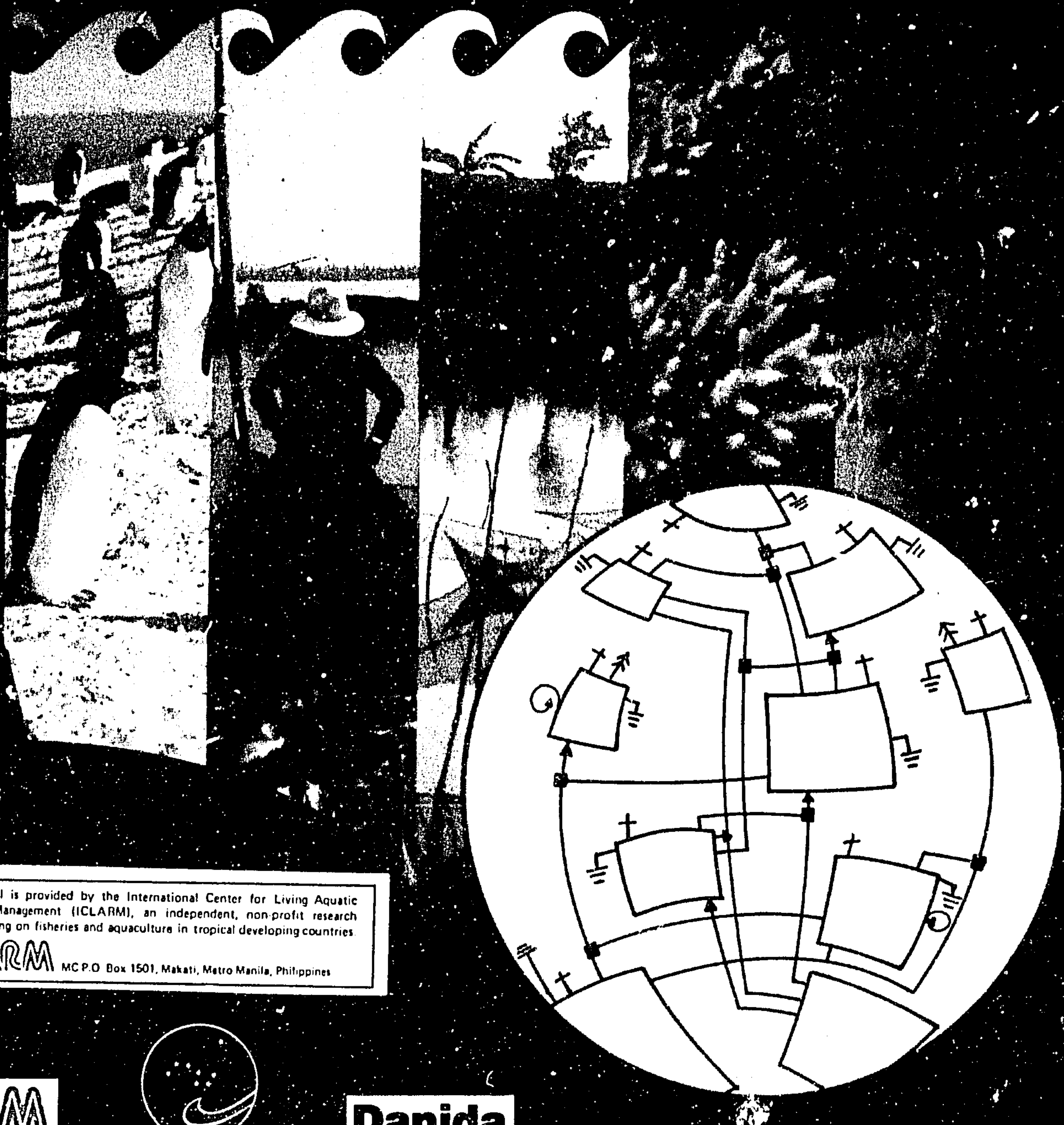
Trophic Models of Aquatic Ecosystems

Edited by
V. Christensen and D. Pauly



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International Center for Living Aquatic Resources Management

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Definition and Construction of Ecosystem Models

Preface

This book is the light at the end of a long tunnel. It was not one of th dark tunnels, though, but one of those you may find in highlands, with numerous open parts *en route* where you can stop, breathe fresh air, enjoy the view, and ensure yourself and others that you know where you are and where you are going.

The notion that steady-state representation of aquatic ecosystems provides a good starting point for modelling of fisheries resources was clear from the early 1980s on to one of us. Later in the mid-1980s, when Jeff Polovina presented his profound work on the French Frigate Shoals and the steady-state model he called ECOPATH, the skeleton of a useful tool emerged. Jeff has described what happened around the French Frigate Shoals project rather nicely in his foreword below. To carry on his initiative was not a quick process, but you can now see at least one result. Surely the start was slow. It took a lot of talking, explanation and persuasion, to get going, and of course our activities on other fronts didn't help to speed up the process.

The first result of the exercises we obtained is presented below in the section on "Definition and Construction of Ecosystem Models". This is a paper on construction and parametrization of ecosystem models, which originally was presented at a workshop in Kuwait in 1987. In this paper, the concept of the original ECOPATH model was re-interpreted, and the foundation was presented for what has since developed into an easily accessible tool for construction, parametrization, and balancing of steady-state models. In addition, another step was taken through adaptation of the network-flow analysis presented by theoretical ecologists, notably by Robert E. Ulanowicz. The paper from the Kuwait meeting had never been published. It was in press in the *Kuwait Bulletin of Marine Research* at the time of the invasion of Kuwait. Therefore, we have decided to include it here, largely unmodified as the first application of what was called the ECOPATH II model.

In the most recent years, the pace of development has increased. One major step was the kind offer from the International Council for the Exploration of the Sea (ICES) to the present editors to convene a Poster Theme Session on "Trophic Models of Aquatic Ecosystems" at the Statutory Meeting of ICES in Copenhagen in October 1990. In the process of planning this Theme Session, we contacted a large number of scientists around the world and many responded with a commitment. The result was some 46 contributions from all over the world. Ecosystems as diverse as ponds, lakes, lagoons and shelves covering all latitudes and salinities were presented. It was noteworthy that a large proportion of the contributions were prepared using the first release of the ECOPATH II software, which we had rushed to distribute some months before the ICES meeting.

The present publication presents a large proportion of the contributions to the ICES Theme Session on "Trophic Models of Aquatic Ecosystems". In addition, we invited a number of scientists to contribute papers later in order to enrich and add diversity to the book. We hope you will find that we have succeeded in this.

You will find, in this book, contributions by very experienced ecosystem modellers. These are, however, vastly outnumbered by contributions from scientists who had never before published anything resembling an ecosystem model. We have heard that many found it appealing to take the step from assembling and analyzing data on a single-species basis to gathering all available data from an area.

In the course of preparing this book, we encountered considerable and very positive interactions with the authors. This led to improvement of the ECOPATH II system and of many of the contributions included here. We were happy to learn from several of our colleagues that the exercise was fruitful for the cooperation achieved internally at their laboratories.

Many chapters are multiauthored. To derive these models, scientists from various fields had to share the burden. Some even found that information from other fields (e.g., predator consumption) could provide useful input to their own (e.g., prey productivity). We send our warmest thanks to the 103 authors.

We would also like to mention that most of the models in the book-all those using ECOPATH II - were offered extra attention from our side. We realize that by pushing the authors to standardize their models in order to facilitate comparisons across ecosystems, we caused problems and extra work for many. We hope, however, that they will forgive us and that our interaction was useful. Certainly, it was an enriching and encouraging experience for us.

A number of distinguished scientists helped to improve the quality of the contributions in this book

(Appendix 5). We appreciate their time and effort in reviewing the contributions. Special thanks go to Robert E. Ulanowicz and Sven E. Jϕrgensen, both of whom were willing to read the draft of the entire book, and give us their comments. Thanks also to Sandra Gayosa of ICLARM who over the past three years had the major task of keeping track of the many manuscripts and the correspondence with authors and reviewers. In addition she has checked the calculation and designed most of the flowcharts in the book.

We also wish to thank ICES, and especially the ICES Secretariat. The offer to convene the Theme Poster Session and to use the ICES apparatus gave us the possibility of establishing contact with a wide array of scientists and to enjoy the benefits of a well-organized meeting. Before, during and after the ICES meeting, John Pope, then Chairman of the ICES Consultative Committee, contributed greatly to making the event successful.

Thanks to an invitation from the Danish International Development Agency (DANIDA), three scientists from Asia were invited to participate in the ICES meeting. In addition, the Norwegian Agency for Development Cooperation (NORAD) supplied funding for a colleague from Mozambique, Africa. Last, but certainly not least, thanks and appreciation to DANIDA, and especially to Ebbe Schiϕler, Head of its Research Department, for seeing the potential in the approach presented here, for continuous funding of the ECOPATH II project at ICLARM, and for ever-pleasant interactions. This book is one result of their support.

The First ECOPATH

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POLOVINA, J.J. 1993. The first ECOPATH, p. vii-viii. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

When I joined the Honolulu Laboratory in the fall of 1978, it was active in a multiagency resource assessment program with considerable effort directed toward the study of the ecosystem at French Frigate Shoals, an atoll near the center of the Northwestern Hawaiian Islands. Although specialists were estimating biological parameters for each component of the ecosystem, no one had attempted to put all the components together to construct a quantitative picture of the atoll's ecosystem. I was assigned that task by the laboratory director at that time, Richard Shomura.

I was aware that Taivo Laevastu and his colleagues at what is now the Alaska Fisheries Science Center in Seattle had an ecosystem model for the Bering Sea (Laevastu and Larkins 1981), so I paid them a visit to determine whether their model might be appropriate for our tropical coral reef ecosystem. It quickly became clear that the information needed for Laevastu's model greatly exceeded the information that would be available for the French Frigate Shoals studies; hence, a much simpler model was needed. I simplified Laevastu et al.'s biomass budget approach by developing a system of simultaneous linear biomass budget equations to balance biomass production and loss.

I felt fairly comfortable working with the simple ECOPATH approach because most of the major components of the ecosystem at French Frigate Shoals were being studied; thus, I had good parameter estimates and expertise to validate the model's approach and output. The cooperation and support from all the researchers were fantastic even though at times it appeared painful for a scientist - trained to measure biological parameters specific to species, age, and sex - to give parameter estimates aggregated over an entire species group. Once ECOPATH estimated the biomasses and production for the components of the atoll, these estimates were compared with the available estimates from field data. The best field estimates were for primary production. The agreement between the model's estimate of primary production and the field data was excellent. No one was more surprised than I. Further checks between the model's estimates and some field estimates generally showed good agreement (Polovina 1984). Thus the objective of the modelling work - to bring together common information from studies on the components of the ecosystem to construct a quantitative picture of the atoll's ecosystem structure - was achieved.

After fitting ECOPATH to the French Frigate Shoals data and publishing the results, I was content to let ECOPATH languish in the literature. I was busy elsewhere and I had doubts about ECOPATH's acceptance, given some criticism that the model was overly simplistic. After I described ECOPATH and its application to Daniel Pauly in 1983, he exclaimed that such a model was exactly what was needed to construct ecosystem box models. To some people, the simplicity meant the model could be widely applied to take advantage of the power of comparative studies. He told me that if I made ECOPATH user-friendly and wrote a user's manual, he would see that it was applied around the world. I did my part and he certainly did his. For several years, the requests I received for ECOPATH material often arrived in batches by country; thus, I could track the locations of Daniel's seminars on ECOPATH.

Although the objective of the ECOPATH approach is to describe ecosystem structure, future work might consider looking at a time dimension for some insight into the dynamics of ecosystems. For example, when I was developing ECOPATH, I felt that a time dimension, such as the mean generation time of each component of the ecosystem, contained useful information about the dynamics of the system. Within an ecosystem, mean generation time and trophic level are likely to be positively correlated, but mean generation time at the same trophic level may vary considerably between different ecosystems. This variation may be important in understanding the differences in dynamics between ecosystems. Thus ECOPATH II users might consider using estimates of mean generation time as an axis in some of the output - for example, displaying the distribution of biomass or production as a function of generation time.

To go further, it might be possible to use the structure of the box model estimated from ECOPATH II as the input to construct a dynamic ecosystem model by using a particle tracking simulation approach. Particle tracking models are used to simulate the dynamics of particle movement in space and time as functions of a production, advection, and diffusion grid (Okubo 1980). Since an ecosystem can largely be described by the movement of particles of energy between the different components, the box model produced by ECOPATH II might be thought of as an advection and diffusion grid. If the mean generation time or some other time dimension is added to each box, then it might be possible to simulate the temporal movement of energy through the ECOPATH II ecosystem grid by coupling it with a particle tracking model that uses primary production as input and tracks the movement of discrete packets of energy through the ecosystem grid.

With its strong theoretical foundation and much improved computation, ECOPATH II represents a major advance from ECOPATH. Villy Christensen and Daniel Pauly are to be congratulated for their considerable efforts which resulted in a tool that, as indicated by this book, will contribute to significant advances in our understanding of ecosystems. Specifically, comparative studies of ecosystems which have long been advocated will now, with ECOPATH II, be easier to achieve and interpret and, I believe, will prove as useful as envisioned. ECOPATH certainly has come a long way, and as this book indicates, the future for ECOPATH II is very promising indeed.

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Inventing the Ecoscope

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ULANOWICZ, R.E. 1993. Inventing the ecoscope, p. ix-x. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

When asked what analytical methods one should employ to investigate the behavior of whole ecosystems, most ecologists likely would point to simulation modelling as the avenue of choice. Sensing the potential of this tool and its growing popularity in other realms of ecology, the governors of the Scientific Committee for Oceanic Research (SCOR) invoked in 1977 a Working Group (WG#59) to assess the potential that simulation modelling offered to biological oceanographers. The ensuing critique (Platt et al. 1981) was less than a ringing endorsement of mathematical modelling. The Group encouraged the use of mathematical models to quantify isolated biological processes, such as photosynthesis by algae or filter feeding by mesocrustaceans. Single processes often were dominated by one or a few controlling parameters, and frequently models of the mechanisms behind these processes yield reasonably accurate predictions.

As the horizons of biological models are expanded to include multiple process, however, their track record of predicting system behavior quickly wanes. Many ecologists still believe that all that is necessary to achieve acceptable predictions from whole ecosystem models are more precise parameter estimates and greater resolution into component processes. The Working Group warns against false optimism in this regard, pointing out that prediction ability more often than not erodes as models are resolved into finer components. They warned that the underlying idea of ecosystems as a mechanical clockwork (an implicit assumption of all coupled process modelling) is flawed, possibly fatally so.

Criticism is a relatively easy task, and the Group was anxious lest biological oceanographers get the mistaken message that it is futile to attempt to describe whole marine ecosystems in quantitative fashion. WG#59 thus set about to recommend other avenues via which investigators could quantitatively describe biological communities. One of their recommendations was that biologists have placed too much emphasis on stocks of organisms and chemicals and not enough on the more difficult to measure processes that link populations together. Accordingly, the Group sponsored a North Atlantic Treaty Organization (NATO) Advanced Research Institute to foster greater awareness of the importance of measuring and describing material and energy flows among ecosystem compartments (Fasham 1984).

I was an active member of WG#59 and its successor WG#73, Ecosystem Theory in Relation to Biological Oceanography, and our consensus to encourage research on ecosystem flows engendered a major shift in my own research directions. I was aware that merely assembling flow measurements into "spaghetti diagrams" or "bird's nests" rarely leads to significant new insights into ecosystem functioning. Absent for the most part were methods for appraising such diagrams in systematic and analytic fashion. My first "discovery" lay in finding a way to quantify what could be called the dual features of activity level and organization that lie inherent in every flow diagram. I was enthralled to find that increases in the measure I called "network ascendency" (Ulanowicz 1980, 1986) appeared to encapsulate most of the attributes of developing ecosystems that had been enumerated by Eugene Odum (1969).

Encouraged by what I perceived to be a new way to look at ecosystem development, I searched for other ways to make sense of the jumble of transfers that occur in any ecosystem. One method for quantifying indirect bilateral transfers in ecosystems had been borrowed from economic analysis by Hannon (1973). Janusz Szyrmer and I were able to reformulate this "Input-Output" methodology so as better to address the particular concerns of the ecologist (Szyrmer and Ulanowicz 1987). Furthermore, with encouragement from Michael Kemp, I was able to transform most complicated webs of exchanges into something that resembles Lindeman's "trophic pyramid," or linear chain of transfers via discrete trophic levels (Ulanowicz and Kemp 1979; Ulanowicz, in press). Finally, I spent much effort finding a way to identify and isolate the pathways for recycle within a network of flows (Ulanowicz 1983).

I assembled these four basic network analyses into one computer package, NETWRK (Ulanowicz and Kay 1991). Meanwhile, WG#73 sponsored a workshop to test evolving methods (including NETWRK) for analyzing ecological flow networks (Wulff et al. 1989). However, it soon became obvious to all concerned that developments in theory and methodology were fast outpacing the acquisition of full data sets with which these methods could be tested and exercised. To find data on each and every exchange in an ecosystem is a laborious and too often an impossible task. If any progress were to be made in characterizing ecosystem function via their network configurations, some way had to be found to interpolate and/or extrapolate from an incomplete ensemble of available data on a particular network to its full complement of flow values.

The development of such "inverse methods" was already underway within WG#73 (e.g., Veziña and Platt 1988; Vezina 1989), unfortunately without any knowledge of the earlier accomplishments of J. J. Polovina et al. in creating ECOPATH. Drs. Pauly and Christensen, however, were quite aware of the potential of Polovina's methods and astutely decided that what was needed was to put ECOPATH into a "user-friendly" form and to promulgate its use among that diverse network of aquatic ecologists worldwide with whom ICLARM maintains close contact. The result was ECOPATH II - the foundation upon which this book is based - and the motivation they provided their associates to use the package was the ICES poster session held in Copenhagen. I had been unaware that they were circulating some of my analytical methods as part of ECOPATH II, when one day a parcel appeared in my mailbox containing some 50 or more quantified foodwebs, replete with accompanying ascendencies. It was perhaps the most startling and gratifying moment of my professional career.

The heavens were opened to us by Galileo and his telescope; the world of microbes by Pasteur and his microscope. It may not be much of an exaggeration to say that the realm of ecosystems is being opened to us by Polovina, Pauly and Christensen through their "ecoscope". For that is what ECOPATH II and its associated analyses represent - a macroscope through which to view the structure and functioning of entire ecosystems. Anytime the barriers to observing a new scale of phenomena fall, a flurry of exciting discoveries inevitably follows. For now vision through the ecoscope may be akin to looking "through a glass darkly," but the picture is certain to sharpen during the next few years.

For my own part, I am confident that what we are seeing through the ecoscope is no clockwork. Nor is it, as Clements suggested, an organism. It is an "organic system," which is to say that certain components behave in mechanical fashion, whilst the ensemble as a whole possesses a "propensity" (Popper 1990) to develop in a particular direction. What is most important is that this propensity is in some measure autonomous of the specific nature of its parts.

Currently our attention is focused on the structure of organic systems. Perhaps the best analogy to the present state of affairs in ecosystem research is that we are at the point where medicine was at the time of Leonardo Da Vinci and his marvelous drawings of the human anatomy. It is thus that the burgeoning endeavor of comparing ecosystem networks might aptly be called "comparative ecosystem anatomy" (Wulff and Ulanowicz 1991). In due time the ecosystem's counterpart to physiology will emerge, but for now this book represents the largest exposition to date of models that can be used by both practitioners and theoreticians alike.

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Improved Construction, Parametrization and Interpretation of Steady-State Ecosystem Models*

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Abstract

An improved version of J.J. Polovina's ECOPATH program for the construction of steady-state multispecies ecosystem models from fisheries data is presented. This new version, called "ECOPATH II," differs from the original, aside from being more user-friendly, in a number of important features, among others: (1) use of a "generalized inverse" matrix routine allowing the system of linear equations used to estimate model parameters to be over- or slightly underdetermined; (2) estimation of (almost) any set of unknowns and not only of biomasses; (3) explicit consideration of respiratory, egestive and excretory losses (with defaults provided for inputs) and of the detritus pathways; (4) estimation of numerous derived quantities on species group or whole-system basis, such as gross and net efficiencies, trophic levels, food electivity, pathways and cycles involving any groups and "ascendancy" *sensu* R.E. Ulanowicz. The preliminary version of an empirical multiple regression model for the estimation from easy-to-estimate parameters of relative food consumption by fish populations is presented; this model provides reasonable values of the input into ecosystem models that were to date most difficult to estimate. An application to the coral reef ecosystem of French Frigate Shoals (Hawaii) is presented, along with some suggestions as to how this methodology could be applied to Kuwait waters.

Introduction

In the last ten years, i.e., since the creation of the Mariculture and Fisheries Department of the Kuwait Institute for Scientific Research (KISR), a vast amount of biological information on the various fisheries resource species of Kuwait has become available (see, e.g., contributions in Mathews 1985) which deepened previous, less focused knowledge on the fishery resources of the gulf (e.g., FAO 1981a, 1981b).

This information, gathered to answer fisheries management questions, was recently complemented, moreover, by numerous basic studies on the oceanography and marine biology of the gulf, especially its inner part (e.g., Halwagy et al. 1986 and contributions therein).

We think that the time has come, therefore, for a modelling effort to synthesize this information, identify crucial knowledge gaps and eventually allow for a fisheries management scheme to emerge in Kuwait which would consider all major resource species simultaneously. Such scheme would, for example, consider the biological (and economic) effects of either exploiting or of not exploiting fish known to consume large quantities of penaeid shrimps (Pauly and Mathews 1986; Euzen 1987; Pauly and Palomares 1987).

This contribution presents a recently developed methodology and related computer program, called "ECOPATH II" for straightforwardly constructing and validating steady-state ecosystem models, as could be used along with the generalizations in Appendices A - D to construct a model of the

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ecosystem upon which Kuwait shrimp and fin fisheries depend.

Description of a New Model

ECOPATH II is derived from the ECOPATH program of Polovina and Ow (1983) and Polovina (1984a, 1984b, 1985, 1986). The latter may be viewed as a system of biomass equations which for any given group (group of) species (i) can be represented for any time interval by

Production by (i) - all predation on (i) - nonpredation losses of (i) - catch of (i) = 0, for all i ...1)

As described by Polovina (1984a, 1985), the ECOPATH model "expresses each term of the budget equation as a linear function of the unknown mean annual biomass (B_i's), so the resulting biomass budget equations become a system of simultaneous linear equations". The inputs needed for ECOPATH are few and these will be presented further below and contrasted with those required by ECOPATH II. We shall first note here, however, five features of ECOPATH II in which it differs markedly from its predecessors:

1. The matrix inversion routine built in ECOPATH and used for solving the system of linear equations cannot handle surplus information, i.e., cannot handle a situation where the system is "overdetermined" in that there are less unknowns than equations (or "i's"). Also, ECOPATH as implemented in Polovina and Ow (1983), can handle only up to 20 groups while ECOPATH II can handle up to 50.
2. The description of ECOPATH cited above appears to imply that the system of equations "linear in the B_i's" may be solved only for the biomasses. This is obviously not so and, presumably, J.J. Polovina chose this solution because it was the one he needed for the system he was working on.
3. ECOPATH does not explicitly consider respiratory, egestive or excretory losses (i.e., the flows into and out of a group's "box" need not be balanced).
4. No check is made as to whether the model outputs (i.e., estimated biomasses and flows) are mutually compatible and thermodynamically possible.
5. The outputs are underutilized; no use is made of the rich, theoretical developments now available to interpret systems of biomasses and flows (see Platt et al. 1981; Ulanowicz and Platt 1985; Ulanowicz 1986).

To deal with (1), we have incorporated into ECOPATH II a "generalized inverse" routine (Mackay 1981) which allows for the system of equations mentioned above to be solved even when the number of equations (i.e., of i's) and the number of unknowns are unequal. This routine, which resolves a problem addressed, but not solved, by Polovina (1986), computes least-square estimates of the unknowns when the system of equation is overdetermined. As an added bonus, this routine also provides (non-unique) solutions when the system is slightly underdetermined.

To deal with (2), we have incorporated into ECOPATH II routines such that (with few exceptions) any parameter may be unknown and hence estimated by the program. Thus, when biomasses are known, other parameters such as e.g., production/biomass (P/B) ratios, or relative food consumption may be estimated, given sufficient degrees of freedom.

To deal with (3), we have incorporated into the interactive entry routine of ECOPATH II, for all consumers, a request for the percentages of ingestion that are lost due to egestion (feces) and to excretion (urine), and provided default values of 15% and 5%, respectively (Winberg 1956). The entries (or defaults) are subsequently used for the computation of net conversion efficiencies (see below) and of the flows to the "detritus box". Detritus is derived from nonpredatory "leaks" (including egestion and excretion) of organic carbon (or other substances, see below) from any trophic level.

To deal with (4), ECOPATH II was provided with checks for i's that do not balance, i.e., production larger than or equal to food consumption is unacceptable for any i. Such simple verification appears particularly useful in the case of models in which numerous species occur and in which thermodynamically impossible "knots" can remain long undetected. Also, ecotrophic efficiency (EE), which is, throughout, a required input for ECOPATH, may be an output of ECOPATH II, depending on whether the two sets of equations for estimating production balance or not (see below).

To deal with (5), finally, we have (a) added to our program a number of routines for computing a variety of straightforward statistics and (b) incorporated into the listing of ECOPATH II the routines adapted from Ulanowicz (1986) for the computation of the "ascendancy" and related statistics of an ecosystem.

Some of the straightforward statistics derived from each group - except for primary producers and in addition to the biomass and flows already estimated by the original ECOPATH - are:

- gross conversion efficiency (= production/ ingestion);
- net conversion efficiency (= production/ingestion - egestion);

- mean trophic level (= 1 + trophic level of preys, weighted over all preys by the amounts ingested);
- omnivory index (= variance of mean trophic level);
- Ivlev's electivity index (I), defined for prey item j of species (group) i as

$$I_{ij} = (DC_{ij} - Br_j)/(DC_{ij} + Br_j) \qquad ...2)$$

where DC_{ij} is the fraction of the prey j in the diet of the predator i (an input to the ECOPATH program, see below), and Br_j is the relative biomass of j in the ecosystem (Ivlev 1961; Parsons and LeBrasseur 1970).
- all pathways leading from the primary producer(s) to group i; and
- all cycles of which group i is a part.

Incorporation of approaches in Ulanowicz (1986) allows ECOPATH II to compute, once the biomasses and derived i-specific statistics have been computed, the following quantities, describing holistic properties of ecosystems: total system throughput, full development capacity, full ascendancy, overhead on inputs, overhead on exports, internal capacity, internal ascendancy, tribute to other systems, dissipation and system redundancy (see Ulanowicz 1986 and other contributions in this volume for the theory leading to these quantities).

Inputs Required by ECOPATH and by ECOPATH II

In the following, a commented list of the inputs required for each group considered explicitly in a given ecosystem by ECOPATH and/or ECOPATH II is presented. These comments refer to (1) methods of estimation with special emphasis on Kuwait waters and/or, in the case of ECOPATH II, to (2) the reason why a given input was added.

- Production/biomass ratio (P/B): equal to instantaneous rate of total mortality (Z) in steady-state systems, when the growth of individual animals can be described by the von Bertalanffy growth function (VBGF, see Allen 1971). Numerous methods exist for estimation of Z in fish and other aquatic animals (reviews in Ricker 1975; Gulland 1983; Pauly 1984) and they have been widely discussed and applied by KISR researchers (e.g., contributions in Mathews 1985). P/B is harder to estimate in primary producers, but indirect methods (empirical equations) exist for production of P/B in phytoplankton (Lafontaine and Peters 1986), while useful P/B estimates for benthic algae and seagrasses may be found in Mann (1982).
- Diet composition (DC): for a given (group of) species (i), the diet composition is the fraction of each species (groups) it consumes, usually estimated from studies of stomach contents. Note that it does not matter much which weighting scheme is used for quantifying relative stomach contents; volume, calories, weight, etc. may be used (Macdonald and Green 1983). Note also that only species (groups) occurring within the system may be consumed and, that, at least in ECOPATH II, care should be taken to have some species (group) feeding on detritus, as also happens in reality. Thus, in the French Frigate Shoals example below, the heterotrophic benthos should feed at least in part on dead benthic algae (detritus) rather than derive all its energy from algae presumed to be grazed while alive. A few food and feeding studies of Kuwait fishes of the type needed here are available (Abdullah and Hussein 1977; Euzen 1987) which could be used for model construction.
- Annual fishery catch (or quantity killed by fishing and discarded): needed for all exploited species. Estimates of this quantity are available for major species taken in Kuwait waters.
- Habitat area: this is an input of ECOPATH which was deleted from ECOPATH II, as it appears straightforward to adjust biomass and flows to any standard area.
- Ecotrophic efficiency: an input of ECOPATH II expressing the fraction of total production consumed by predators or caught by a fishery and usually assumed to range from 0.7 to 0.9 (Ricker 1969; Polovina 1984a, 1984b). In ECOPATH II, ecotrophic efficiency (EE) must be either entered (when biomass is unknown) or is estimated by the program (when biomass is known and was entered). In ECOPATH II, the fraction 1-EE of production is directed toward the detritus box, from which it may be exported out of the system.
- Primary production (PP, in $g \cdot C \cdot m^{-2} \cdot year^{-1}$); PP is not an input for ECOPATH. However, this is a required input for ECOPATH II, in order to (1) encourage users to obtain independent, i.e., "external" estimates of a parameter which closely correlates with a number of important characteristics of a system; (2) to allow for validation of internally generated PP (which should be smaller than or equal to the externally input value) and more importantly; (3) to allow for the difference between observed (= external) and computed (= internal) PP to be added to the detritus box and thus quantify a linkage important in virtually all ecosystems (i.e., the transfer of uningested, dead phytoplankton and algal biomass to the detrital pool, from where it

becomes available to a variety of consumers and/or for burial or export).

- Detritus biomass: this is not an input in ECOPATH, but is needed by ECOPATH II for various computations when detritivores are included in a system, e.g., to compute the "electivity" of detritivores for detritus. An empirical equation is provided in Appendix D which provides rough estimates of detritus (in $g{\cdot}C{\cdot}m^{-2}$) as a function of primary production and euphotic depth.
- Food consumption per unit biomass: the number of times per year a population of, e.g., hamoor (*Epinephelus tauvina)* consumes its own weight per year. This quantity (obviously not needed for primary producers) is usually difficult to estimate and Polovina (1984b), in the absence of anything better, used estimates of consumption by Pacific salmon for the reef fishes in Fig. 2. Polovina (1984a, 1984b) called this input the "food required" (FR). Following Pauly (1986), we shall instead use the notation "Q/B", with the caveat that such estimates must refer to age-structured populations, i.e., consider the fact that there usually are, in natural fish populations, more young than old fish, and that the former eat (per unit weight) more than the latter.

An analytical method has been recently developed by Pauly (1986) which is well suited to estimate Q/B, and which has been successfully applied to Kuwaiti fishes (Pauly and Palomares 1987). This method, however, still requires inputs that may be hard to obtain in some fish species, and we present an empirical model which allows direct, if preliminary estimates of Q/B:

$$\ln Q/B = 1.117 - 0.202 \ln W_\infty + 0.612 \ln T + 0.516 \log_{10} A + 1.26 f \quad ...3)$$

where Q/B ($year^{-1}$) is as defined above, W_∞ the asymptotic weight (as defined by the VBGF) of the fish of a given population (live weight, in g), A an index of the mean activity level of the fish of a given species, derived from the shape ("aspect ratio") of their caudal fin (see Fig. 1) and the food type (f) - here either: carnivore, f=0, or herbivore, f=1.

The derivation of this model is documented in Palomares and Pauly (1989). It is based on Q/B estimates for 33 demersal and pelagic fish stocks ranging in size from myctophids to tuna and occurring in waters with mean annual temperatures ranging from 10 to 28°C. Eighty percent of the variance in the original dataset was explained by equation (3), which hence provides reasonable estimates of Q/B for modelling purposes.

This model provides lower estimates of Q/B than suggested by Pauly (1982) and Caddy and Sharp (1986); this is due to the use by these authors of (uncorrected) feeding data from captive fish generally fed to satiation. Note that, for obvious reasons, Q/B - (egestion + excretion) must be higher than P/B (or Z) for any consumer.

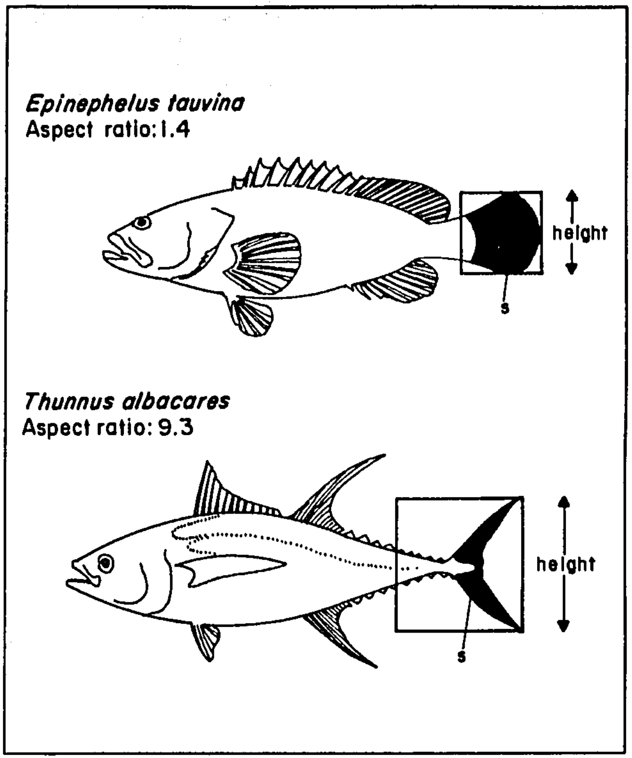

Fig. 1. Definition of aspect ratio ($A = h^2/s$) in two fishes (hamoor and yellowfin tuna) with different surface areas (s, in black) and height (h) of their caudal fins. High A values correspond to a high level of activity and hence to high food consumption.

Application Example of ECOPATH II

Pending the construction of a model of the marine ecosystem off Kuwait, we present here an application of ECOPATH II using the data set used by Polovina and Ow (1983) to document the operation of their program for implementing ECOPATH (Tables 1 and 2). This dataset differs in details from that in Polovina (1984a), whose estimated primary production was very close to observed primary production (see also Atkinson and Grigg 1984).

Fig. 2 shows the model of French Frigate Shoals estimated from the data in Tables 1 and 2 by either ECOPATH or ECOPATH II. As might be seen, the figure presents only that part of the flows that go up the food web and omits backflows to the detritus as well as respiration (fishery catches are here omitted because French Frigate

Table 1. Input values for ECOPATH model of the French Frigate Shoals ecosystem, as given in Polovina and Ow (1983).[a]

No.	Group name	Biomass[b]	P/B[c]	Q/B[d]	Habitat area[e]
1.	Phytoplankton	-	70.000	-	1,200
2.	Benthic algae	-	12.500	-	700
3.	Zooplankton	-	40.000	280.00	1,200
4.	Heterotrophic benthos	-	3.000	12.50	700
5.	Small pelagics	-	1.100	7.50	1,200
6.	Lobster and crabs	-	0.520	8.20	700
7.	Reef fishes	-	1.500	9.50	700
8.	Bottom fishes	-	0.320	3.60	300
9.	Green turtle	-	0.150	3.50	1,200
10.	Seabirds	15.00	5.400	80.00	1,200
11.	Monk seal	63.00	3.000	40.00	1,200
12a.	Tiger sharks	42.00	0.500	4.50	1,200
12b.	Reef sharks	-	0.175	3.80	1,200
12c.	Jacks	-	0.350	3.80	1,200
12d.	Tuna	-	0.660	5.30	900

[a] These values differ slightly from those in Polovina (1984b), but were used here because they are part of the complete dataset distributed with the original listings of the ECOPATH program.

[b] Missing biomasses (here: kg·km^{-2}) are estimated by ECOPATH and ECOPATH II; the three values provided here help to estimate the parameters of the model from the "top down".

[c] Equivalent, under the steady-state assumption, to an estimate of total mortality (Z, year^{-1}).

[d] Termed FR, i.e., "food required" in Polovina and Ow (1983) and in all of Polovina's contributions.

[e] In km^2; not an input in ECOPATH II (in which the biomass estimates for nos. 10, 11 and 12a were adjusted by the ratio 1,200/700).

Table 2. Diet composition of components of the French Frigate Shoals ecosystem (from Polovina and Ow 1983).[a]

		Predator												
	Prey	3	4	5	6	7	8	9	10	11	12a	12b	12c	12d
1.	Phytoplankton	0.91	-	-	-	-	-	-	-	-	-	-	-	-
2.	Benthic algae	0.09	0.85	-	-	0.248	-	0.90	-	-	-	-	-	-
3.	Zooplankton	-	-	0.94	0.021	0.170	0.104	0.10	0.05	-	-	-	-	0.36
4.	Heterotrophic benthos	-	0.15	-	0.979	0.459	0.258	-	-	-	-	-	-	-
5.	Small pelagics	-	-	0.06	-	-	0.125	-	0.68	-	0.08	0.05	0.08	0.48
6.	Lobster and crabs	-	-	-	-	-	0.018	-	-	0.15	0.14	0.05	0.12	-
7.	Reef fishes	-	-	-	-	0.123	0.469	-	0.15	0.85	0.28	0.90	0.80	0.08
8.	Bottom fishes	-	-	-	-	-	0.026	-	-	-	-	-	-	0.08
9.	Green turtle	-	-	-	-	-	-	-	-	-	0.01	-	-	-
10.	Seabirds	-	-	-	-	-	-	-	-	-	0.30	-	-	-
11.	Monk seals	-	-	-	-	-	-	-	-	-	0.08	-	-	-
12a.	Tiger sharks	-	-	-	-	-	-	-	-	-	0.01	-	-	-
12b.	Reef sharks	-	-	-	-	-	-	-	-	-	0.03	-	-	-
12c.	Jacks	-	-	-	-	-	-	-	0.10	-	0.05	-	-	-
12d.	Tuna	-	-	-	-	-	-	-	0.02	-	0.02	-	-	-
	Sum	1.00	1.00	1.00	1.000	1.000	1.000	1.00	1.00	1.00	1.00	1.00	1.00	1.00

[a] Dashes represent zeros.

Shoals is an unexploited ecosystem; both ECOPATH and ECOPATH II can handle fisheries catches).

Fig. 3, derived using ECOPATH II, presents backflows as should occur in an ecosystem such as French Frigate Shoals. They consist of:

- all egested and excreted matters (here 10 and 5%, respectively, of food consumption, see above); and
- the production not consumed by predators (i.e., (B·Z)·(1-EE)), important in apex predators.

Fig. 3 also shows respiration for all boxes for which this parameter could be straightforwardly computed, i.e., from the difference (assimilated food - excretion) - production. ECOPATH II has a routine to identify and list cycles within food webs. Such cycles may be zero-order cycles (i.e., involving only one box which cannibalizes itself), first-order cycles (involving two predators that are also mutual prey, as often occurs with fishes in the course of their ontogeny), second-order cycles, etc.

The data in Table 1, used here to construct a model using ECOPATH II, do not imply more than zero-order cycles; hence, this routine of ECOPATH II cannot be illustrated here (note that the French Frigate Shoals ecosystem probably includes, in reality, a large number of first-, second-, and higher-order cycles, especially when detritivory is considered; note also that Fig. 2 suggests a first-order cycle between the seabirds and box 12; this is an artifact of grouping).

ECOPATH II also has a routine to identify all pathways leading from the primary producers to a given box. Table 3 provides, as an example of this type of output, a list of all flows leading from the primary producers up the food web to the birds. As might be seen, even animals as peripheral as these birds are involved in a large number of pathways, despite the outward simplicity of a graph such as Fig. 2.

Table 4 presents some important biological statistics extracted by ECOPATH II from the data in Tables 1 and 2, while Table 5 presents the electivity indices for all consumers in the French Frigate Shoals model. These two tables, examined jointly with Figs. 2 and 3, help characterize the role of a given group within the system.

Table 6 compares some holistic properties of the French Frigate Shoals ecosystem with the same properties of seven other ecosystems.

Table 3. Food flows (pathways) leading, in the French Frigate Shoals ecosystem, from the primary producers (#1 and 2) to the seabirds (no. 10); see Figs. 2 and 4 for the numbers of the other groups.

1 → 3 → 10
2 → 3 → 10
1 → 3 → 5 → 10
2 → 3 → 5 → 10
1 → 3 → 7 → 10
2 → 3 → 7 → 10
2 → 4 → 7 → 10
2 → 7 → 10
1 → 3 → 5 → 12 → 10
2 → 3 → 5 → 12 → 10
1 → 3 → 7 → 12 → 10
2 → 3 → 7 → 12 → 10
2 → 4 → 7 → 12 → 10
2 → 7 → 12 → 10
1 → 3 → 6 → 12 → 10
2 → 3 → 6 → 12 → 10
2 → 4 → 6 → 12 → 10
1 → 3 → 5 → 8 → 12 → 10
2 → 3 → 5 → 8 → 12 → 10
1 → 3 → 7 → 8 → 12 → 10
2 → 3 → 7 → 8 → 12 → 10
2 → 4 → 7 → 8 → 12 → 10
2 → 7 → 8 → 12 → 10
1 → 3 → 6 → 8 → 12 → 10
2 → 3 → 6 → 8 → 12 → 10
2 → 4 → 6 → 8 → 12 → 10
1 → 3 → 8 → 12 → 10
2 → 3 → 8 → 12 → 10
2 → 4 → 8 → 12 → 10
1 → 3 → 12 → 10
2 → 3 → 12 → 10

Table 4. Some summary statistics of the groups considered in the French Frigate Shoals ecosystem.

	Group	A	B	C	D
1.	Phytoplankton	-	-	0.00	0.000
2.	Benthic algae	-	-	0.00	0.000
3.	Zooplankton	0.14	0.17	1.00	0.000
4.	Heterotrophic benthos	0.24	0.28	1.15	0.167
5.	Small pelagics	0.15	0.17	2.06	0.063
6.	Lobster and crabs	0.06	0.07	2.15	0.001
7.	Reef fishes	0.16	0.19	1.94	0.364
8.	Bottom fishes	0.09	0.10	2.66	0.200
9.	Green turtle	0.04	0.05	1.10	0.090
10.	Seabirds	0.07	0.08	3.09	0.150
11.	Monk seal	0.08	0.09	2.97	0.005
12a.	Tiger sharks	0.11	0.13	3.52	0.292
12b.	Reef sharks	0.05	0.05	2.96	0.003
12c.	Jacks	0.09	0.11	2.98	0.005
12d.	Tuna	0.12	0.15	2.72	0.317

A-Gross efficiency = production/food consumption.
B-Net efficiency = production/(food consumption - egestion).
C-Mean trophic level, as defined in the text.
D-Index of omnivory, as defined in the text.

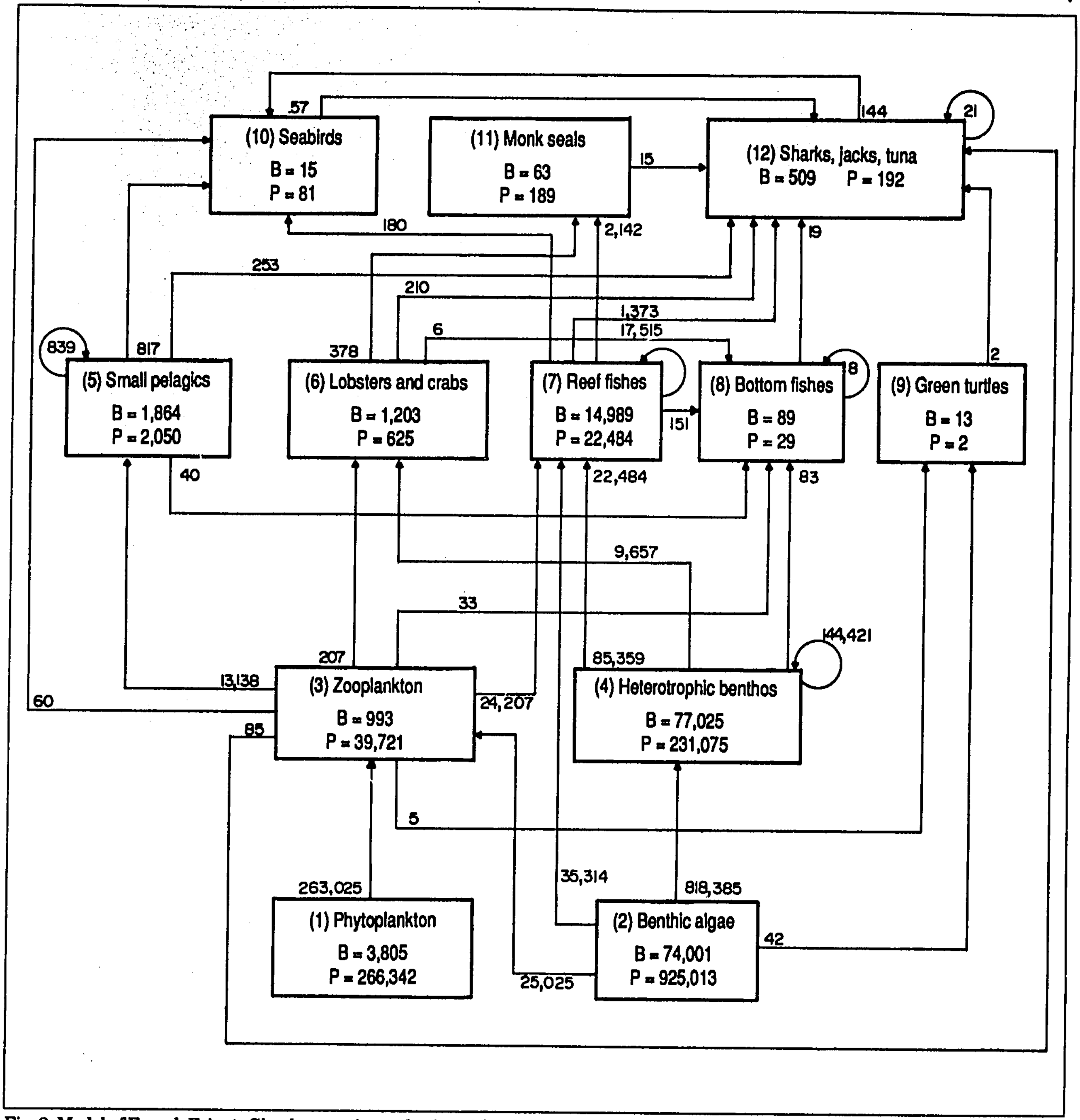

Fig. 2. Model of French Frigate Shoals, as estimated using either ECOPATH or ECOPATH II from the input data in Tables 1 and 2, with all biomasses expressed in kg and all flows in kg·year^{-1}. Note absence of a detritus box and of detritivores (see Fig. 3).

Discussion

The present paper, which is intended to have a methodological emphasis, is not the proper place to discuss at length the results presented here (Figs. 2 and 3, Tables 3-6). Rather, we wish to stress how far one can get in understanding a given ecosystem using rather limited inputs (here: Tables 1 and 2) and an appropriate model (here: ECOPATH II).

We are confident that ECOPATH II could be successfully used to describe the marine ecosystem in the northern end of the Gulf, and hence increase understanding of the system which forms the bases of Kuwait shrimp and other fisheries.

The database available for such an exercise differs, however, in some important characteristics from that used here to illustrate the use of ECOPATH II, the main differences being that:

1. a substantial catch is extracted from the marine ecosystem off Kuwait; and
2. biomasses are known (at least approximately) for most resource species.

These two features represent extremely powerful constraints on the parameter estimates which

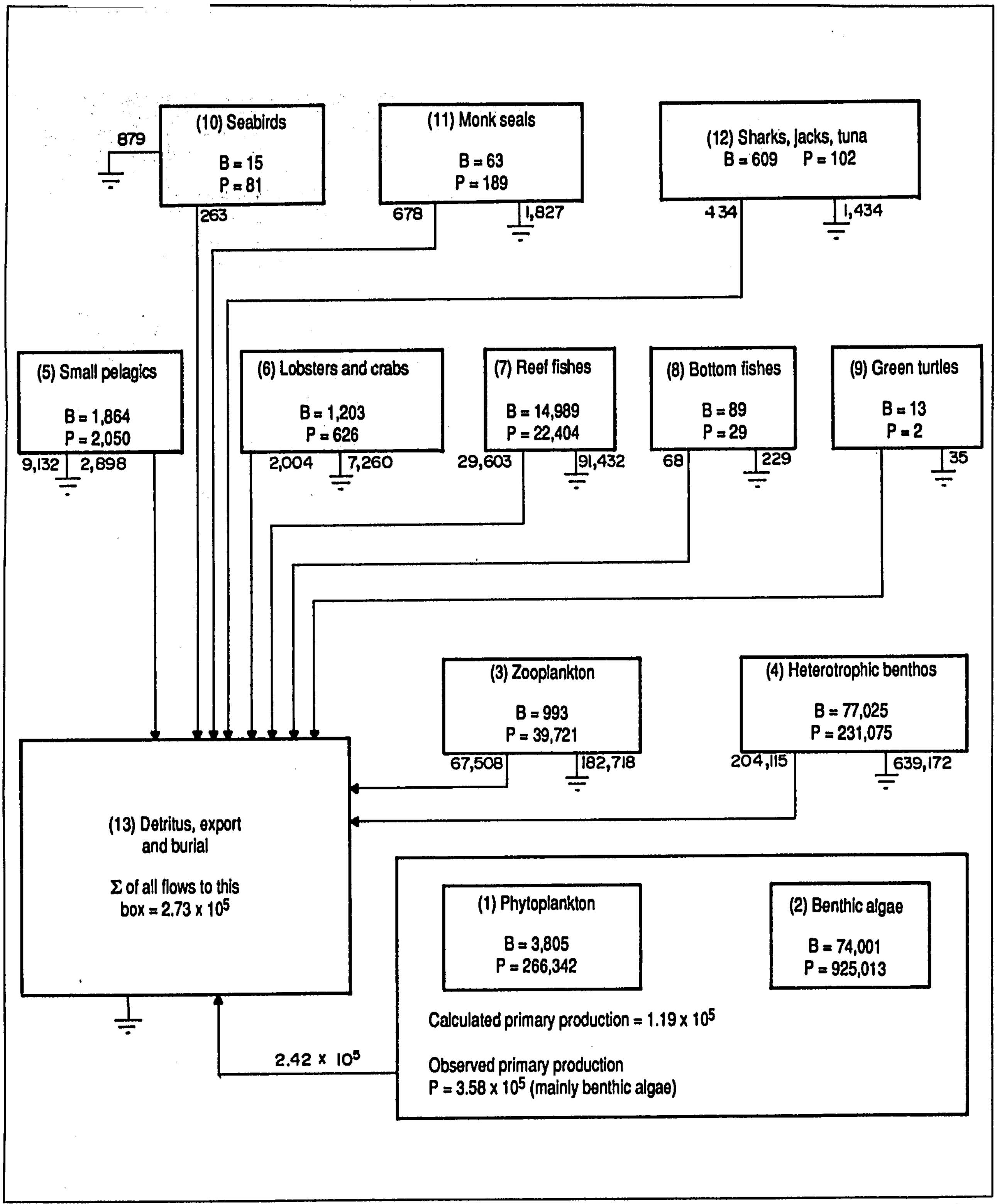

Fig. 3. "Backflows" of French Frigate Shoals model, as estimated using ECOPATH II (see Fig. 2 for flows up the food web). Note large sum of flows to detritus box (units are kg·km^{-2} and kg·km^{-2}·year^{-1}, based on an area of 1,200 km).

ECOPATH II can be expected to provide, given a feeding matrix such as illustrated here by Table 2.

In fact, these constraints are so powerful that they resulted in the failure of our initial attempts to identify, based on a feeding matrix of Kuwait fishes, for the marine ecosystem in question, a set of parameters that are biologically tenable.

Two approaches may be pursued to make the constraints (i.e., the known catches, biomasses, P/B ratios, etc.) compatible with a food matrix. One of

Table 5. Electivity index values of various preys for the consumers of the French Frigate Shoals ecosystem, as computed by ECOPATH II, based on the data in Tables 1 and 2.[a]

Prey	Predator												
	3	4	5	6	7	8	9	10	11	12a	12b	12c	12d
1. Phytoplankton	0.95	-	-	-	-	-	-	-	-	-	-	-	-
2. Benthic algae	0.65	0.33	-	-	0.26	-	0.36	-	-	-	-	-	-
3. Zooplankton	-	-	0.99	0.57	0.94	0.90	0.89	0.80	-	-	-	-	0.97
4. Heterotrophic benthos	-	0.49	-	0.38	0.02	0.26	-	-	-	-	-	-	-
5. Small pelagics	-	-	0.70	-	-	0.84	-	0.97		0.77	0.65	0.77	0.96
6. Lobster and crabs	-	-	-	-	-	0.45	-	-	0.91	0.91	0.76	0.89	-
7. Reef fishes	-	-	-	-	0.18	0.69	-	0.27	0.82	0.53	0.83	0.81	0.04
8. Bottom fishes	-	-	-	-	-	0.96	-	-	-	-	-	-	0.99
9. Green turtle	-	-	-	-	-	-	-	-	-	0.99	-	-	-
10. Seabirds	-	-	-	-	-	-	-	-	-	1.00	-	-	-
11. Monk seals	-	-	-	-	-	-	-	-	-	0.99	-	-	-
12a. Tiger sharks	-	-	-	-	-	-	-	-	-	0.95	-	-	-
12b. Reef sharks	-	-	-	-	-	-	-	-	-	0.99	-	-	-
12c. Jacks	-	-	-	-	-	-	-	0.96	-	0.92	-	-	-
12d. Tuna	-	-	-	-	-	-	-	0.98	-	0.98	-	-	-

[a] Dashes, implying total avoidance of a given item and actually corresponding to an electivity of -1, are here left out for the sake of clarity.

Table 6. Summary statistics of various marine and brackishwater ecosystems.[a]

A Area	Chesapeake Bay[b]	Baltic Sea[b]	Celtic Sea I[b]	Celtic Sea II[b]	Benguela Current[b]	Peru Current I[c]	Peru Current II[c]	French Frigate Shoals[d]
B Type of ecosystem	estuary	brackish sea	temperate sea	temperate sea	kelp bed	upwelling, before 1972	upwelling, after 1972	coral reef
C Number of boxes	39	13	12	12	7-8	13	13	16[e]
D Currency	Carbon	Carbon	Carbon	Nitrogen	Carbon	Carbon	Carbon	Wet weight[f]
E Total system throughput	8,989	620	4.55	15.37	8,864	2,660	2,485	2,605 (4,973)
F Capacity	28,522	1,844	15.00	49.35	24,941	5,857	5,279	538,692 (8,893,465)
G Ascendency (%)	54	54	58	52	67	64.6	61.4	45.3 (14.2)
H Respiration overhead (%)	25	2.3	12.9	0	8.1	24.3	17.6	36.5 (74.8)
I Redundancy (%)	15	16.7	24.4	40	24.6	12.8	15.1	18.2 (11.0)

[a] See Ulanowicz (1986) and other contributions in this volume for the background of these summary statistics and their interpretation.

[b] From Fasham et al. (1985).

[c] From Pauly (1987), based on box models in Walsh (1981) and BASIC program in Ulanowicz (1986).

[d] This study (see Tables 1 and 2 for inputs, and Figs. 2 and 3 and Tables 3 to 5 for other outputs); values in brackets consider direct flow from primary producers to detritus, the other values do not; wet weight in $t \cdot km^{-2}$.

[e] Computations all performed with the 15 groups in Tables 1 and 2, plus one implicit detritus compartment (only 12 respiration; 13 boxes are shown in Figs. 2 and 3).

[f] Wet weight is approximately = carbon x 10.

them is to modify the constraints such that a biologically tenable model emerges when they are combined with the food matrix. (This would imply the assumption that the catches, biomasses, P/B ratios, etc. of Kuwait fisheries are not as accurately known as the diet composition of Kuwaiti fishes).

The more promising approach, we believe, is to assume the constraints to be correct and to use them along with e.g., the empirical equations in Appendices A-D and similar relationships to derive, indirectly, a "possible" diet matrix.

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We wish to acknowledge the late J.A. Gulland for reviewing the first draft of this contribution. Also Daniel Pauly wishes to thank the staff of the Marine Fisheries Department, Kuwait Institute of Scientific Research for their invitation to the workshop, held in December 1987 at which this contribution was originally presented. The occupation of their country by Iraqi forces, and the subsequent destructions prevented the publication of the workshop proceedings (in the Kuwait Bull. Mar. Sci.), which had reached the page proof stage when Kuwait was invaded. Our now slightly dated contribution was included in this book not only to show how ECOPATH II emerged, but also to make a point: we dedicate this paper to our Kuwaiti colleagues who resisted.

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Appendices

The following four appendices present empirical relationships linking important features of marine ecosystems as can be used for ecosystem modelling. In all four cases, data points were read off published graphs, and fitted with an equation "which captures the major qualitative features of the data" (Silvert 1981).

These equations may be used as components of simulation models or to check whether estimates derived using ECOPATH II are acceptable.

Appendix A

Primary production, in aquatic systems, is generally based on two types of nutrients:

1. nutrients that cycle through the system (and lead to "regenerated production");
2. nutrients that are added to, or "flow through," the system, leading to "new production".

Values of the ratio "f" of regenerated production to total production have been compiled and plotted as a function of total annual primary production by Eppley (1981). We have fitted these data with an equation of the form

$$f = a + b \exp(c * PP) \qquad \text{...A1)}$$

where f is the ratio of regenerated/total production, a, b and c are fitted parameters, and PP is the total primary production in g $Cm^{-2}year^{-1}$.

Fig. A1 reproduces Eppley's data, and our fitted line, derived for the equation

$$f = 0.325 + 0.675 \exp(-0.0046PP) \qquad \text{...A2)}$$

and which may be used, e.g., to assess the fraction of total primary production which, in a given system, should be flowing into the detritus box to be later released as recycled nutrients (see Kirchman and Ducklow 1987 for a recent review).

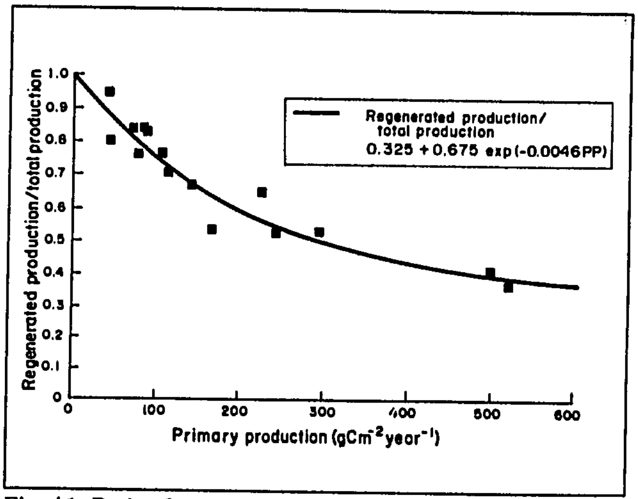

Fig. A1. Ratio of regenerated to total primary production as a function of total production. Squares are observations from Fig. 2 in Eppley (1981).

Appendix B

The efficiency with which zooplankton organisms transform their food (mainly phytoplankton) into animal biomass accessible to other consumers is usually difficult to estimate. Cushing (1973) estimated "transfer efficiencies" of zooplankton in the Indian Ocean. These efficiencies, roughly corresponding to ecologi-

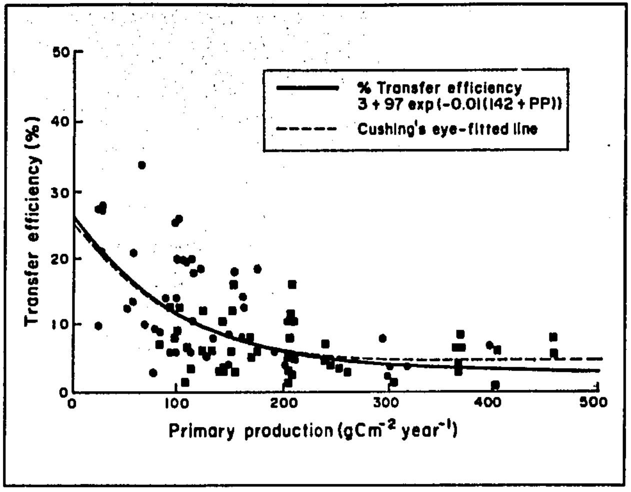

Fig. A2. Transfer efficiency (roughly equal to ecological efficiency) from primary production to secondary (i.e., zooplankton) production expressed as a function of primary production. Adapted from Fig. 7 of Cushing (1973), with ■ referring to the NE monsoon, and • to the SW monsoon, in the Indian Ocean, from 25°N to 40°S.

cal efficiencies, decline as a function of primary production and this is shown in Fig. A2.

We have fitted Cushing's data, after standardizing the ordinate for "180-day monsoons" to a whole year, with the equation

$$TE = 3 - (97 \exp(-0.01(142 + PP)) \qquad \text{...A3)}$$

where TE is the transfer efficiency, in percent. This equation (and the scatter of data on Fig. A2) may be used to assess whether one's estimates of ecological efficiency in tropical zooplankton are compatible with Cushing's data.

Table A1. Data used to derive a multiple regression model for prediction of pelagic detritus abundance as a function of primary production and euphotic layer depth, including observations from all three oceans, from temperate to tropical waters.[a]

No.	Primary production ($g{\cdot}C{\cdot}m^{-2}{\cdot}year^{-1}$)	Euphotic depth (m)[b]	Detritus ($g{\cdot}C{\cdot}m^{-2}$)
1.	25	150	5.2
2.	30	150	5.5
3.	31	150	8.0
4.	40	150	5.8
5.	150[b]	8[c]	2.0[d]
6.	70	75	11.0
7.	100	75	15.8
8.	200	40	8.0
9.	44	100	13.5
10.	73	30	2.2
11.	45	50	10.0
12.	150	20	9.0
13.	190	40	20.0
14.	350	10	8.0

[a] Values from Table 1 and Fig. 4 in Finenko and Zaika (1970), except for no. 5.

[b] From Lenz (1981).

[c] From Krey (1974)..

[d] From Tables 1, 2 and 4 in Lenz (1974).

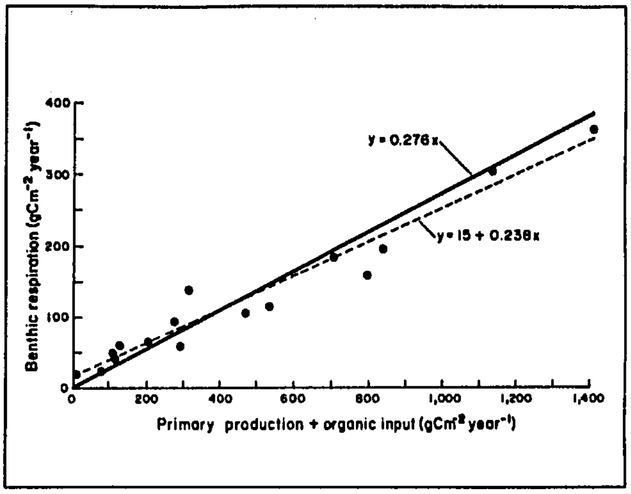

Fig. A3. Relationship between primary production and benthic respiration in US and Canadian estuarine and nearshore waters (from Nixon 1986, with solid line added).

Appendix C

Nixon (1986) presented data showing, for temperate estuaries and nearshore waters at least, that benthic respiration (i.e., "remineralization") is a close linear function of primary production (plus other organic inputs). This is shown here in Fig. A3, which suggests

$$BR = 0.276\,(PP + ORG.INPUTS) \qquad \text{...A4)}$$

where BR is the benthic respiration, and PP the primary production, in $g{\cdot}C{\cdot}m^{-2}{\cdot}year^{-1}$.

It should be considered with regard to this equation, that no points referring to tropical locations are included in Fig. A3, and that the relationship applies only to shallow water (down to 5-7 m).

Appendix D

ECOPATH II and related models express biomasses on a per area basis (e.g., m^{-2}); the explicit inclusion of detritus as an element of an ecosystem thus requires that this component also be expressed on a surface area basis.

As detritus standing stock estimates in the literature are generally expressed on a volume basis (e.g., $g{\cdot}C{\cdot}m^{-3}$), we present here one of the few readily available dataset on detritus standing stock per area, for various areas of the world ocean (Table A1). This dataset was fitted with the equation

$$\log_{10}D = -2.41 + 0.954 \log_{10}PP + 0.863 \log_{10}E \qquad \text{...A5)}$$

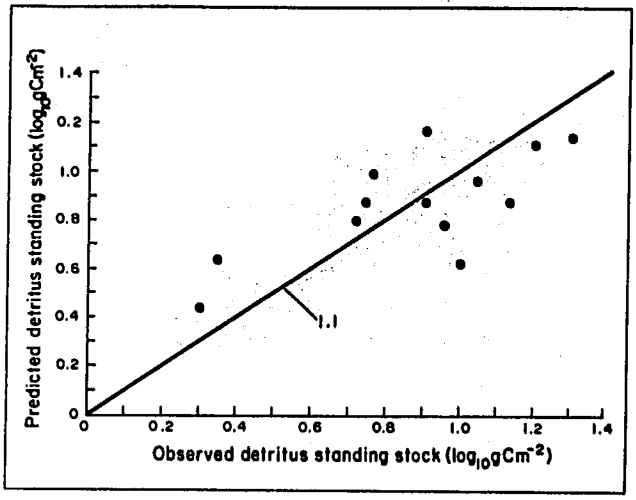

Fig. A4. Relationship between observed (from Table A1) and detritus standing stock as predicted using equation A5 (see text).

where D is the detritus standing stock in $g{\cdot}C{\cdot}m^{-2}$, PP is the primary production in $g{\cdot}C{\cdot}m^{-2}{\cdot}year^{-1}$ and E is the euphotic depth, in m. This equation, with R = 0.718, explains 52% of the variation in the dataset in Table 1A, and both of its partial regression coefficient are significant (s.e. = 0.305 and 0.256, respectively, df = 11). Fig. A4 shows a plot of observed *vs.* predicted detritus standing stock values. As might be seen, the fit is not particularly tight, but might be considered sufficient in cases where no other information is available.

On Steady-State Modelling of Ecosystems*

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Abstract

This paper provides a brief description of the rationale behind steady-state modelling, and of the implementation of the ECOPATH II software system, a system for straightforward construction, parametrization, and balancing of steady-state trophic models of (aquatic) ecosystems. ECOPATH II is written for MS DOS computers and is available as a public domain software from the ICLARM Software Project.

ECOPATH II is structured around a system of linear equations initially proposed by J.J. Polovina and coworkers. Also, it incorporates routines for computation of several maturity and network flow indices proposed by various theoretical ecologists, notably the Odum brothers and R.E. Ulanowicz.

Modelling of Ecosystems

The word "model" has several meanings; for scientists and, more specifically, for biologists working at the ecosystem level, "models" may be defined as *consistent* descriptions, emphasizing certain aspects of the system investigated, as required to *understand* their function.

Thus, models may consist of a text ("word models") or a graph showing the interrelationships of the various components of a system. Models may also consist of equations, whose parameters describe "states" (the elements included in the models) and "rates" (of growth, mortality, food consumption, etc.) of the elements of the model.

The behavior of mathematical models is difficult (often impossible) to explore without computers. This is especially the case for "simulation models", i.e., those representations of ecosystems which follow, through time, the interactive behavior of the (major) components of an ecosystem.

Simulation models are difficult to build, and even more difficult to get to simulate realistically the behavior of a system over a long period of time, without "crashing" or "exploding", where populations go either extinct or grow without bound, respectively. This is one reason why most aquatic biologists shy away from constructing such models, or even from interacting with "modellers" (who, often being nonbiologists, may have scant knowledge of the intricate interactions between living organisms). Another reason is that one needs to be able to describe the dynamics of all key biological processes (growth, reproduction, mortality, etc.) to build realistic dynamic models. Obtaining sufficient knowledge to do this is difficult for most ecosystems.

However, "modelling" does not necessarily imply "*simulation* modelling". There are various ways of constructing quantitative models of ecosystems which avoid the intricacies of dynamic simulation modelling, yet still provide many of the benefits of fully-fledged modelling, *viz*:

- requiring the biologist/ecologist to review and standardize all available data on a given ecosystem and identify information gaps;
- requiring the would-be modeller to identify estimates (of states and/or rates) that are mutually incompatible, and which, if true, would prevent the system from maintaining itself (e.g., prey productions that are too low relative to assumed food requirements of predators);

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*Includes extracts from the ECOPATH II manual of Christensen and Pauly (1992a). ICLARM Contribution No. 831.

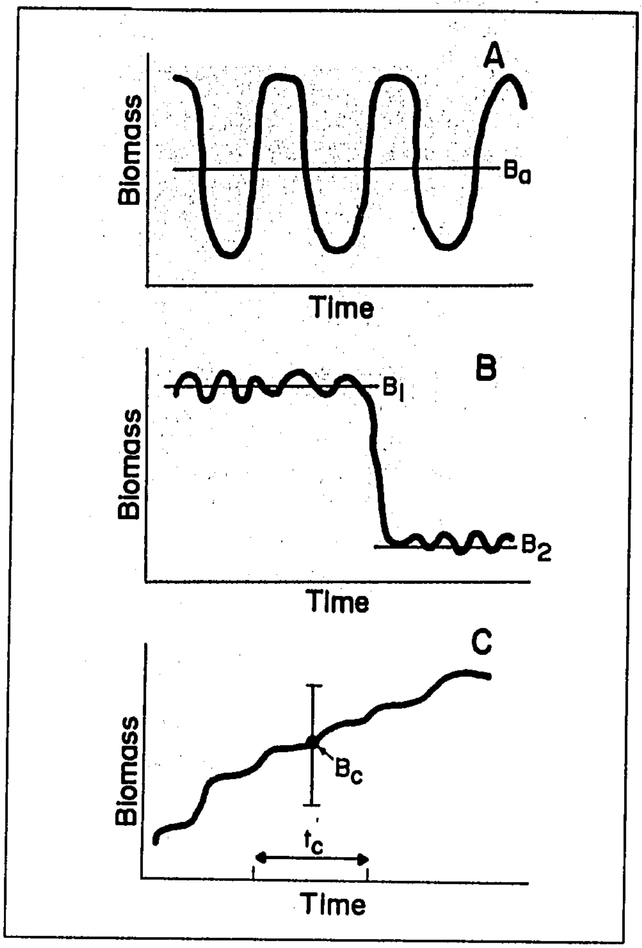

Fig. 1. Schematic representation of possible biomass trends in an ecosystem. (A) Strong, regular changes as, e.g., due to the succession of seasons, not well represented by an annual mean (B_a). (B) Rapid transition between two stable states, of which each is well represented by its own mean (B_1, B_2). (C) Example of a biomass that does not reach equilibrium. During a brief period (t_c), this biomass can be represented by a single value (B_c) whose confidence interval will usually bracket the change of biomass during the interval t_c.

- requiring the same would-be modeller to interact with specialities other than her/his own, e.g., a plankton specialist will have to either cooperate with fish biologists and other colleagues working on various consumer groups, or at least read the literature they produce.

To avail of these and other related advantages without having to get involved in simulation modelling, one's models can be limited to describing "average" (or "steady-state") states and rates. This limitation, as we shall see, is not as constraining as it may appear at first sight. It is consistent with the work of most aquatic biologists, whose state and rate estimates also represent "averages", applying to a certain period (although this generally is neither stated by the authors, nor realized by the readers).

The approach we propose is to use states and rates estimated for single species in a multispecies context to describe aquatic ecosystems in rigorous, quantitative terms, during the (arbitrary) period to which the state and rate estimates apply (Fig. 1).

In many cases, the period considered will be one (typical) year, with the state and rate estimates used for model construction pertaining to different years. Such models may represent a decade or more, during which little changes have occurred.

When ecosystems have undergone massive changes, two or more models may be needed, representing the ecosystem before, (during) and after the changes (Fig. 1). As an example, three models of the Peruvian upwelling ecosystem were constructed, covering different periods before and after the collapse of the anchoveta fisheries (Jarre et al. 1991). Other examples of this can be found in this volume for Lake Tanganyika, Lake Victoria, and Lake Turkana, all in Africa.

When seasonal changes are to be emphasized, different models may be constructed for each season, or for extreme situations ("summer" *vs.* "winter"). As an example, Baird and Ulanowicz (1989) constructed four models describing the seasons in Chesapeake Bay and one "average" model to represent the whole year. Likewise, Jarre and Pauly (this vol.) describe the dynamics of the annual cycle of the Peruvian upwelling system using 12 steady-state models, each representing a monthly period.

The same idea can be applied to aquaculture situations, where a pond and its producers and consumers can be described for instance at the beginning, midpoint and end of a growing season. Alternatively, a pond can be modelled as the average of such states. Ruddle and Christensen (this vol.) illustrate this approach.

Judicious identification of periods long enough for sufficient data to be available, but short enough for massive changes not to have occurred, will thus solve most problems associated with the lack of a time dimension in "steady-state" models.

The ECOPATH II Model

The ECOPATH II system combines an approach by Polovina (1984a) for estimation of biomass and food consumption of the various elements (species or groups of species) of an aquatic ecosystem with an approach proposed by Ulanowicz (1986) for analysis of flows between the elements of ecosystems (Christensen and Pauly 1992b).

As described by Pauly et al. (this vol.), the core routine of ECOPATH II is derived from the ECOPATH program of Polovina and Ow (1983) and Polovina (1984b, 1985).

The ecosystem is modelled using a set of simultaneous linear equations (one for each group *i* in the system), i.e.,

Production by *(i)* - all predation on *(i)* - nonpredation losses of *(i)* - export of *(i)* = 0, for all *(i)*.

This can also be put as

$$P_i - M2_i - P_i\,(1\text{-}EE_i) - EX_i = 0 \qquad ...1)$$

where P_i is the production of *(i)*, $M2_i$ is the total predation mortality of *(i)*, EE_i is the ecotrophic efficiency of *(i)* or the proportion of the production that is either exported or predated upon, $(1 - EE_i)$ is the "other mortality", and EX_i is the export of *(i)*.

Equation (1) can be re-expressed as

$$B_i{*}PB_i - \sum_{j=1}^{n} B_j{*}QB_j{*}DC_{ji} - PB_i{*}B_i\,(1\text{-}EE_i) - EX_i = 0$$

or

$$B_i{*}PB_i{*}EE_i - \sum_{j=1}^{n} B_j{*}QB_j{*}DC_{ji} - EX_i = 0 \qquad ...2)$$

where B_i is the biomass of *(i)*, PB_i is the production/biomass ratio, QB_i is the consumption/biomass ratio and DC_{ji} is the fraction of prey *(i)* in the average diet of predator *(j)*.

Based on (2), for a system with n groups, n linear equations can be given in explicit terms,

$$B_1PB_1EE_1\text{-}B_1QB_1DC_{11}\text{-}B_2QB_2DC_{21}\text{-}...\text{-}B_nQB_nDC_{n1}.EX_1 = 0$$
$$B_2PB_2EE_2\text{-}B_1QB_1DC_{12}\text{-}B_2QB_2DC_{22}\text{-}...\text{-}B_nQB_nDC_{n2}\text{-}EX_2 = 0$$
:

:

$$B_nPB_nEE_n\text{-}B_1QB_1DC_{1n}\text{-}B_2QB_2DC_{2n}\text{-}...\text{-}B_nQB_nDC_{nn}\text{-}EX_n = 0$$

This system of simultaneous linear equations can be solved through matrix inversion. In ECOPATH II, this is done using the generalized inverse method described by Mackay (1981), which has features making it generally more versatile than standard inverse methods.

For example, if the set of equations is overdetermined (more equations than unknowns) and the equations are not consistent with each other, the generalized inverse method provides least squares estimates which minimize the discrepancies.

If, on the other hand, the system is underdetermined (more unknowns than equations), an answer that is consistent with the data (although not unique) will still be output.

Generally only one of the parameters B_i, PB_i, QB_i, or EE_i may be unknown for any group i. In special cases, however, QB_i may be unknown in addition to one of the other parameters (Christensen and Pauly 1992a). Exports and diet compositions are always required for all groups.

The Energy Balance of a Box

A box, in an ECOPATH II model, may be a group of (ecologically) related species, a single species, or a single size/age group of a given species.

In a "steady-state" model, the energy input and output of all living groups must be (or are) balanced, by definition.

The basic ECOPATH equation (1) includes only the production of a box. Here production equals predation mortality plus export plus other mortality. When balancing the energy flow of a box, other flows should be included. Thus,

Consumption = production + respiration + unassimilated food

From this the respiration can be estimated as a difference (but see below).

Parametrization

The data requirements of steady-state models are very limited in comparison to those of simulation models. At the same time, steady-state models are very useful for making summaries of available data and trophic flows in a system. Also, and quite importantly, these models help identify gaps in one's knowledge about an ecosystem. Together, this makes steady-state models a good starting point for ecosystem modelling.

Consumption

There are various approaches for obtaining estimates of consumption/biomass ratio (QB); they may be split into (i) analytical methods and (ii) holistic methods.

(i) The analytical methods involve estimation of ration, pertaining to one or several size/age classes, and their subsequent extrapolation to a wide range of size/age classes, representing an age-structured population exposed to a constant or variable mortality.

The required estimates of ration are obtained from laboratory experiments, from studies of the dynamics of stomach contents in nature (Jarre et al. 1991; see Fig. 2), or by combining laboratory and field data (Pauly 1986).

(ii) The existing holistic methods for estimation of QB are empirical regressions for prediction of QB from some easy to quantify characteristics of the animals for which the QB values are required (Palomares and Pauly 1989; Pauly et al. 1990; Palomares 1991; Pauly et al., this vol.).

Production

Production includes all matter elaborated by a group (whether it is ultimately eaten, fished or dies of other causes) over the period considered. Total

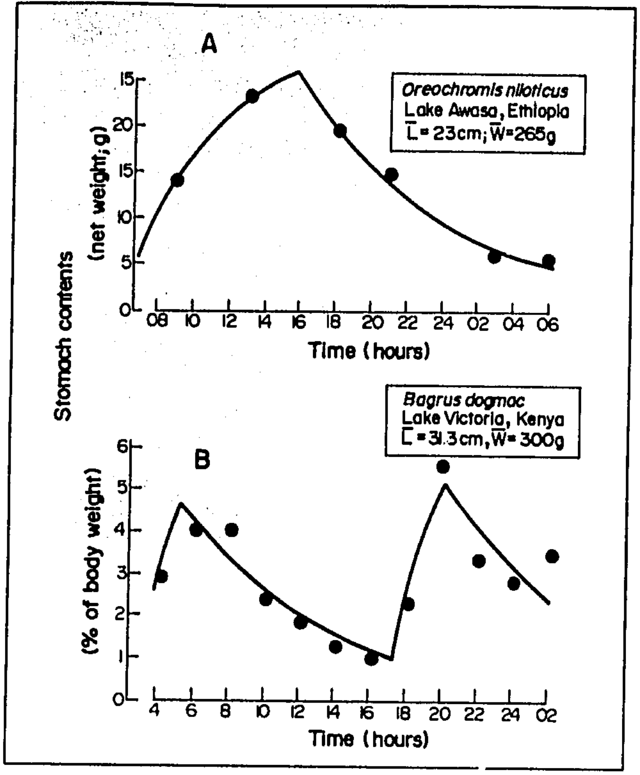

Fig. 2. Two daily cycles of stomach contents of African fishes (from Palomares 1991), fitted by means of the MAXIMS software of Jarre et al. (1990). (A) *Oreochromis niloticus* (Cichlidae), based on data in Getachew (1987). Note single feeding period, from 7 to 16 hours. (B) *Bagrus dogmac* (Bagridae), based on data in Okach and Dadzie (1988). Note two feeding periods per day, at dawn and dusk, as often occurs in piscivores (Hobson et al. 1981).

mortality, when constant, is equal to production over biomass. Therefore, in steady-state models, it is safe to treat estimates of total mortality (Z) as equivalent to the production/biomass ratio (P/B) (Allen 1971).

Predation

In a trophic model such as constructed by ECOPATH II, it is predation that links the groups in a system. Thus, what is consumption for one group is mortality (production) for its prey. Therefore, information on predation is important for understanding the dynamics of ecosystems. Unfortunately, properly presented information on diet composition is sparse - fish population dynamics has traditionally treated fish populations as if they were independent, and a large part of the available information on diet compositions is expressed on a "per cent occurrence" or "point" basis or as "dominance", all of which are of little use for quantification of diets. What are needed are measures based on energy, weight or volume.

For quantified ecosystem models such as ECOPATH II, the diet compositions should be expressed as the proportion (weight, volume or energy) each prey constitutes to the overall diet.

Respiration

As mentioned above, respiration is estimated by ECOPATH II as a difference, and hence is not a required parameter. If, however, explicit estimates of respiration are available, these can be used for "calibration", i.e., a model's inputs can be modified until, for any given box, the computed respiration matches the available estimate; this approach makes it possible for another parameter of that box, e.g., PB, to be unknown.

Network Flow Indices

The ECOPATH II software links concepts developed by theoretical ecologists, especially the theory of Ulanowicz (1986), with those used by biologists involved with fisheries and aquaculture management. The following section gives a brief account of some of the concepts from theoretical ecology that are included in ECOPATH II.

Ascendency is a measure of the average mutual information in a system, scaled by system throughput. These quantities are derived from information theory (Ulanowicz 1986; Ulanowicz and Norden 1990). If one knows the location of a unit of energy, the uncertainty of where it will go next is reduced by an amount known as the "average mutual information",

$$I = \Sigma_{ij}\, f_{ij}\, Q_i \quad \log(f_{ij}/\Sigma_k(f_{kj}\, Q_k)),$$

where, if T_{ij} is a measure of the energy flow from j to i, f_{ij} is the fraction of the total flow from j that is represented by T_{ij}, or

$$f_{ij} = T_{ij}/\Sigma_k\, T_{kj}.$$

Q_i is the probability that a unit of energy passes through i, or

$$Q_i = \Sigma_k\, T_{ki} \,/\, \Sigma_{lm}\, T_{lm}.$$

I is a probability and is scaled by multiplication with the total throughput of the system, T, where

$$T = \Sigma_{ij} T_{ij}.$$

Thus,

$$A = T * I,$$

where A is called "ascendency". There is an upper limit for the size of the ascendency, estimated from

$$C = H * T,$$

where C is called "development capacity" and H is called "statistical entropy" and is estimated from

$$H = - \Sigma_i Q_i \log Q_i.$$

The difference between capacity and ascendency is called "system overhead". This provides a limit for the increase of ascendency and reflects the system's "strength in reserve" from which it can draw to meet unexpected perturbations (Ulanowicz 1986).

Ascendency, overheads and capacity can all be split into contributions from imports, internal flow, exports and dissipations (respiration). These contributions are additive; examples can be found in several of the contributions in this volume.

The unit for these measures is "flowbits", or the product of flow (e.g., $t \cdot km^{-2} \cdot year^{-1}$) and bits, an information unit corresponding to the amount of uncertainty associated with a single binary decision.

Trophic Aggregation

In addition to including a routine for calculating group-specific fractional trophic levels, as suggested by Odum and Heald (1975), we have included a routine in the ECOPATH II system that aggregates the entire system into discrete trophic levels *sensu* Lindeman (1942). This routine is used by a number of the authors in this volume, and is based on an approach suggested by Ulanowicz (in press) which reverses the routine for calculation of fractional trophic levels. For example, if a group obtains 40% of its food as a herbivore and 60% as a first-order carnivore, 40% and 60% of the flow through the group are attributed to the herbivore level and the first consumer level, respectively.

Based on these computations, the efficiency of transfer between discrete trophic levels can be calculated as the ratio of the flow that is transferred from one trophic level to the next (or to the fishery) and the throughput at the trophic level.

Mixed Trophic Impacts

Leontief (1951) developed a method to quantify the direct and indirect interactions of various sectors of the economy of the USA, using what has since been called the Leontief matrix. This was first used in ecology by Hannon (1973) and Hannon and Joiris (1989) to assess the impact of any group in a system on all other groups.

Ulanowicz and Puccia (1990) developed a similar approach, and a routine based on their method has been incorporated in the ECOPATH II system. Examples of the use and interpretation of mixed trophic impacts are given in a number of the contributions in this volume.

Conclusion

We hope that the rationale presented in this paper, together with the other contributions in this volume, will help establish the potential of steady-state modelling as a tool to improve our understanding of ecosystems, especially for data-sparse areas.

ECOPATH II, and forthcoming new developments (Christensen 1991), will, we hope, build a bridge between methodologies commonly used by fisheries biologists and by theoretical ecologists.

Acknowledgement

The development and dissemination of the ECOPATH II system was made possible by the "Global comparisons of aquatic ecosystems" project, financed through a grant to ICLARM from the Danish International Development Agency (DANIDA).

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Graphical Representation of Steady-State Trophic Ecosystem Models*

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Abstract

The traditional method of representing steady-state ecosystem models, usually by scattering interconnected boxes across a page, underutilizes the potential descriptive and explanatory power of graphical representations. Some alternative approaches are proposed: (1) drawing boxes with areas proportional to the logarithms of the biomasses they represent, ordered along the ordinate in terms of their weighted mean trophic levels; (2) plotting boxes as in (1) along the ordinate, but using box-specific particle size for ordering along the abscissa (which leads to "size-shifted" models); and (3) mapping the fluxes between boxes, arranged as in (2), in terms of isolines.

Introduction

Construction and parametrization of steady-state models of aquatic ecosystems have a tradition dating back several decades - see, e.g., Odum and Odum's (1957) model of Eniwetok Reef. Yet, consistently applied rules do not seem to have emerged regarding the graphic representation of such models.

The only approach we have seen used repetitively is the energy circuit language of Odum (1972). In this representation, different symbols are used for producers, consumers, storage groups, etc. We find, however, that the symbols add more complexity than information and would not recommend that language.

We wonder if the absence of usable rules of graphic representation of steady-state models could be caused by the perception that steady-state trophic box models are intrinsically too simple - they consist only of boxes and arrows - for their graphical representation to require much thought about symbols or effort by a graphic artist.

It seems paradoxical to us, however, to devote as much time as is generally done to the construction and parametrization of ecosystem models and so little to the elaboration of the graph representing the model, i.e., the final product.

We believe, indeed, that the same criteria should apply for representations of ecosystem models as for scientific graphs in general, for which Tufte (1983) wrote:

> "Excellence in statistical graphics consists of complex ideas communicated with clarity, precision, and efficiency. Graphical displays should
> - show the data
> - induce the viewer to think about the substance rather than about methodology, graphic design, the technology of graphic production, or something else
> - avoid distorting what the data have to say
> - present many numbers in a small space
> - make large data sets coherent
> - encourage the eye to compare different pieces of data
> - reveal the data at several levels of detail, from a broad overview to the fine structure
> - serve a reasonably clear purpose: description, exploration, tabulation, or decoration
> - be closely integrated with the statistical and verbal descriptions of a data set."

As we hope to show below, there are ways to represent box models such as to (1) increase the descriptive and explanatory impact of the graph and (2) facilitate comparisons between ecosystems.

The first of these two points does not need

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elaborating, but the second does: the baroque cacophony of style used by different authors and illustrated in Fig. 1 may be one key reason why few useful generalizations have emerged to date from the comparisons of models of different ecosystems.

We suggest, in the following, some rules for representing trophic models of ecosystems. These rules, if adopted, could help overcome some of the

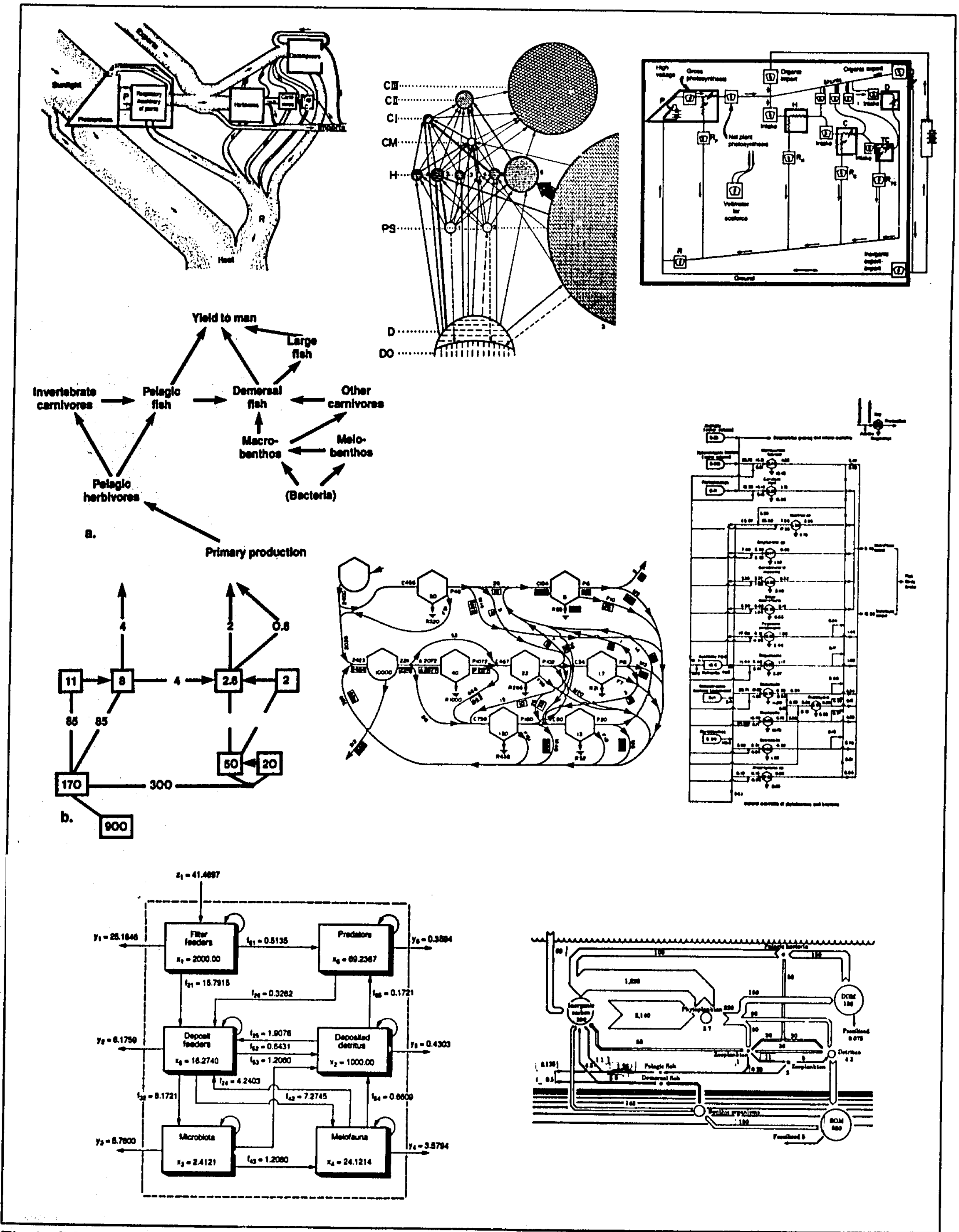


Fig. 1. Selected examples of published representations of steady-state trophic models of aquatic ecosystems.

problems in (1) and (2) above, mainly by making creative use of the ordinate and abscissa implied in each graph, and of the quantitative scale which - since Descartes - comes along with these axes, if only implicitly.

Using the Y-Axis

Often, trophic models are drawn such that the boxes representing organisms low in the food chain (or web) are placed in the lower part of the graph, along with the plants, while the boxes representing organisms high in the food chain (web) are put higher up.

We propose to make explicit use of this mode of graphing, i.e., to plot the boxes representing the organisms of an ecosystem such that the horizontal axis of symmetry of each box is aligned with the trophic level of the box in question (Fig. 2). This implies estimating these trophic levels, as opposed to making *a priori* assumptions about them (as, e.g., some cases included in Fig. 1). The estimation in question can be performed using various methods, notably the ECOPATH II software discussed elsewhere in this volume. Note that the trophic levels so estimated need not be (and generally are not) whole numbers, as assumed in some food chain theories (e.g., Pimm 1982).

Using the X-Axis (I)

Using trophic level as Y-axis is not sufficient to define the relative position of the elements of a model, and two approaches may be considered for ordering the boxes along the X-axis:

1. arranging the boxes such that they do not overlap, and/or with emphasis on some symmetry, i.e., such that the resulting graph is esthetically pleasing, or
2. arranging the boxes such that the arrows linking the boxes cross each other as little as possible, hence, maximizing intelligibility of the graph.

We have tried to incorporate (1) and (2) in the construction of Fig. 2. We note in this context that software for electronic hardware development exist, e.g., SCHEMA II and ORCAD, which can be used to optimize the positioning of elements and to conduct check of energy pathways and that such software is of use for constructing ecosystem flow charts as well.

As the astute reader will have noted, the sizes of the boxes plotted on Fig. 2 themselves contain information: their area is proportional to the logarithm of the biomass in each box.

We found this trick to be particularly useful in helping the reader visualize the relative role and impact of the organisms in each box - something which boxes of equal sizes do not even attempt, and which boxes with dimensions directly proportional to biomass fail to do well. To avoid the problem of taking logarithms of values less than 1 we have also found it useful to make the box sides equal to the third root of the biomasses, thus assuming the boxes to be three-dimensional.

We have introduced another rule of construction in Fig. 2. All flows entering a box do this on the lower half of the box, while flows exiting a box do it from the upper half. Flows that enter a box can be combined, while flows that leave a box cannot branch, but they can be merged with flows exiting other boxes. This ensures compatibility with shortcut circuit checks in electronic hardware design software, and at the same time it simplifies the flow chart. "Cannibalism" or zero-order flows are shown as circles originating from the top half of a box and entering the lower half.

On the other hand, we abstain here from representing flows through arrows of different sizes (i.e., with thickness proportional to the log of the flow represented) because we found that this cluttered up our models. Indeed, it is often necessary to omit, for clarity's sake, lesser flows from graphs representing highly interconnected systems. Moreover, there appear to be far more effective ways of representing flows, as will be shown below.

Using the X-Axis (II)

Powerful holistic approaches have recently emerged in biology and ecology which demonstrate that the *size* of organisms is their key attribute. The relevant compilations (see, e.g, Bonner 1965; Calder 1984; Ulanowicz and Platt 1985) show that virtually all important characteristics of organisms, ranging from their physiology to their population dynamics and from their gross anatomy to their ecology, can be expressed as tight double logarithmic plots, often ranging in size from bacteria to whales (24 orders of magnitude). This suggests that insights could be gained by using size as the abscissa scale of graphic representation of ecosystems.

Following common usage, we assume a weight-to-volume conversion based on a specific weight equal to unity. This enables comparability between organisms with different shapes. One problem here is the choice of the appropriate "mean weight" for the aggregate of organisms within a box, which may consist of (1) a single-species, steady-state population, including lots of small, young organisms and fewer larger, old organisms, or (2) several species, each with its own size composition. In the second case, the model builder may have to construct either a cumulated multispecies size distribution or use the

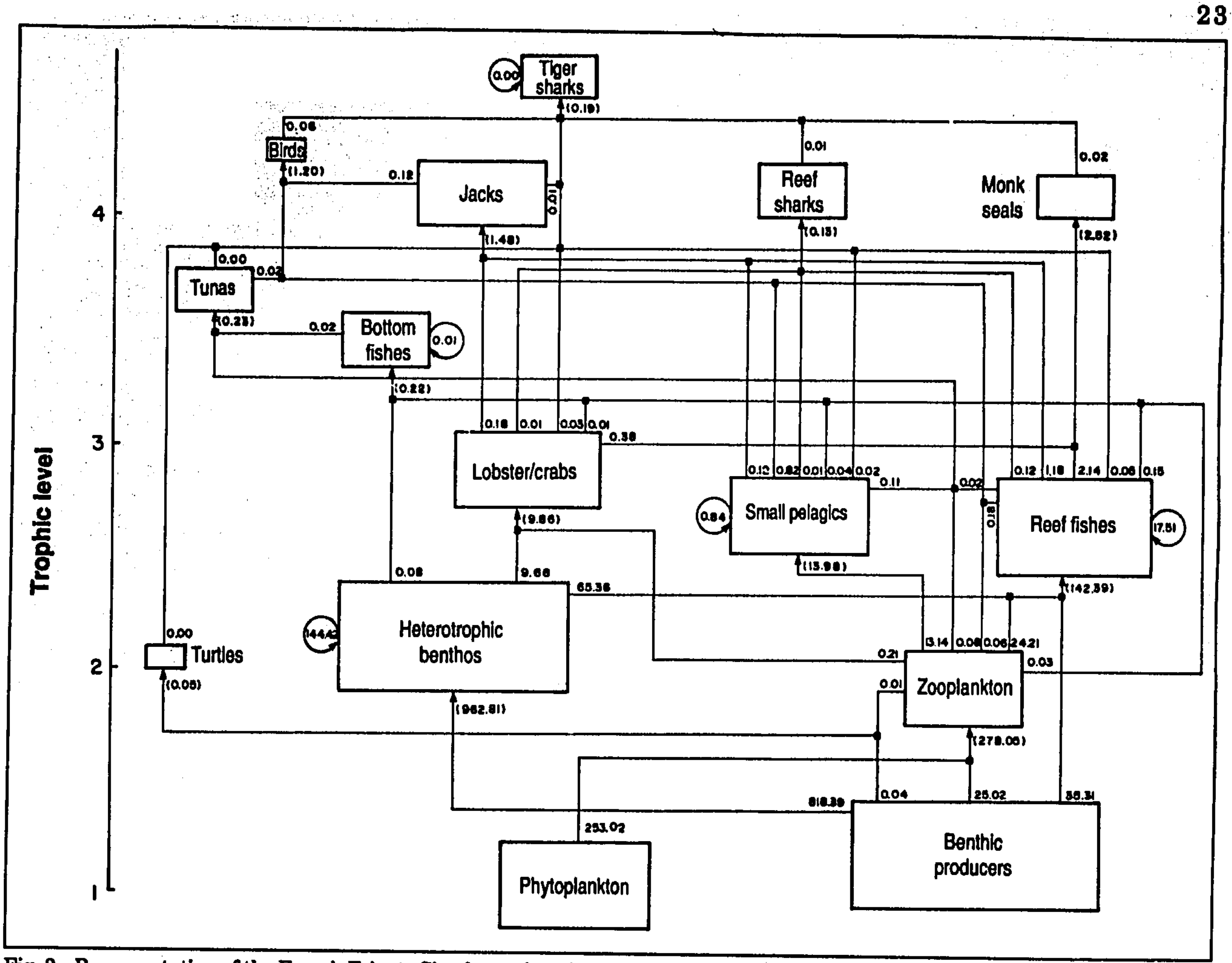


Fig. 2. Representation of the French Frigate Shoals coral reef ecosystem (Polovina 1984). The area of each box is proportional to the logarithm of the biomass of each group. Flows exit the top half of a box and enter the bottom half (see text for further constructional details).

size distribution of a single species representative of the other taxa in the box.

Whatever choice is taken, some measure of central tendency of the size distribution will have to be used, i.e.,

- a statistically based index, e.g., the mean, mode or median, or
- a biologically based index, e.g., (a) a representative size of adults, i.e., the mean of size at first maturity (W_m) and of asymptotic (W_∞) or maximum size (W_{max}), as used in Pauly (1982), or (b) W_m itself which, in fishes, roughly corresponds to the peak of the biomass curve, and to $0.3 * W_\infty$, or (c) the size at which relative food consumption is highest (this generally occurs at the juvenile stage, below $0.3 * W_\infty$).

Here, we have chosen a measure of size which, due to its simplicity, needs some explanation. The measure of size should represent the "average" organism in a group. For a given population this size will among others be a function of the total mortality of the population. This is illustrated in Fig. 3, which shows population mean weight as a function of total mortality (within the range of mortality normally found for organisms of this size [i.e., from unexploited to heavily exploited]).

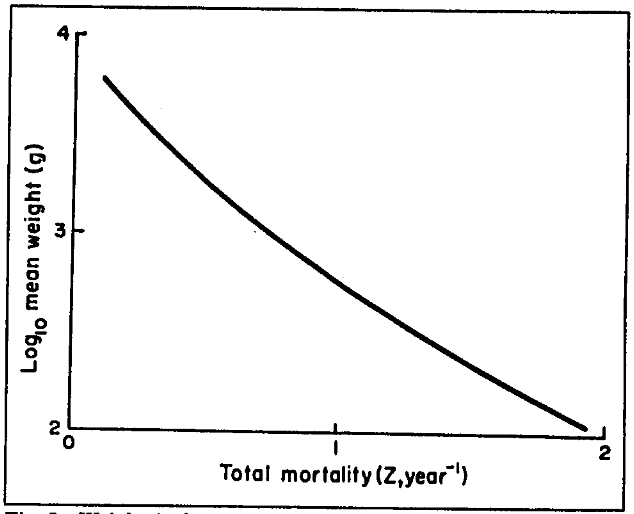


Fig. 3. Weight (g, log scale) for the average fish in a population with growth following the von Bertalanffy growth function, with parameters $W_\infty = 10^4$ g, $t_0 = -0.1$ year, $K = 0.5$ year^{-1}, as a function of total mortality, Z (year^{-1}).

As can be seen from the figure, weight is strongly correlated with total mortality rates in the observed range. If the population is in steady state (as all populations considered here are assumed to be), total mortality rate is equivalent to production/biomass ratio (P/B; Allen 1971). As the correlation is negative, we suggest to use the inverse log (B/P) as a measure of (log) size. The unit for biomass/production is time, e.g., year.

To further explore the proportionality between P/B and size, we have extracted 58 cases of reported total mortality rates (or production/biomass ratios) and corresponding organism weights from published data (Table 1).

The correlation between the measure of size, i.e., log (B/P) and weight is shown on Fig. 4. As can be seen, the two variables are highly correlated (r = 0.88). However, there is considerable variation around the regression line. This is partly due to the measure of size we used, which varies with the exploitation rate (c.f. Fig. 3).

Using log (biomass/production) as an indirect measure of size (or any of the other above-mentioned direct measures of size), it is straightforward to plot the compartments of a trophic model on a surface defined by trophic level *vs.* organism size. This leads to what we shall call here *size-shifted models.* This name was selected because in aquatic ecosystems, predators are usually much larger than their preys, which induces a rightward shift in the resulting graphs (Fig. 5).

Figs. 6a and 6b show size-shifted graphs of two ecosystems, in which the flows are represented by straight lines. Fig. 6a illustrates a case in which size and trophic level correlate rather well, for all groups. On the other hand, at least three of the groups in Fig. 6b are outliers. A closer examination justifies the position of group (5), i.e., of turtles. These are large organisms feeding on small plants. For the other groups that seem misplaced, i.e., (2) monk seals, (3) birds, and perhaps (1) tiger sharks, it should be noted that the P/B ratios used were preliminary estimates, and it might be that these groups do not have the high P/B ratios that were assumed. These and similar observations suggest the general usefulness of this approach, and of outliers to pinpoint questionable P/B ratios.

The shift that is observed on Figs. 6a and 6b can be quantified by calculating the slopes of all nonrespiratory and nondetrital flows in a system, then taking the geometric mean of all positive slopes weighted by the size of the flows. For the two systems on Figs. 6a and 6b, the slopes are almost the same, 1.00 and 0.98, respectively (disregarding flows from the three outlier groups on Fig. 6b).

We propose that the value of this slope for a given ecosystem be used to characterize the way trophic levels and size interact in the ecosystem in question.

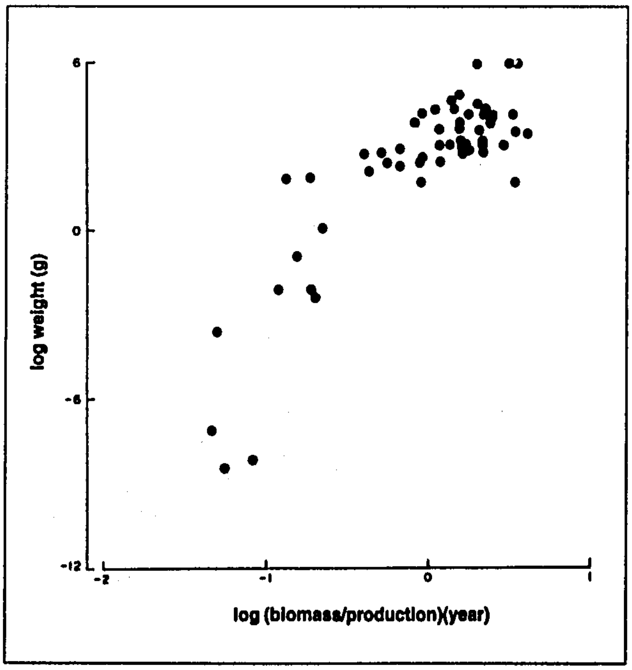


Fig. 4. Average weight (log) as a function of inverse mortality (or B/P) rate for 58 groups (see Table 1).

Using the Z-Axis - Flow Intensity

The size-shifted models described above and in Figs. 5 and 6 have two dimensions: trophic level and organism size. However, since the publication of Fasham (1984), awareness of the importance of flows has considerably increased and new approaches for deriving indices of ecosystem structure exclusively from network of flows have been developed (e.g., Ulanowicz 1986).

Similar developments have not occurred at the graphical level, however, i.e., no approach appears to have been proposed to date to graphically express the "signature" of an ecosystem's network of flows.

We propose that such a signature be obtained by adding a third dimension to graphs such as Fig. 6, i.e., by expressing the (nonrespiratory and nondetrital) flows as arrows with a width proportional to the log of their intensity, adding up overlapping flows (by grid squares) then drawing isolines of the log flow intensity for the whole system (Fig. 7).

As might be seen, this approach leads to complete obliteration of the boxes of a system, and of the individual flows between them, leaving only an isopleth diagram to characterize the system as a whole.

We suggest that such graphs, perhaps even better than the index b (see above) could be used to characterize the size-shifted nature of the network of flows used to represent steady-state trophic ecosystem models.

Table 1. Reported total mortality rates (Z) (or production/biomass ratios [P/B]) and the organism weights for 58 groups of organisms.

Species/group	P/B or Z (year^{-1})	Weight (g)[a]	References
Bacteria	197.00	$1.00 \cdot 10^{-12}$	Lewis (1981)
Microbial population	21.90	$6.67 \cdot 10^{-8}$	Sorokin (1981)
Eurocercus lamellatus	20.00	$2.00 \cdot 10^{-4}$	Jϕrgensen (1979)
Microbial population	18.25	$3.33 \cdot 10^{-9}$	Sorokin (1981)
Microbial population	12.17	$6.25 \cdot 10^{-9}$	Sorokin (1981)
Nematoda	8.38	$6.85 \cdot 10^{-9}$	Warwick et al. (1979)
Shrimps	7.57	$6.00 \cdot 10^{1}$	Abarca-Arenas and Valero-Pacheco (this vol.)
Tantarsini	6.50	$1.00 \cdot 10^{-1}$	Jϕrgensen (1979)
Shrimps	5.38	$6.00 \cdot 10^{1}$	Arreguín-Sánchez et al. (this vol.)
Shrimps	5.38	$6.00 \cdot 10^{1}$	Chávez et al. (this vol.)
Meiofauna	5.33	$6.40 \cdot 10^{-3}$	Elmgren (1984)
Zooplankton	5.00	$3.31 \cdot 10^{-3}$	Reyes-Marchant et al. (this vol.)
Hyalella	4.50	1.00	Jϕrgensen (1979)
Crabs	2.50	$4.00 \cdot 10^{2}$	de la Cruz-Aguero (this vol.)
Anchoveta	2.30	$1.00 \cdot 10^{2}$	Lewis (1981)
Goat fish	1.92	$4.59 \cdot 10^{2}$	Mendoza (this vol.)
Sardine	1.80	$2.00 \cdot 10^{2}$	Lewis (1981)
Loligo spp.	1.50	$1.50 \cdot 10^{2}$	Cohen et al. (1982)
Illex spp.	1.50	$6.00 \cdot 10^{2}$	Cohen et al. (1982)
Mugil spp.	1.20	$5.00 \cdot 10^{3}$	Chávez et al. (this vol.)
Anchovies and sardines	1.13	$2.01 \cdot 10^{2}$	Mendoza (this vol.)
Herrings	1.11	$4.00 \cdot 10^{1}$	Chávez et al. (this vol.)
Octopus	1.10	$1.09 \cdot 10^{4}$	Chávez et al. (this vol.)
Mojarra	1.09	$3.00 \cdot 10^{2}$	Chávez et al. (this vol.)
Bonito	0.91	$1.50 \cdot 10^{4}$	Lewis (1981)
Horse mackerel	0.85	$3.00 \cdot 10^{3}$	Lewis (1981)
Mackerel	0.85	$8.00 \cdot 10^{2}$	Lewis (1981)
Squids	0.84	$2.07 \cdot 10^{2}$	Mendoza (this vol.)
Mackerel	0.73	$8.00 \cdot 10^{2}$	Sheridan et al. (1984)
Cod	0.72	$3.04 \cdot 10^{4}$	Cohen et al. (1982)
Lutjanus spp.	0.70	$1.50 \cdot 10^{4}$	Chávez et al. (this vol.)
Porgies	0.65	$5.00 \cdot 10^{3}$	Chávez et al.(this vol.)
King mackerel	0.65	$5.00 \cdot 10^{4}$	Chávez et al. (this vol.)
Croakers	0.64	$3.14 \cdot 10^{3}$	Mendoza (this vol.)
Yellowtail flounder	0.63	$1.20 \cdot 10^{3}$	Cohen et al. (1982)
Catfish	0.62	$6.62 \cdot 10^{2}$	Mendoza (this vol.)
Mackerel	0.62	$4.16 \cdot 10^{2}$	Mendoza (this vol.)
Silver hake	0.59	$9.00 \cdot 10^{2}$	Cohen et al. (1982)
Scombrids and barracudas	0.57	$9.41 \cdot 10^{3}$	Mendoza (this vol.)
Grunts	0.57	$5.86 \cdot 10^{2}$	Mendoza (this vol.)
Sharks	0.50	$6.26 \cdot 10^{5}$	Browder (this vol.)
Red grouper	0.50	$2.30 \cdot 10^{4}$	Chávez et al. (this vol.)
Snappers and groupers	0.49	$2.98 \cdot 10^{3}$	Mendoza (this vol.)
Other flounders	0.46	$1.20 \cdot 10^{3}$	Cohen et al. (1982)
Red hake	0.46	$8.00 \cdot 10^{2}$	Cohen et al. (1982)
Pollock	0.46	$1.00 \cdot 10^{4}$	Cohen et al. (1982)
Carangids	0.45	$4.78 \cdot 10^{2}$	Mendoza (this vol.)
Snappers	0.44	$0.50 \cdot 10^{4}$	Chávez et al. (this vol.)
Haddock	0.41	$5.40 \cdot 10^{3}$	Cohen et al. (1982)
Small sharks	0.40	$7.00 \cdot 10^{3}$	Mendoza (this vol.)
Grunts	0.40	$1.00 \cdot 10^{4}$	Chávez et al. (this vol.)
Mackerel	0.34	$8.00 \cdot 10^{2}$	Cohen et al. (1982)
Sharks	0.32	$6.26 \cdot 10^{5}$	Chávez et al. (this vol.)
Hake	0.30	$1.00 \cdot 10^{4}$	Lewis (1981)
Arius spp.	0.29	$2.60 \cdot 10^{3}$	Chávez et al. (this vol.)
Herring	0.29	$4.00 \cdot 10^{1}$	Cohen et al. (1982)
Sharks	0.28	$6.26 \cdot 10^{5}$	Sheridan et al. (1984)
Redfish	0.24	$2.00 \cdot 10^{3}$	Cohen et al. (1982)

[a] Reported mean weights or maximum reported weight * 0.3, to approximate mean weight in population.

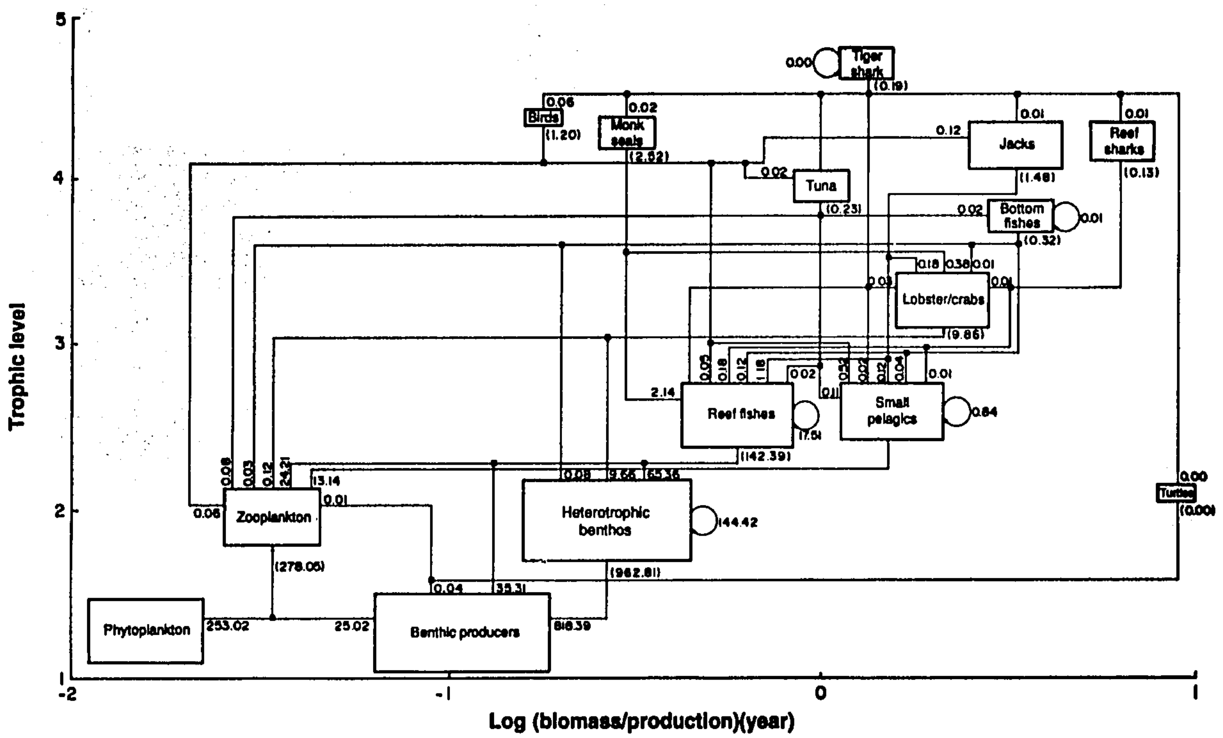


Fig. 5. Size-shifted representation of the French Frigate Shoals ecosystem model. The positions of the boxes are based on the average "size" of the organisms they contain (as represented by log B/P) and their trophic level.

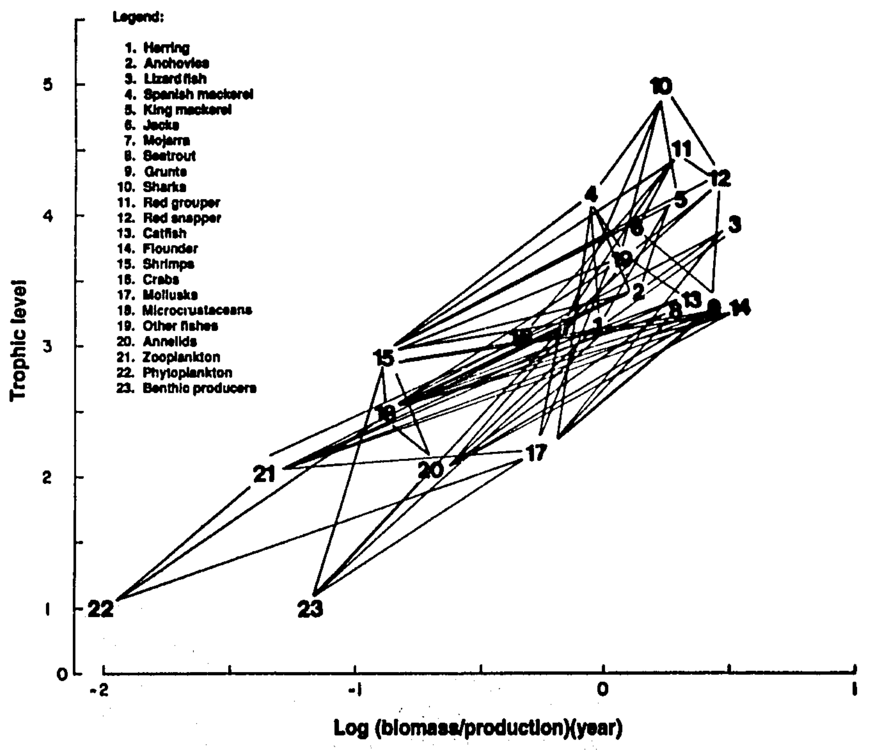
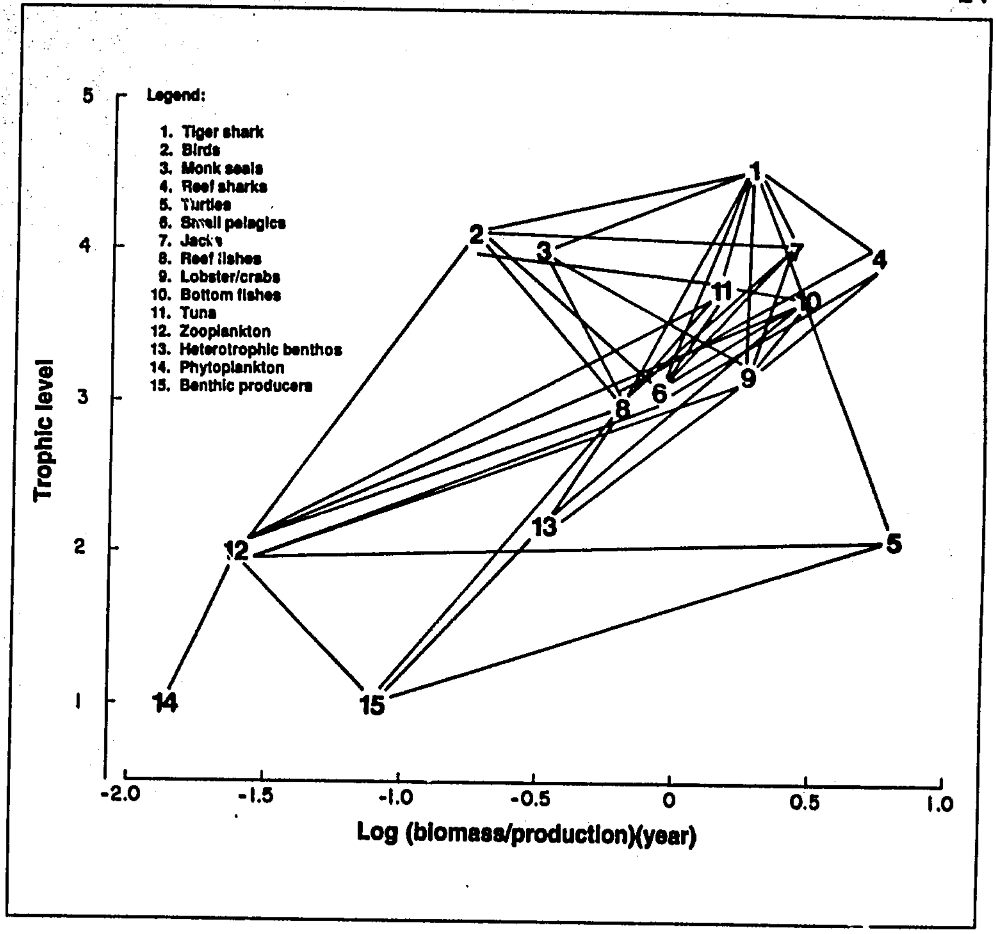


Fig. 6a. Size-shifted representation of the Western Gulf of Mexico ecosystem (Chávez and Arreguín-Sánchez, this vol.). Lines indicate presence of flow (>5% of total flow) between boxes.

Fig. 6b. Size-shifted representation of the French Frigate Shoals ecosystem (Polovina 1984). All flows are included. (Cf. with Fig.2)



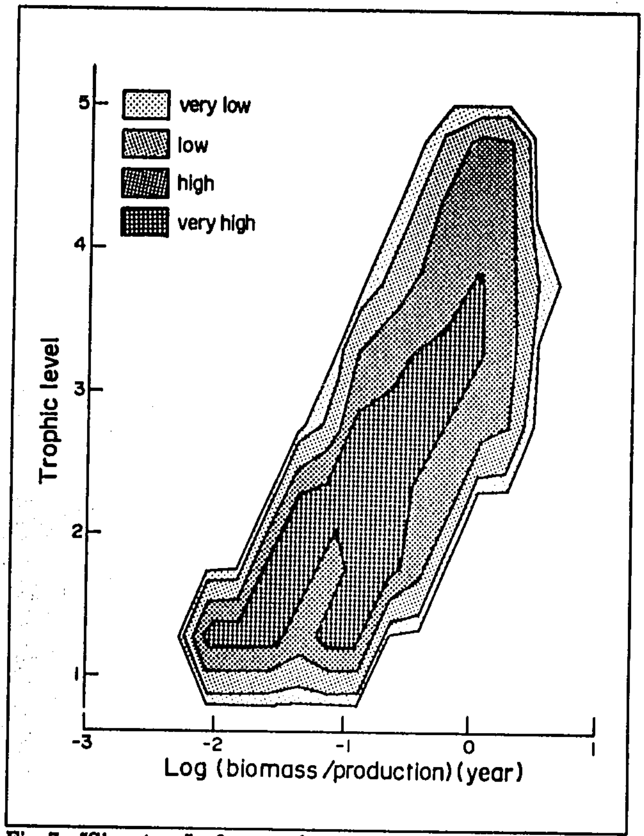


Fig. 7. "Signature" of a steady-state trophic ecosystem model (Western Gulf of Mexico, Chávez and Arreguín-Sánchez, this vol.) as an isopleth of flow intensity.

Conclusion

Time will tell whether any of the suggested new approaches for graphical representation of steady state trophic models will become widely accepted. We hope, however, to have initiated a discussion and that the rapidly improving software for graphing will not just lead to an increased occurrence of the "ducks" or junk-graphs justifiably criticized by Tufte (1983), but that the constructors of ecosystem models will use their creative abilities to make graphs that are of pleasure for the eye as well as for the mind.

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Lake Ontario Food Web, an Energetic Mass Balance

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Abstract

Lake Ontario is one of the Great Lakes of North America. The lake has been intensively studied for many decades and only now is there enough information to attempt development of an energy food web. Unfortunately, not all parameters for the food web are obtainable from the lake itself. Therefore, where necessary, information has been collected from laboratory work or from other lakes in the region with similar climate and ecosystem structure. Yearly solar energy input to Lake Ontario is 8.3×10^{19} J. Our results show that phytoplankton has a yearly production of 3.13×10^{17} J. This production leads to yearly salmonines production of 2.20×10^{14} J. This calculation is representative over the past 20 years. Assumptions, missing data and research needs are stated as a necessary basis for understanding of the food web. Since the food web is not balanced, the AUTOMOD program was used for model construction.

Introduction

The food web structure of Lake Ontario, one of the Great Lakes of North America, has been reconstructed mostly using published data. This food web is cumulative (Schoenly and Cohen 1991) in the sense that information was gathered over many occasions, about 20 years. All data presented here are in energy terms (joules). Flint (1986) published a food web of Lake Ontario in terms of carbon flow; however, his representation and ours differ significantly. Our food web contains a detrital compartment and the top predator compartment is not aggregated but is replaced by the five most important species. Much information from phytoplankton to fish, are missing or contained in databases not available to the scientific community at large. Where assumptions are necessary, they are explicitly stated. Note that *Pontoporeia hoyi* (in Tables 1, 2 and Figs. 1-3) is now considered a species of *Diporeia* (Bousfield 1989).

The Food Web Compartments

Some compartments were aggregated, such as phytoplankton, zooplankton and benthos, while others were at the species level. Ideally, we would have liked to subdivide some compartments (such as the benthos compartment into tubificids and chironomids and the zooplankton compartment into cladocerans, copepods and omnivorous zooplankton); however, lack of data prevented us from doing this procedure for all organisms. Two species were left out completely because of the lack of an energy budget, the lamprey and the zebra mussel. Both species are important in the food web but until more knowledge regarding these species has been published they have to be left out. Trophic links were established with information concerning the diet habits of the major compartments (usually from stomach contents).

The computation of the energy balance is presented in Schito and Halfon (1992). The main assumption is that the energy flux through the living compartments can be calculated with the equation:

Consumption = respiration + SDA + production + egestion + excretion ...1)

where all terms are expressed in joules (J) per day and where SDA refers to "specific dynamic action" (see e.g. Jobling 1983). In all calculations we used a volume of 1.68×10^{12} m^3 and an area of 1.95

x 10^{10} m^2 for Lake Ontario. All data for living organisms are expressed in fresh weight; when dry weights were reported in the literature they were converted (Table 1). Data reported on a per hour or per year basis were reexpressed on a daily basis.

In many instances, data were not available on metabolic processes of fish. In this case, we used bioenergetic models for alewife (Stewart and Binkowski 1986), for chinook and coho salmon (Hewett and Johnson 1987), for brown trout (Elliott 1976) and for lake trout (Stewart et al. 1983). To estimate the energetics of slimy sculpin and rainbow smelt, we used a bioenergetic model for northern pike (Hewett and Johnson 1987). We evaluated the bioenergetics of rainbow trout based on a lake trout model (Stewart et al. 1983).

Table 1. Model components, and conversion values used to build a Lake Ontario food web.

Compartment	Assumptions	Sources
Detritus	4,421 kcal·g^{-1} dry weight	Cummins and Wuycheck (1971)
Phytoplankton	3,482 kcal·g^{-1} dry weight	Cummins and Wuycheck (1971)
	dry weight = 0.1·wet weight	
Zooplankton	1,987 J·g^{-1} wet weight	calc. from Stewart and Binkowski (1986)
	dry weight = 0.1·wet weight	
	1 g O_2 respired = 14,150 J	approx. from Elliott and Davison (1975), and Brinkhurst and Austin (1979)
Other benthos	3,558 J·g^{-1} wet weight	calc. from Gardner et al. (1985)
	dry weight = 0.15·wet weight	Strayer and Likens (1986)
	1 g O_2 respired = 14,150 J	approx. from Elliott and Davison (1975), and Brinkhurst and Austin (1979)
Mysis relicta	4,604 J·g^{-1} wet weight	Stewart et al. (1983)
	dry weight = 0.21·wet weight	Evans and Landrum (1983)
	preferred temperature = 4°C	J. Elrod (pers. comm.)
	average weight = 2.6 mg dry weight	Borgmann (1985)
	1 g O_2 respired = 14,150 J	approx. from Elliott and Davison (1975), and Brinkhurst and Austin (1979)
Pontoporeia hoyi (= *Diporeia* sp.)	4,185 J·g^{-1} wet weight	Stewart et al. (1983)
	dry weight = 0.27·wet weight	Evans and Landrum (1983)
	preferred temperature = 5°C	J. Elrod (pers. comm.)
	average weight = 1.34 mg dry weight	Borgmann and Whittle (1983)
	1 g O_2 respired = 14,150 J	approx. from Elliott and Davison (1975), and Brinkhurst and Austin (1979)
Slimy sculpin (*Cottus cognatus*)	5,743 J·g^{-1} wet weight	Rottiers and Tucker (1982)
	dry weight = 0.25·wet weight	
	preferred temperature = 5°C	Coutant (1977)
	average weight = 10 g wet weight	assumption
	1 g O_2 respired = 13,560 J	Elliott and Davison (1975)
Rainbow smelt (*Osmerus mordax*)	6,656 J·g^{-1} wet weight	Rottiers and Tucker (1982)
	dry weight = 0.25·wet weight	
	preferred temperature = 11.1°C	Olson et al. (1988)
	average weight = 5 g dry weight	Borgmann (1985)
	1 g O_2 respired = 13,560 J	Elliott and Davison (1975)
Alewife (*Alosa pseudoharengus*)	6,000 J·g^{-1} wet weight	calc. from Stewart and Binkowski (1986), J. Elrod (pers. comm.), Rottiers and Tucker (1982)
	dry weight = 0.25·wet weight	
	preferred temperature = 17.4°C	Olson et al. (1988)
	average weight = 20 g wet weight	assumption
	1 g O_2 respired = 13,560 J	Elliott and Davison (1975)
All salmonines	10% of population weight is juvenile	assumption
	10% of population removed by fishing	Flint (1986)
	2.91 x 108gC·yr^{-1} of salmonines stocked	Flint (1986)

continued

Table 1 continued.

Compartment	Assumptions	Sources
	total biomass = 0.1·(alewife+sculpin + smelt biomass)	assumption
	1 g O_2 respired = 13,560 J	Elliott and Davison (1975)
Lake trout (*Salvelinus namaycush*)	average weight = 500 g dry weight	Borgmann (1985)
	preferred temperature = 10.1°C	Olson et al. (1988)
	10,646 J·g^{-1} wet weight for adults	calc. from Stewart et al. (1983)
	juvenile average weight = 260 g wet weight	Stewart et al. (1983)
	6,501 J·g^{-1} wet weight for juveniles	calc. from Stewart et al. (1983)
	31% of total salmonid biomass	based on Savoie and LeTendre (1990)
	31% (by weight) of total stocked	based on Savoie and LeTendre (1990)
Chinook salmon (*Oncorhynchus tshawytscha*)	average weight = 250 g dry weight	assumption
	preferred temperature = 14.4°C	Olson et al. (1988)
	6,749 J·g^{-1} wet weight for adults	calc. from Stewart and Ibarra (1991)
	juvenile average weight = 160 g wet weight	calc. from Niimi (1981)
	5,921 J·g^{-1} wet weight for juveniles	calc. from Stewart and Ibarra (1991)
	36% of total salmonid biomass	based on Savoie and LeTendre (1990)
	36% (by weight) of total stocked	based on Savoie and LeTendre (1990)
Coho salmon (*Oncorhynchus kisutch*)	average weight = 250 g dry weight	Borgmann (1985)
	preferred temperature = 14°C	adjusted using Coutant (1977)
	6,749 J·g^{-1} wet weight for adults	calc. from Stewart and Ibarra (1991)
	juvenile average weight = 160 g wet weight	calc. from Niimi (1981)
	5,921 J·g^{-1} wet weight for juveniles	calc. from Stewart and Ibarra (1991)
	10% of total salmonid biomass	based on Savoie and LeTendre (1990)
	10% (by weight) of total stocked	based on Savoie and LeTendre (1990)
Brown trout (*Salmo trutta*)	average weight = 2,000 g wet weight	assumption
	preferred temperature = 13.4°C	Olson et al. (1988)
	6,500 J·g^{-1} wet weight	calc. using P/B
	juvenile average weight = 260 g wet weight	assumption
	13% of total salmonid biomass	based on Savoie and LeTendre (1990)
	13% (by weight) of total salmonines	based on Savoie and LeTendre (1990)
Rainbow trout (*Oncorhynchus mykiss*)	average weight = 250 g dry weight	assumption
	preferred temperature = 13.8°C	adjusted using Coutant (1977)
	8,780 J·g^{-1} wet weight for adults	calc. using Stewart et al. (1983)
	juvenile average weight = 160 g wet weight	assumption
	6,193 J·g^{-1} wet weight for juveniles	calc. using Stewart et al. (1983)
	10% of total salmonid biomass	based on Savoie and LeTendre (1990)
	10% (by weight) of total stocked	based on Savoie and LeTendre (1990)

The Food Web

Fig. 1 shows the Lake Ontario food web. This figure integrates the information available as late as the summer of 1991. Table 2 summarizes all available data and the procedures used to compute the values in Fig. 2. The five species of predatory fishes are sustained through the food chain from energy originally synthesized from the sun by phytoplankton. This food web is not balanced in energy terms, the major problem being that there is not enough measured zooplankton production to sustain alewife. Conversely, alewife biomass might have been overestimated. A second problem is that good lakewide measurements of phytoplankton production in Lake Ontario are missing in the 1980s; thus, it is difficult to present a really up to date description of the food web. More details and a complete discussion of the food web are presented in Schito and Halfon (1992).

Food Web Analysis

The problem of assembling literature data from different sources is that they are not necessarily compatible. Ulanowicz (1989) suggested the use of a mathematical model to interpret food web data, for which he developed a computer program,

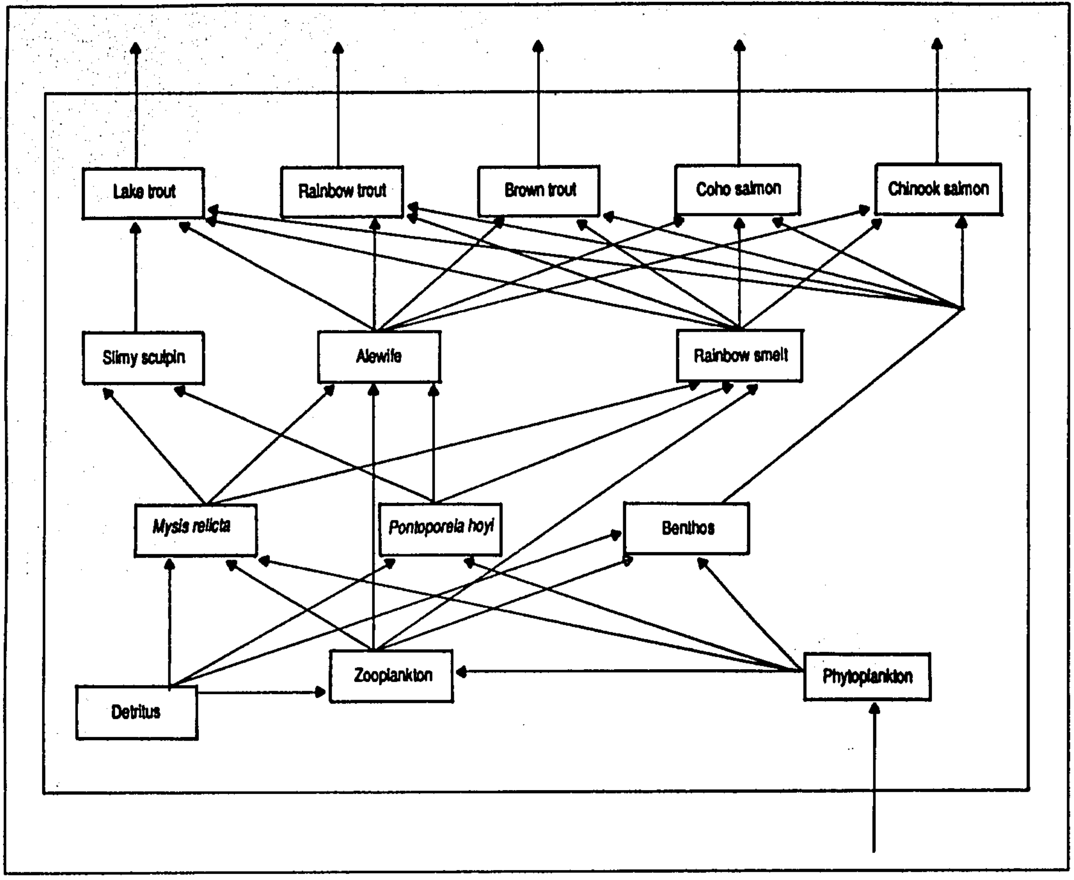

Fig. 1. A simplified description of the Lake Ontario food web.

AUTOMOD, that integrates all available information and produces a simulation. AUTOMOD is "a generic simulation model for treating incomplete sets of data. This software provides the user with an objective means for balancing a dataset or for inferring the values of missing data (or for doing both simultaneously)." AUTOMOD has two options that work in a mass balanced way, one linear donor-controlled, the other predator-controlled. With the available data for Lake Ontario, the predator controlled model became unstable and some species, such as alewife went extinct. The results presented in Table 3 were obtained, therefore, with the linear, donor-controlled model.

A linear model provides generality and stability but cannot generate surprising results. The model is a good tool to integrate the information and assess where errors lie. AUTOMOD was ran four times; the first run, based on unprocessed food web data, showed that the estimate of energy entering and being used by phytoplankton was much too large, with biomasses exceeding many times over the observed values. In the second run, the input to phytoplankton was reduced from 44,000 to 6,340 J·day^{-1}. This amount was calculated to keep phytoplankton biomass steady at 44,000 J m^{-2}. In this run, however, detritus was increased from 1.6 million J m^{-2} to 3.8 million J m^{-2}. Since the concentration of detritus in Lake Ontario is well known, we increased, in the third run of AUTOMOD, the loss of detritus to the environment to keep detritus concentration steady. This change of parameter values removes detritus from the food web through sedimentation to the bottom. Detritus that sediments to the bottom but remains a component of the food web, is taken into account through flows to benthos and to *P. hoyi*. The result of the third run was that both phytoplankton and detritus biomasses were kept at the observed levels of 44,000 and 1,600,000 J m^{-2}, respectively. Fig. 3 shows the balanced food web obtained from AUTOMOD.

In the food web, the other 12 compartments assumed a new equilibrium value, reached after the simulation was ran for 2,070 days. Table 3 shows the initial and final values of the simulations. Benthos biomass increases about 20% to a new steady state, which is probably due to uncertain initial conditions. The biomass of alewife, rainbow smelt, slimy sculpin, *P. hoyi*, *Mysis* and zooplankton decreased; this suggests that the energy flows among compartments are lower than we estimated from the literature.

The biomass of the five fish at the top of the food chain, i.e., lake trout, chinook salmon, rainbow trout, coho salmon and brown trout, barely changed from the second run. Thus, detritus seems to play a minor role in determining the fish carrying capacity of the lake. Rather these top five fish species appear to

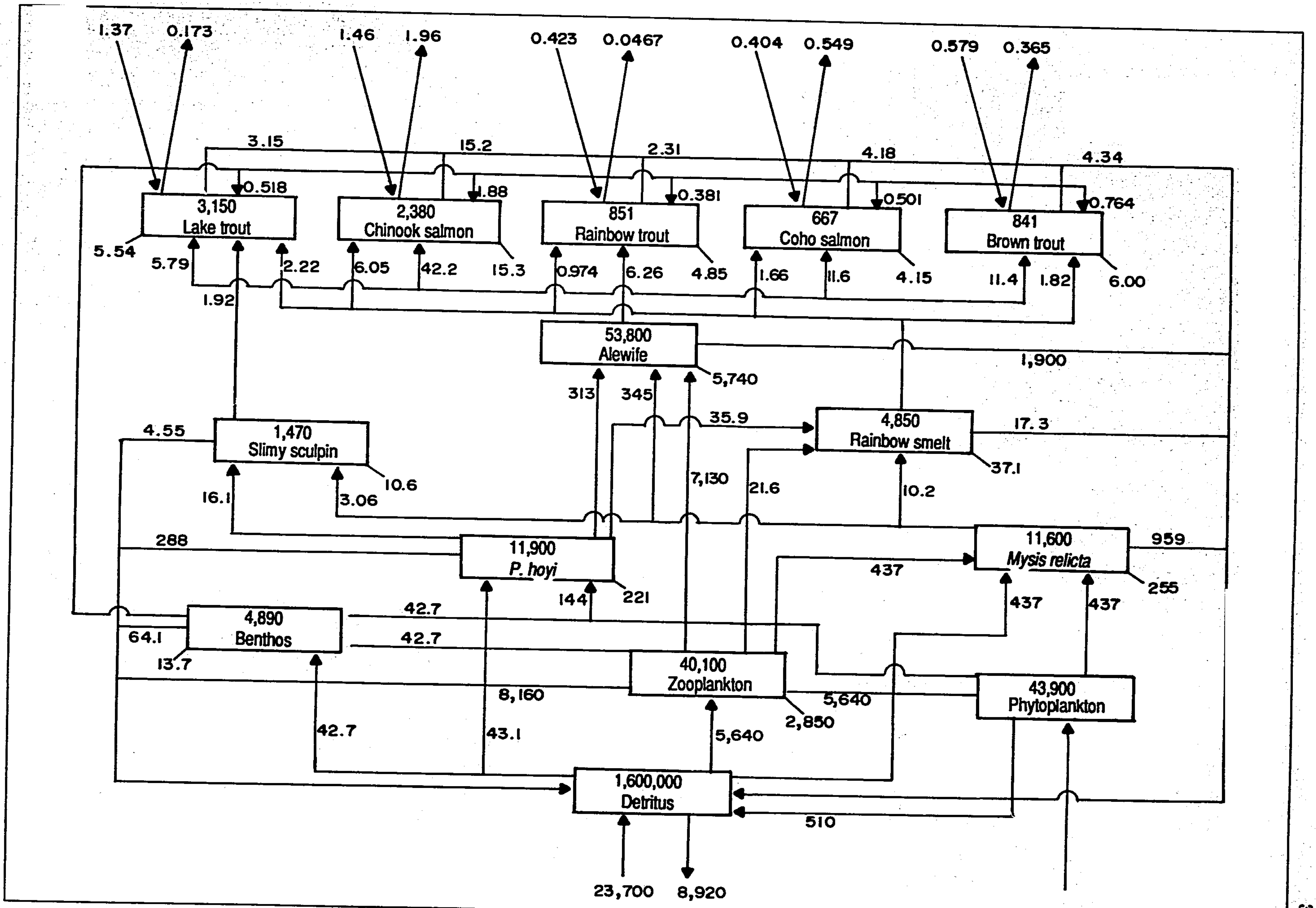

Fig. 2. The food web as obtained from the data analysis.

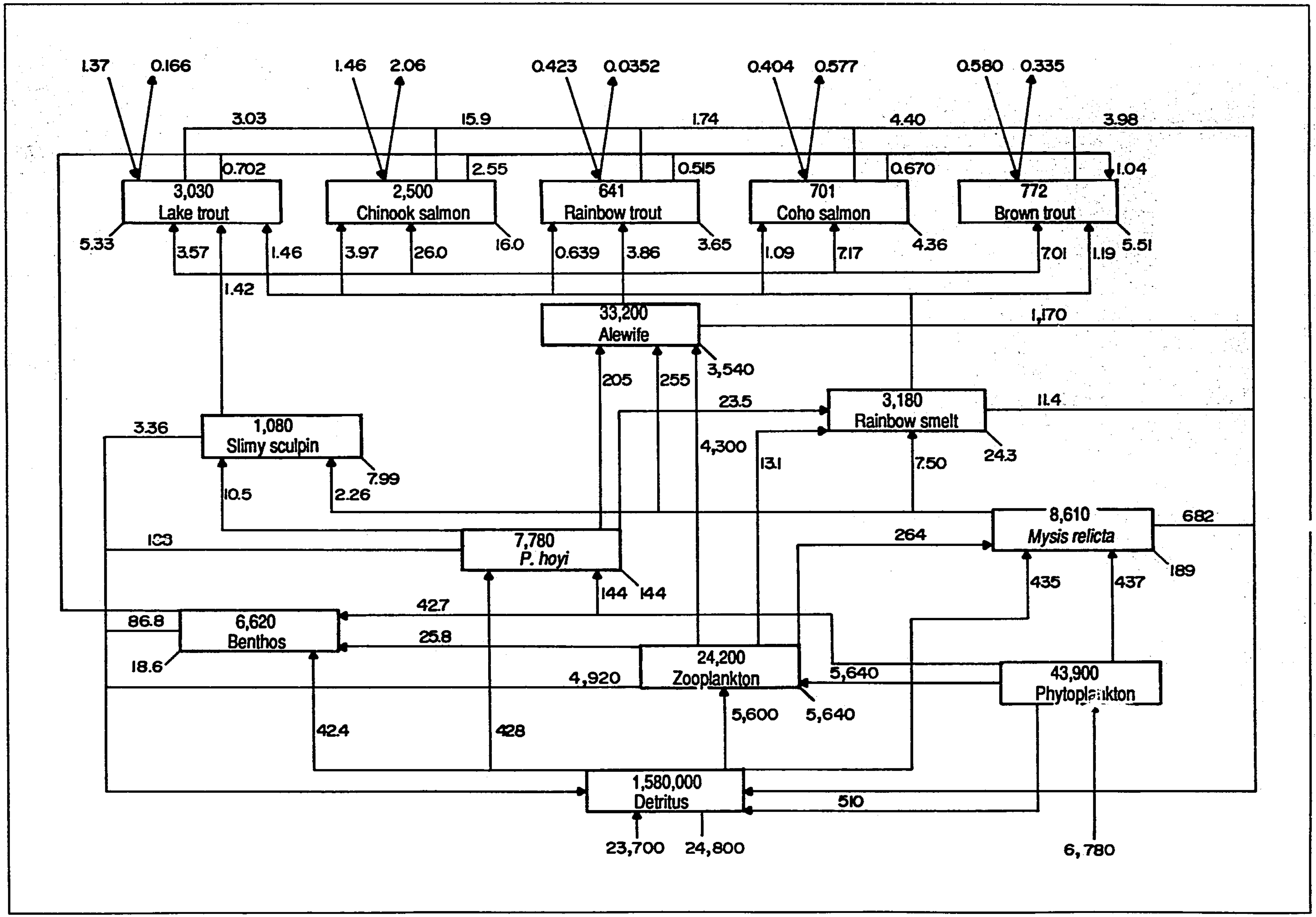

Fig. 3. The Lake Ontario food web balanced using AUTOMOD.

Table 2. Data used to construct food web model of Lake Ontario.

Compartment and process	Value		Sources
	Reported	Converted*	
Detritus			
Mass	1 mg dry weight·L^{-1}	3.11 x 10^{16} J	
Import (all sources)	9.14 x 106 t·year^{-1}	4.63 x 10^{14} J·day^{-1}	Kemp and Harper (1976)
Export	3.44 x 106 t·year^{-1}	1.74 x 10^{14} J·day^{-1}	Kemp and Harper (1976)
Phytoplankton			
Biomass	0.35 g fresh weight·m^{-3}	8.57 x 10^{14} J	Munawar et al. (1987)
Production	P/B = 365·year^{-1}	8.57 x 10^{14} J·day^{-1}	Borgmann and Whittle (1983)
Sedimentation	1 m·day^{-1}	9.95 x 10^{12} J·day^{-1}	
Zooplankton			
Biomass	23.41 mg dry weight·m^{-3}	7.81 x 10^{14} J	Makarewicz and Jones (1990)
Production	13.99 g dry weight·m^{-2}·year^{-1} (calc.)	1.49 x 10^{13} J·day^{-1}	Johannsson and O'Gorman (1991)
Respiration	0.01 g O2·g^{-1}·day^{-1}	5.56 x 10^{13} J·day^{-1}	Park et al. (1974), Scavia et al. (1974)
SDA	none	none	none
Excretion	3% of consumption	6.60 x 10^{12} J·day^{-1}	Park et al. (1974), Scavia et al. (1974)
Egestion	65% of consumption	1.43 x 10^{14} J·day^{-1}	Park et al. (1974), Scavia et al. (1974)
Sedimentation	1 m·day^{-1}	9.07 x 10^{12} J·day^{-1}	
Consumption	computed	2.20 x 10^{14} J·day^{-1}	this study
Benthos			
Biomass	206.1 mg dry weight·m^{-2} (calc.)	9.53 x 10^{13}	Johannsson et al. (1985)
Production	0.012 kcal·m^{-2}·day^{-1}	9.80 x 10^{11} J·day^{-1}	Stadelmann et al. (1974)
Respiration	0.14 µL O2·dry mg^{-1}·hour^{-1}	2.68 x 10^{11} J·day^{-1}	Brinkhurst et al. (1972)
SDA	none	none	assumption
Excretion+egestion	50% of consumption	1.25 x 10^{12} J·day^{-1}	Welch (1968)
Consumption	computed	2.50 x 10^{12} J·day^{-1}	this study
Mysis relicta			
Biomass	0.53 g dry weight·m^{-2} (calc.)	2.27 x 10^{14} J	Shea and Makarewicz (1989)
Production	1.64 g dry weight·m^{-2}·year^{-1}	1.92 x 10^{12} J·day^{-1}	Shea and Makarewicz (1989)
Respiration	equation; see reference	4.98 x 10^{12} J·day^{-1}	Lasenby and Langford (1972)
SDA			included in respiration
Excretion	3% of consumption	7.68 x 10^{11} J·day^{-1}	Park et al. (1974), Scavia et al. (1974)
Egestion	70% of consumption	1.79 x 10^{13} J·day^{-1}	Thomann and Connolly (1984)
Consumption	computed	2.56 x 10^{13} J·day^{-1}	this study
Pontoporeia hoyi			
Biomass	14.96 x 10^{3} t dry weight below 10 m	2.32 x 10^{14} J	Johannsson et al. (1985)
Production	30.99 x 10^{3} t dry weight·year^{-1}	1.32 x 10^{12} J·day^{-1}	Johannsson et al. (1985)
Respiration	equation; see reference	4.30 x 10^{12} J·day^{-1}	Johannsson et al. (1985)
SDA	included in respiration		
Excretion+egestion	50% of consumption	5.62 x 10^{12} J·day^{-1}	Welch (1968)
Consumption	computed	1.12 x 10^{13} J·day^{-1}	this study
Slimy sculpin	modelled after northern pike		
Biomass	2,502 t in U.S. water	2.87 x 10^{13} J	Gray (1979)
Production	P/B = 1·year^{-1}	7.86 x 10^{10} J·day^{-1}	Borgmann (1985), Flint (1986)
Respiration	equation; see reference	1.64 x 10^{11} J·day^{-1}	Hewett and Johnson (1987)
SDA	11.2% of consumption**	4.18 x 10^{10} J·day^{-1}	Hewett and Johnson (1987)
Excretion	5.7% of consumption**	2.13 x 10^{10} J·day^{-1}	Hewett and Johnson (1987)
Egestion	18.1% of consumption	6.75 x 10^{10} J·day^{-1}	Warren and Davis (1967)
Consumption	computed	3.73 x 10^{11} J·day^{-1}	this study
Rainbow smelt	modelled after northern pike		
Biomass	1.20 x 109 g	9.45 x 10^{13} J	calc. from O'Gorman et al. (1987) and Gray (1979)
Production	P/B = 1·year^{-1}	2.59 x 10^{11} J·day^{-1}	Borgmann (1985), Flint (1986)
Respiration	equation; see reference**	5.75 x 10^{11} J·day^{-1}	Hewett and Johnson (1987)
SDA	11.2% of consumption	1.48 x 10^{11} J·day^{-1}	Hewett and Johnson (1987)
Excretion	5.6% of consumption	7.39 x 10^{10} J·day^{-1}	Hewett and Johnson (1987)
Egestion	20% of consumption	2.64 x 10^{11} J·day^{-1}	Hewett and Johnson (1987)
Consumption	computed	1.32 x 10^{12} J·day^{-1}	this study

continued

Table 2 continued.

Compartment and process	Value		Sources
	Reported	Converted*	
Alewife			
Biomass	887,700 t in U.S. waters	1.05 x 10^{15} J	calc. from O'Gorman et al. (1987)
Production	P/B = 1·year^{-1}	2.87 x 10^{12} J·day^{-1}	Borgmann (1985), Flint (1986)
Respiration	equation; see reference	8.99 x 10^{13} J·day^{-1}	Stewart and Binkowski (1986)
SDA	14.7% of consumption	2.23 x 10^{13} J·day^{-1}	Stewart and Binkowski (1986)
Excretion	8.4% of consumption	1.28 x 10^{13} J·day^{-1}	Stewart and Binkowski (1986)
Egestion	16% of consumption	2.43 x 10^{13} J·day^{-1}	Stewart and Binkowski (1986)
Consumption	computed	1.52 x 10^{14} J·day^{-1}	this study
Lake trout			
Biomass			
adult	5.41 x 109 g	5.76 x 10^{13} J	based on Savoie and LeTendre (1990)
juvenile	6.01 x 108 g	3.91 x 10^{12} J	assumption
Production			
adult	P/B = 0.2·year^{-1}	3.16 x 10^{10} J·day^{-1}	Borgmann (1985)
juvenile	P/B = 0.2·year^{-1}	2.14 x 10^{09} J·day^{-1}	Borgmann (1985)
Respiration			
adult	equation; see reference	6.77 x 10^{10} J·day^{-1}	Stewart et al. (1983)
juvenile	equation; see reference	1.38 x 10^{10} J·day^{-1}	Stewart et al. (1983)
SDA			
adult	13.1% of consumption**	2.31 x 10^{10} J·day^{-1}	Stewart et al. (1983)
juvenile	13.6% of consumption**	3.71 x 10^{09} J·day^{-1}	Stewart et al. (1983)
Excretion			
adult	6.8% of consumption**	1.20 x 10^{10} J·day^{-1}	Stewart et al. (1983)
juvenile	7.0% of consumption**	1.91 x 10^{09} J·day^{-1}	Stewart et al. (1983)
Egestion			
adult	23.8% of consumption**	4.19 x 10^{10} J·day^{-1}	Stewart et al. (1983)
juvenile	21.0% of consumption**	5.73 x 10^{09} J·day^{-1}	Stewart et al. (1983)
Consumption			
adult	computed	1.76 x 10^{11} J·day^{-1}	this study
juvenile	computed	2.73 x 10^{10} J·day^{-1}	this study
Import	31% of total salmonid import	2.68 x 10^{10} J·day^{-1}	calc. using Flint (1986) and Savoie and LeTendre (1990)
Export	10% of production	3.37 x 10^{09} J·day^{-1}	Flint (1986)
Chinook salmon			
Biomass			
adult	6.28 x 109 g	4.24 x 10^{13} J	based on Savoie and LeTendre (1990)
juvenile	6.98 x 108 g	4.13 x 10^{12} J	assumption
Production	modelled after coho salmon		
adult	P/B = 3.0·year^{-1}	3.49 x 10^{11} J·day^{-1}	assumption
juvenile	P/B = 3.0·year^{-1}	3.40 x 10^{10} J·day^{-1}	assumption
Respiration			
adult	equation; see reference	1.42 x 10^{11} J·day^{-1}	Hewett and Johnson (1987)
juvenile	equation; see reference	2.45 x 10^{10} J·day^{-1}	Hewett and Johnson (1987)
SDA			
adult	13.4% of consumption**	1.17 x 10^{11} J·day^{-1}	Hewett and Johnson (1987)
juvenile	13.9% of consumption**	1.40 x 10^{10} J·day^{-1}	Hewett and Johnson (1987)
Excretion			
adult	8.5% of consumption**	7.44 x 10^{10} J·day^{-1}	Hewett and Johnson (1987)
juvenile	8.8% of consumption**	8.89 x 10^{09} J·day^{-1}	Hewett and Johnson (1987)
Egestion			
adult	22.0% of consumption**	1.93 x 10^{11} J·day^{-1}	Hewett and Johnson (1987)
juvenile	19.1% of consumption**	1.92 x 10^{10} J·day^{-1}	Hewett and Johnson (1987)
Consumption			
adult	computed	8.75 x 10^{11} J·day^{-1}	this study
juvenile	computed	1.01 x 10^{11} J·day^{-1}	this study
Import	36% of total salmonid import	2.84 x 10^{10} J·day^{-1}	calc. using Flint (1986) and Savoie and LeTendre (1990)
Export	10% of production	3.83 x 10^{10} J·day^{-1}	Flint (1986)
Coho salmon			
Biomass			
adult	1.75 x 109 g	1.18 x 10^{13} J	based on Savoie and LeTendre (1990)

continued

Table 2 continued.

Compartment and process	Value		Sources
	Reported	Converted*	
juvenile	1.94 x 108 g	1.15×10^{12} J	assumption
Production			
adult	P/B = 3.0·year^{-1}	9.70×10^{10} J·day^{-1}	Borgmann (1985)
juvenile	P/B = 3.0·year^{-1}	9.45×10^{09} J·day^{-1}	Borgmann (1985)
Respiration			
adult	equation; see reference	3.85×10^{10} J·day^{-1}	Hewett and Johnson (1987)
juvenile	equation; see reference	6.27×10^{09} J·day^{-1}	Hewett and Johnson (1987)
SDA			
adult	13.4% of consumption**	3.24×10^{10} J·day^{-1}	Hewett and Johnson (1987)
juvenile	13.9% of consumption**	3.77×10^{09} J·day^{-1}	Hewett and Johnson (1987)
Excretion			
adult	8.4% of consumption**	2.03×10^{10} J·day^{-1}	Hewett and Johnson (1987)
juvenile	8.8% of consumption**	2.39×10^{09} J·day^{-1}	Hewett and Johnson (1987)
Egestion			
adult	22.2% of consumption**	5.37×10^{10} J·day^{-1}	Hewett and Johnson (1987)
juvenile	19.3% of consumption**	5.23×10^{09} J·day^{-1}	Hewett and Johnson (1987)
Consumption			
adult	computed	2.42×10^{11} J·day^{-1}	this study
juvenile	computed	2.71×10^{10} J·day^{-1}	this study
Import	10% of total salmonid import	7.88×10^{09} J·day^{-1}	calc. using Flint (1986) and Savoie and LeTendre (1990)
Export	10% of production	1.07×10^{10} J·day^{-1}	Flint (1986)
Brown trout			
Biomass			
adult	2.27 x 109 g	1.48×10^{13} J	based on Savoie and LeTendre 1990
juvenile	2.52 x 108 g	1.64×10^{12} J	assumption
Production			
adult	computed	6.02×10^{10} J·day^{-1}	this study
juvenile	computed	1.09×10^{10} J·day^{-1}	this study
Respiration			
adult	equation; see reference	9.90×10^{10} J·day^{-1}	Elliott (1976)
juvenile	equation; see reference	1.76×10^{10} J·day^{-1}	Elliott (1976)
SDA			
adult	included in respiration		
juvenile	included in respiration		
Excretion			
adult	8.7% of consumption**	2.01×10^{10} J·day^{-1}	Elliott (1976)
juvenile	8.7% of consumption**	3.59×10^{09} J·day^{-1}	Elliott (1976)
Egestion			
adult	22.4% of consumption**	5.17×10^{10} J·day^{-1}	Elliott (1976)
juvenile	22.4% of consumption**	9.25×10^{09} J·day^{-1}	Elliott (1976)
Consumption			
adult	equation; see reference	2.31×10^{11} J·day^{-1}	Elliott (1976)
juvenile	equation; see reference	4.13×10^{10} J·day^{-1}	Elliott (1976)
Import	13% of total salmonid import	1.13×10^{10} J·day^{-1}	calc. using Flint (1986) and Savoie and LeTendre (1990)
Export	10% of production	7.11×10^{09} J·day^{-1}	Flint (1986)
Rainbow trout			
Biomass			modelled after lake trout
adult	1.75 x 109 g	1.54×10^{13} J	based on Savoie and LeTendre (1990)
juvenile	1.94 x 108 g	1.20×10^{12} J	assumption
Production			
adult	P/B = 0.2·year^{-1}	8.44×10^{09} J·day^{-1}	assumption
juvenile	P/B = 0.2·year^{-1}	6.58×10^{08} J·day^{-1}	assumption
Respiration			
adult	equation; see reference	6.32×10^{10} J·day^{-1}	Stewart et al. (1983)
juvenile	equation; see reference	1.13×10^{10} J·day^{-1}	Stewart et al. (1983)
SDA			
adult	13.4% of consumption**	1.72×10^{10} J·day^{-1}	Stewart et al. (1983)
juvenile	13.9% of consumption**	2.86×10^{09} J·day^{-1}	Stewart et al. (1983)
Excretion			
adult	8.4% of consumption**	1.08×10^{10} J·day^{-1}	Stewart et al. (1983)

continued

Table 2 continued.

Compartment and process	Value		Sources
	Reported	Converted*	
juvenile	8.7% of consumption**	1.79 x 10^{09} J·day^{-1}	Stewart et al. (1983)
Egestion			
adult	22.3% of consumption**	2.85 x 10^{10} J·day^{-1}	Stewart et al. (1983)
juvenile	19.4% of consumption**	4.00 x 10^{09} J·day^{-1}	Stewart et al. (1983)
Consumption			
adult	computed	1.28 x 10^{11} J·day^{-1}	this study
juvenile	computed	2.06 x 10^{10} J·day^{-1}	this study
Import	10% of total salmonid import	8.24 x 10^{09} J·day^{-1}	calc. using Flint (1986) and Savoie and LeTendre (1990)
Export	10% of production	9.10 x 10^{08} J·day^{-1}	Flint (1986)

* values converted through application of assumptions outlined in Table 2.

** computed using equation from reference cited.

Table 3. Comparison of compartment biomasses (J m^{-2}). See text.

Compartment	Literature value	AUTOMOD simulations (steady state)	
		Input to phytoplankton (calibrated)	Input to phytoplankton and export to detritus (calibrated)
Lake trout	3,150	5,000	3,030
Chinook salmon	2,390	4,190	2,500
Rainbow trout	851	1,060	641
Coho salmon	667	1,180	701
Brown trout	841	1,290	772
Alewife	53,900	56,100	33,200
Rainbow smelt	4,850	5,900	3,180
Slimy sculpin	1,470	2,120	1,080
Pontoporeia hoyi	11,900	15,700	7,780
Benthos	4,890	11,100	6,620
Mysis relicta	11,600	14,400	8,610
Zooplankton	40,100	40,500	24,200
Phytoplankton	44,000	43,900	43,900
Detritus	1,600,000	3,730,000	1,580,000

depend on primary production, which is transferred to them both through the pelagic food chain through zooplankton, *Mysis*, smelt and alewife, and through the bottom food chain, *P. hoyi* and sculpin.

Discussion

Knowledge of the complete food web of a large lake, such as Lake Ontario can be put to different uses. One is that the information on the food web can be combined with knowledge of toxic pollutants. Thus, it is possible to assess the transfer of such pollutants through food chains and improve a "fate" model of Lake Ontario. Another use is to assist limnologists and fish specialists to assess the role that each organism plays in biomass production in Lake Ontario.

The food web presented here requires improvement since the data stem from a variety of sources, and were collected in different years and seasons with a variety of techniques. Coordinated research efforts are now occurring in Canada and the United States, but it might be a few more years before the resulting information can be summarized. Improvements would result if more data on the bioenergetics of rainbow trout, rainbow smelt and slimy sculpin became available. Rainbow trout is the only stocked species whose bioenergetics in a natural environment has not been studied in detail. Presently, bioenergetic models for these species are being developed (D. Stewart, pers. comm.), and they are expected not only to assist in the improvement of the Lake Ontario food web, but also to aid other researchers studying the ecology of these organisms.

Another factor is the occurrence of zebra mussels in Lake Ontario, where they have established themselves as a significant component of the ecosystem. Considering the impact they can be expected to have on the resources of the lake, it will become necessary to incorporate them soon into models of Lake Ontario.

Simulation models, such as AUTOMOD, can help in the analysis of difficult groups, such as the zooplankton compartment; however it must be realized

that the solution they offer are only provisional, and must be verified by appropriate field studies.

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Size-Structured Models of Continental Shelf Food Webs

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Abstract

A generic model of continental shelf ecosystems has been developed which uses size as a proxy for trophic level in characterizing food web structure. The model parameters can be adjusted to represent a wide range of continental shelf environments differing in physical characteristics such as temperature and mixing rates. The model also allows for different nutrient levels and types.

Introduction

The role of size in determining how organisms are constructed and how they function has long been appreciated (Galileo 1638; Thompson 1942; Bonner 1965). The use of size-structured models to describe aquatic ecosystems was pioneered by Sheldon and coworkers (Sheldon and Parsons 1967; Sheldon et al. 1972, 1977). The concept originated with the empirical observation that the slope of a *biomass spectrum*, i.e., a plot of the biomass concentration expressed in $g \cdot m^{-3}$ of particles in logarithmically equal size ranges, is close to constant.

Subsequent research has established a solid foundation for the use of size to classify marine organisms (Fenchel 1974; Kerr 1974; Platt and Denman 1977, 1978; Silvert and Platt 1978, 1980; Platt and Silvert 1981; Schwinghamer 1981; Sprules and Munawar 1986). The major supporting factors include:

- the slope of the biomass spectrum is an indicator of the health and productivity of the ecosystem;
- the shape of the biomass spectrum is characteristic of the environment;
- the biomass spectrum is easily measured with devices such as calibrated nets, sieves and Coulter counters;
- predation can easily be described on the basis of size;
- size is a good predictor of metabolic rates, life span, and other ecologically important quantities; and
- aggregation on the basis of size generally leads to far more realistic models than other aggregation schemes.

These advantages have been exploited by using size as a primary descriptive variable in constructing dynamic models of marine environments. In cases where description solely on the basis of size is not acceptable, an extended biomass spectrum can be extended to include size classes within a coarse-grained taxonomic framework (Fig. 1). This approach has been used successfully for modelling both estuarine and continental shelf ecosystems (Gordon et al. 1986; Keizer et al. 1987; Silvert 1988). As shown here for a typical continental shelf pelagic submodel (Silvert 1988), this approach lets us generalize a single size category to describe as many functional groups as required by the model, while still retaining many of the advantages of using size as a primary descriptor.

Trophic Interactions

One of the great advantages of using size-structured models is that trophic interactions are largely determined by particle size. Pelagic predators

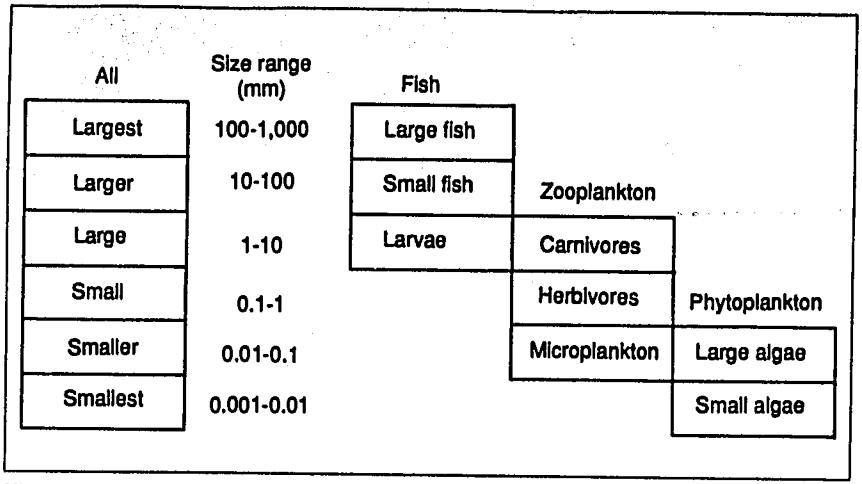

Fig. 1. A possible aggregation scheme for a mixed size and taxonomically structured model.

generally eat particles that are one or two orders of magnitude smaller than themselves. Since the size classes used in the models shown here cover a range of x10 in Effective Spherical Diameter (ESD), predation is modelled by assuming that organisms in one size class eat those in the next two smaller size classes. For example, organisms in the 10-100 mm size range (identified as mostly small fish), feed on organisms in the range 0.1-10 mm ESD, corresponding to fish larvae and two size classes of zooplankton.

In a strictly size-structured model, each size class is connected to the two classes below it (as a predator) and to the two above it (as prey). In the more general extended size structure approach, a single size class may include more than one functional group, such as the 10-100 μm range which covers both microzooplankton and algae. The result is a food web structure which in many ways resembles a food chain. Energy flows through this web from smaller to larger organisms. In the annual simulation shown in Figs. 2 and 3, this is reflected by the pattern of peaks, where the spring diatom bloom is followed by blooms, first of all smaller zooplankton (mostly small herbivores) and then of larger zooplankton (consisting of larger herbivores as well as carnivores which feed on the small herbivores). The 10-100 mm ESD organisms (mostly planktivorous fish) show less intra-annual variation, but they do peak in the fall after the zooplankton bloom.

Because this is not a strict food chain, the energy flow is dispersed as it moves up the size spectrum, and the peaks in the larger classes are broader and less pronounced than in the smaller size classes. The largest size category exhibits virtually no dynamics (the largest two size groups can of course migrate, but this is not incorporated in this simulation).

Annual Dynamic Patterns

The annual pattern of life in marine ecosystems shows an interesting regularity when viewed in terms of size structure changes rather than species succession. Some typical results of simulations with a generic continental shelf model are presented here which show how these patterns develop. The seasonal cycle of phytoplankton and bacteria is shown in Fig. 2, and the response of four size classes of grazers is shown in Fig. 3.

As is normal on continental shelves, there is a marked spring bloom of diatoms which represents the chief pulse of primary production into the system. The simulations shown in Fig. 2 also show a

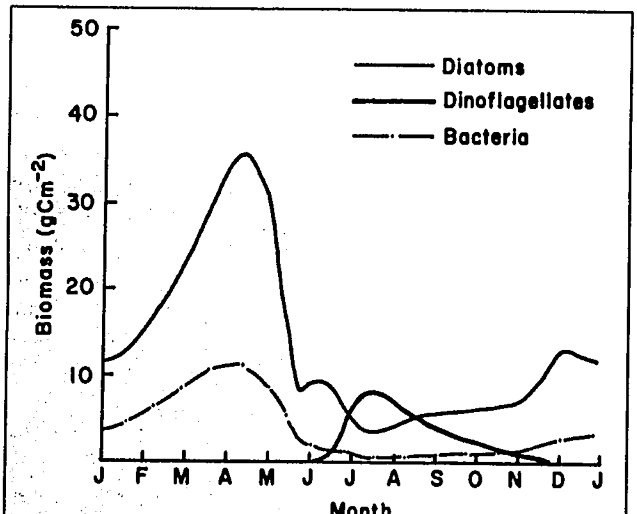

Fig. 2. Seasonal cycle of phytoplankton and bacteria.

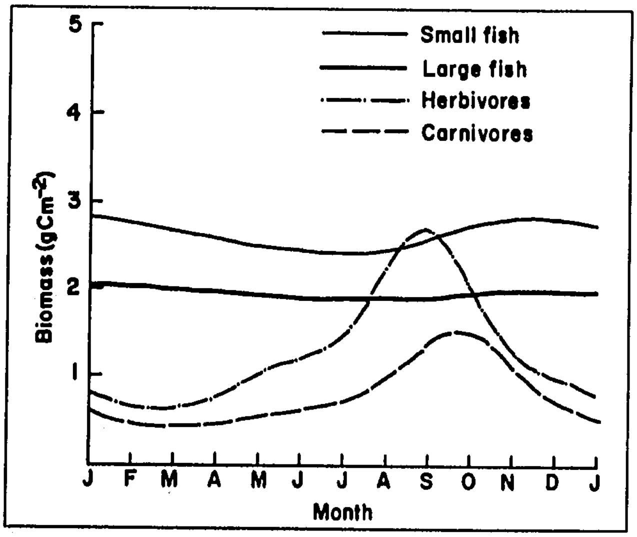

Fig. 3. Seasonal cycle of animal populations.

smaller diatom fall bloom as well as a summer dinoflagellate bloom. The timing and magnitude of these blooms depend largely on the physical environment, represented by such factors as the strength of summer stratification and the speed with which this becomes established (rapid stratification causes sudden crash of the spring bloom due to nutrient depletion of the euphotic zone, while slower stratification permits grazing to play a larger role in controlling the phytoplankton populations).

Of greatest interest are the dynamics of the animal populations. Four size classes are shown in Fig. 3, and although these are labelled by the dominant taxa, their formal description in the model is as follows (sizes expressed as ESD):

Large fish	100-1,000 mm ESD
Small fish	10-100 mm ESD
Carnivores (invertebrate)	1-10 mm ESD
Herbivores (invertebrate)	0.1-1 mm ESD

It is interesting to note that although the populations vary in size from 0.1 mm to 1,000 mm, the biomass concentrations differ by little more than a factor of two at any time during the year. This is consistent with the empirical results of Sheldon et al. (1972) which laid the foundation for size-structured modelling.

Ecosystem Stability

One of the most interesting questions in ecology is whether natural ecosystems are naturally stable, or whether at least part of the naturally observed variability can be attributed to instabilities in their internal dynamics.

Formal stability analysis of complex ecosystem models is very difficult, but the dynamical behavior of these models can be investigated by simulation *experiments* over extended periods of time, varying only the parameter values and initial conditions.

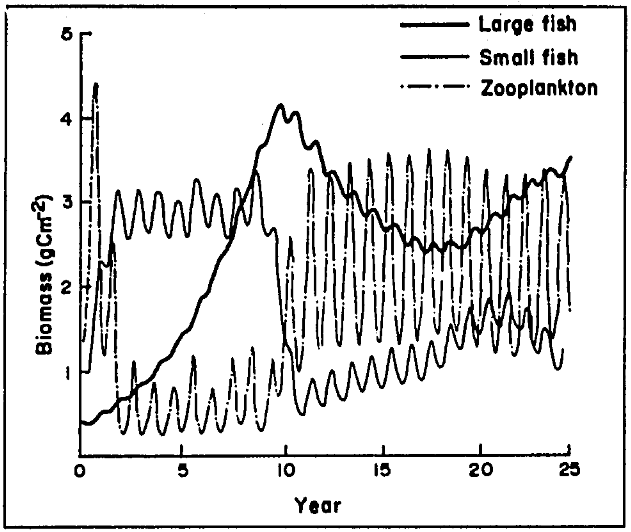

Fig. 4. Dynamics of animal populations over a 25-year simulation.

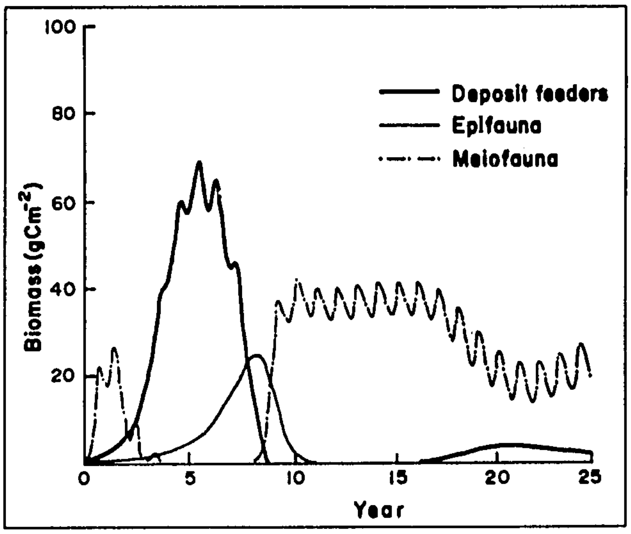

Fig. 5. Dynamics of benthic populations over a 25-year simulation.

A series of such simulations has been carried out with the Theoretical Macrocosm, a size-structured model of one spatial compartment in a continental shelf ecosystem (Silvert 1988). Many of these runs indicate that the system can jump between multiple quasi-stable points. The accompanying figures show the results of a 25-year simulation in which, after a two-year period of initial adjustment, the ecosystem appears to stabilize in a state where the pelagic community is dominated by organisms in the 10-100 mm ESD size range, as shown in Fig. 4. These are mostly small planktivorous fish, as reflected by the low levels of the planktonic size class. The benthic community shown in Fig. 5 is dominated by deposit feeders. During a relatively stable 10-year interval the only marked changes are a large increase in the abundance of larger fish and benthic epifauna, both of which can be viewed as top predators. The result is an almost instantaneous transition to another nearly stable state with a low biomass of small fish, large zooplankton biomass, and the virtually complete replacement of the macrobenthic community by meiobenthic organisms.

This behavior is very unlike the more familiar cyclic changes found in Lotka-Volterra models and suggests that internal dynamics may contribute to the variability and long-term changes in marine ecosystems.

Conclusion

- Size-structured simulation models of marine ecosystems are valuable tools for understanding their dynamics and their responses to environmental factors.
- Size-structured models have been used

successfully in modelling both estuarine and continental shelf systems.

- The energy flow through pelagic marine ecosystems proceeds along the size spectrum from small to large organisms.
- Even deterministic simulation models can generate multistable complex behavior that may cast light on changes in community structure.
- Size-structured models cannot answer all questions; for example, they cannot be used to predict the population dynamics of individual fish stocks. They should however be considered an essential tool in the investigation of marine ecosystems.

The model is written in Fortran and runs on a wide variety of computers, including MS-DOS, Macintosh, and Atari ST desktops as well as minicomputers and mainframes, using the BSIM modelling software to handle input, output and integration. Please contact the author for further information.

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The Detrital Cycle and Its Interaction With Higher Trophic Levels

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Abstract

Attempts to simulate an annual nitrogen cycle show that for semi-realistic results, a minimum of five nitrogen "pools" is essential. These are: animals, phytoplankton, inorganic nitrogen and two pools of dead organic nitrogen. Of these five compartments, the two pools of dead organic nitrogen make up at least 80% of the total nitrogen in the system. The formation and breakdown of this material therefore has a considerable influence on the living components of the system.

After the spring bloom, there is typically a period during which the relative magnitudes of the various nitrogen compartments do not appear to vary very much. Attempts have been made to replicate this observation using simulation studies and to determine values of the various parameters and flow rates that had to be used in these simulations. Attention is drawn to the uptake of inorganic nitrogen by microorganisms. This nitrogen is required for the manufacture of proteins by those microorganisms that utilize the soluble organic carbon that is released by phytoplankton.

The magnitude of this flow can be calculated from simulation studies or steady-state calculations which indicate that inorganic nitrogen uptake by microorganisms must be during the summer, of the same order of magnitude as the uptake by phytoplankton. A better perception of the formation and breakdown of dead organic matter is essential for simulation studies and for understanding how ecosystems work.

Introduction

This paper summarizes an attempt to simulate an annual nitrogen cycle for a hypothetical region based largely on the area off the east coast of Scotland. This area is characterized by the fact that during the summer, nitrate levels remain relatively very low throughout the whole of the water column. Also interchange with adjacent water masses appears to be relatively small. To a first approximation therefore it is appropriate to try to account for the annual nitrate cycle without having to consider significant horizontal interchange with other areas, nor significant vertical interchange across a thermocline. Fuller details and references are given in Jones and Henderson (1987).

The Basic Framework

One objective of this study was to discover the simplest nitrogen flow model that could be used for producing realistic-looking simulations of annual cycles of, for example, inorganic nitrogen and phytoplankton nitrogen. Fig. 1 shows the results in the form of a flow diagram based on five nitrogen "pools". Estimates have been obtained of the magnitudes of the various pools, and the ways in which these vary throughout the year. Details are given in Jones and Henderson (1987).[d]

The main conclusions from this study are as follows: In summer, living material adds up only to about 2 $g \cdot N \cdot m^{-2}$. In winter, inorganic nitrogen is equal to 5-6 $g \cdot N \cdot m^{-2}$. Throughout the year, dead

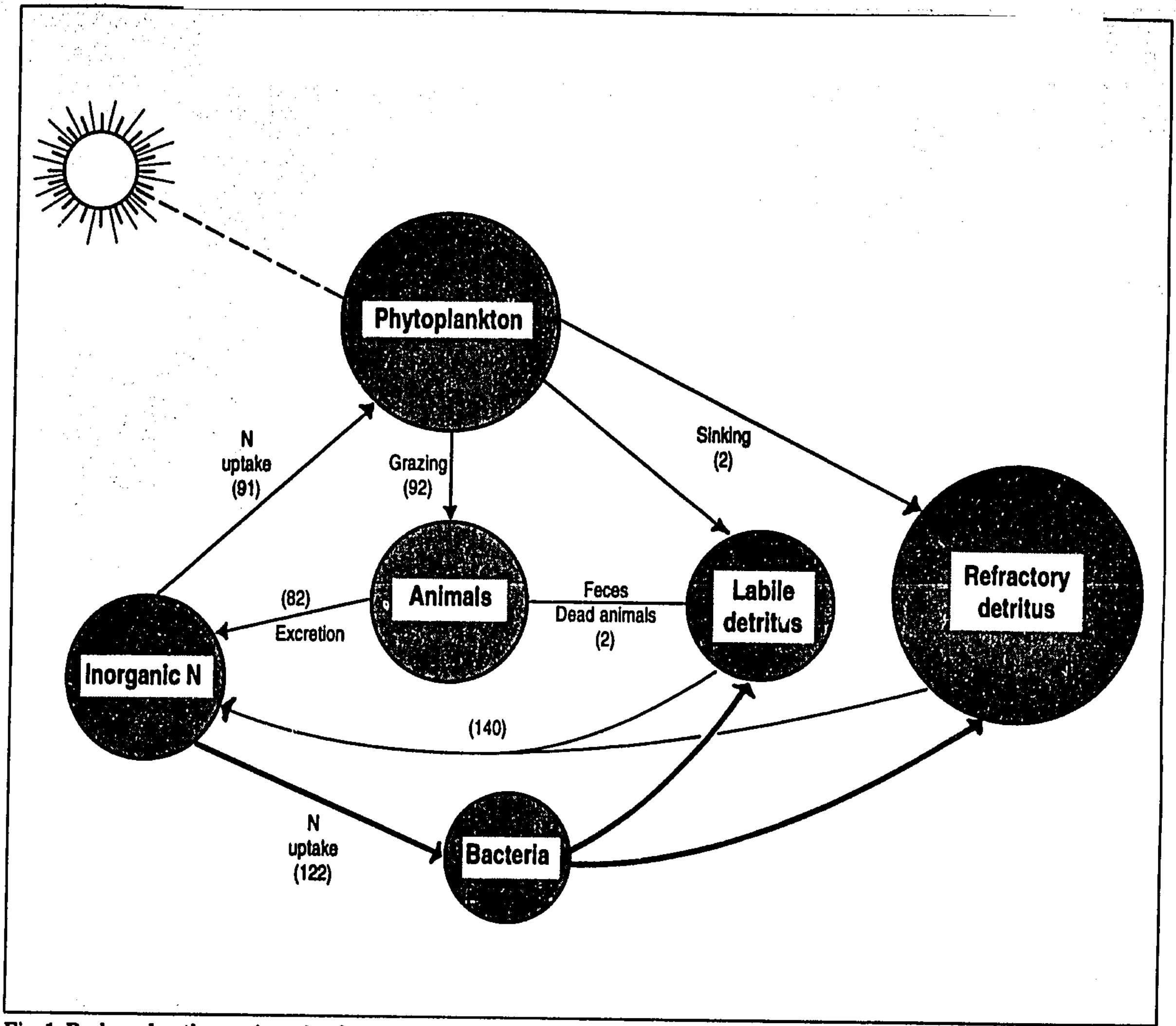

Fig. 1. Pools and pathways in a simple nitrogen model. Numbers are representative of daily flows in mg $N{\cdot}m^{-2}{\cdot}day^{-1}$ during the summer, postbloom period.

organic nitrogen, most of which is in the sediments, amounts to about 18-30 $g{\cdot}N{\cdot}m^{-2}$, depending on the depth of sediment included. Dead organic nitrogen makes up by far the largest part of the total nitrogen, thus, so much emphasis is placed on its importance.

Dead organic matter is broken down by microorganisms on time scales that range from hours to thousands of years. For simulation purposes, it is appropriate to distinguish, at the very least, between time scales of less than a productive season, and time scales longer than a productive season. This has been done and the terms "labile" and "refractory," respectively, have been adopted as a convenient way of referring to these two groups of dead organic matter.

Seasonal Variations in Nitrogen and Nitrate

The decline in inorganic nitrogen in spring and its subsequent reappearance in autumn is a striking and readily observable phenomenon. Off the east coast of Scotland, the decline is from a winter value of 5.6 $g{\cdot}N{\cdot}m^{-2}$ to a summer value that is less than 1 $g{\cdot}N{\cdot}m^{-2}$.

Regarding the spring bloom of phytoplankton, measured spring peak values are about 1.2 $g{\cdot}N{\cdot}m^{-2}$. Due to the transitory duration of the peak at any one location, however, it is likely that higher values than this could occur for brief periods.

Although the various values given above are very approximate, they do have one very important implication. That is, that only some of the winter inorganic nitrogen is transformed into living animals by the summer. It is not certain how much of the winter nitrate nitrogen is transitorily incorporated into the spring bloom. However great this may be, it is clear that by the end of the bloom, a large part of the winter nitrate nitrogen is not in living material, but is presumably in the form of dead organic nitrogen.

The values above show that only a small part of the autumn reappearance of nitrate can be accounted for by the rundown of living biomass. The remainder must come from the breakdown of labile organic matter.

The conclusions reached so far are: Winter nitrate nitrogen is converted, in summer, partly into living

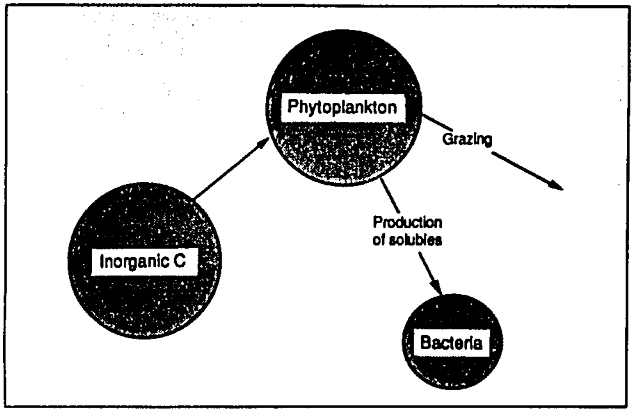

Fig. 2. Position of bacteria in a carbon flow model.

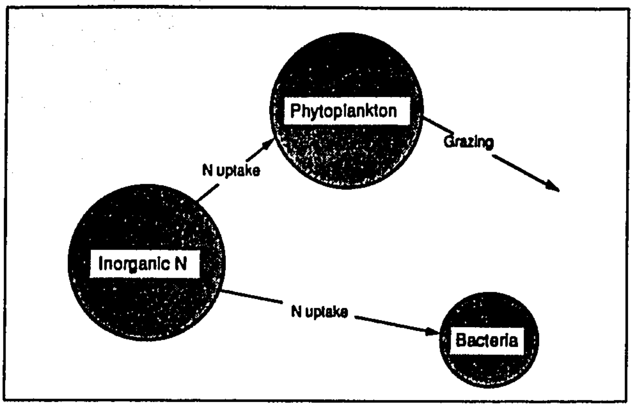

Fig. 3. Position of bacteria in a nitrogen flow model.

material, and partly into dead organic nitrogen. In autumn, nitrate nitrogen reappears in the water column, partly from a rundown of living material, and partly from a breakdown of labile dead organic matter.

Major Flows

For about 100 days after the decline of the spring bloom, there are only relatively small variations in the magnitudes of the various pools. The simulations must replicate this observation as closely as possible.

Using computer simulations, values have been derived for the magnitudes of the various pools and flows and for a hypothetical 50 meter mixed water column, based on parameter values from various sources. The resulting flow rates, shown in Fig. 1, are in units of mg N $m^{-2}day^{-1}$ and represent a typical set of summer values from a simulation run.

A particularly important feature of Fig. 1 is the flow from inorganic nitrogen to bacteria, and from bacteria to dead organic matter. From a simulation viewpoint, this flow is essential. Without it, it is not possible to maintain a semi steady-state system for a period of as long as 100 days, as is necessary for the postspring bloom period. In real terms it seems reasonable to suppose that this flow represents the uptake of inorganic nitrogen by microorganisms, and its eventual incorporation into dead organic nitrogen. Just how this happens, is largely surmise. A likely explanation, however, is that this process is connected in some way with the production and breakdown of soluble organic carbon.

A characteristic of phytoplankton, is the production of soluble organic carbon, and during summer, when nutrient levels are low, the quantities produced can be relatively large. This material is taken up by bacteria and presumably converted into microorganism biomass. Those microorganisms that die without being ingested by something larger, add some combination of labile and refractory matter to the dead organic pools.

If one were dealing with a carbon flow model, one might visualize the flows shown in Fig. 2. Phytoplankton takes up inorganic carbon. Some carbon is incorporated into plant biomass and follows the grazing pathway. The other carbon is released in soluble organic form, and is taken up by bacteria and incorporated into the detrital pathway.

Here, however, one is dealing with a nitrogen flow model, and phytoplankton does not produce a great deal of soluble organic nitrogen, and certainly does not do so on a scale comparable with the release of soluble organic carbon. To utilize soluble organic carbon, bacteria have to obtain nitrogen (for proteins) from some other source. The simplest assumption, then, is that bacteria obtain inorganic nitrogen directly from the inorganic nitrogen pool (Fig. 3). There is experimental evidence that, in the presence of glucose, bacteria do take up inorganic nitrogen directly.

Conclusion

Inorganic nitrogen is seen to be a common source of nitrogen for the "detrital pathway" and the "grazing pathway". Therefore, bacteria that take up inorganic nitrogen to utilize soluble carbon, compete directly with phytoplankton for inorganic nitrogen at a time when inorganic nitrogen concentrations are typically low. The resultant flow diverts nitrogen to the dead organic compartment at the expense of higher trophic levels and sets a limit to the effective level of animal production.

Simulation studies also suggest that differences in the relative magnitudes of the detrital and living pathways, could be large enough to account for the differences observed between different ecosystems.

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CULTURE SYSTEMS

Most modelling in aquaculture is process-oriented. One tries to describe, e.g., the dynamics of a pond, by describing all the component processes, linking processes and submodels to form a synthesis that can represent the system. Barnard's paper in this section on waterfowl management modelling is a good example.

Models of the process-oriented type have shown to be very useful in agriculture, e.g., for designing optimum schemes for irrigation, fertilization, and pest control, and other forms for crop-oriented optimization. Less obvious is how they can be used to optimize larger (integrated) systems due to the complexity of the systems and the limited success in making predictions for them.

For work with such systems, other approaches should be considered instead of, or to supplement process-oriented modelling. The alternative that will be discussed by the four other contributions in this section is steady-state modelling on a system level. The four contributions discuss very different systems, from a traditional Chinese integrated polyculture system, over small ponds, rice-fish systems to fishpens in a large lake. Yet all models show that it is possible to construct simple steady-state models of the trophic interactions in the respective systems based on available data and information from the literature. And what is more: the models, although first attempts, can be used to raise and discuss questions and just as important to show gaps in knowledge and to pinpoint questionable parameter estimates.

An added benefit is that this form for models is, as concluded by Baird et al. (1991), useful for comparisons between systems. Comparisons are of interest in ecology for designing structural dynamic models (Jϕrgensen 1992), while the discussion in aquaculture has concentrated on development of "sustainable" systems through farming systems research and extension (FSRE, see Lightfoot and Pullin 1991). Because of this interest, we now see data collection schemes designed with (steady-state) modelling in mind popping up; as an example, the rice-fish group in the Philippines, whose first model is presented here, has since, the model was constructed, collected data in order to improve their model. Also of interest is the work going on now with data collection at a farm level. Models like those discussed here are not restricted to aquatic systems - the Chinese model to some extent shows this - but can be used to describe whole farming enterprises. A detailed data collection on farms is intended to supply enough data at the farm level to be able to describe (through quantified models) the energy or economic flow for individual farms, and to explore ways of expressing sustainability using key output parameters.

Where we (the editors, as fisheries biologists) hope some day to have enough material on individual ecosystems to describe interactions in perhaps a hundred ecosystems so that we, through proper stratification, can come up with worldwide figures for biological productivity on a global scale, we hope to see us overtaken by approaches within aquaculture, where the ecosystem is one farm. The possibilities this raises for comparisons and generalizations are enormous, and we are certain that the interaction between fisheries biologists and aquaculturists, of which this book is one small example, is more than worthwhile.

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An Energy Flow Model of the Mulberry Dike-Carp Pond Farming System of the Zhujiang Delta, Guangdong Province, China*

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Abstract

This paper describes an integrated dike-pond farming system in South China, one with a history that goes back to the mid-fourteenth century. The energy flows through the system, which includes among other components, eight fish species (*Ctenopharyngodon idellus, Hypophthalmichthys molitrix, Aristichthys nobilis, Mylopharyngodon piceus, Cirrhinus molitorella, Cyprinus carpio, Megalobrama bramula, Oreochromis* sp.) are quantified. The system has a very high throughput and production, caused by high imports of manure and concentrated feeds, together with elephant grass, vegetables and mulberry leaves that are produced on the dikes.

Introduction

This paper describes the dike-pond polycultures of South China. The main source for the description is field research conducted by the senior author jointly with Chinese counterparts, as documented by Ruddle and Zhong (1988). For the present study, data have been extracted from that monograph and available literature and used to construct a steady-state energy flow model using the ECOPATH II model (Christensen and Pauly 1992).

Historical and Socioeconomic Context

In the Zhujiang (Pearl River) Delta of Guangdong Province, South China, which sprawls over some 12,000 km^2 south of the city of Guangzhou (Canton), an elaborate integrated system of intensive agriculture and polyculture of carps and other freshwater fishes is operated on a geographic and economic scale unmatched elsewhere in the world. This system has evolved over centuries and is now developed over 800 km^2. It is more tightly integrated than elsewhere in Shunde County of the central delta (Fig. 1). In total it supports an estimated 1.2 million persons.

The system has three components: fishponds, mulberry dikes and sugarcane dikes. Where this is the dominant land use type, 52,128 ha or 76% of the agricultural land use is devoted to the system, with 22,239 (43%) in fishponds, 9,814 ha (18%) under sugarcane and 8,094 ha (15%) planted to mulberry. Fig. 2 gives an aerial view of an intensively used dike-pond area.

The principal fish cultured are Chinese carps: grass carp (*Ctenopharyngodon idellus*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Aristichthys nobilis*), black or snail carp (*Mylopharyngodon piceus*), mud carp (*Cirrhinus molitorella*) and common carp (*Cyprinus carpio*). In addition, bream (*Megalobrama bramula*) and tilapia (*Oreochromis* sp., probably a hybrid of *O. mossambicus* and *O. niloticus*) are cultured to some

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* ICLARM Contribution No. 648.

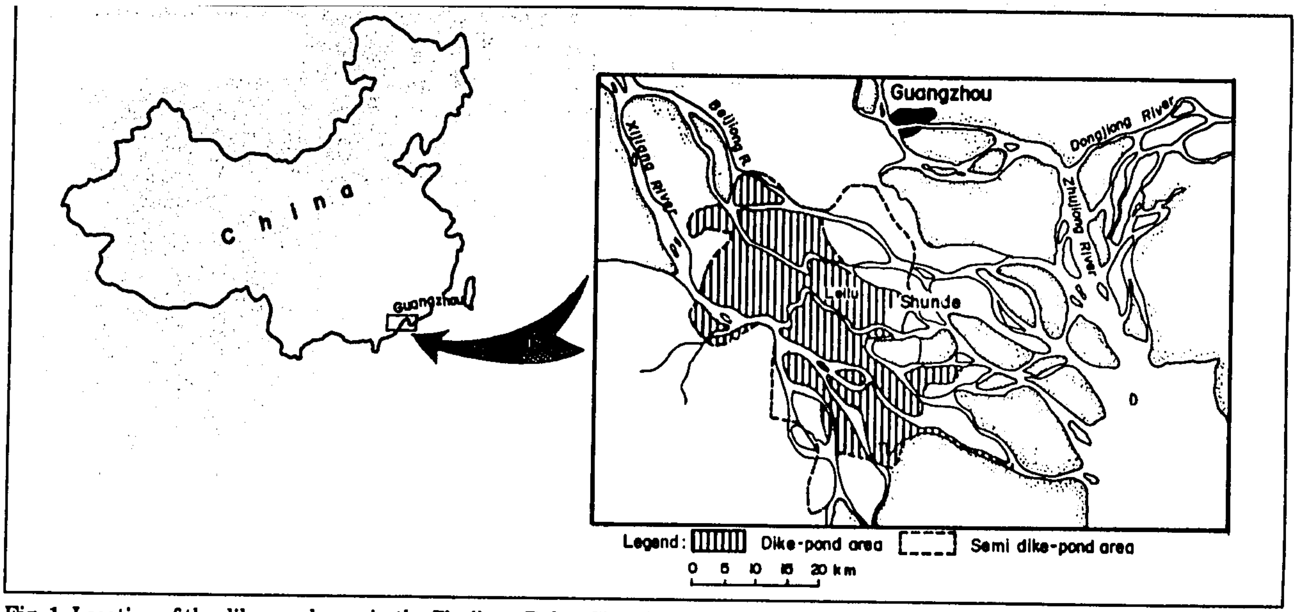


Fig. 1. Location of the dike-pond area in the Zhujiang Delta, Shunde District, South China.

Fig. 2. Aerial view of part of Leliu Commune, central Zhujiang Delta, showing the intricate patchwork of nearly rectangular fishponds segregated by crop dikes (drawn after photo in Ruddle and Zhong 1988).

extent. Most are marketed live, mainly to Guangzhou, Hong Kong and Macao. Fish sales are the largest source of income in the region's agricultural sector, the Zhujiang Delta yielding 90,000 $t \cdot year^{-1}$ (1979) or 50% of the total production of Guangdong Province and 80% of the nation's live fish exports.

This is one of the few integrated agriculture-aquaculture systems for which a reasonably precise historical record can be reconstructed. About 1,000 years ago, village economies in the Zhujiang Delta were based mainly on the capture and collection of marine, riverine and wetland resources. At nearby higher elevations, however, fruit cultivation, especially of litchi (*Litchi chinensis*) and longan (*Euphoria longana*), developed rapidly during the Han Dynasty, some 2,000 years ago. Sugarcane has been cultivated in the region for two millennia, mostly in upland areas. Mulberry-growing had also been undertaken for some 2,000 years in the Zhujiang Delta and had developed into a substantial industry by the early Tang dynasty (7th century A.D.).

During the 1350s (A.D.), water control began in some lower-lying areas to make fishponds so as to drain wetlands and natural waterbodies, thereby creating cultivable land on intervening dikes. The early artificial ponds were devoted mainly to nursing wild fry to fingerlings, and the dikes to fruits, especially litchi and longan. There was no integrated system at that time.

Mulberry-growing and silkworm-rearing remained separate both geographically and conceptually from fish cultivation in the 14th century, as demonstrated by the fact that few dikes were planted to mulberry. By the 1620s, however, mulberry was being widely cultivated on the dikes between the fishponds, experience having shown that the economic returns from integrated mulberry dike-fishpond systems were greater than those obtained from cultivating fruit trees on the dikes. Moreover, pond mud enriched with silkworm excrement and other wastes which had first been utilized to fertilize the pond and to feed the fish, was found to be a superior fertilizer for mulberry bushes than was the raw silkworm waste used hitherto. This discovery led to the rapid development of the integrated mulberry dike-carp pond system, such that by 1800 A.D. most farms in Shunde County were devoted exclusively to it.

The yields of the dike-pond system make Shunde County one of the most productive regions of China. Annual yields ($t \cdot ha^{-1}$) are: fish (7), sugarcane (75), mulberry leaf (20-30), silkworm (1.9-2.25), mixed vegetables (80) and bananas (22-30).

As a consequence, per capita income in households surveyed in 1982 ranged from US$253 to US$331. In comparison, the average per capita rural income in China at the time was US$152. Incomes per "able-bodied worker" were US$456-670.

Since the early 1980s, as a result of the implementation of the household responsibility system and the concomitant decline of the centrally planned economy, variations began to emerge among households, particularly in terms of the allocation of working capital and labor to the dike-pond system, management strategies and levels of productivity, household economies, and the energy efficiency of household ponds.

Field Research Methodology

Research was conducted jointly with the Guangzhou Institute of Geography, Chinese Academy of Sciences, from 1980 until 1983 on the socioeconomic, biological and physical aspects of the dike-pond system. Biological and physical research concentrated mainly on the quantitative analysis of energy exchange.

The fundamental concept underlying highly intensive, integrated aquaculture-agriculture farming systems is that outputs of subsystems become inputs for other subsystems. Thus, in the dike-pond system of the Zhujiang Delta, not only are the media for the growth of fish and crops provided but also the environment in which their food and fertilizer requirements are produced. This results in higher yields for all commodities produced and a wider range of products than could otherwise be obtained. It also results in lower costs for inputs, which, in the absence of such integration, would have to be imported from outside the system. Such inputs are also a part of the system described here but the integration tends to limit the imports.

To understand how the fundamental processes operate, field research was conducted on (1) net solar radiation on the dike and over the pond, reflex radiation and photosynthetically active radiation (PAR) on the dike and beneath the pond surface; and (2) primary productivity of the pond, fish production, productivity of mulberry, mulberry detritus fall, and silkworm productivity.

A Steady-State Model of a Developing Culture System

It may be conceived as impossible to use a steady-state model for a rapidly developing culture system, but by averaging the flows and biomasses over the production period, which is nearly a year, the *average* system can be described, even with a steady-state model (see also Fig. 1C, Christensen and Pauly, this vol.).

Components

The ecosystem model as we have chosen to make it consists of a total of 16 groups, of which six are carp species, one bream, and one tilapia. Silkworms, though not present in the ponds, form yet another group, and the invertebrates in the system are divided between zooplankton and macrobenthos. The primary producers are mulberry, elephant grass, and vegetables, all growing on the dikes, and of course phytoplankton in the pond, well nourished from the continuous supply of manure, human, as well as from poultry and livestock.

The dike-pond system is highly productive, mainly dependent on the supplies of manure, elephant grass, and concentrated feeds for maintaining its high productivity. The input parameters are given in Table 1.

Fish Groups

The biomasses have been calculated as the mean of the biomasses at stocking and at harvest, thus *not* taking the fact into account that growth (and consumption) rates vary throughout the culture period. The marked seasonality in the ponds will however tend to minimize the error due to averaging, as the main biological activity takes place during the warm summer months, in the middle of the culture period.

The production (P/B) ratios are readily available for the fish species as the ratio between harvest less

Table 1. Input parameters (without brackets) for the Chinese polyculture system. Biomass is an average on a t·ha^{-1} scale. P/B (year^{-1}) is the production/biomass ratio; production (t·ha^{-1}·year^{-1}) corresponds to B•P/B; Q/B (year^{-1}), the consumption/biomass ratio; GE, the gross efficiency (production/consumption); unassimilated food is the proportion of the consumption that is not assimilated. Exports are in t·ha^{-1}·year^{-1}. EE is the ecotrophic efficiency (estimated parameters are presented in brackets).

Group	Biomass	P/B	Production	Q/B	GE	Unassimilated food	Export	EE
Grass carp	1.240	0.90	-	50.0	(.02)	0.75	1.110	(1.00)
Silver carp	0.212	0.90	-	-	(.07)	0.30	0.191	(1.00)
Bighead carp	0.506	2.00	-	-	(.25)	0.20	1.013	(1.00)
Mud carp	1.781	0.90	-	-	(.13)	0.30	1.594	(0.99)
Black carp	0.036	1.80	-	-	(.39)	0.20	0.064	(0.99)
Common carp	0.068	1.97	-	-	(.24)	0.30	0.134	(1.00)
Bream	0.034	0.98	-	-	(.05)	0.40	0.033	(1.00)
Tilapia	0.173	0.95	-	-	(.05)	0.30	0.164	(1.00)
Silkworm	2.000	1.05	-	15.0	(.07)	0.20	2.100	(1.00)
Zooplankton	(0.652)	20.00	-	(133.3)	.15	0.40	0.0	0.95
Macrobenthos	(1.179)	20.00	-	(133.3)	.15	0.20	0.0	0.95
Mulberry	-	-	30	0.0	-	-	0.0	(1.00)
Elephant grass	-	-	225	0.0	-	-	0.0	(0.25)
Vegetables	-	-	3.75	0.0	-	-	0.750	(0.90)
Phytoplankton	0.750	298.67	-	0.0	-	-	0.0	(0.39)
Detritus	90.000	-	-	-	-	-	444.405	(0.25)

stocking and mean biomass. The consumption rates (Q/B) for all fish species except grass carp were estimated from the empirical model of Palomares and Pauly (1989).

The grass carp are known to be voracious, albeit inefficient feeders. In China, they are considered as "mobile fertilizer factories", and hence a vital part of the integrated pond systems. The food conversion efficiencies of grass carp depend very much on feed type, and have, for grass carps feeding on grass, been reported as 0.025 to 0.04 by Shigang (1989). Adopting a value of 0.04 for our study and assuming the average biomass corresponds to half the gain in weight, the Q/B ratio can be calculated to be approximately 50 year^{-1}.

Invertebrates

For zooplankton and macrobenthos, the P/B ratio was set to a value in the range observed in other studies (e.g., Jϕrgensen 1979) as this resulted in reasonable estimates for the respiration/biomass ratio of zooplankton. The Q/B ratios were calculated from assumed gross efficiencies of 0.2. Due to expected high predation rates, the ecotrophic efficiencies were set to 0.95, so that only very small parts of the zooplankton and macrobenthos production were directed to the detritus.

Primary Producers and Detritus

Production data for the primary producers are available from the field research. The manure and concentrated feeds that are added to the system are treated as imports to the detritus box. The total input to the detritus is estimated as 160 t·ha·year^{-1}.

Diet Compositions

For most of the groups there are only qualitative statements of the diet composition to be found in the available literature (Yan and Yao 1989; Edwards 1992). The diets are therefore chiefly based on a general knowledge of the trophic ecology of the described groups. The system was then balanced by changing the diet compositions based on the general knowledge until acceptable values of the ecotrophic efficiencies were obtained (i.e., very close to 1 for all consumers and lower for producers). It should be noted, however, that hardly any (and only small) changes had to be made to the originally assumed diet compositions to make the system balance.

Unassimilated Food

The proportion of the food that is not assimilated was set to vary between groups as a function of the degree of herbivory/detritivory (Table 1). The value for grass carp is based on Yan and Yao (1989).

Results and Discussion

Fig. 3 gives a qualitative representation of the energy and matter linkages in the dike-pond system. A simplified version of this was analyzed with the ECOPATH II model.

The flowchart from this analysis is shown in Fig.

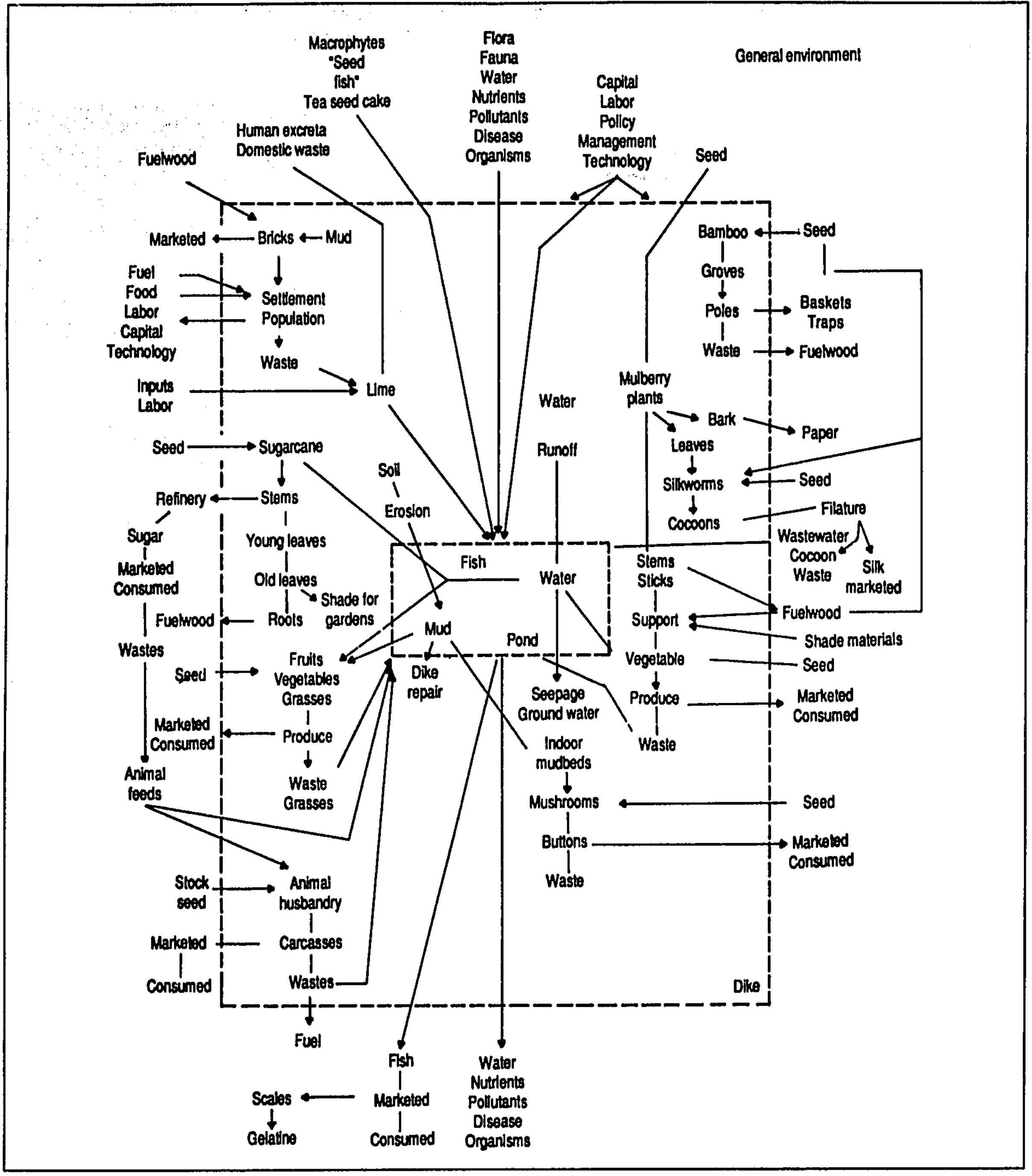
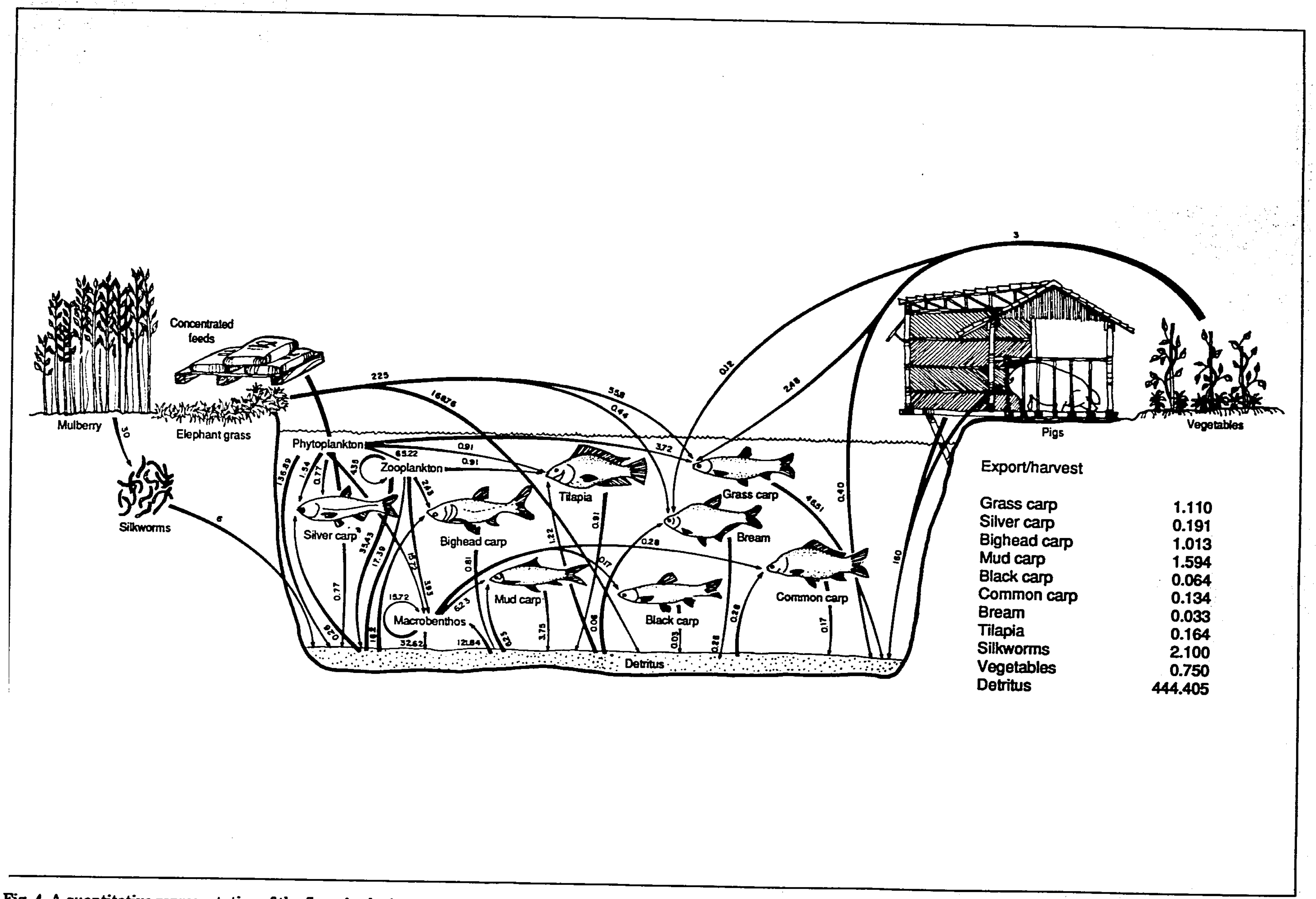


Fig. 3. Energy and matter linkages in the dike-pond system (after Ruddle et al. 1983).

4 while Table 1 includes some of the parameters estimated by ECOPATH II. The system is characterized by a true network of flows. Yet its short path lengths make it resemble the aquaculture system one sees in other areas. The highest trophic level in the system is thus 3.14 (Table 2), i.e., only slightly higher than the trophic level of a first-order carnivore. The average trophic level of the harvestable groups is 2.42 (weighted after production), roughly intermediate between a herbivore/detritivore and a first-order carnivore.

The parameter estimates for the individual groups are difficult to compare with other studies, as only very few investigations have been conducted in comparable systems.

Phytoplankton production can be compared, though, with findings of Colman and Edwards (1987) of maximum sustained rates of photosynthesis in a tropical fishpond of about 0.3 t dw·ha^{-1}·year^{-1}. The present investigation yields 224 t ww·ha^{-1}·year^{-1}, somewhat higher than the maximum rate reported by Colman and Edwards (1987). Mean phytoplankton biomass in septage-fed ponds with Nile tilapia was estimated by Edwards et al. (1984,



Export/harvest

Grass carp	1.110
Silver carp	0.191
Bighead carp	1.013
Mud carp	1.594
Black carp	0.064
Common carp	0.134
Bream	0.033
Tilapia	0.164
Silkworms	2.100
Vegetables	0.750
Detritus	444.405

Fig. 4. A quantitative representation of the flows in the integrated dike-pond polyculture system of the Zhujiang Delta, South China. Flows are expressed in t·ha^{-1}year^{-1}.

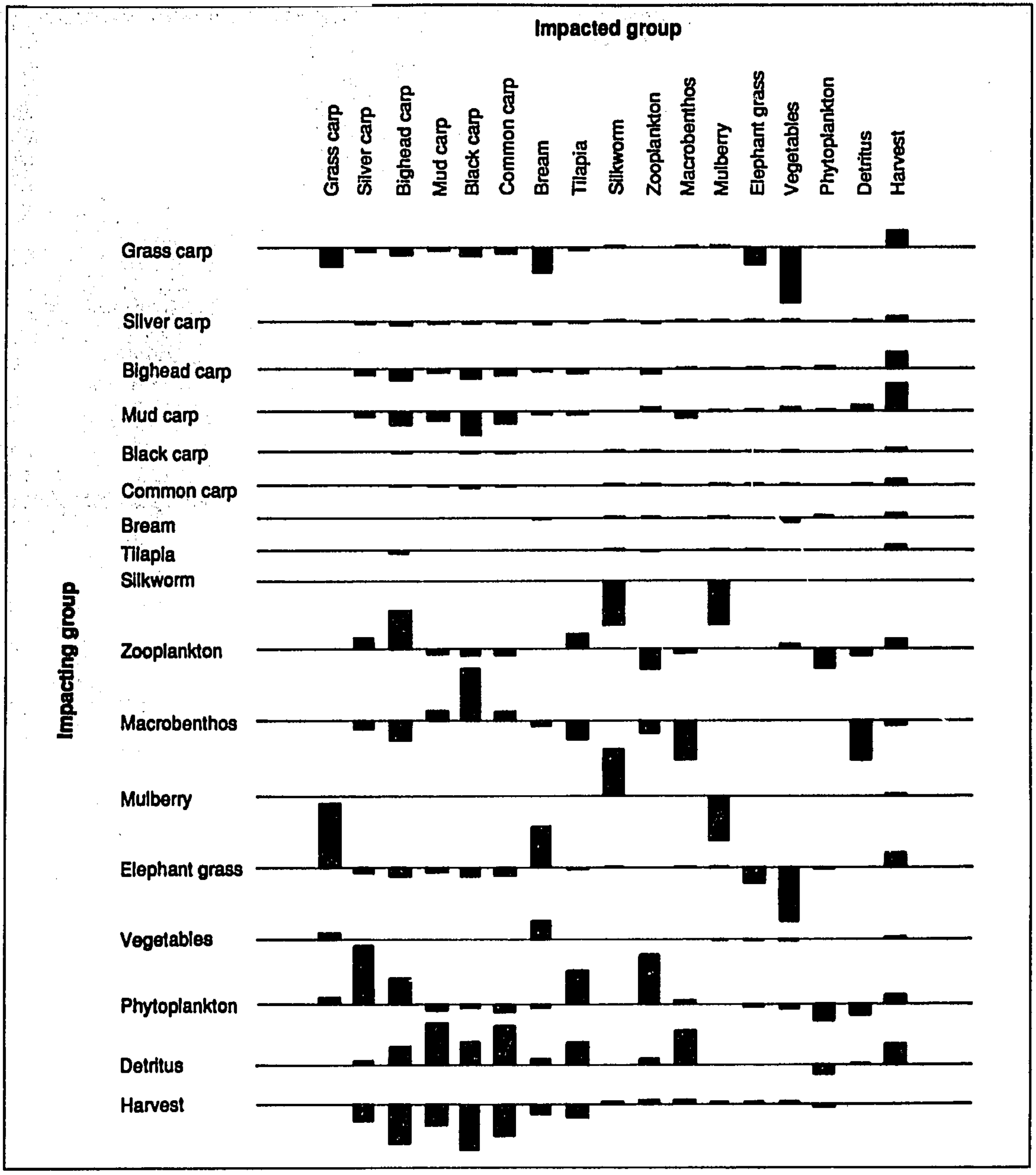


Fig. 5. Mixed trophic impact in a mulberry dike-carp pond farming system, China, as obtained from the ECOPATH II program (Christensen and Pauly 1992). The bars show the impact of the groups to the left of the bars on all other groups in the entire system. Positive impacts are shown above the baseline, and negative ones below. The impacts are relative, but comparable between groups.

1987) to be around 30 mg·l^{-1}. This corresponds to a biomass of around 0.75 t·ha^{-1} for ponds with an average depth of 2.5 m as the Chinese ponds. A phytoplankton production of 224 t·ha^{-1}·year^{-1} and a biomass of 0.75 t·ha^{-1} correspond to a P/B ratio of some 300 year^{-1} for the Chinese ponds. This seems to be a reasonable estimate considering the high energy input to the phytoplankton.

Zooplankton biomass was reported by Edwards et al. (1984, 1987) to be almost an order of magnitude lower than those of phytoplankton. Here we found the zooplankton biomass to be nearly as large as that of the phytoplankton. Clearly, this calls for a closer study of the zooplankton in the system. For comparable systems, Hallock and Ziebell (1970) estimated a total benthic productivity of 14.2 t·ha^{-1}·year^{-1}. This can be compared to estimates from the present study of 23.6 t·ha^{-1}·year^{-1}.

Using the trophic aggregation routine of ECOPATH II (Christensen and Pauly 1992), the flows in the system can be aggregated on discrete trophic levels. The results of this aggregation are shown in Table 3. As can be seen, the system has very few trophic levels, and the bulk of the flows are at trophic levels I and II. The trophic transfer efficiencies are rather low on trophic level II (5.9%,

Table 2. Parameters for estimation of consumption/biomass (Q/B) ratio for various fish species in a Chinese mulberry dike-carp pond model. Q/B is estimated using the empirical model of Palomares and Pauly (1989) modified to take the proportion of food derived from herbivory/detritivory (PHD) into account, and solved for T = 16°C.

Species	W_∞ (g)	Caudal fin aspect ratio[a]	PHD ($year^{-1}$)	Q/B
Grass carp	32,000	2.67	1.0	12.0
Silver carp	8,000	2.52	0.7	12.1
Bighead carp	11,000	3.05	0.3	8.0
Mud carp	12,850	1.55	0.5	7.0
Black carp	35,000	5.00	0.0	4.6
Common carp	19,170	2.54	0.5	8.3
Bream	3,000	2.39	1.0	18.3
Tilapia	850	2.17	0.7	17.6

[a] See Fig. 1 in Pauly et al. (this vol.).

Table 3. Trophic transformation matrix for the Chinese mulberry dike-carp pond ecosystem showing how flows ($t \cdot ha^{-1} \cdot year^{-1}$) for each group in the system are distributed on discrete trophic levels. The bottom line gives trophic transfer efficiencies by trophic levels.

Group	Average trophic level	Trophic level I	II	III	IV
Black carp	3.14	-		0.16	0.005
Bighead carp	2.63	-	1.62	2.43	-
Mud carp	2.57	-	6.23	6.06	0.175
Common carp	2.57	-	0.28	0.27	0.008
Silver carp	2.32	-	1.80	0.77	-
Tilapia	2.32	-	2.13	0.91	-
Macrobenthos	2.14	-	152.81	4.40	-
Zooplankton	2.05	-	86.96	-	-
Grass carp	2.00	-	62.00	-	
Bream	2.00	-	0.62	-	-
Silkworm	2.00	-	30.00	-	
Mulberry	1.00	30.00	-	-	-
Elephant grass	1.00	225.00	-	-	-
Vegetables	1.00	3.75	-	-	-
Phytoplankton	1.00	224.00	-	-	-
Detritus	1.00	593.30	-	-	-
Total	-	1,076.05	344.45	15.00	0.188
Trophic transfer efficiencies	-	0.059	0.124	0.139	-

the herbivore level), and higher on the two predatory levels (12.4% and 13.9%). The flows are predominantly of detrital origin, with 58% of all flows originating from this source as estimated using ECOPATH II.

From the mixed trophic impact analysis presented in Fig. 5, it can be concluded that remarkably little negative impact occurs between the harvested groups. This can be seen as a sign of a well designed system, developed over hundreds of years. Only mud carp seems to have some negative effect on the other groups, mainly due to its high biomass. The analysis in its present form does not show the important role of grass carp in producing manure, thus making elephant grass nutrients available for other groups. This was discussed by Yan and Yao (1989) who found that for every ton of grass carp produced, there may be enough food for "Wuchang fish" (*Megalobrama amblycephala*) to increase by 0.2 t, and for common carp and crucian carp to increase by 0.5 t. The mixed trophic impact routine of ECOPATH II could be modified to take the positive impact of detritus production into account, and this would show the beneficial impact of grass carp on the other groups in the system.

Conclusion

The comparisons made above seem to indicate that the estimates for the organisms at the lower trophic levels of the dike-pond system are quite reasonable. Considering that this is the part of the system for which we have least *a priori* information, we take the findings as a sign of the robustness of the modelling approach.

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Preliminary Steady-State Nitrogen Models of a Wetland Ricefield Ecosystem With and Without Fish*

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Abstract

Rice and fish are the most important food sources in Asian diets. Up to now the supplies of rice and fish have come from different sources. The traditional practice of catching wild fish in ricefields is insignificant today. Recent investigations indicate, however, that integrated rice-fish systems offer possibilities of increasing rice yields by as much as 15% and at the same time harvesting fish up to 500 kg·ha^{-1} every rice crop.

Modern rice production has become heavily dependent on insecticides. Through the integration of fish in rice paddies the possibility exists for reducing insecticide use. Similarly, chemical fertilizers could be partially substituted with farm by-products fed to the fish.

To improve our understanding of ecological interactions in rice-fish systems, we have used ECOPATH II to construct initial models of rice systems, one with and one without fish. While these preliminary models were constructed from limited field data, they do provide indicators for critical field measurements and experimentation. Future models will assist in the development of guidelines for optimum management of rice-fish integrated systems.

Introduction

By the year 2000, Asian farms must provide food for 3.6 billion people. A prerequisite will be higher production of rice and fish, the mainstays of Asian diets. Asian farming systems are predominantly rice-based and depend upon, among other things, water control. Thus they could theoretically at least produce large quantities of high-value fish. Integrating the production of rice and fish in the same water on the same land can help to achieve high food production requirements. Even modest adoption of such integration could dramatically increase fish production (Lightfoot et al. 1990). More than one hundred and fifty fold increases in fish production (500 to 79,000 t) could be achieved in Vietnam, for example, if 300 kg·ha^{-1}·year^{-1} of fish were harvested from only 5% of its riceland. India and Thailand, with current productivity levels of 450 and 1,044 kg·ha^{-1}, respectively, could increase their fish production by similar orders of magnitude. On 5% of their ricelands, the Philippines and Bangladesh could theoretically produce 45,000 and 140,000 t of fish, respectively. Rice-fish integration may also

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provide incentives for farmers to reduce levels of pesticide use and fertilizer application without reducing rice production.

Adoption of rice-fish farming will depend greatly on what happens to rice yields. An analysis of rice-fish data from research stations and farms in several Asian countries by Lightfoot et al. (1989) showed that even though some negative effects on rice yields were reported, positive effects in the order of 5 to 30% were typical. They concluded that "from these data it is not unreasonable to assume a 10-15% increase in rice yield when fish are present." Little empirical evidence exists and even less is known about the underlying ecological processes of the synergistic effects in rice-fish farming.

Fish may consume rice pests including weeds. Work conducted in Indonesia showed ricefield weed biomasses to be significantly reduced by grazing of carps and tilapia (Moody 1988). Chinese studies report similar findings (Xu and Guo 1988). Rice pest predation by fish has been observed in China. Rice stemborer egg masses, leaf folders and plant hopper populations have been reduced by fish (Spiller 1985; Yuan 1988).

Fish may contribute to soil fertility. Differences in soil nitrogen, phosphorus, potassium and organic matter have been detected between paddy soils where rice was grown with and without fish (Li 1988; Xu and Guo 1988). The nitrogen cycle to be presented below helps explain how nitrogen accumulation might occur.

Fish not only contribute to nitrogen accumulation through their feces, but they may also reduce nitrogen losses. In irrigated rice-fish culture, a continuous flooding of the field is expected and therefore high losses by denitrification observed in fields subjected to alternate dessication and submergence are not expected to occur.

Fish may reduce the strong nitrogen losses by ammonia volatilization in rice monoculture system. The high level of fertilizer directly applied in the floodwater causes pH increases. Ionized NH_4^+ increasingly converts to unionized NH_3 which may escape from the water as a gas. Major factors affecting ammonia loss by volatilization are pH and ammonia concentration and wind speed at the floodwater surface (De Datta 1981). Aquatic photosynthetic organisms, especially microalgae, have a key role in NH_3 volatilization by causing diurnal changes in floodwater pH, by 1-2.5 units. Large populations of algae are not required to increase floodwater pH to levels that support rapid N losses (Fillery et al. 1986). Losses by NH_3 volatilization range from 2 to 60% of N applied. Most losses occur at the beginning of the crop cycle, when there is almost no canopy and the resulting high light availability permits microalgae to develop while their biomass is not large enough to limit N losses through immobilization.

The introduction of the plankton feeder Nile tilapia (*Oreochromis niloticus*) with rice at the beginning of the culture period may decrease ammonia volatilization by reducing the biomass of microalgae that increase floodwater pH. The bottom feeding action of common carp (*Cyprinus carpio*) could cause turbidity that would limit light available for photosynthetic activity of phytoplankton. Therefore, with fish in the ricefields it is expected that nitrogen loss through ammonia volatilization is reduced.

Ecological processes involved in irrigated rice monoculture differ from that of rice-fish culture. This paper attempts to use ecological models constructed using the ECOPATH II software of Christensen and Pauly (1992) to compare these different systems.

Methodology

Quantitative data were obtained from measurements performed in irrigated ricefields without fish on the International Rice Research Institute (IRRI) research farm in Los Baños, Philippines. Input parameters for the rice-fish model other than the fish biomass and diet were estimated from data collected in irrigated ricefields. Fish biomass and diet data are average values of available data from rice-fish experiments conducted at the Freshwater Aquaculture Center, Central Luzon State University research station in the Philippines. Other data and nitrogen conversions were based on Jφrgensen (1979). The input parameters for the models are given in Table 1. Details of data sources for each component in both models follow. Due to the paucity of data, especially on fish and biological productivity, this model must be considered preliminary.

Fish Component

While reported fish yields from irrigated rice-fish systems in China, Indonesia, the Philippines and Thailand ranged from 100 to 1,800 $kg \cdot ha^{-1} \cdot crop^{-1}$ (dela Cruz et al. 1988), we have selected a very conservative figure of 300 $kg \cdot ha^{-1}$ for our model, of which 180 $kg \cdot ha^{-1}$ is Nile tilapia (*Oreochromis niloticus*) and 120 $kg \cdot ha^{-1}$ is common carp (*Cyprinus carpio*). Nile tilapia, an omnivorous plankton feeder, contributes more to total production as it is a better food converter than common carp, an omnivorous benthic feeder. Fish flesh nitrogen content is equivalent to 13% of dry matter (Cagauan 1990). Based on this, a whole fish is assumed to have 7% N and a dry matter of 20%; therefore, fish N equivalents are 2.5 $kg N \cdot ha^{-1} \cdot crop^{-1}$ for tilapia and 1.7 $kg N \cdot ha^{-1} \cdot crop^{-1}$ for common carp.

Table 1. Input parameters and consumption of static nitrogen models in irrigated ricefields with and without fish. Values in parenthesis are estimated by ECOPATH II.

	Production		Consumption	
	Rice (kg N·ha^{-1}·crop^{-1})	Rice-fish (kg N·ha^{-1}·crop^{-1})	Rice (kg N·ha^{-1}·crop^{-1})	Rice-fish (kg N·ha^{-1}·crop^{-1})
Phytoplankton	25.0	25.0	27.8	27.8
Weeds	8.0	6.4	8.9	7.1
Rice	(104.9)	(114.6)	(116.5)	(127.3)
Aquatic macrophytes	17.0	17.0	18.9	18.9
Snails	4.0	4.0	13.3	13.3
Benthos	8.0	4.0	26.6	13.3
Zooplankton	7.0	7.0	16.3	16.3
Insects	0.9	0.7	3.0	2.4
Microbial biomass	(130.0)	(114.9)	(162.5)	(143.7)
Tilapia	-	(2.6)	-	12.5
Carp	-	(1.8)	-	9.0
BNF	12.0	12.0	0.0	0.0

Rice

Nitrogen exported by rice was estimated on the basis of 1.5% N in grain, 0.8% N in straw and on a harvest index of 1, based on a six-crop experiment at IRRI with five modern varieties of rice. On the basis of the quantity of N fertilizer offered, we used an average 4 t grain yield in the rice model equivalent to 92 kg N exported when straw is not incorporated. An analysis of rice-fish data by Lightfoot et al. (1989) shows rice yield increase ranging from 5 to 30% in rice-fish systems. We assumed a conservative average increase of 10%.

Fertilizer

INORGANIC N FERTILIZER

In wetland ricefields, the efficiency of fertilizer is low. Twenty to 40% N applied is recovered by the crop, depending on the N source, management, and agroecological conditions. In thirty-eight ^{15}N balance experiments with 20-80 kg N·ha^{-1}, N losses ranged from 10 to 65% of N applied (average: 37%), N recovery in the soil ranged from 12 to 76% (average: 35%), and N recovery in the plant ranged from 1 to 54% (average: 28%) (Fillery and Vlek 1986).

ORGANIC MANURE

No information is available on the fate of N applied as chicken manure and pig manure. Part of the N in chicken/pig manure is already in a humified form and is not available for rice. It is unknown how much is eaten by fish, added to detritus as unavailable N, and immobilized in the photosynthetic aquatic biomass (PAB). When applied into the water, probably a significant part of the N is rapidly ammonified and lost by ammonia volatilization. We assumed that 37% of the 74 kg N applied as inorganic fertilizer in both models was lost.

In the rice-fish system the additional N input due to the application of 3 t·ha^{-1} of chicken manure (1.7% N) and 2 t·ha^{-1} pig manure (1.3% N) was estimated to be 49 kg N·ha^{-1} after losses by volatilization (28 kg N·ha^{-1}) were subtracted.

Biological Nitrogen Fixation

With regard to the high level of nitrogen fertilizer applied in both systems, the contribution of biological nitrogen fixation (BNF) was expected not to be high. Using average values summarized by Roger and Ladha (1990) we assumed a contribution of 12 kg ha^{-1}, with photodependent BNF contributing about 5 kg ha^{-1} and heterotrophic BNF contributing 7 kg N·ha^{-1}·crop^{-1}. We assumed the same N contribution by BNF in both models.

Gross Primary Production in Floodwater

In wetland ricefields, phytoplankton and aquatic macrophytes are responsible for primary production in floodwater. Phytoplankton is dominant during the first part of the crop cycle, then macrophytic algae and submerged macrophytes become dominant. Planktonic algae generally have lower productivity than macrophytes (Roger and Watanabe 1984) but a higher N content and probably a faster turnover. Estimates of productivity for the rice model were derived from data summarized by Roger et al. (1989). We assumed a total gross primary production of 600 kg C·ha^{-1}·crop^{-1} split as 300 kg microalgal carbon and 300 kg of aquatic macrophyte carbon in the rice model. This would correspond to 25 kg N for micro- and filamentous algae (C/N of about 12) and 17 kg N from submerged aquatic weeds (C/N of about 18).

We assumed a lower standing phytoplankton biomass in the rice-fish system but a faster turnover because of a better recycling by fish, leading to the same phytoplankton productivity. We assumed that aquatic macrophyte biomass was not significantly affected by the presence of fish.

Weeds

Measurements conducted in 65 plots of the IRRI farm with various managements show a total N content in weeds harvested at two weedings that average about 8 kg N·ha^{-1}·crop^{-1} (Roger et al. 1989).

This average value is used in the rice model. We assumed that fish reduced the standing weed biomass by 20%.

Invertebrates in Rice Canopy

No quantitative data are available for the biomass of arthropods in the rice canopy. A theoretical estimate was calculated assuming that the biomass of a single dominant species during a bloom or an outbreak is an estimate of the upper limit of the biomass of the balanced population of the corresponding group of organisms (e.g., zooplankton, phytoplankton, arthropods) in an ecological niche such as the floodwater or the rice canopy. That is, an estimate of the biomass of brown plant hopper (BPH) during an outbreak is an estimate of the upper limit of arthropod populations in rice canopy when such a population is balanced among consumers and predators. Using this BPH population as a proxy for all invertebrates is probably an underestimate.

The calculation considers populations of 1,000 BPH m^{-2}, 0.4 mg·dw each, 7% N, which is a total of 4 kg·ha^{-1} dw as standing biomass or 0.3 kg N·ha^{-1}. Assuming the standing biomass has a 3 times turnover, this leads to contribution of 0.9 kg N·ha^{-1} for the rice model.

We assumed that fish pressure on arthropods in rice canopy and the surface water reduced the standing biomass of arthropods by 20%.

Zooplankton

Standing biomasses of zooplankton were estimated from data summarized by Roger and Kurihara (1988) in wetland ricefields. These data mostly refer to ostracods and therefore we used the same type of calculation as for the invertebrates in rice canopy.

A maximum biomass of 150 kg·ha^{-1} ww was extrapolated for populations of 50,000 animals m^{-2}. Assuming three turnovers during the crop and an average biomass of half the peak biomass, this leads to an estimate of 2.3 kg N·ha^{-1} (.5 x 150 x 3 x 15% dw x 7% N) in the rice model.

Data on nitrogen excretion by zooplankton were obtained from the values presented by Roger and Kurihara (1988). We assumed that the productivity of zooplankton was primarily limited by that of phytoplankton and therefore was the same in the rice and in the rice-fish model.

Snails

Populations up to 1,000 m^{-2} (1.5 t·ha^{-1} ww) have been observed in Philippine ricefields (Roger and Kurihara 1988). Some large species (*Pila* spp., *Pomacea* spp., and *Ampullaria* spp.) may additionally develop biomass of a few hundred kg·ha^{-1} ww.

Snail biomass estimated by recent counts in the IRRI farm in plots where *Pomacea canaliculata* was dominant ranged from 0 to 1 t·ha^{-1} ww. Based on average biomasses of 400-500 kg·ww·ha^{-1} and assuming 80% water, 25% shell, 5.5% N, and one turnover this leads to a production estimate of 4 kg N·ha^{-1}·$crop^{-1}$.

Benthos: Oligochaetes and Nematodes

Surveys of oligochaete populations in experimental plots in the IRRI farm and 32 farmers' fields of Laguna Province (Philippines) showed that populations ranged from 0 to 630 kg·ha^{-1} ww. Relatively large populations of aquatic oligochaetes are expected to develop when large quantities of organic nutrients are added in the field.

In the rice model, we used a biomass of 300 kg·ha^{-1} ww for oligochaetes and the same value for saprophytic nematodes, which was calculated to the equivalent of 8 kg N·ha^{-1}·$crop^{-1}$ using 6.5% N content at 20% dry matter. Because of the benthic feeding habit of common carp, we estimated that soil meiofauna was reduced by half in the rice-fish model.

Microbial Biomass

Research on nitrogen nutrition of rice has shown that, whatever the quantity of N fertilizer applied, between 75 and 60% of the nitrogen absorbed by the plant usually originates from soil (Fig. 1). But only a small fraction of total soil N is available to the plant, and most of this available nitrogen originates from the turnover of the microbial biomass in soil which represents only a small per cent of total soil N (Watanabe et al. 1988). Crop residues, rhizosphere exudates and the photosynthetic aquatic biomass (algae and aquatic plants) contribute nutrients that allow the replenishment of microbial biomass. Crop residues are incorporated at the beginning of the crop while nutrients accumulating in PAB (including biologically fixed nitrogen) are continuously recycled and reincorporated into the deeper soil by zooplankton and soil fauna, which are therefore key components of the ricefield fertility (Roger et al. 1987).

Preliminary studies, under a restricted number of cultural conditions in the IRRI farm, indicated that microbial biomass might be about 50 kg N·ha^{-1} at the beginning of the crop and then decreases to reach a value of about 30 kg N·ha^{-1} at harvest. The turnover of this biomass has not been determined yet but should be 20-30 days (4 times) to ensure rice nutrition.

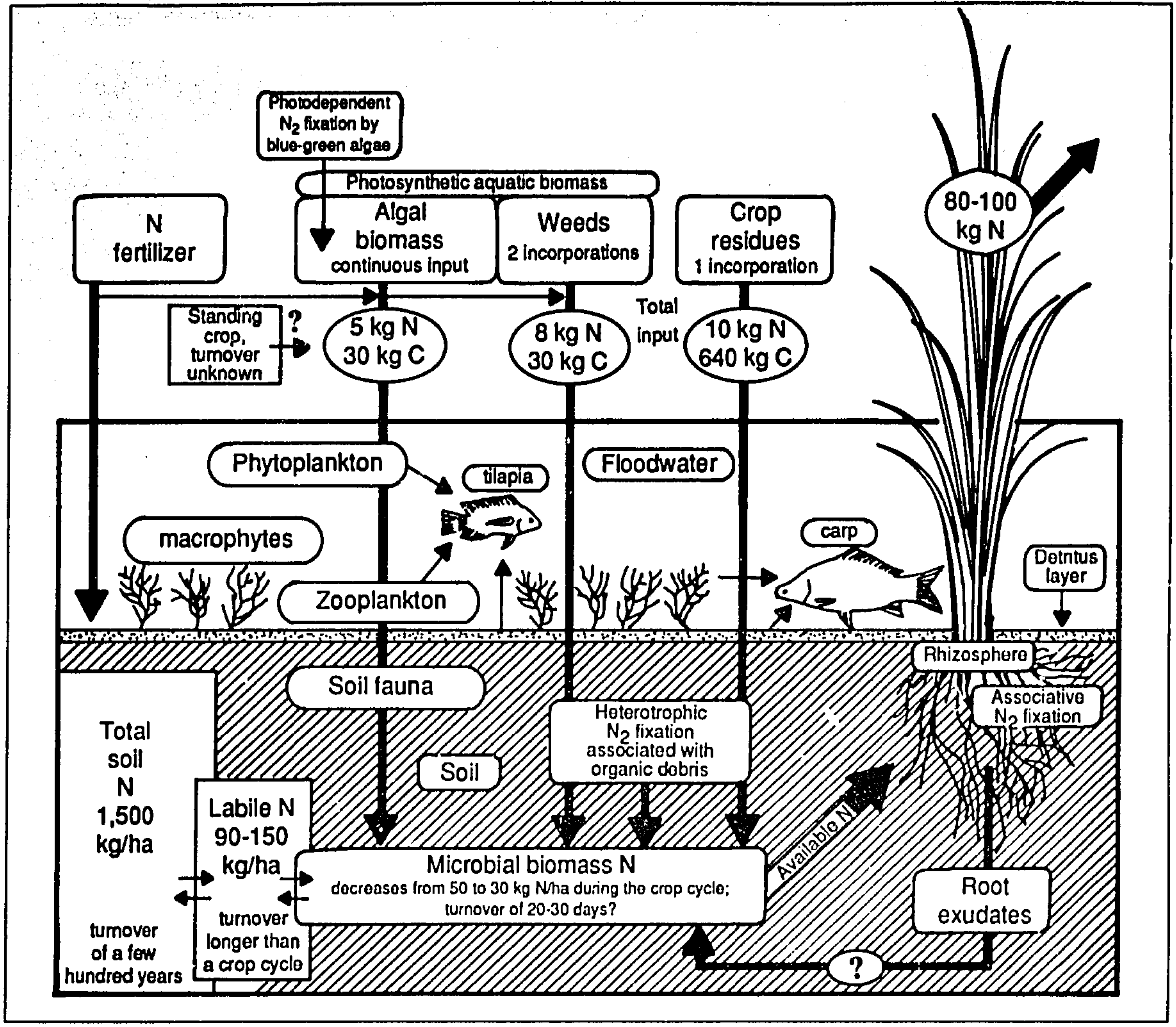

Fig. 1. Schematic representation of the rice-fish ecosystem with a conceptual representation of the origin of the nitrogen absorbed by rice, the role of the microbial biomass in providing available nitrogen to rice, and the pathways involved in the replenishment of the microbial biomass.

Results

Comparison of Box Models

The box models in Fig. 2 compare the two systems. The greater complexity of the system that includes fish is evident, both in terms of number of boxes and complexity of flows. Note that most boxes in the rice-fish model have more consumers or exit paths than they do in the rice model. Less evident is the reduction of weed, insect, and benthic fauna boxes and increase in the rice box by fish, as shown in the P values. Trophic levels of components are not different between systems. Noteworthy is that carp and tilapia both have lower trophic levels than the insects. As the "currency" for these models is a nutrient (N), the primary producers do not appear on trophic level I in the models as they do in energy-based models. Instead BNF is found together with detritus on trophic level I. This is apparent from Table 2, which shows how the relative flows by groups are distributed on discrete trophic levels. The dominance of pests at the highest trophic level (IV) in the rice model indicates a loss of

Table 2. Trophic transformation matrix for nitrogen models of wetland irrigated ricefields without and with cultured fish. The table shows how the relative flows of the groups in the systems are allocated to trophic levels.

	Relative flows by trophic level				
Group	I	II	III	IV	V
Insects	-	-	0.43	0.57	-
Tilapia[a]	-	0.15	0.48	0.32	0.06
Snails	-	0.25	0.63	0.12	-
Rice	-	0.40	0.60	-	-
Aquatic macrophytes	-	0.40	0.60	-	-
Carp[a]		0.67	0.17	0.13	0.03
Benthos	-	0.50	0.45	0.05	-
Weeds	-	0.50	0.50	-	-
Zooplankton	-	0.60	0.31	0.09	-
Phytoplankton	-	0.75	0.25	-	-
Microbial biomass	-	1.00	-	-	-
BNF	1.000	-	-	-	-
Detritus	1.000	-	-	-	-

[a] Included in rice-fish model only.

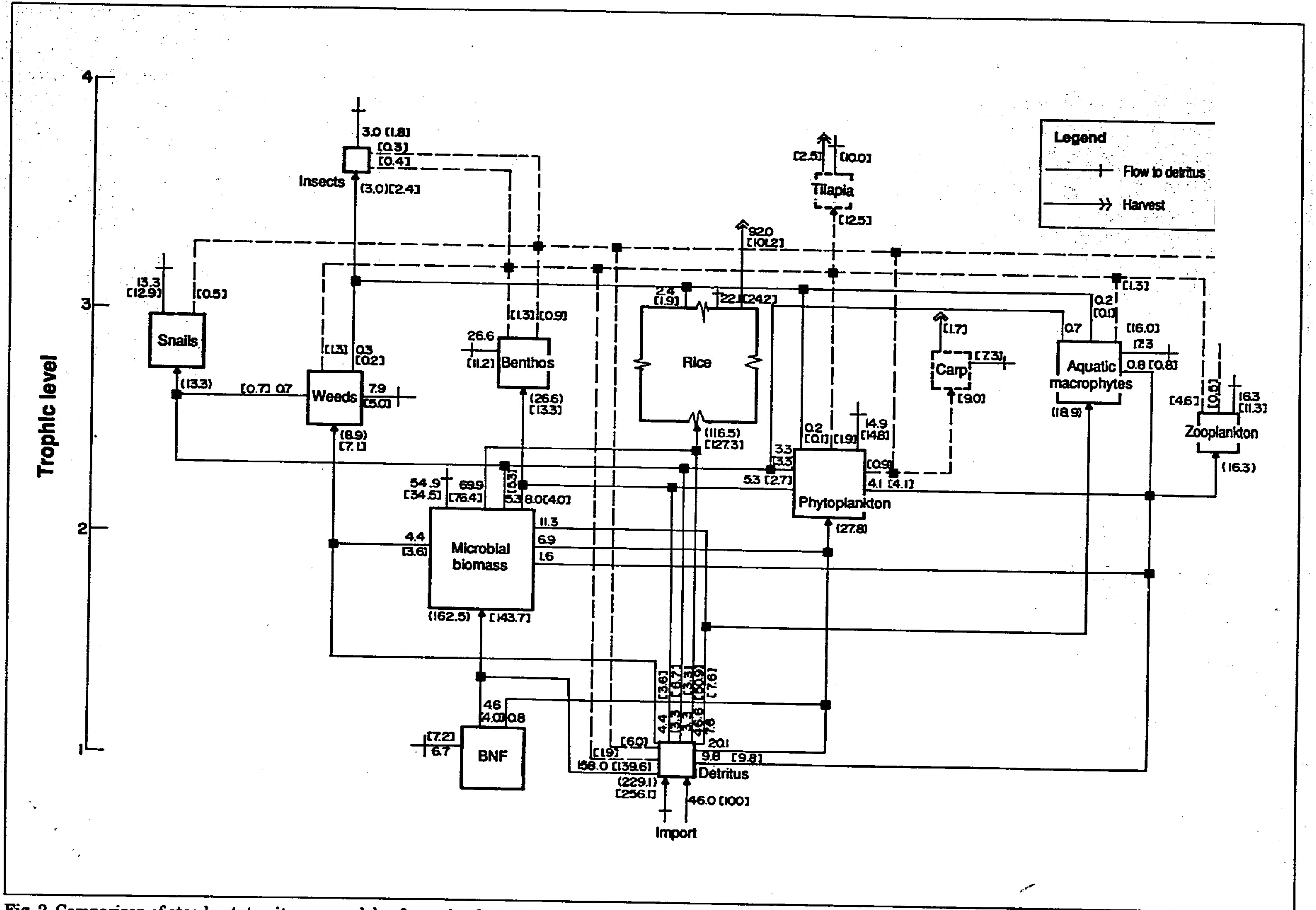

Fig. 2. Comparison of steady-state nitrogen models of a wetland ricefield ecosystem with (rice-fish-model) and without fish (rice-model). Rates with square brackets apply to the rice-fish model only, while other rates apply to the rice model and also to the rice-fish model where no rates in square brackets are given. Dotted lines show flows that are present in the rice-fish model only. All rates are in kg N ha^{-1} crop^{-1}.

high-value N. However, in systems with fish some of this high-value N is captured.

Based on the allocation of nutrient flows to trophic levels shown in Table 2, the trophic transfer efficiencies by discrete levels can be estimated as the percentage of flow entering a trophic level that is ultimately harvested or transferred to the next trophic level (Christensen and Pauly 1992). These transfer efficiencies for the two systems are given in Table 3. It can be seen that the transfer efficiencies in all trophic levels are highest for the system including fish which suggests that fish improve the utilization of nutrients within the systems.

Table 3. Trophic transfer efficiencies by trophic levels for two nitrogen models of rice systems without and with fish.

	Trophic level			
Model	I	II	III	IV
Rice only	-	58%	51%	0.0%
Rice-fish	-	66%	57%	20%

The summary statistics of Table 4 suggest that rice-fish ecosystems hold more nitrogen in the system, put more nitrogen through the system and have a higher capacity than rice alone. This is possibly because rice-fish systems have more consumers and more flow paths. This suggests that fish may impart greater efficiency to rice production systems. However, less nitrogen is cycled in rice-fish systems, possibly because less nitrogen flows to the detritus. This is also shown by the mean path length which gives the number of groups an average nutrient unit passes through from entering the system until exiting.

Table 4. ECOPATH II summary statistics for nitrogen models of wetland irrigated ricefields with and without fish.

	Rice	Rice-fish	Unit
Total production	316.8	310.0	kg N·ha^{-1}·crop^{-1}
Total flow to detritus	229.1	256.0	kg N·ha^{-1}·crop^{-1}
Total throughput	714.9	759.6	kg N·ha^{-1}·crop^{-1}
Throughput cycled	304.7	244.8	kg N·ha^{-1}·crop^{-1}
Cycling index	42.6	32.2	%
Mean path length	7.8	6.8	-

Comparison of Ecotrophic Efficiencies

Ecotrophic efficiencies (i.e., proportion of production harvested or utilized for consumption in the system) among the components of the ecosystem most affected by the introduction of fish are zooplankton, benthic fauna, weeds and insects (Table 5). Efficiency has increased through the consumption of invertebrates (mostly grazers of PAB) by fish. There is a better utilization of weed biomass through tilapia grazing.

The trophic levels for all components (other than fish) are alike in the two models. As noted above, the trophic levels of carp and tilapia (2.53 and 3.28, respectively) are lower than that of insects (3.57).

The nutrient throughputs by groups are shown in Table 5. As expected, the largest throughput among the living groups involves the bacteria, which may even have a considerably higher throughput than conservatively estimated here.

Table 5. ECOPATH II-generated values for efficiencies, trophic levels and nutrient throughput in irrigated ricefields with and without fish.

	Ecotrophic efficiency		Gross	Trophic	Nutrient throughput	
	Rice	Rice-fish	efficiency	level	Rice	Rice-fish
Phytoplankton	0.52	0.52	0.90	2.25	27.8	27.8
Weeds	0.12	0.34	0.90	2.50	8.9	7.1
Rice	0.90	0.90	0.90	2.60	116.5	127.3
Aquatic macrophytes	0.10	0.17	0.90	2.60	18.9	18.9
Snails	0.00	0.11	0.30	2.87	13.3	13.3
Benthos	0.00	0.54	0.30	2.55	26.6	13.3
Zooplankton	0.00	0.73	0.43	2.49	16.3	16.3
Insects	0.00	0.90	0.30	3.57	3.0	2.4
Microbial biomass	0.83	0.95	0.80	2.00	162.5	143.7
Tilapia[a]	-	0.95	0.21	3.28	-	12.5
Carp[a]	-	0.95	0.20	2.53	-	9.0
BNF	0.44	0.40	-	1.00	12.0	12.0
Detritus	-	-	-	1.00	229.1	256.0
Import	-	-	-	-	46.0	100.0

[a] Included in rice-fish system only.

Comparison of Mixed Trophic Impacts

Rice, being the largest biomass component of the ecosystem, has higher impacts than fish on other components. Impact values range from -0.50 to 0.47 for rice, from -0.25 to 0.02 for tilapia and from -0.07 to 0.01 for carp (Fig. 3). Besides an expected negative impact on itself, rice has a marked negative effect on soil microbial biomass (mainly due to competition for nitrogen resources). It may be that rice absorbs most of the available soil nitrogen, thus not allowing the replenishment of the microbial biomass. This is important as it indicates that intensification of rice production might lead to a decrease in soil microbial biomass and thus, possibly of soil-available N and of fertility. Such a hypothesis has indeed to be tested by *in-situ* measurement in long-term experiments. Increasing rice biomass also leads to a reduction of the biomasses of weeds and the components of the floodwater. This can be related with competition for nutrients and an expected decrease in floodwater productivity under a dense rice canopy. Rice has a positive effect on the accumulation of BNF (a larger rice root biomass and exudation is expected to

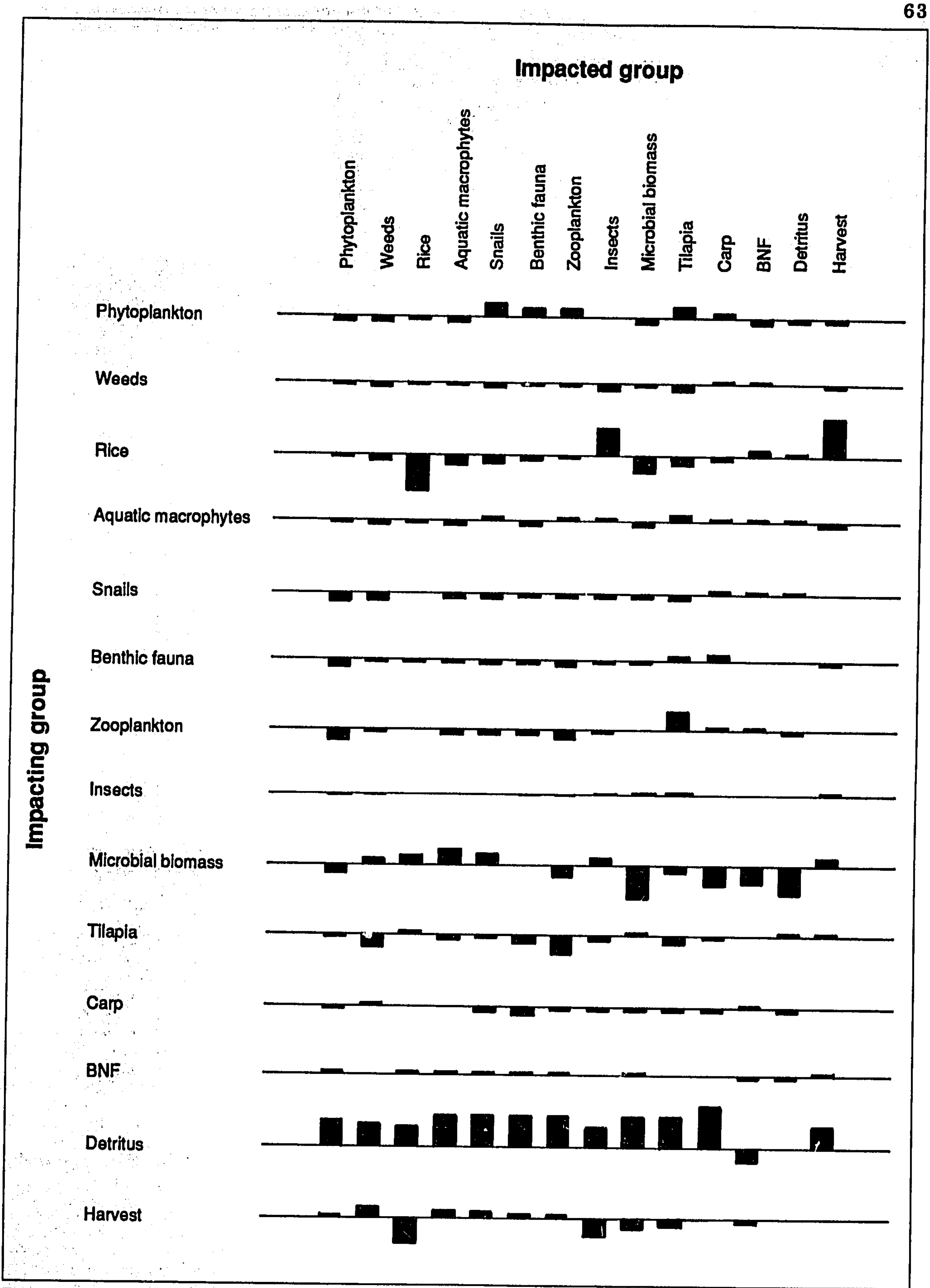

Fig. 3. Matrix of mixed trophic impacts of components in wetland irrigated ricefield ecosystem stocked with tilapia and carp. The histogram shows the relative response of the *impacted* groups resulting from an increase in the biomass of the *impacting* group.

increase heterotrophic BNF in the rhizosphere) and on insects living in the rice canopy.

Tilapia as an omnivorous fish has negative impacts on most of the living components of the ecosystem except rice and microbial biomass. The slight beneficial effect of tilapia on rice might be related to an increased production of detritus contributing to the replenishment of soil microbial biomass and a negative effect on insect pests and weeds. Carp has a very moderate effect on the other components of the ecosystem. The main negative effect is on benthic fauna which reflects the feeding habit of this fish. Carp has a negative impact on snails, benthos and zooplankton and hardly any effect on other groups.

The harvest is affected positively by the rice, detritus, and microbial biomass groups. Obviously, insects have a negative impact on the harvest, indicating potential for increasing the harvest through pest control.

Conclusion

ECOPATH II results raise the intriguing possibility that stocking ricefields with fish not only produces fish, but also leads to greater efficiency in rice production. Ricefields with fish hold more nitrogen, move more nitrogen through the ecosystem and are more efficient. Even more interesting is the suggestion that intensifying monocropped rice might lead to a decrease in microbial biomass and therefore soil fertility in the long term. Microbial biomass is the most important actor in the ecosystem in terms of N cycling.

We cannot conclude from these preliminary models that optimum management of ricefields as an ecosystem and as a production system may require the integration of fish. Our information has too many gaps and our rice-fish model is too hypothetical. Nevertheless, none of the results disagree with current knowledge of N cycling in ricefields. We conclude that the questions raised warrant more studies using ECOPATH II.

ECOPATH II deserves further trial not only because its results raise important questions about ricefield management, but also because they suggest critical long-term experiments and important parameters to study for better understanding of how these ecosystems work. Moreover, ECOPATH II allows environmental impact of rice-fish experiments using different field layouts, fish species, rice varieties, etc., to be compared. We believe that ecological models such as ECOPATH II could provide insights on sustainability in agricultural systems.

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Trophic Interactions in a Napier Grass (*Pennisetum purpureum*)-fed Aquaculture Pond in Malaŵi*

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Abstract

The trophic relationships in a small fishpond stocked with a polyculture of *Tilapia rendalli* and *Oreochromis shiranus shiranus* and fed with napier grass (*Pennisetum purpureum*) are analyzed using the ECOPATH II program for construction of ecosystem box models. The preliminary model contains boxes for fish of the two species, phytoplankton, zooplankton, planktonic microbes, benthic microbes, macrobenthos, meiobenthos, frogs and detritus, and is based on research ponds at the Domasi Experimental Fish Farm, Malaŵi, and from the literature.

Construction of this model demonstrated gaps in our knowledge on food web structure and on the productivity of the groups of organisms in grass-fed ponds. Nevertheless, the model was useful as it suggested research directions for improvement of pond productivity.

Introduction

Napier grass (*Pennisetum purpureum*) may be a substitute as a pond input for the widely used maize bran in Malaŵian fishponds. Because maize bran is not always available to fish farmers in Malaŵi, napier grass, which is available throughout the year and has little or no opportunity costs, is being tested for use as an alternative pond input. Experiments show that napier grass can result in yields equal to those obtained using maize bran (Chikafumbwa 1990).

In this study, a steady-state modelling method using the ECOPATH II model was used to study trophic interactions in a grass-fed pond. The principles of this kind of modelling are explained elsewhere (Polovina and Ow 1985; Christensen and Pauly 1992, this vol.). Not all the information necessary for constructing the model was available from the published literature, and some parameters had to be guessed.

Description of the Model

The model describes a 200 m^2 pond with napier grass as the only external input besides sunlight. It is assumed that 200 fingerlings each of *Tilapia rendalli* and *Oreochromis shiranus shiranus* are stocked at an average individual size of 10 g. Napier grass is put into the pond at 2 kg dry matter per day. Based on previous experiments (Chikafumbwa 1990), the fish are expected to have a specific growth rate of 0.50 and 0.35% day^{-1} for *T. rendalli* and *O. shiranus*, respectively. The farming household catches fish for home consumption and cash sale regularly, with a yearly total of 15.7 kg (783 $kg \cdot ha^{-1} \cdot year^{-1}$).

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Ten boxes are distinguished in the model. A short description of their characteristics follows:

Tilapia rendalli is usually considered a herbivore but has been found to feed on a variety of other foods as well (Pullin 1983). In the ponds it feeds almost exclusively on the napier grass (this was corroborated by delta carbon analysis of experimental pond samples [F.J.K.T. Chikafumbwa, unpubl. data]). When feeding on *Ceratophyllum demersum*, *T. rendalli* was found to have an assimilation efficiency of about 59% (Caulton 1982). Napier grass contains about 30-40% crude fiber (Gomide et al. 1969; Crowder and Cheda 1982; Kaunda 1988) and hence assimilation by *T. rendalli* was relatively inefficient. Egestion was assumed to be 40% of the food consumed.

The specific growth rate is assumed to be 0.5%·day^{-1}, resulting in 9,924 g of *T. rendalli* at the end of the year. Production from growth is thus 39.62 g·m^{-2}·year^{-1}. Apart from growing, the stocked fish reproduce as well, resulting in 3,500 g of fingerlings or 17.5 g·m^{-2}. Average biomass is therefore 7,712 g or 38.58 g·m^{-2} and total production is 57.12 g·m^{-2}·year^{-1}.

Oreochromis shiranus has a diverse diet with vegetative materials predominating (Philippart and Ruwet 1982). It can eat macrophytes, but in competition with a macrophagous fish it is more likely to eat other food. In the experimental ponds, it was found to feed on a variety of food sources but not so much on added grass (as shown by delta carbon analysis [F.J.K.T. Chikafumbwa, unpubl. data]). Based on a 0.35%·day^{-1} specific growth rate and 3,500 g of fingerling biomass, average biomass is calculated as 28.10 g·m^{-2} and production as 36.20 g·m^{-2}·year^{-1}. The assimilation rate for *O. shiranus* was assumed to be the same as for *T. rendalli*.

Phytoplankton. Chlorophyll concentration in the ponds ranged from 48 to 112 μg·l^{-1}. Using the average 80 μg·l^{-1}, this resulted in 28.44 g·m^{-2} (1 gChla = 39.1 g C, 50% C in dry matter and 22% dry matter, [Lind 1974]). Daily phytoplankton productivity was measured to be 1.1 mg O_2·l^{-1}·day^{-1}. This resulted in an average estimated production of 1,325 g·m^{-2}·year^{-1} and a P/B ratio of 46.59 year^{-1}.

Zooplankton. No data on zooplankton in the ponds were available so a P/B ratio of 40 year^{-1} and Q/B = 280 year^{-1} were assumed as generic estimates; see other publications in this volume.

Planktonic and benthic microbial biomass and productivity were not measured in the experiments. Moriarty (1986), in shrimp ponds in Malaysia, found bacterial productivities of 0.43-2.10 and 0.24-0.50 gC·m^{-2}·day^{-1} in the water column and sediment, respectively. Assuming carbon to be 15% of cell mass and taking the mid-range, this results in productivities of 3,077 and 902 g·m^{-2}·year^{-1}, respectively. Schroeder (1987) estimated the weight of microorganisms at a maximum of 5% of detrital organic weight which results here in a total microbial biomass of 4.5 g·m^{-2} (detritus biomass was 90 g·m^{-2}). Which part of this is benthic and which planktonic is not known; it was assumed here that planktonic microbial biomass was 20% and benthic biomass 80% of total microbial biomass. Resulting P/B ratios are very high, so we decided to use P/B ratios of 90 year^{-1} and 150 year^{-1} for benthic and planktonic microbes, respectively. Moriarty (1986) estimated conversion efficiencies for planktonic and benthic bacteria to be 50 and 30%, respectively, but these bacteria were utilizing high-protein pellets with digestible carbohydrates. Lower values must be assumed here. Therefore, egestion was guessed to be 40% of consumption for both groups. Q/B was guessed to be 500 year^{-1} for both groups.

Macrobenthos. These consist mainly of a variety of insect larvae. Biomass at the end of the culture period was 11.3 g·m^{-2}, which was used as the average biomass here. P/B ratio was guessed to be 1.2 year^{-1}.

Meiobenthos. These were mainly nematodes, which feed on bacteria (Warwick 1987). Data on production of nematodes were not found. Biomass at the end of the culture period was 3.2 g·m^{-2}, which was entered as the average biomass here. P/B ratio was guessed to be 9 year^{-1}.

Frogs (*Xenopus* sp.) were quite abundant in the grass-fed ponds. At harvest, their biomass can be as high as 2 kg per pond. An average of 5 g·m^{-2} was assumed here. Tadpoles consume primarily phytoplankton while the adults are carnivores; their P/B ratio was estimated at 2 year^{-1}.

Detritus consisted mainly of unconsumed napier grass parts, especially the fibrous stems. Based on havests at the end of experiments, grass detritus "biomass" was estimated at 90 g·m^{-2}. Napier grass was added to the pond at a rate of 2 kg dry matter per day. With 20% dry matter content (Chikafumbwa 1990), this equals to 50 g·m^{-2}·day^{-1}. Total grass input was 18,250 g·m^{-2}·year^{-1}.

The available information is summarized in Table 1 (biomass, production, food consumption, excretion and egestion) and Table 2 (diet composition).

All information was entered into the ECOPATH II program. Ecotrophic efficiencies were estimated by the program for all groups, except for the zooplankton, where biomass was estimated.

Results and Discussion

Some of the results are presented in Tables 1 and 3, while Fig. 1 summarizes the flows in the system. Total system throughput (sum of all flows) is around 44 kg·m^{-2}·year^{-1}, the bulk of which is not properly utilized for production in the system, i.e. productivity is low, 2.1 kg·m^{-2}·year^{-1}, with fish harvest of only 78 g·m^{-2}·year^{-1}. For comparison the highly productive integrated Chinese mulberry dike/carp pond system

Table 1. Biomass and production data for all groups in the pond model. Values in brackets indicate figures that are estimated by ECOPATH.

Group	Import (g·m⁻²·year⁻¹)	Harvest (g·m⁻²·year⁻¹)	Biomass (g·m⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE
1. *T. rendalli*	-	49.62	38.65	1.48	10.3	(0.87)
2. *O. shiranus*	-	28.70	28.10	1.29	5.4	(0.79)
3. Frogs	-	-	5.00	2.00	20.0	(0.50)
4. Zooplankton	-	-	(4.58)	40.00	200.0	0.95
5. Planktonic microbes	-	-	0.90	150.00	500.0	(0.39)
6. Benthic microbes	-	-	3.60	90.00	500.0	(0.59)
7. Meiobenthos	-	-	3.20	9.00	33.3	(0.97)
8. Macrobenthos	-	-	11.30	1.20	10.0	(0.37)
9. Phytoplankton	-	-	28.44	46.59	0.0	(0.51)
10. Detritus	18,250	-	90.00	-	-	-

Table 2. Diet composition of various biota in a napier grass-fed pond. Group 1 is *T. rendalli*; group 2 is *O. shiranus*.

	Predator							
Prey	1	2	3	4	5	6	7	8
3. Frogs			0.05					
4. Zooplankton	0.12	0.31	0.35	0.05				
5. Planktonic microbes		0.05		0.05				
6. Benthic microbes							0.95	0.80
7. Meiobenthos							0.05	0.20
8. Macrobenthos			0.05					
9. Phytoplankton	0.12	0.45	0.25	0.60				
10. Detritus	0.77	0.19	0.30	0.30	1.00	1.00		

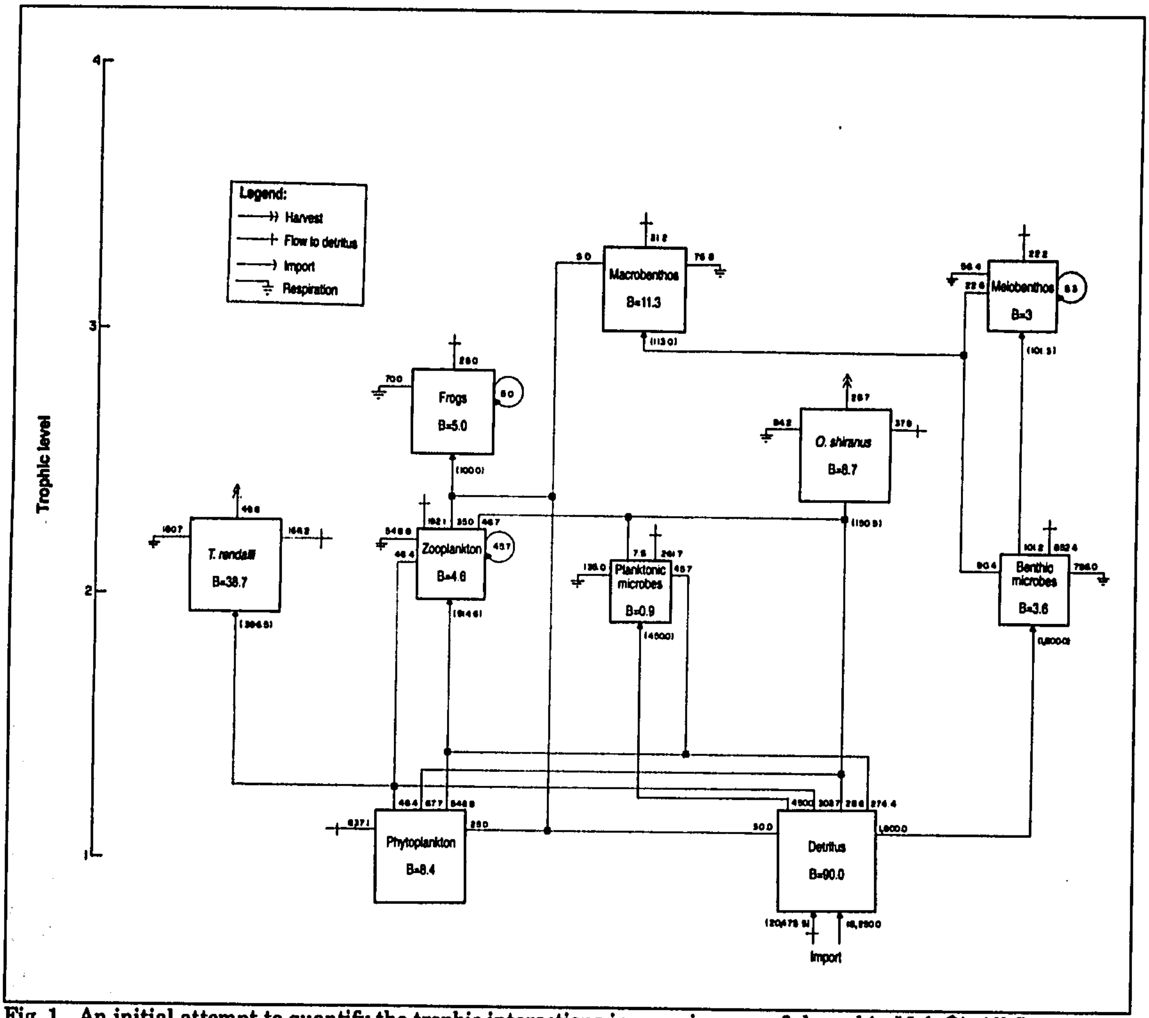

Fig. 1. An initial attempt to quantify the trophic interactions in a napier grass-fed pond in Malaŵi. All flows are in g·m⁻²·year⁻¹.

Table 3. Summary of results for a model of a napier grass-fed pond (flow in g·m^{-2}·year^{-1}).

Sum of all consumption	4,031.2
Sum of all exports	17,667.1
Sum of all respiratory flows	1,907.9
Sum of all flows into detritus	20,475.5
Total system throughput	44,081.6
Sum of all production	2,112.8
The harvest has a "mean trophic level" of	2.23

described by Ruddle and Christensen (this vol.), shows a total production of 50.7 kg·m^{-2}·year^{-1} of which the fish harvests account for 714 g·m^{-2}·year^{-1}, an order of magnitude more than in the napier grass-fed Malaŵian ponds.

The harvested groups have an average trophic level of 2.23, i.e., only slightly higher than that of a herbivore or detritivore. This suggests that the low production in the system is not caused by the fish being too high in the food chain.

The overall production/respiration ratio for the system is rather low, 0.69, indicative of a nonoptimal system (Odum 1971).

Napier grass-fed ponds, as modelled here, are rather inefficient systems. The largest part of the napier grass added to the system is removed again as sediments in the form of grass detritus. However, the transfer efficiencies at the higher trophic levels seem reasonable. The trophic transfer efficiency was 12.0% for trophic level III (first-order carnivore level), while for the second-order carnivore level (IV) an efficiency of 5.3% was estimated. This apparently low efficiency for the top level is, however, an artifact caused by the system description. The top level mainly includes frogs and macrobenthos, which are only partly (about 50%) used within the system; the remaining production of these groups is probably exported as adult frogs and emerging insects which is not quantified in the present model.

The uptake of phytoplankton and zooplankton by both fish species are of the order of 100 g·m^{-2}·year^{-1}, with *T. rendalli* additionally taking some 300 g·m^{-2}·year^{-1} detritus. The two species compete for resources, while other resources such as frogs and macrobenthos are not properly utilized.

Addition of a carnivorous/omnivorous fish species could remove this problem and lead to increased fish production. Possible candidates that are native to Malaŵi include *Clarias gariepinus* and *Bathyclarias* sp.

Much more basic knowledge about the food web in fishponds is needed to construct a more reliable model. At this stage, modelling mainly serves to make us aware of the shortcomings in our knowledge and to direct research efforts. Apart from that, the question remains whether the steady-state modelling approach used here is suitable for a system that is continuously evolving.

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Trophic Dynamics in a Gravel Pit Lake Ecosystem

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Abstract

Work by The Game Conservancy at the ARC Wetlands Research Centre at Great Linford, England, UK, has suggested that fish (especially bream, *Abramis brama*, and perch, *Perca fluviatilis*) can limit the supply of insects, especially the nonbiting midges (Chironomidae) as food for wildfowl. This competition reduces the breeding success of both dabbling and diving ducks.

Removal of the existing stocks of fish in the Main Lake at WRC resulted in an increase in the biomass of dipteran (principally chironomid) larvae in the following summer and a perceived improvement in the breeding success of a diving duck species (tufted duck, *Aythya fuligula*). The larvae of the alder fly, *Sialis lutaria*, are predators of chironomid larvae and are thus potential competitors whose effects must be considered in parallel with those of fish. Their predation was being quantified and modelled.

Changes in phytoplankton and zooplankton production are included in the model because of the potential for zooplankton to be utilized as an alternative food source by fish such as bream, so effectively reducing the predation pressure experienced by the chironomid population. The model cannot be used as a predictive tool until it is properly validated. A model is being developed to understand what effects partial removal of fish stocks would have on the availability of chironomid larvae, and hence on the breeding success of wildfowl. Predictive simulations, while desirable, will be available once the model is validated with more data.

Introduction

The decision to model the trophic dynamics of the gravel pit lake called Main Lake, Great Linford, UK, was taken to explain in detail the observed effects that fish removal has upon the production of chironomid larvae and subsequently upon the survival prospects of wildfowl in the system. A strong response was recorded when the entire fish population was removed from the lake, with chironomid standing crops improving after removal of its fish from the system (Giles et al. 1989). However, experiments had not been carried out to examine the likely graded response of partial fish removal.

A simplified foodweb was drawn up (Fig. 1) as a basis for a model. Chironomid productivity is effectively reduced by bream predation on the larval phase, perch predation on the ascending (pharate) pupal stage and invertebrate (alder fly, *Sialis lutaria*) predation on the larval stage. The potential predation pressure exerted by bream is modified by the availability of zooplankton as an alternative food source, and so it will be necessary to include subroutines to predict zooplankton stocks (via phytoplankton stocks) from water chemistry and environmental data.

The final goal, once attained, is to have a predictive tool to enable management decisions to be taken regarding the likely outcomes of fish stock manipulation, especially in terms of the likely impacts on duckling survival. It is hoped that by using a complete predictive model effective management policies can be developed which are tailored to the main end-use objectives of flooded gravel pit sites.

Methods

To assess the impact that fish have upon the benthic fauna of the lake, staff at Great Linford

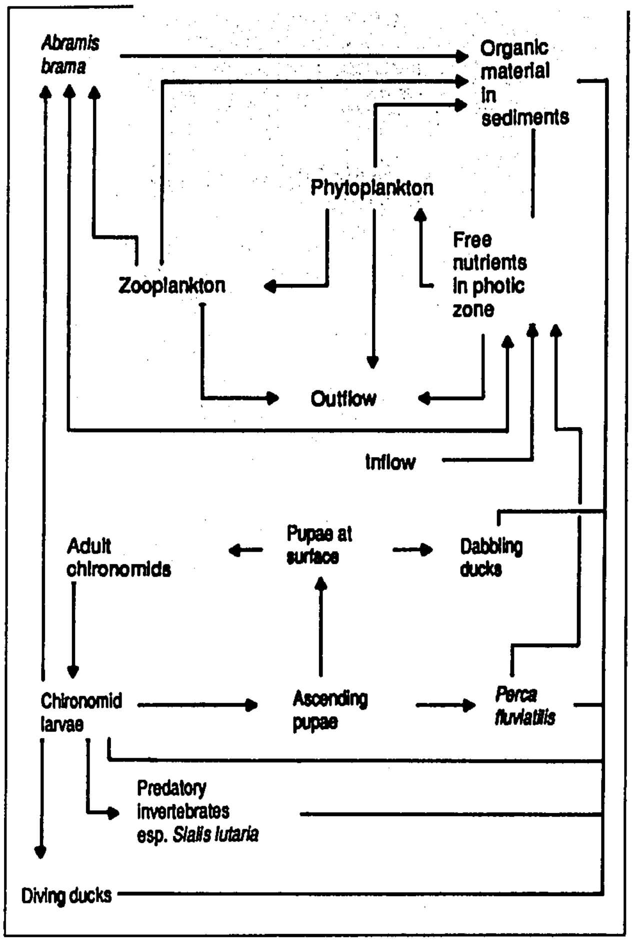

Fig. 1. A simplified foodweb of a gravel pit lake (Main Lake, Great Linford, UK).

carried out fortnightly benthic invertebrate sampling. Ten cylinder samples (0.05 m^2) were taken and, after rinsing through a 300 µm mesh sieve, were sorted by hand in the laboratory. The environment of the Main Lake was altered over the five-year period by the removal, and subsequent reintroduction, of fish. This provided good field evidence of the effects of fish predation on chironomid standing crops (see Fig. 2).

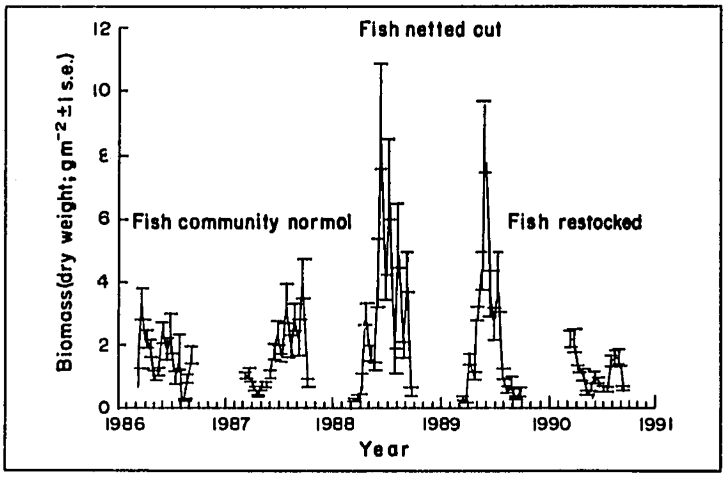

Fig. 2. Dipteran larval biomass in Main Lake (sampling bay only).

Subsequently, a series of experimental ponds were set up in an attempt to highlight the effects that the main benthivorous fish species present in the Main Lake system, bream (*Abramis brama*), has upon the standing crop of dipteran larvae. Each of nine uniform ponds, measuring approximately 12 m x 32 m, was divided into two halves by a mesh curtain, and bream were introduced into one-half of each pond. The density of bream in the "fish half" was varied, from low (80 kg ha^{-1}), through medium (the density previously present in the natural lake system, 160 kg ha^{-1}) up to high (320 kg ha^{-1}), with three replicates of each stock density. Two months after the introduction of fish the chironomid larvae were sampled by taking ten random cores (1.13 x 10^{-3} m^2) in each half pond. Samples were rinsed through a 300 µm mesh sieve and chironomid larvae sorted by hand and weighed.

As potential invertebrate competitors of dabbling and diving ducks, the larvae of the alder fly (*Sialis lutaria*) form another sink for chironomid production. Work by England (1989) suggests that the predation rate of alder fly larvae upon chironomid larvae is a function of both alder fly and chironomid larval population densities. This process, lends itself very well to inclusion into a dynamic model, but obviously requires an estimation of alder fly populations to be made in parallel with chironomid populations.

Experimental work on tufted ducklings (Giles 1990) examined their ability to capitalize on improved food availability. In this work foraging success under laboratory conditions was estimated over ranges of prey (chironomid larvae) densities found naturally (see Giles 1990 for details). This experimental work was intended in part to predict how natural populations of tufted duck might respond to changes in chironomid abundance in the wild.

The increased dipteran larval biomass resulting from the removal of fish from the Main Lake provided the opportunity to compare the results from the laboratory experiments with the response of field populations of tufted duck. Regular brood observations by staff at Great Linford were used to compare tufted duck brood survival when fish were absent to earlier observations made when fish were present.

The foodweb comprising chironomids, bream, perch, mallard, tufted duck and alder fly larvae is complicated by the tendency of bream to switch from feeding almost exclusively on chironomid larvae to feeding on zooplankton during "blooms" (Fig. 3 and see Lammens et al. 1987). This requires a separate, water quality-based system to

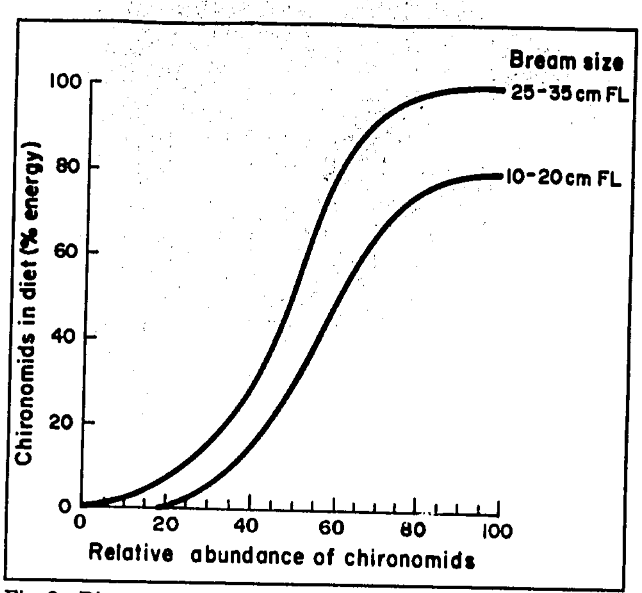

Fig. 3. Dietary switching of breams between chironomids and zooplankton as a function of relative abundance of chironomid (expressed as % of energy in chironomids and energy in zooplankton); after Lammens et al. (1987). Chironomids in diet is expressed as % of overall dietary energy intake. Chironomid availability is expressed as %, where chironomic energy content + zooplankton energy content = 100%.

be built into the model in order to be able to predict phytoplankton and, in turn, zooplankton abundance. "AQUASIM," a computer simulation developed by lecturers at the University of Wales College of Cardiff (Bowker and Randerson 1989) to predict phytoplankton and zooplankton densities from basic environmental data and nutrient (phosphate) availability was used for this purpose (see Fig. 4 and text below).

Results and Discussion

The long-term study on the benthos of the Main Lake gave results for dipteran (principally chironomid) larvae as shown in Figs. 2 and 5. It would appear that the presence of fish has a dramatic depressing effect on the production of chironomids by reducing their standing crop through the summer to approximately half that of normal (i.e., that seen without fish predation).

This is supported by the results from the experimental ponds (Fig. 6). In all but one pond the biomass of larvae on the side with fish was less than that on the side without. It should be noted that no clear trends were apparent as regards the effects of different densities of bream, perhaps indicating that there is an upper threshold (less than or equal to the lower fish stock density used) above which an increase in the fish stock density has no further effect on the standing crop of chironomid larvae.

Analysis of England's (1989) work leads to the following empirical equation relating the predation pressure exerted by alder fly larvae on chironomid larvae to the larval densities of the alder fly and chironomid populations present:

$$P = 1.06 - (3.85 \times 10^{-3} \times S) + (1.53 \times 10^{-3} \times C)$$

where P = number of chironomids consumed per alder fly larva per 24 hours; S = alder fly density (number of larvae per m^2); and C = chironomid density (number of larvae per m^2).

Relationships between the average size (wet weight) of prey (chironomid) handled in terms of the size (again, wet weight) of the predator (alder fly) can be derived by combining England's (1989) work with weight and size values for chironomid larvae from the detailed paper by Potter and Learner (1974); this leads to the following equation:

$$\mathrm{Log}\,(Sw) = 10^{0.18} * Cw^{0.16}$$

where Sw = wet weight (g) of *Sialis lutaria* (alder fly) larva; and Cw = mean wet weight (mg) of potential chironomid prey.

The results from laboratory experiments on the feeding abilities of young tufted ducklings (Giles 1990) demonstrated that under such conditions, foraging success increases linearly with increasing

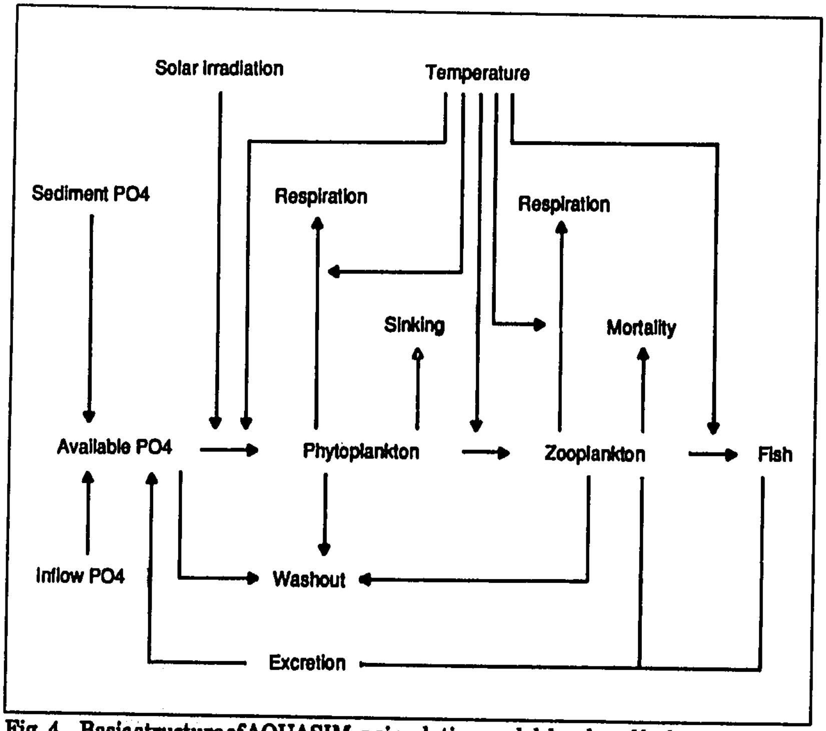

Fig. 4. Basic structure of AQUASIM, a simulation model developed by lecturers at the University of Wales College of Cardiff (Bowker and Randerson 1989).

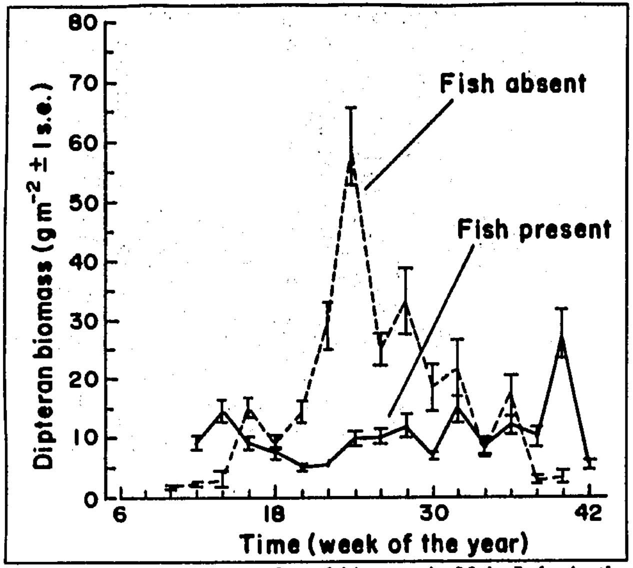

Fig. 5. Trends in dipteran larval biomass in Main Lake in the absence and the presence of fish.

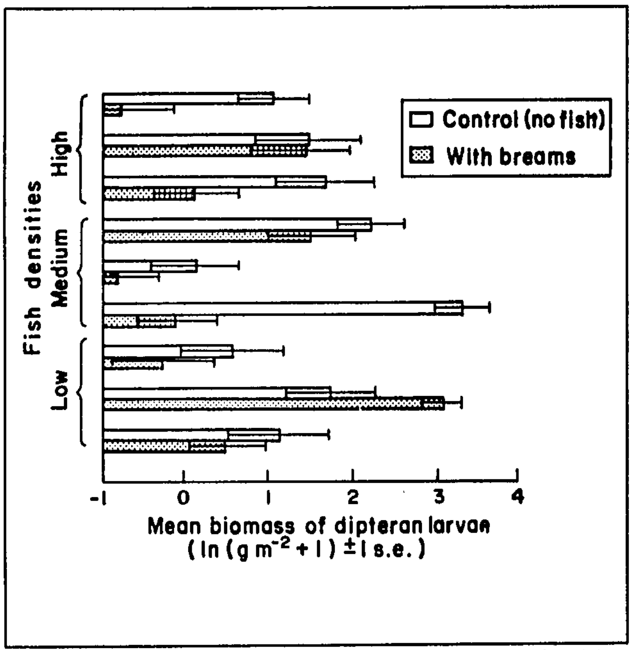

Fig. 6. Larval dipteran biomass with different bream densities; mean of ten samples for August 1989.

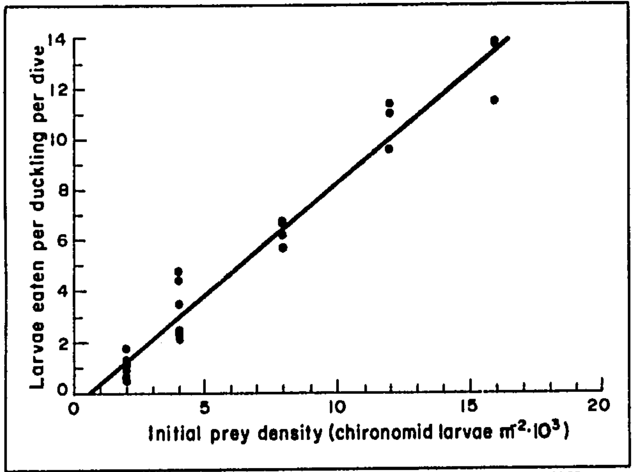

Fig. 7. Feeding success of downy tufted ducklings at different prey densities.

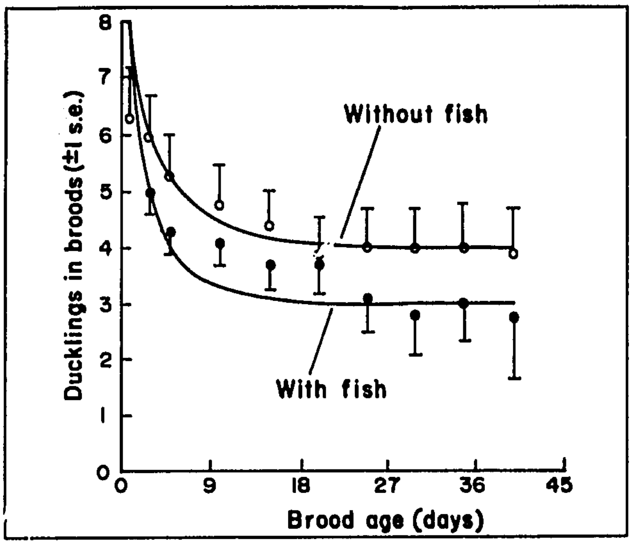

Fig. 8. Tufted duck brood size at Great Linford, as a function of time and competition by fish.

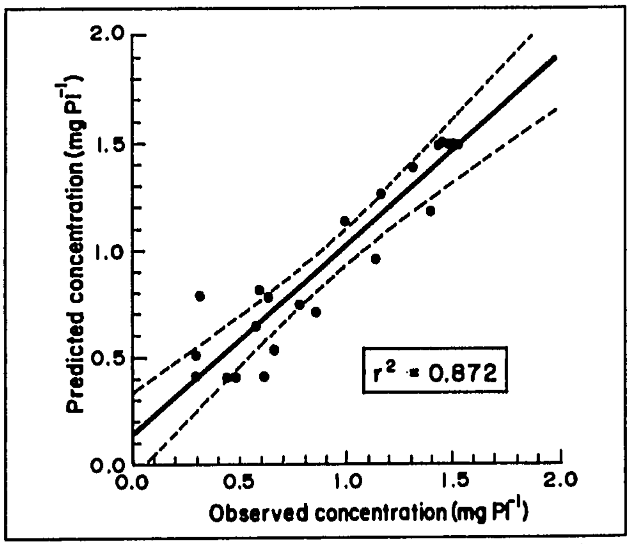

Fig. 9. Showing the close fit between observed phosphate concentrations in lake inflow water and predicted values used as the input to the AQUASIM model (dotted line: 95% confidence belt of regression line).

food availability (Fig. 7). This suggests that an increase in the natural abundance of chironomid larvae in the Main Lake would benefit the wild populations of tufted duck. It would be most likely that such benefits would be manifested as an improved survival of fledging birds, as measured by brood survival.

Field observations indicated an improvement in tufted duckling fledging success (Fig. 8) concomitant with the observed increase in dipteran larval biomass (Fig. 5). The average size of a brood surviving through to fledging rose from approximately three young per successful pair of breeding adults to four. Such an increase demonstrates quite well that manipulation of the environment through "stock control" can result in marked changes in elements related via the foodweb. In addition to the improved fledging success subsequent to the fish removal from the Main Lake, tufted duck began to use the area to rear their broods. Formerly they had taken their broods onto the adjacent River Great Ouse where feeding conditions for young ducklings appeared to be more favorable (Traill-Stevenson and Giles 1990).

It is possible to use a simulation, such as "AQUASIM," to develop a subroutine for the Gravel Pit Lake Model to furnish estimates of the likely levels of phytoplankton and zooplankton densities from environmental data and basic nutrient loading data. The latter (based principally on the phosphate levels in the lake inflow water) can be predicted quite accurately (Fig. 9) and so it should be feasible to complete likely levels of zooplankton throughout a yearly cycle. In turn, calculations could be made regarding the likely prey preference of bream by reference to the relative (calorific) availability of chironomid larvae and zooplankters (again see Fig. 3).

The above points can be taken together as a convincing argument for the need for synergism, i.e., a need to view the gravel pit lake ecosystem not as a series of independent relationships but rather as a whole interdependent system.

A model of a simplified foodweb (Fig. 1) can be constructed, whilst other environmental driving functions, such as water temperature or phosphate concentration of the lake inflow water (which tend by their nature to be seasonal) can be modelled with time-based functions. In this way the changes in biomass of the components of the system (as wet weight per square meter) can be calculated on a day to day basis.

Ultimately it is hoped to be able to use the model to describe the likely benefits of different management policies (principally the control of fish stocks) to wildfowl in terms of increased survival potential through increased food availability. At this stage it is envisaged that the "ECOPATH II" system (Christensen and Pauly 1992) will be used to show the "steady state" of the gravel pit lake ecosystem at different times of the year (such as spring, summer, autumn and winter) with different fish stock levels. This should provide easily comparable schematic representations of the trophic state of the lake with various management regimes.

Acknowledgements

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Fishpen Culture and Its Impact on the Ecosystem of Laguna de Bay, Philippines

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Abstract

This paper presents quantitative trophic models of the Laguna de Bay ecosystem, Philippines, for two different time periods. The first (late 1960s) describes the system without fishpen culture in the system while the second (early 1980s) emphasizes the role of the introduced planktivorous species, especially milkfish (*Chanos chanos*). Highlights of the results are: (1) total finfish biomass increased due to the cultivation of milkfish; (2) ecotrophic efficiency of phytoplankton increased with the development of pen and cage enclosures; (3) phytoplankton flow to detritus was much higher in the prefishpen period than in the fishpen period and the sum of all flows to detritus decreased about 4 times for the whole system; and (4) the calculated total net primary production decreased by a factor of two in the fishpen period.

Introduction

Laguna de Bay is the largest lake in the Philippines and lies southeast of Metropolitan Manila in the island of Luzon (Fig. 1). It has a surface area of 911 km^2 and a watershed area of 2,920 km^2. The lake is shallow with an average depth of 2.8 m. It is separated into four main bays: (1) West Bay, industrial urban nearest to Metro Manila; (2) South Bay, mostly flat terrain with irrigated rice; (3) East Bay, rising steeply towards a plateau; and (4) Central Bay, close to denuded hills with some flat areas where rice is grown.

Early descriptions of the lake mentioned the presence of crocodiles and of *Pristis microdon*, the sawfish - one of the many marine fish of the Philippines recorded from freshwater habitats (Herre 1958; Pauly 1982). However, they became extinct before the turn of the century. Also, the clupeid, *Anodontostoma chacunda* and penaeid shrimps occurred in the lake in large numbers some 50 years ago (IESAM 1991) but pollution has been responsible for a depletion of wildlife resources and decline of fish species.

In the 1960s, there were 23 known species of fish in Laguna de Bay of which two-thirds were omnivorous and the rest carnivorous (Parsons 1961; Delmendo and Bustillo 1968). Vallejo (1985) reported 25 species, 5 of which were new Laguna de Bay records. Table 1 lists the species of fish found in Laguna de Bay and their key properties.

The native fishes utilize a relatively small part (about 7%) of the primary production of the lake (Delmendo 1968; LLDA/BCEOM 1984). In the prefishpen period, fisheries production was high in terms of bulk catch but consisted of small fish of low market value (Rabanal et al. 1964). Most of the catch was used for animal feeds, mainly for the duck-raising industry, and only 15% was used for human consumption (Mercene 1983).

By altering the environment, biological food chains can be modified to provide more food for humans. This has been the case for the Laguna de Bay ecosystem, where the economic resource use has been changed during the past three decades. The introduction of milkfish (*Chanos chanos*) culture in pen enclosures in the 1970s and its development in the 1980s coupled with the development of tilapia (*Oreochromis* spp.) culture in cages have changed the situation in the lake.

In an effort to make better use of the primary production of the lake, the Laguna Lake Development Authority (LLDA), following a recommendation of a United Nations Fishery Study documented in LLDA

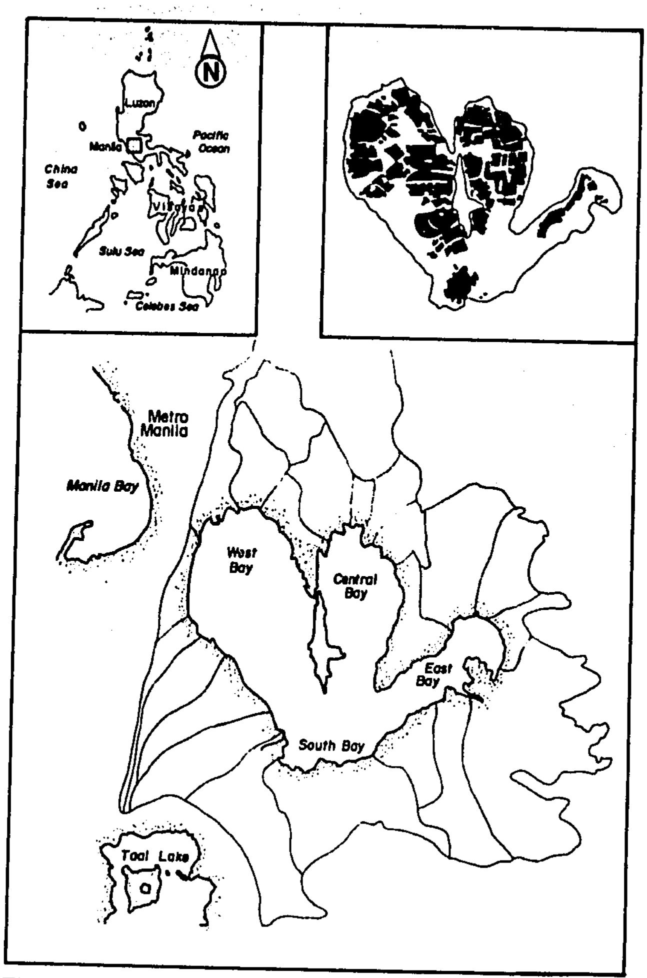

Fig. 1. Map of Laguna de Bay, Philippines. Right inset shows extent of fishpens in the mid-1980s.

(1974), introduced milkfish into pen enclosures. Milkfish is popular for human consumption and efficiently converts energy by feeding directly on phytoplankton and algal felts.

Fishpens are enclosures for culturing fish. The walls are formed by nets that are held up by bamboo and palm-tree poles dug into the bottom mud. The size of the fishpen can vary from 0.5 to 100 ha. Double walling is often used to protect the pens from fields of water hyacinths. Pen culture is capital-intensive and the main fish species is milkfish sold to Metro Manila markets and nearby towns. Use of fishpens for fish culture was discussed thoroughly in a report on the small-scale pen and cage culture for finfish published by FAO/UNDP-SCSP (1982).

The LLDA introduced and experimented with fishpens on a 0.38-km^2 pilot project in Looc, Cardona, Rizal in Central Bay in 1970. They were further developed in 1980 over 104 km^2 and proliferated in 1985 over 290 km^2, almost one-third of the lake area (Delmendo 1987) (Fig. 1). Since then there has been a decreasing trend, down to less than 70 km^2 in 1991 (F. Francisco, LLDA Lake Management Division, pers. comm.).

This study presents quantitative trophic models for two different periods of the Laguna de Bay ecosystem. The first model, referring to the late 1960s, describes the food web without milkfish while the second model, referring to the early 1980s, emphasizes the role of the introduced planktivorous species with emphasis on the dynamics of primary production of the lake.

A Dying Lake: Socioeconomic Impact

Since the 1980s, Metro Manila residents often describe Laguna Lake as a "dying lake" as did some researchers (LLDA/SOGREAH 1974; Cruz 1982). Situated in the densest region in the country, the lake has become a convenient sink for domestic and industrial sewage for more than eight million people and over 1,155 industrial establishments located around the lake, despite its primary use for fisheries. Illegal logging is a problem in the area resulting in land erosion of the watershed and siltation in the lake. The southern part of the lake is mostly agricultural and here use of chemical fertilizers and pesticides has been a routine since the 1960s. The net result is water pollution, fish kills and diseases, decreased productivity, low income and lowering of the socioeconomic status of the fishers.

According to the Inter-church Center for Development study (ICED, n.d.) and Rivera (1983), living conditions in the fishing villages are even worse than that of urban poor settlers in Manila. This is because of the rapid urbanization of the lake area and the aggravated economic condition of the lake inhabitants. The housing units of most fishing families are built close to each other and very near the lake. The lack of wide open roads and pre-dominance of narrow paths leading to the lakeshore are signs of congestion. Most houses are made of wood; only a few can afford to cement their floors, posts and walls.

The health conditions are equally poor. Most fishing household members, especially the small children, are thin and malnourished. There is no efficient and widespread use of community waste disposal systems. Faced with low incomes, most fishers cannot afford to buy medicines for their illness which are often related to lack of food. Fishers are able to support about 50% of their children up to grade school level and 41% to high school. A minority (3.4%) are able to send their children to college while 5.2% cannot provide any education for their children at all.

Competition between small-scale fishers and fishpen owners is intense, and has resulted in the death of numerous fishers, for which fishpen guards have been blamed (Maranan 1982).

Table 1. List of finfish species found in Laguna de Bay and their key properties.

Scientific Sources	English	Local	Common/abundant species	Introduced species	Carnivorous species	Omnivorous species	Planktivorous species	New Laguna de Bay records	Sources
Gobiidae									
Chonophorus melanocephalus	Rock goby	*Biyang bato*			●				
Glossogobius biocellatus	Sleeping goby	*Biyang tulog*			●				
Glossogobius giurus	White goby	*Biyang puti*	●	●	●				Vallejo 1985
Microgobius lacustris	Goby	*Bulong*			●				
Taenioides gracilis	-	-						●	
Taenioides sp.	Eel goby	*Baliga*			●				
Cyprinidae									
Carassius auratus	Golden carp	*Tawes*							LLDA/WHO (1978) vols. 3 and 8
Cyprinus carpio	Common carp	*Karpa*	●	●		●			
Puntius javanicus	Tawes	*Tawes*				●			
Cichlidae									
Oreochromis aureus	Blue tilapia	*Pla-pla*						●	
Oreochromis mossambicus	Tilapia	*Tilapia*	●	●			●		Parsons (1961)
Belontiidae									
Trichogaster pectoralis	Snakehead	*Plasalid*		●		●			
Trichogaster tricopterus	Three spot	*Placalid*		●		●			
Anabantidae									
Anabas testudineus	Climbing perch	*Martiniko*				●			
Anguillidae									
Anguilla mauritiana	Eel	*Igat*				●			
Ariidae									
Arius manilensis	Sea catfish	*Kanduli*	●		●				Mercene (1983)
Carangidae									
Caranx sp.	Jack	*Talakitok*				●			
Chanidae									
Chanos chanos	Milkfish	*Bangus*		●			●		
Channidae									
Channa striata	Mudfish	*Dalag*	●		●				Delmendo and Bustillo (1968)
Clariidae									
Clarias batrachus	Freshwater catfish	*Hito*	●		●				ICED (n.d.)
Eleotridae									
Ophiocara aporos	Sleeper	*Papalo*				●			
Hemiramphidae									
Hemiramphus sp.	Halfbeak	*Kansusuwit*				●			
Megalopidae									
Megalops cyprinoides	Tarpon	*Buan-buan*			●				
Mugilidae									
Mugil sp.	Mullet	*Talilong*				●			
Scatophagidae									
Scatophagus argus	Spadefish	*Kitang*				●			
Synbranchidae									
Ophisternon bengalensis	Swamp eel	*Igat*						●	
Syngnathidae									
Doryichthys brachyurus	Pipefish	-						●	
Terapontidae									
Terapon plumbeus	Grunter	*Ayungin*	●			●			LLDA/URS (1989)

Materials and Methods

The main purpose of this study is to compare two different states of the Laguna de Bay ecosystem and hence to provide a scientific basis to attempts to mitigate the competition between the small-scale fishers and fishpen owners. This can be done using steady-state box modelling in the form of the ECOPATH II model system by Christensen and Pauly (1992) as modified from Polovina (1984). The model has a budget equation of the form:

$$P_i - M_{pi} - M_{ni} - C_i = 0$$

where P_i is the production of species i, M_{pi} its predation mortality, M_{ni} other mortality and C_i the fisheries catch of species i.

Information necessary for construction of two preliminary trophic models of the Laguna de Bay ecosystem was gathered from the literature. These represented the 1968 and 1980 time frames, i.e., the prefishpen and fishpen periods where most of the data needed were available. The data inputs were assembled, standardized and converted to t·km^{-2}. Not all parameters were available; however, missing values and other ecosystem processes such as respiration, assimilation, and food conversion efficiencies were estimated by the model. Parameters used in ECOPATH II such as fisheries catch, biomass, production/biomass ratio, consumption/biomass ratio, diet composition, and ecotrophic and gross efficiencies are presented in Table 2.

Finfishes

Fisheries harvest (catches) for the periods 1968 and 1980 were taken from Shimura and Delmendo (1969) and Mercene (1983), respectively. The

Table 2. Parameters inputted (without brackets) in the ECOPATH II model for the periods 1968 and 1980 in Laguna de Bay. Parameters in bracket are estimate. by the program. Gross efficiencies (GE) refer to both the 1968 and 1980 models.

Common/scientific names	Catch		Biomass		P/B		Q/B^o		EE		GE
	1968^a	1980^b	1968	1980	1968	1980	1968	1980	1968	1980	
1. Grunter/*Terapon plumbeus*	29.60	18.50	(7.87)	(7.39)	3.98^h	2.64^i	9.42^p	8.65^r	.95	.95	-
2. Goby/*Glossogobius giurus*	11.30	4.20	(3.22)	(1.65)	3.77^h	2.72^i	7.67^p	7.23^r	.95	.95	-
3. Catfish/*Arius* sp. *Clarias batrachus*	0.59	1.25	(0.40)	1.32^c	1.55^i	1.55^i	4.31^r	4.64^r	.95	-	-
4. Common carp/*Cyprinus carpio*	0.79	0.07	(0.67)	0.06^e	1.24^j	1.24^j	8.30^n	8.30^n	.95	-	-
5. Mudfish/*Channa striata*	2.04	0.10	(3.36)	0.14^e	0.75^j	0.75^j	5.02^q	5.02^q	.95	.95	-
6. Tilapia/*Oreochromis* spp.	0.30	7.21	(0.26)	1.42^e	1.20^k	1.20^k	24.53^r	24.53^r	.95	-	-
7. Milkfish/*Chanos chanos*	0.00	41.656	-	9.13^f	-	4.800^f	-	41.52^r	-	-	-
8. Shrimps/2 species, dominant: *Macrobrachium lanceifrons*	30.61	8.189	12.0^c	12.00	(3.16)	(0.94)	(12.64)	(3.77)	.95	.95	0.25
9. Snails/5 families, dominant: Family Malaniidae	107.43	199.70	40.0^c	40.00	(2.88)	(5.27)	(11.53)	(21.07)	.95	.95	0.25
10. Midges/7 species, dominant: Family Chironomidae	0.00	0.00	1.6^c	1.60	(3.92)	(1.69)	(15.70)	(6.76)	.95	.95	0.25
11. Annelids/2 species, dominant: Family Tubificidae	0.00	0.00	0.7^c	0.70	(13.09)	(3.50)	(52.35)	(13.99)	.95	.95	0.25
12. Microcrustaceans	0.00	0.00	2.0^c	2.00	(28.53)	(14.98)	(114.12)	(59.91)	.95	.95	0.25
13. Higher aquatic plants/ water hyacinth	0.00	0.00	11.0^c	11.10	5.00^l	5.00^l	0.00	0.00	-	-	-
14. Zooplankton	0.00	0.00	12.0^d	16.90^g	70.00^d	89.70^g	282.00	358.00	.20	.20	-
15. Phytoplankton	0.00	0.00	82.0^d	60.55^g	268.36^d	146.90^g	0.00	0.00	-	-	-
16. Juvenile fish	0.00	0.00	(4.3)	(1.97)	3.00^m	3.00^m	8.00^m	8.00^m	.95	.95	-

[a] From Shimura and Delmendo (1969).

[b] From Mercene (1983).

[c] From Rabanal et al. (1964).

[d] Derived from LLDA/WHO study (1978), with zooplankton biomass of 500 ind./l and phytoplankton biomass of 27.5 mg/l (average of 1973, 1974 and 1976 biomasses).

[e] Based on biomass (B) x production/biomass (P/B) ratio x ecotrophic efficiency (EE) = catch + predation mortality (M_p).

Derived from LLDA/WHO (1978) and computed from two harvests per year with five months culture period each with a lag of two months between harvests.

Derived from Nielsen (1983) with zooplankton biomass of 16.9 t·km^{-2} from the average of Central Bay (21.5 g·m^{-2}) and West Bay (12.3 g·m^{-2}) and phytoplankton biomass of 60.55 t·km^{-2} from the average of Central Bay (96.6 g·m^{-2}) and West Bay (24.5 g·m^{-2}).

[h] Derived from Ingles and Pauly (1984).

[i] Derived from length-frequency data of Mercene (unpubl.) using the Compleat ELEFAN software.

[j] 15% of QB.

[k] Derived from LLDA/WHO (1978) and computed from two harvests per year with 4.5 months culture period each with a lag of three months between harvests.

[l] Assumed value.

[m] From Liew and Chan (1987).

[n] From Ruddle and Christensen (this vol.).

[o] Computed using the model of Palomares and Pauly (1989).

[p] Derived from h.

[q] Derived from Kilambi (1986).

[r] Derived from i.

differences between the two periods are mainly caused by the presence of milkfish with a harvest of 41.64 $t \cdot km^{-2} \cdot year^{-1}$ and the increased harvest of tilapia with 7.21 $t \cdot km^{-2} \cdot year^{-1}$ of which 6.88 $t \cdot km^{-2} \cdot year^{-1}$ were taken from cages in 1981 and the rest from open fisheries.

Biomasses of catfish (*Arius manilensis*), carp (*Cyprinus carpio*), mudfish (*Channa striata*) and tilapia (*Oreochromis mossambicus*) in 1980 were estimated from B = (C+M)/(EE*P/B), given that biomass (B) x production/biomass ratio (P/B) x ecotrophic efficiency (EE) = catch (C) + predation mortality (M). The estimate of biomass for milkfish in the same period was derived from LLDA/WHO (1978) and computed from two harvests per year with a five-month culture period each and a lag of two months between harvests.

Under steady-state conditions, production/biomass ratio (P/B) is equal to the total mortality (Z) (Allen 1971). For the prefishpen period, values of Z for grunter and goby were taken from Ingles and Pauly (1984) and those for tilapia were derived from data in Mercene (1979) using ELEFAN I and II (Gayanilo et al. 1989). Values for carp and mudfish were assumed to be 15% of their Q/Bs and those of tilapia were computed from the ratio of their known production and biomass. During the fishpen period, the P/B values of grunter (*Terapon plumbeus*), goby (*Glossogobius giurus*) and catfish (*Arius manilensis*) were also taken as the total mortality (Z) estimated from the 1978-1979 length frequency data of Mercene (unpubl. data) using ELEFAN I and II. For carp, mudfish and tilapia, the same values of the prefishpen period were used. The P/B of milkfish was computed from the ratio of production over biomass for the species. The value of P/B for juvenile fishes was taken from Liew and Chan (1987) for both periods.

Consumption/biomass ratio (Q/B) estimates of finfishes were derived from the method proposed by Palomares and Pauly (1989) with known asymptotic weight (W_∞), caudal fin aspect ratio (A), average habitat temperature and feeding type (predator vs. herbivore). For the prefishpen period, data on grunter and goby were taken from Ingles and Pauly (1984) and those for catfish were taken from the 1978-1979 data of Mercene (unpubl. data). For the fishpen period, values for grunter, goby and catfish were also adapted from Mercene (unpubl. data). Data on mudfish were taken from Kilambi (1986). The Q/B values of carp and juvenile fishes for both periods were taken from Ruddle and Christensen (this vol.) and Liew and Chan (1987), respectively. Data for tilapia and milkfish were taken from LLDA/WHO (1978). For milkfish, estimates were derived from two harvests per year with a five-month culture period each and a lag of two months between harvests and for tilapia, from two harvests per year with a 4.5 month culture period each and a lag of three months between harvests.

Invertebrates/Benthos

Shrimp and snail harvest/catches were obtained from Shimura and Delmendo (1969) and Mercene (1983); no value for the harvest of other invertebrates was available. Biomass estimates for shrimps, snails, midges, annelids and microcrustaceans in the prefishpen period were taken from Rabanal et al. (1964). The same values were used during the fishpen period since no information was available for that period.

Plankton and Aquatic Plants

Phytoplankton biomass does not appear to have been recorded in 1968; therefore, data were taken from the averages of 1973, 1974 and 1976 records gathered by LLDA/WHO (1978). Biomass of phytoplankton during this period was 27.5 $mg \cdot l^{-1}$ or 82.5 $t \cdot km^{-2}$ in wet weight. For the fishpen period, a value of 60.55 $t \cdot km^{-2}$ was obtained from Nielsen (1983). This estimate was the average of Central Bay (96.6 $t \cdot km^{-2}$) and West Bay (24.5 $t \cdot km^{-2}$) estimates. The values were relatively high because during these two periods there were phytoplankton blooms in the lake. The zooplankton biomass in the prefishpen period was converted using a table of Jϕrgensen (1979) from the value of 500 organisms l^{-1} (= 12 $t \cdot km^{-2}$ wet weight). In the 1980 period, the biomass was 16.9 $t \cdot km^{-2}$, the average of Central Bay (21.5 $t \cdot km^{-2}$) and West Bay (12.3 $t \cdot km^{-2}$) estimates. Production/biomass ratios of phyto- and zooplankton were simply the ratio of the estimated production and biomass. The 1968 biomass value for higher aquatic plants was taken from Rabanal et al. (1964) and the same estimate was used in the 1980 value as no information was available for that period. The P/Bs of aquatic plants and Q/Bs of zooplankton were assumed.

Diet Composition

Finfish diet compositions (Table 3) were obtained from LLDA/WHO (1978), Delmendo and Gedney (1974) and Delmendo (1968). These data were adapted, to include juvenile fishes, which comprise young perch, goby, catfish, carp and mudfish. The same was done with microcrustaceans; some were included with the zooplankton to avoid inconsistencies found in the literature.

Ecotrophic and Gross Efficiencies

Ecotrophic efficiency (EE) is defined as the part of production that goes to export or to predation mortality. EE is difficult to measure and was assumed to be 0.95 for finfishes and invertebrates of Laguna de Bay,

Table 3. Diet composition of species/groups in Laguna de Bay (%). Group 15 is phytoplankton, group 17 detritus.

Predator	Year	Prey 1	2	8	9	10	11	12	14	15	16	17
1. Grunter	1968	0.1	0.2			0.4		30.0	40.0	29.3		
	1980		0.1			0.4		30.0	39.5	30.0		
2. Goby	1968			13.7						30.0	56.3	
	1980			10.0						40.0	50.0	
3. Catfish	1968	0.5		20.0	8.0	35.5		2.0		14.0	20.0	
	1980	0.4		20.0	6.1	35.5		2.0		10.0	26.0	
4. Carp	1968				20.0		5.0	15.0	10.0	15.0	35.0	
	1980				20.0		10.0	10.0	10.0	15.0	35.0	
5. Mudfish	1968	0.5	0.5	10.0	5.0	30.0	5.0	4.5	22.0	22.5		
	1980	0.6	0.7	20.0		20.0	2.2	10.0	25.0	21.5		
6. Tilapia	1968								5.0	90.0	5.0	
	1980								5.0	90.0		5.0
7. Milkfish	1980									100.0		
8. Shrimps	1968 + 1980						5.0	20.0	20.0	10.0		45.0
9. Snails	1968 + 1980									10.0		90.0
10. Midges	1968								20.0	5.0		75.0
	1980								10.0	5.0		85.0
11. Annelids	1968								5.0	10.0		85.0
	1980								2.5	10.0		87.5
12. Microcrustaceans	1968 + 1980									50.0		50.0
14. Zooplankton	1968 + 1980							5.0	9.50			
16. Juvenile fish	1968 + 1980							80.0	10.0		10.0	

indicating that most of the production is assumed to be used. (1-EE) is the fraction of production that dies off, resulting in the decay and bacterial decomposition of the products, which in turn become nutrients for new production. Gross efficiency (GE) values, defined as the ratio between production and consumption, and required for estimation of Q/B ratios were assumed to be 0.25 for the invertebrates of Laguna de Bay, which is within the range of physiologically possible values (V. Christensen, pers. comm.).

Results and Discussion

As shown in Table 2, the Laguna de Bay openwater fisheries in 1968 generated an annual average finfish catch of 45.0 t·km^{-2} and about 138.0 t·km^{-2} of shrimps and snails. The three dominant species, which comprised more than 93% of the catch, were *Terapon plumbeus*, *Glossogobius giurus* and *Arius manilensis*. Close to 8,000 full-time and about 2,000 part-time fishers operated on the lake using 43 different types of fishing gear (Shimura and Delmendo 1969). The most common gears were traps, gill nets and push nets.

Milkfish production in 1980 amounted to 42.0 t·km^{-2}, about two times more than all other finfish species combined (at 31.0 t·km^{-2}) and only slightly less than the catch of all finfish species in 1968 (at 45.0 t·km^{-2}). The total finfish biomass is higher in the fishpen period at 21.0 t·km^{-2} than in the prefishpen at 16.0 t·km^{-2} as shown in Tables 2 and 4. This is due to the presence of milkfish in the latter period. The fishpens covered an area of 104 km^2. More than 4,000 full-time and less than 1,000 part-time fishers fished in the lake, half as many as in 1968. They used four major gears, namely, gill nets, fish corrals, motorized push nets and longlines (Mercene 1987).

Tilapia was caught from open waters at 0.3 t·km^{-2} in 1968 compared to 7.21 t·km^{-2} in 1981, of which 0.33 t·km^{-2} was contributed by the openwater fisheries and the rest by fishcage culture. Thus, the catches of tilapia from openwater fisheries did not decline; as one-third of the lake was closed to fishing in the latter period, the catch rates actually seem to have increased.

There was a considerable decrease in fish production of the openwater fisheries from 1968 to 1980, resulting in low income for the fishers. The following might be thought as having contributed to the decline: (1) a decrease in the number of fishers on the lake; (2) a reduction of the available openwater areas for fishing due to the expansion of fishpens; and (3) limited circulation of lake water in congested areas resulting in the depletion of food organisms and in turn led to

Table 4. Computed parameters of the Laguna de Bay ecosystem using ECOPATH II model.

Group/species	Biomass ($t \cdot km^{-2}$)		P/B ($year^{-1}$)		Q/B ($year^{-1}$)	
	1968	1980	1968	1980	1968	1980
Grunter	7.873	7.388	-	-	-	-
Goby	3.220	1.652	-	-	-	-
Catfish	0.401	-	-	-	-	-
Carp	0.668	-	-	-	-	-
Mudfish	3.355	-	-	-	-	-
Tilapia	0.263	-	-	-	-	-
Milkfish	-	-	-	-	-	-
Shrimps	-	-	3.160	0.942	12.640	3.768
Snails	-	-	2.882	5.268	11.528	21.071
Midges	-	-	3.923	1.691	15.698	6.764
Annelids	-	-	13.087	3.498	52.350	13.993
Microcrustaceans	-	-	28.530	14.978	114.122	59.912
Aquatic plants	-	-	-	-	-	-
Zooplankton	-	-	-	-	-	-
Phytoplankton	-	-	-	-	-	-
Juvenile fish	4.306	1.971	-	-	-	-

poor fish growth (LLDA/WHO 1978; LLDA/URS 1989). Further, the downward trend in fish and snail production, according to Mercene (1987), might be the result of ecological imbalance such as siltation and sedimentation, poor water quality and the destructive effects of some gears like motorized push nets and small-meshed gill nets.

Regarding the invertebrate components, such as shrimps and snails, intensive harvesting had been applied prior to and during the fishpen periods. The shrimps harvest declined from 30.61 to 8.18 $t \cdot km^{-2}$ while the snails increased from 107.43 to 199.70 $t \cdot km^{-2}$. The influence of intensive harvesting on the food chain, specially on snails was not established due to little information on causes and effects. However, it is certain that the removal of large quantities of shrimps and snails must reduce the amount of food for benthic feeding fishes.

Table 5 presents a summary of important changes in the Laguna de Bay ecosystem. The mean trophic level of the catches/harvest in the prefishpen period was 3.26 while that in the fishpen period had decreased to 3.08 due to the phytoplanktivorous milkfish. These levels are relatively low compared to the level of ecosystems in this volume.

The efficiency of the fisheries (fisheries catch/primary production) in the prefishpen and fishpen periods were 0.0082 and 0.0314, respectively. The increase in the latter period means that the utilization of the primary production has increased since the prefishpen period. This is due to the introduction of milkfish and the increase in the catch of tilapia.

Phytoplankton flow to detritus was much higher in the prefishpen period at 18,732 $t \cdot km^{-2}$ than in the fishpen period at 2,553 $t \cdot km^{-2}$. In general, the sum of all flows to detritus decreased more than three times

Table 5. Summary of the important changes in the Laguna de Bay ecosystem calculated using ECOPATH II models. Except for the total biomass (excl. detritus), which is in $t \cdot km^{-2}$, all units are in $t \cdot km^{-2} \cdot year^{-1}$.

	1968	1980
Sum of all consumption	4,426.7	7,605.1
Sum of all exports	20,451.7	5,935.6
Sum of all respiratory flows	1,743.0	3,014.7
Sum of all flows into detritus	20,936.1	6,522.4
Total system throughput	47,557.4	23,077.7
Sum of all production	23,321.1	10,806.9
The fishery has a 'mean trophic level'	3.26	3.08
Its gross efficiency (catch/prim. prod.) is	0.0082	0.0314
Calculated total net primary production	22,194.7	8,950.3
Total primary production/total respiration	12.7	3.0
Net system production	20,451	5,935
Total primary production/total biomass	122	53
Total biomass/total throughput	0.004	0.007
Total biomass (excl. detritus)	181.9	167.9
Total catches	182.7	280.9

for the whole system. The decrease may be accountable to milkfish and tilapia, both planktivorous species, grazing on phytoplankton in the fishpen period along with a decrease in phytoplankton biomass and productivity.

The sum of all consumption, exports, respiratory flows and flows to detritus gave rise to an estimation of total system throughput (TST) and the sum of all production (SAP), which is an indicator of the size of the two communities during the two periods. The TST and SAP in the prefishpen period were twice as high as those of the fishpen period. The TST and SAP in 1968 were 47,557 and 23,321 compared to 23,098 and 10,807, respectively, in 1980.

Fig. 2 shows the mixed trophic impact the various groups/species had on the other groups in the system in the 1980 model. The impacts for the 1968 model (not shown) are very similar. The graph shows the trophic impact that each group in the system has on all other groups in the given static situation. Interestingly, the zooplankton is found to impact the phytoplankton much more than either milkfish or tilapia. Figs. 3 and 4 illustrate the ECOPATH II models of Laguna de Bay prior to and during fishpen periods. The mudfish (*Channa striata*) and the catfish (*Arius manilensis*) are typical carnivores occupying the highest rank in the aquatic food chain.

In Laguna de Bay, the calculated total net primary production was estimated in 1968 and 1980 at 22,195 and 8,950 t·km^{-2}, respectively. The reduced value during the fishpen period indicates that the presence of milkfish in pens and tilapia in cages may have contributed to the decline. This agrees with the observations of Nielsen (1983) and Oosterberg (1987)

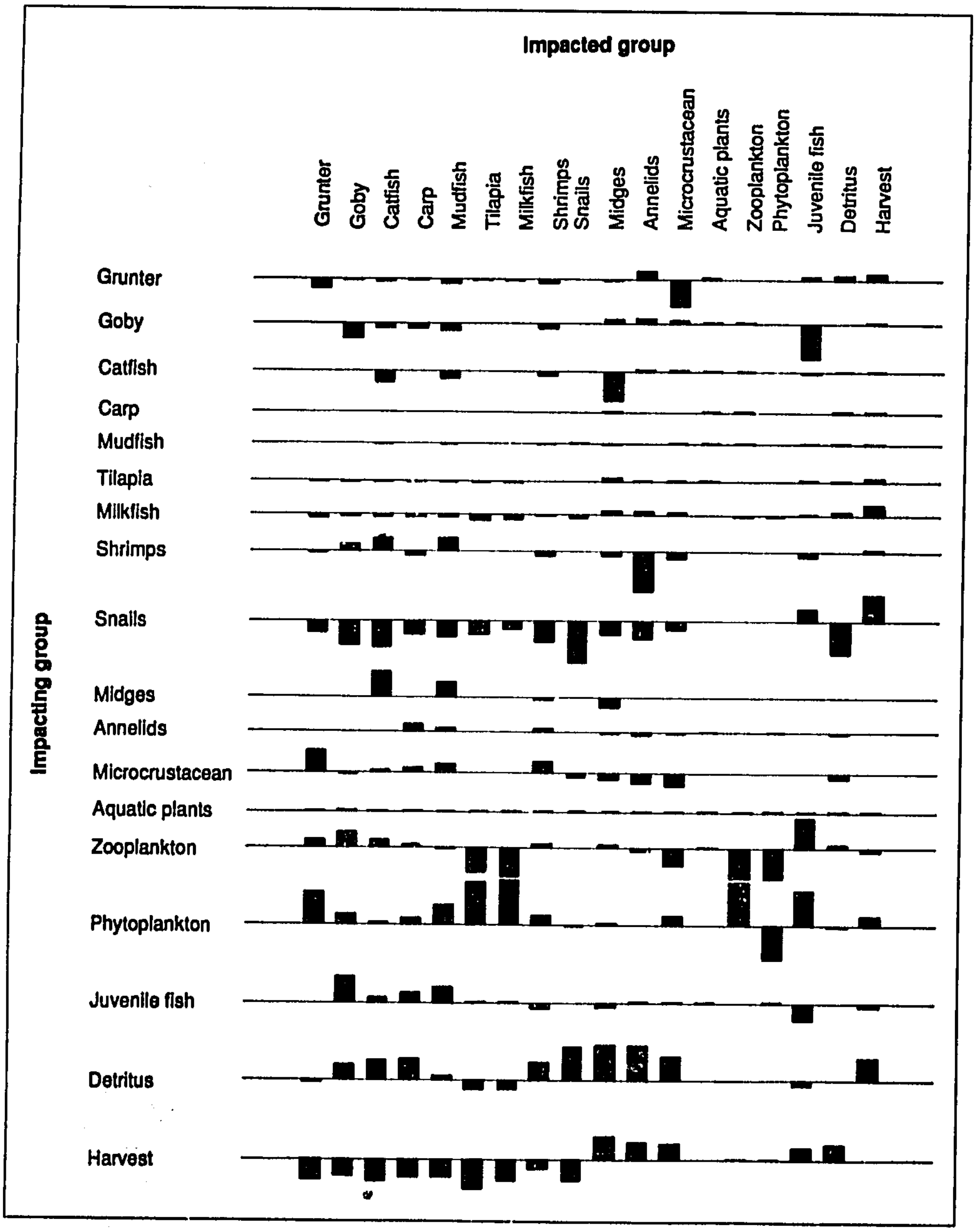

Fig. 2. Impact of the various groups/species on the other groups in the Laguna de Bay ecosystem, Philippines (1980 model).

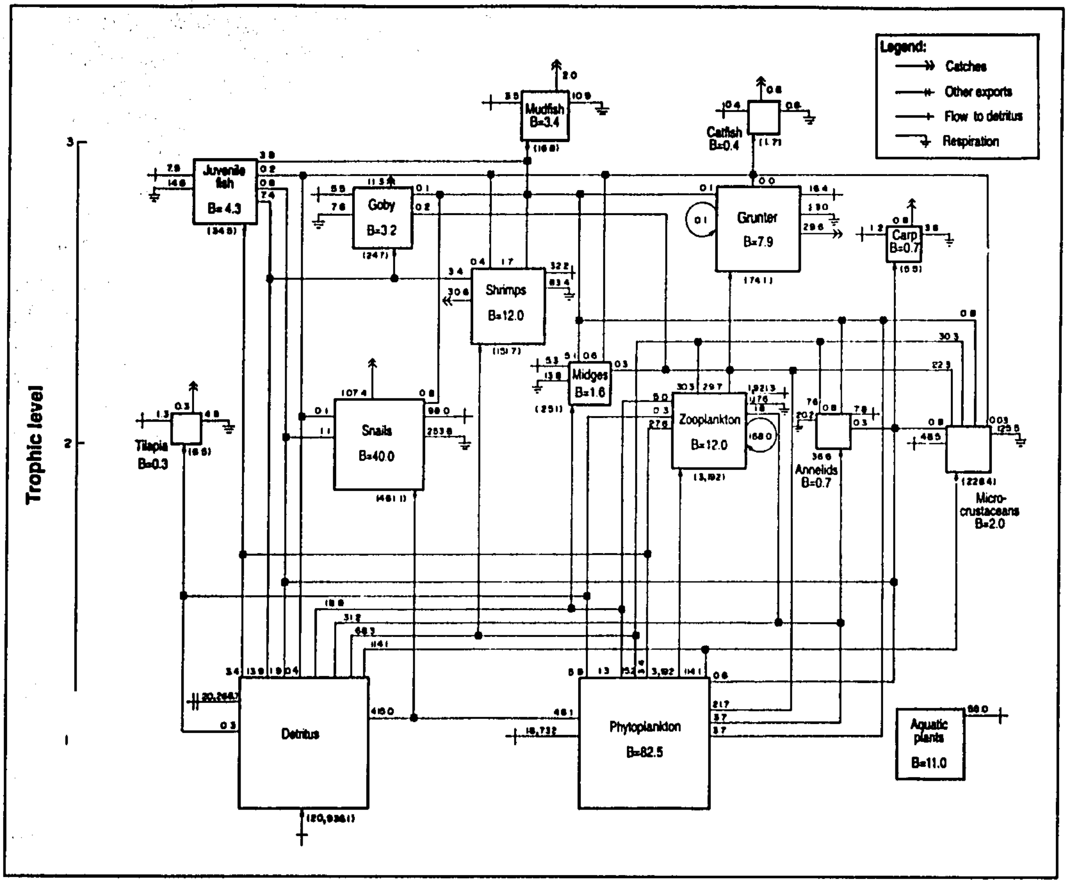

Fig. 3. ECOPATH II model of Laguna de Bay, Philippines, prior to the fishpen period (1968).

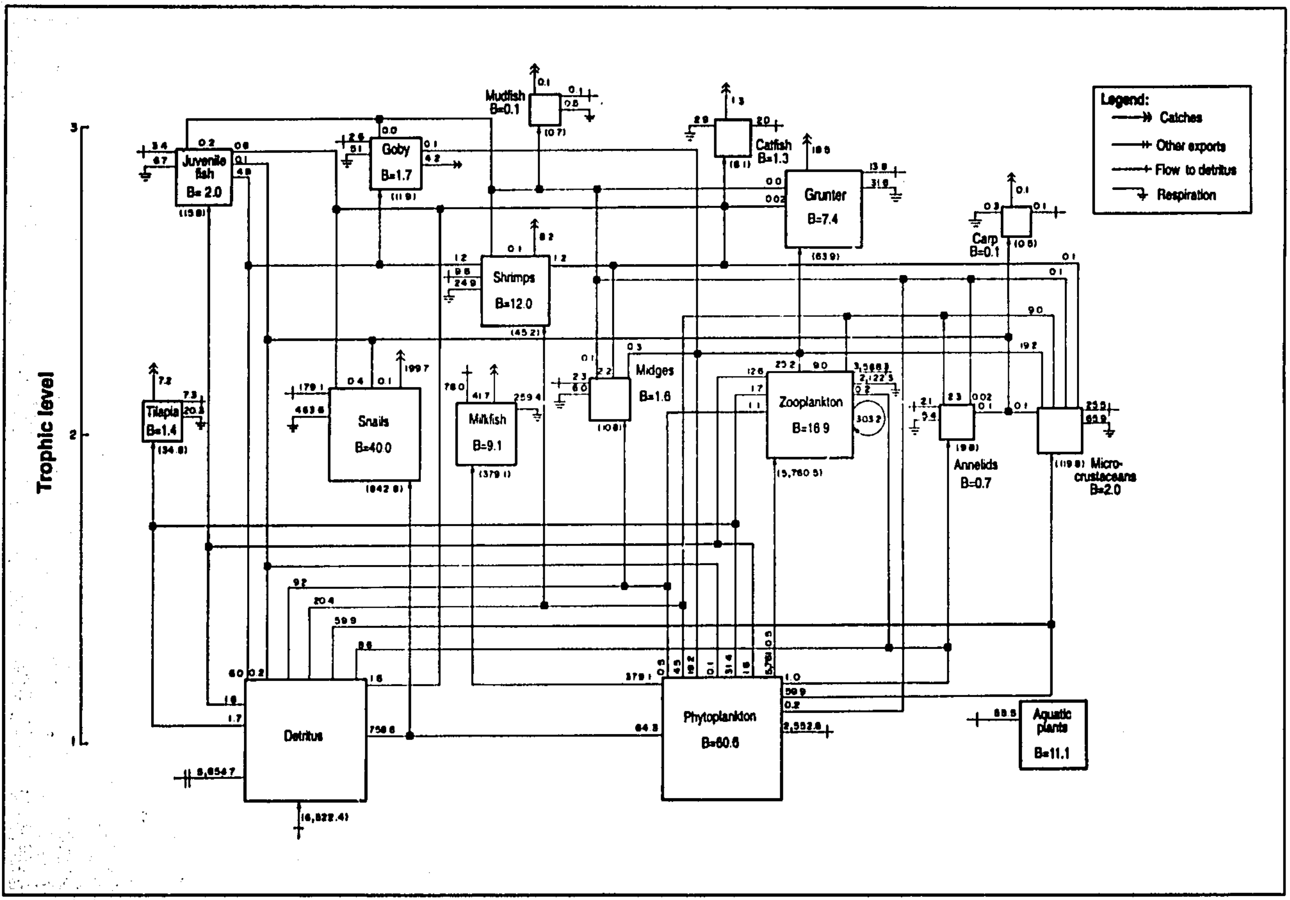

Fig. 4. ECOPATH II model of Laguna de Bay, Philippines, during the fishpen period (1980).

that milkfish and tilapia filter the phytoplankton and zooplankton from the water flowing freely through the pens and cages. These species are therefore important factors in keeping the phytoplankton biomass low and may even indirectly depress primary productivity. There is also a tendency toward shifted species composition of phytoplankton in the lake, creating an excess of very small phytoplankton as a result of milkfish and tilapia grazing.

It is assumed that during the height of fishpen proliferation in the mid-1980s, the carrying capacity of the lake to sustain production was reached, resulting in the strong decline of the capture fisheries. This resulted in death or in growth reduction of milkfish and native fishes as observed by pen operators and fishers. Fishes took a longer time to grow to harvestable size; thus, fishpens suffered from a low production.

There are several reasons (aside from overstocking the pens) why the primary production could not support excessive numbers of milkfish anymore. The production of milkfish excreta probably raised the levels of ammonia and little spacing between pens might have reduced the dissolved oxygen content due to poor water circulation. These conditions might also have increased the incidence of fish diseases as reported in 1983 (Delos Reyes and Belen 1988).

However, this does not necessarily discount other factors than the limited primary production. There has been some controversy on the above issue in Laguna de Bay (Pullin 1981). According to the reports, nitrate (LLDA/SOGREAH 1974), temperature (LLDA/WHO 1978; LLDA/BCEOM 1984) and turbidity (Nielsen et al. 1981) are the limiting factors of primary production. Furthermore, interpretations on the above data were made by LLDA/ERL (1985) and IESAM (1991).

This study interprets biological changes in the Laguna de Bay ecosystem during the past three decades using two ECOPATH II models, sensitive to food chain structure. As part of the author's ongoing study on the geoecology of Laguna de Bay, continued sampling is being done to gather adequate and reliable biological, ecological and fisheries data. This will form part of a third ECOPATH II model, reflecting the present situation of the ecosystem. It is hoped this will help resolve some of the issues raised here.

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LAKES

Traditionally modelling of aquatic ecosystems has concentrated on lakes. There are many reasons for this. Some are practical in nature, e.g., lakes are largely closed ecosystems, therefore fulfilling a key requirement for modelling. Often they are also easily accessible, making cost-effective sampling schemes possible.

Other reasons for modelling lakes are linked with the problems associated with industrialization and/or intensification of agriculture, and increased eutrophication especially in the more developed parts of the world. Because of the nature of these problems, attention has been on describing the dynamics of lake ecosystems whereas few models have been developed with the purpose of describing trophic interactions in lakes. Here the present volume has a contribution to add. From temperate areas four models are presented, two from Europe, one from West Asia and one from North America, while the tropics are represented with models of the largest lake in the Philippines (previous section), of a small and productive lake in India and of a number of African lakes.

In the tropics, lakes are as yet generally of more importance for fisheries than as recipients for pollutants. There is therefore a need for development of models for fisheries management. This need can perhaps be illustrated by a comparison of fish yield and effort on African lakes (Fig. 1), which shows the expected - high fishing pressure leads to less fish per fisher, and the fishing pressure is steadily growing everywhere.

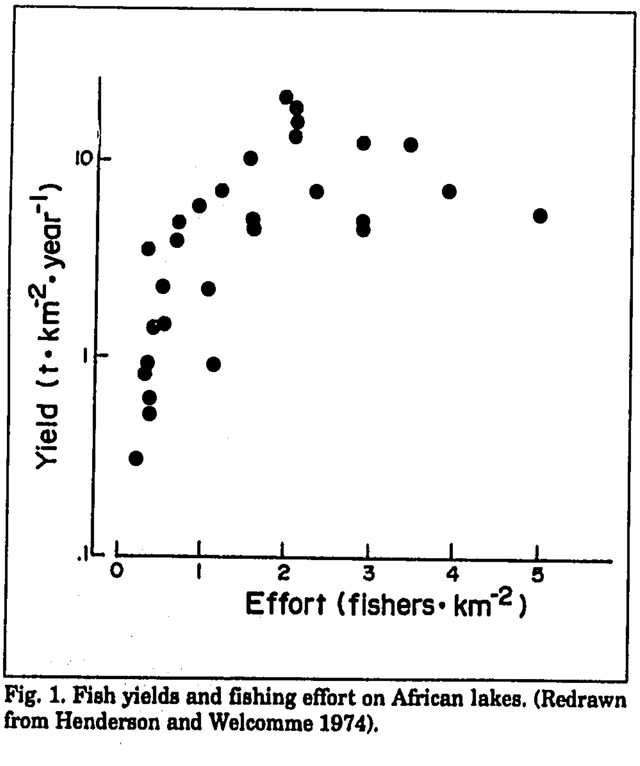

Fig. 1. Fish yields and fishing effort on African lakes. (Redrawn from Henderson and Welcomme 1974).

In the tropics and subtropics, only Africa has large natural lakes. The three largest (Victoria, Malaŵi and Tanganyika) cover a combined area of 134,000 km^2. You will find trophic models of all three of these in this section - along with models of a few other African lakes - Lakes Turkana, George, Chad, and the large artificial lake, Lake Kariba, once the largest in the world.

Artificial lakes, i.e., reservoirs, comprise the greatest areas of stable standing waters in the tropics. In the 56 countries and associated islands of Africa, there are 320 major dams and reservoirs occupying a total of 41,000 km^2. Noting that Africa to a large extent derives her fish production from freshwater, one can add that the reservoirs have come to play an important role for the supply of fish protein. Roughly 10% or 150,000 t·year^{-1} of inland fisheries yields come from reservoirs, and there is good reason to presume that this production can be increased if we learn how to manage the ecosystems in the reservoirs - and for that matter in other resource systems as well. Due to the brief biological history of the reservoirs they do not possess the variety of life forms that characterizes most lakes. This raises a need for careful consideration of introductions as all ecological niches may not be filled, something that often results in inefficient transfer from primary production to fish yield (Fernando and Holcik 1982).

As an example, introduction of "kapenta" (*Limnothrissa miodon*) into Lake Kariba resulted in the niche for small pelagics being filled and in sustainable catches of some 32,000 t·year^{-1} annually. Still, the problem of introduction of new species is not an easy one. The introduction of *Limnothrissa miodon* from Lake Tanganyika in to Lake Kariba may have been a success, but as discussed by Machena and colleagues (this vol.) the system is far from optimized yet.

Actually, even for much older (and mature?) ecosystems, the same problem exists. Degnbol (this vol.) convincingly shows how the pelagic ecosystem of the old Lake Malaŵi produces more lake flies than fish, and he concludes "it takes more than the age of Lake Malaŵi (approx. 10 mio. years) for a cyprinid to accumulate the skills needed for competitive zooplankton grazing". A debate, still unresolved, has been going on for a decade on whether or not to introduce Lake Tanganyika clupeoids to Lake Malawi.

A similar discussion is also continuing on the consequences of the introduction of Nile perch to Lake Victoria, which may be assessed by comparing the role of Nile perch in different lakes. In the present volume, you will find trophic models of Lakes Victoria, Tanganyika and Turkana, all of which (now) have Nile perch as apex predator. In Lake Victoria, Nile perch has apparently reduced the species diversity of the small haplochromines upon which it feeds, thereby also feeding a huge controversy about the wisdom of introductions, a problem discussed in several of the contributions in this section. A tentative - to some extent controversial - conclusion seems to be that this specific introduction has been successful from a fisheries point of view (see Acere 1988) notwithstanding vociferous claims to the contrary (Witte et al. 1992). Yet from a biological point of view it may have been a disaster, although recent evidence suggest that the reduction in abundance ofhaplochromine cichlids and diversity may also be linked to excessive fishing pressure (Harrison et al. 1989). Not only was Nile perch introduced but also fish meal plants to process catches from industrialized haplochromine cichlids fisheries; moreover haplochromine cichlids have been found to thrive in parts of Lake Victoria where they are not exposed to fishing but only to Nile perch predation (Harrison et al. 1989).

Still we do not want to draw firm conclusions from the analyses presented here; that is not even the purpose of these reflections. Instead we want to point out that predator-prey studies in the form of quantified models of trophic interactions are of importance for elucidating questions such as those posed by introductions; the discussion in several of the papers in this section illustrates this.

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Preliminary Trophic Model of Veli Lake, Southern India

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ARAVINDAN, C.M. 1993. Preliminary trophic model of Veli Lake, southern India, p. 87-89. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Abstract

An attempt to construct a trophic model of Veli Lake, southern India, was made using the ECOPATH II approach and software. This was used to estimate the biomasses of exploited fishes such as mullets, *Etroplus*, catfishes and prawns and of their preys. Catches from the lake are very high and, in consequence, high biomasses are estimated for most groups.

Introduction

Veli Lake is a relatively small water body situated 5 km northwest of Trivandrum City, southern India at 08°28' northern latitude and 76°57' eastern longitude (Fig. 1). The lake is 1 km long and 0.3 km wide with an average depth of only 2 m. During the southwest monsoon the lake opens for a few days to the sea through a narrow outlet. Seawater exchange takes place only during these days. Seasonal variations of benthic fauna (Murugan et al. 1980) and zooplankton (Arunachalam et al. 1982) of this area have been studied in detail. Scanty information on the fish fauna of the lake is available, but no details have so far been published.

Even though the lake is small, regular fishing by a few country crafts using small seine nets exists, though no attempt has hitherto been made to assess the stock upon which that fishery is based. In the present study a trophic model of Veli Lake is constructed using ECOPATH II (Christensen and Pauly 1992) with data collected by the author and supplemented by other literature.

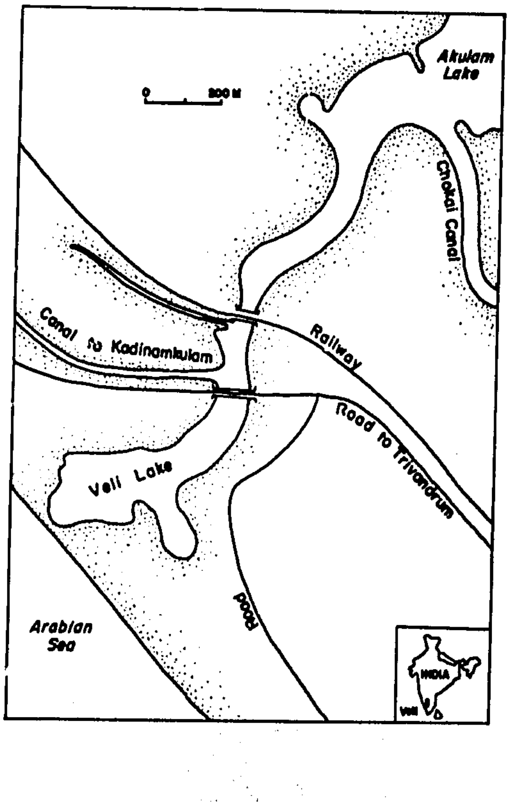

Fig. 1. Veli Lake and surrounding area, southern India.

Materials and Methods

The diet composition of the fishes was estimated by analyzing stomach contents of fish samples. Catch data were obtained from the landing centers and directly from fishers operating in the lake. Data on benthic producers were mainly from published work (Murugan et al. 1980) while primary production estimates were from Arunachalam et al. (1982).

Except for benthic producers, high values (0.95) of ecotrophic efficiency (EE) have been used in the input to imply a high utilization of the fishes by the fisheries and by predators.

No major phytoplankton blooms occur in the lake and only slight fluctuations associated with monsoon occur in the phytoplankton and zooplankton biomass in the lake (Arunachalam et al. 1982). Based on this, a high ecotrophic efficiency can be expected for the phytoplankton.

Table 1 presents the model inputs (except for the diet matrix, not shown).

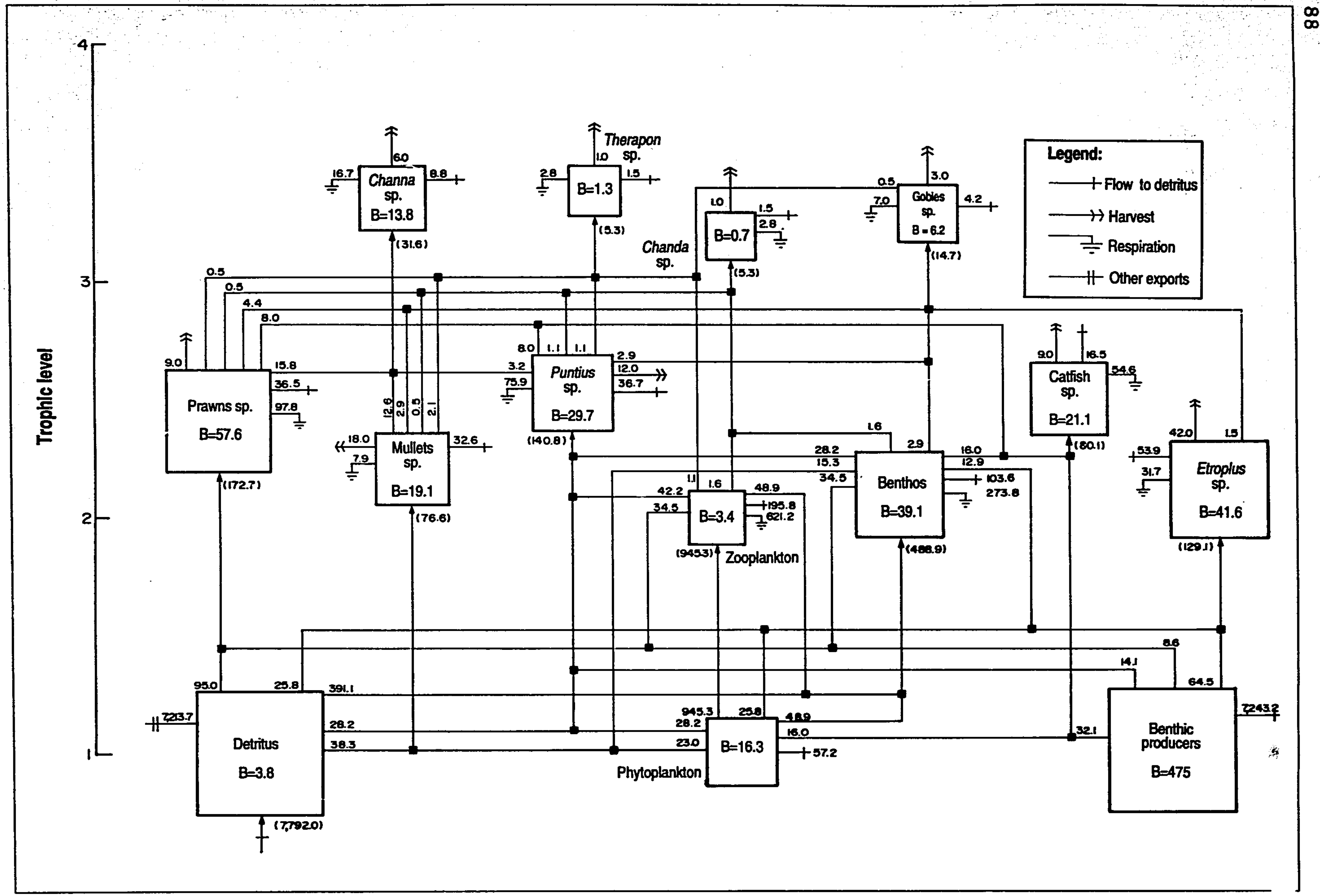

Fig. 2. Trophic flows (g·m⁻²year⁻¹) in an ECOPATH II model of Veli Lake, southern India. Biomasses (g·m⁻²) are given inside the boxes.

Table 1. Inputs used for ECOPATH II model of Veli Lake (with derived estimates in brackets). Exports (catches) are in g·m^{-2}·year^{-1}, P/B and Q/B are annual rates, and biomasses are in g·m^{-2}. EE is the ecotrophic efficiency and GE, the gross efficiency (P/Q); both are dimensionless.

Group	Export	P/B	Q/B	EE	GE	Biomass
Channa sp.	6	(0.46)	2.29	0.95	0.20	(13.8)
Chanda sp.	1	(1.43)	7.17	0.95	0.20	(0.7)
Therapon sp.	1	(0.81)	4.07	0.95	0.20	(1.3)
Gobies	3	0.60	2.38	0.95	(0.25)	(6.2)
Puntius sp.	12	1.00	4.74	0.95	(0.21)	(29.7)
Mullet	18	2.00	4.02	0.95	(0.50)	(19.1)
Etroplus sp.	42	1.10	3.10	0.95	(0.35)	(41.6)
Catfishes	9	0.45	3.81	0.95	(0.12)	(21.1)
Prawns	9	0.70	3.00	0.95	(0.23)	(57.6)
Zooplankton	0	40.00	280.00	0.95	(0.14)	(3.4)
Benthos	0	3.00	12.50	0.95	(0.24)	(39.1)
Phytoplankton	0	70.00	0.00	0.95	-	(16.3)
Benthic producers	0	15.50	0.00	(0.02)	-	475.0
Detritus	(7,213.7)	-	-	(0.07)	-	3.8

Results and Discussion

The estimated biomass and other outputs of ECOPATH II is presented in Table 2 and in Fig. 2. Generally the biomass estimated by ECOPATH II appears high, but perhaps not unrealistically so, noting the high primary production in the lake and the high catches. The high (input) biomass for the benthic production (475 g·m^{-2}) consists of aquatic macrophytes such as *Elodea*, *Hydrilla* and *Nitella* which are found in large quantities in the lake. These constitute a component of the food of herbivores and are also consumed on decay as detritus; still their utilization is far from total and their EE value is thus low.

Table 2. Summary of statistics obtained for Lake Veli from ECOPATH II. (Flows are in g·m^{-2}·year^{-1}; trophic level and gross efficiency are dimensionless)

Sum of all consumption	=	2,090
Sum of all exports	=	7,315
Sum of all respiratory flows	=	1,192
Sum of all flows into detritus	=	7,792
Total system throughput	=	18,389
Sum of all production	=	8,935
Mean trophic level of fishery	=	3.37
Gross efficiency (catch/prim. prod.) of fishery	=	0.0119

The lake is fished regularly but so far no estimates of biomass of any fish or prawn have been made and hence there is no scope for comparison of the estimates. Recently increased catches of prawns and *Etroplus* have been observed.

The main environmental influence in the lake appears to be associated with the monsoon and thus more details for premonsoon, monsoon and postmonsoon seasons should be collected if the present model is to be refined and if attempts to use ECOPATH II, separated or combined models, for these seasons should be made. In the meantime we note that the ECOPATH II model has enabled us to obtain new insights on Veli Lake, notably on the trophic ecology of its fishes.

Acknowledgement

I am thankful to V. Christensen, ICLARM, for helping me with new insights into trophic modeling.

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Elements of a Trophic Model for IJsselmeer (The Netherlands), a Shallow Eutrophic Lake

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Abstract

IJsselmeer in the central part of the Netherlands is a 182,000 ha shallow eutrophic freshwater body with an average depth of 4 m. Commercially important fish species are the eel (*Anguilla anguilla*), two predators, pikeperch (*Stizostedion lucioperca*) and perch (*Perca fluviatilis*) and the short-lived smelt (*Osmerus eperlanus*).

Other important fish species in the ecosystem are ruffe (*Gymnocephalus cernua*), bream (*Abramis brama*) and roach (*Rutilus rutilus*). The fishery consists mainly of a fyke net fishery for eel and spawning smelt and a gill net fishery for pikeperch and perch. Important fish-eating birds are the cormorants (*Phalacrocorax carbo*), grebes (*Podiceps cristatus*), mergansers, gulls and terns. The trophic relations between phytoplankton, zooplankton, fish, birds and the fishery were estimated over the period 1983-1987. The zooplanktivorous smelt, producing 130 $kg{\cdot}ww{\cdot}ha^{-1}{\cdot}year^{-1}$, appeared to be a key species within the food web. Smelt was mainly consumed by perch (59 $kg{\cdot}ha^{-1}{\cdot}year^{-1}$). Birds consumed 48 $kg{\cdot}ha^{-1}{\cdot}year^{-1}$ of fish, of which 42% was smelt. The impact of the fishery consisted of overexploitation of eel and pikeperch stock and of catching large amounts of 0- and 1-group fish as by-catch in the fyke net fishery. The discarded by-catch was utilized by gulls and terns.

Introduction

IJsselmeer, with its 182,000 ha, is one of the larger freshwater lakes in Europe. Due to the nutrient input from the River IJssel, a branch of the Rhine River, and its shallowness, IJsselmeer has a high productivity. It serves many functions, e.g., fisheries, recreation, drinking water supply, transport, and as a rest and forage area for birds.

Some of these functions conflict with each other, e.g., fisheries and birds use the same resource. The fishers blame the cormorants for the decline in the eel catches. The cormorants which forage in IJsselmeer, come mainly from colonies in three nearby marshes: Lepelaarsplassen, Naardermeer and Oostvaardersplassen. These colonies are unique by size in Europe and are therefore of international importance. The impact on the lake ecosystem of both fishery and cormorants has never been quantified simultaneously in the case of IJsselmeer.

IJsselmeer is one of the most important haunts for waterbirds and is thereby a wetland of international importance (van Eerden and Zijlstra 1986). Concerning the fish-eating species, a year-round usage occurs, both by birds from colonies of breeding species (gulls, terns and cormorants) as well as by wintering and migratory species (mergansers, black tern [*Chlidonias niger*]).

The aim of this study is to depict the major routes for the energy flow in the IJsselmeer ecosystem, thus elucidating especially the impact of both fisheries and birds on the ecosystem.

Materials and Methods

Study Area

The situation of IJsselmeer and of the marshes, where the cormorants breed, is presented in Fig. 1. Since 1975, IJsselmeer has been partitioned into a 112,000-ha northern and a 70,000-ha southern parts. The water is supplied for 70% through the River IJssel. The phosphorus load amounted to 7 and 1.4 $g \cdot m^{-2} \cdot year^{-1}$ in the northern and southern parts, respectively. The nitrogen load is about 10 times as high (Berger and Sweers 1988). Total phosphorous levels averaged 0.28 $mg \cdot l^{-1}$ and 0.15 $mg \cdot l^{-1}$ in the northern and southern parts, respectively, over the period 1983-1986. In the southern part, phosphorus is mainly absorbed to suspended silt and clay. Hence only 10% of phosphorus is directly available for growth of algae. From time to time growth of algae can be phosphorus-limited (Berger et al. 1986). Mean depth of the northern and southern parts, 4.5 and 3.6 m, respectively, was averaged (weighted for surface area), since the available information for birds and fisheries could not always be disaggregated.

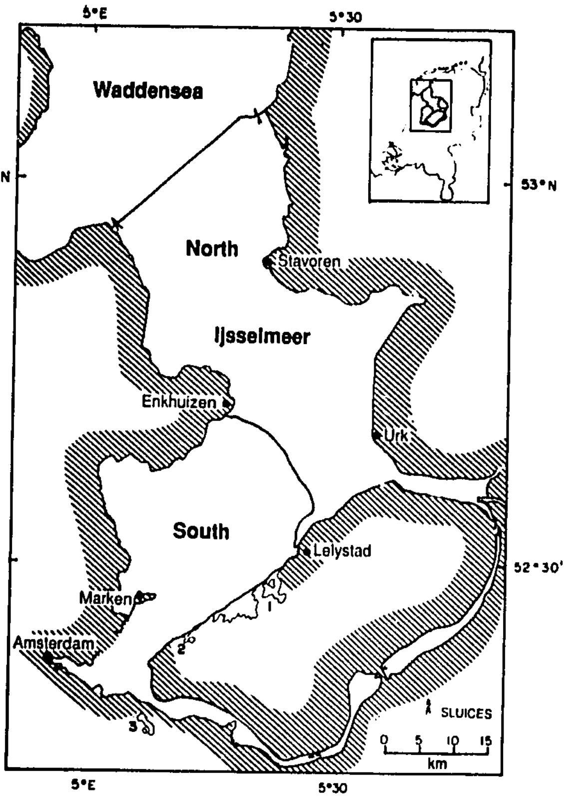

Fig. 1. The location of IJsselmeer and the marshes Oostvaardersplassen (1), Lepelaarsplassen (2) and Naardermeer (3). The insert shows The Netherlands.

Phytoplankton

Diatoms (*Melosira* spp., *Asterionella formosa*) are generally found early in the year. The most abundant green algae are *Scenedesmus* spp., while *Microcystis aeruginosa* is the most abundant blue-green alga. In some years a bloom of *Oscillatoria agardhii* occurs (Berger and Sweers 1988). Phytoplankton concentrations were measured at three stations in the northern and three stations in the southern parts of IJsselmeer. Data were available for the period 1983-1986. Chlorophyll *a* concentrations were converted to wet weight as follows: 1 mg chlorophyll *a* = 100 mg dry weight and 1 g wet weight = 0.15 g dry weight. As primary production data were not available, data from Berger and Sweers (1988) for 1976 were used: daily biomass gross production averaged 14% of total biomass, which results in a gross production/biomass (P/B) ratio of 51.1 $year^{-1}$.

Zooplankton

No zooplankton data were available for the period 1983-1987, so the zooplankton data from a lake-wide survey during June, August and September 1987-1989 were used. Sampling was carried out on 22 stations with a Friendinger or Schlinder-Patalas sampler.

P/B ratios are based on estimates made by Vijverberg et al. (1990) in Tjeukemeer, which is situated in the northern part of the Netherlands and has a similar zooplankton community. *Daphnia galeata, D. cucullata, Bosmina coregoni, B. longirostris, Chydorus sphaericus, Leptodora kindtii* and cyclopoids are the main species. On a yearly basis, mean P/B ratio for these species was 52.7.

Fish

Fish stock biomasses were estimated during November surveys, using a 20-mm stretched mesh bottom trawl. The swept-area method was used to calculate abundance per hectare. For smelt the volume swept was used, since it was the only species which was clearly not confined to demersal layers. Thereby it is assumed that smelt is uniformly distributed over the water column in the shallow IJsselmeer. This asssumption is not yet substantiated by survey data, but is probably close to reality.

Since only the production of predators is known, a transfer efficiency (ratio of the biological production of predator and prey) of 20% from fish to fish (Pauly 1986) and 10% from macrofauna and zooplankton to fish was used.

Birds

Birds were counted by means of aerial surveys on a monthly basis over the entire lake. Fish predation by birds was investigated by examining pellets of gulls and cormorants and stomachs of drowned mergansers and grebes. Some data on bird diets were collected in other years than the period 1983-1987, due to the nonavailability of certain bird species during that period.

Fishery

The yield of the fishery was estimated on the basis of registered landing statistics. Age and size composition were based on market sampling programs. Surveys revealed the amount of by-catch, composed of 0- and 1-group fish, in the fyke net fishery. This by-catch is discarded and is thought to be the main food source for gulls and terns.

Results

The estimated biomass, production and consumption are presented in Fig. 2 and Table 1, while the diet compositions of the major predators are presented in Table 2. The thickness of the lines indicates the amount of energy flow. Solid boxes and lines represent quantified biomass and transfer estimates. Dotted boxes and lines represent predator-prey relationships for which only tentative information is available.

Planktivorous fish consumed about 10% of the zooplankton production. Smelt had the highest production (130 kg·ha^{-1}·year^{-1}) of all fish species. Piscivorous fish and birds utilized 77% of this production. Perch had the highest production of the piscivorous fish (13.9 kg·ha^{-1}·year^{-1}).

Fish predation by birds occurs all over the lake, but is especially prominent in the neighborhood of resting places or colonies. On an annual basis, cormorants consume about 22, gulls and terns 14, mergansers 7 and grebes 6 kg·ha^{-1} of fish. Smelt, ruffe and small perch are important prey for most bird species. Cormorants take larger prey as well, such as adult perch and roach. Although in low abundance (0.01 kg·ha^{-1}), red-breasted mergansers (*Mergus serrator*) consumed the largest amount of eel (0.7 kg·ha^{-1}·year^{-1}). However, the overall consumption of eels by birds nowadays is very small, and eels formed less than 1% of the diet (i.e., 0.1 kg·ha^{-1} year^{-1}).

The impact of the fishery consisted mainly of removing large piscivorous eel, perch and pikeperch. The fyke net fishery for spawning smelt is found to be

Table 1. Biomass, production and consumption estimates of the major components of the various trophic levels in the IJsselmeer ecosystem. Biomass data are in kg·ww·ha^{-1}; production and consumption data are in kg·ww·ha^{-1}·year^{-1}.

Group	Scientific name	Code	Biomass	Production	Consumption
Algae		AL	1,928	98,521	-
Zooplankton		ZO	181	5,723	-
Smelt	*Osmerus eperlanus*	SM	66.1	129.8	1,298.0
Ruffe	*Gymnocephalus cernua*	RU	9.3	8.9	-
Roach	*Rutilus rutilus*	RO	15.0	9.0	-
Bream	*Abramis brama*	BR	9.5	3.1	-
Nonpiscivorous eel	*Anguilla anguilla*	N-EEL	9.6	2.9	-
Piscivorous eel		P-EEL	2.4	0.7	3.5
Nonpiscivorous perch	*Perca fluviatilis*	N-PE	2.5	5.3	52.7
Piscivorous perch		P-PE	14.6	13.9	67.6
Pikeperch	*Stizostedion lucioperca*	PP	2.0	2.0	10.2
Herring gull	*Larus argentatus*	HG	0.0165	-	1.5
Black-headed gull	*Larus ridibundus*	BHG	0.0715	-	10.1
Greater black-backed gull	*Larus marinus*	GBG	0.0071	-	0.4
Little gull	*Larus minitus*	LG	0.0010	-	0.2
Common gull	*Larus canus*	CG	0.0019	-	0.2
Common tern	*Sterna hirundo*	CTE	0.0041	-	0.7
Black tern	*Chlidonias niger*	BTE	0.0053	-	1.1
Great-crested grebe	*Podiceps cristatus*	GR	0.0618	-	5.7
Goosander	*Mergus merganser*	GO	0.0651	-	5.6
Red-breasted merganser	*Mergus serrator*	REM	0.0113	-	1.1
Smew	*Mergus albellus*	S	0.0084	-	1.0
Cormorant	*Phalacrocorax carbo*	COR	0.2918	-	20.7
Fishery			-	23.2	
Total			-	1,503.4	

Table 2. Diet compositions (kg·ha^{-1}·year^{-1}) for some of the groups in the IJsselmeer ecosystem. Diets of consumer not included here have not been quantified. (ZO=Zooplankton; CH=chironomids; GA=*Gammarus* spp.; NE=*Neomysis integer*).

		Prey												
Predator		ZO	CH	GA	NE	SM	RU	RO	BR	N-EEL	P-EEL	N-PE	P-PE	PP
Fish														
Smelt	SM	1,298.0	-	-	-	-	-	-	-	-	-	-	-	-
Piscivorous eel	P-EEL	-	-	-	-	3.5	-	-	-	-	-	-	-	-
Nonpiscivorous perch	N-PE	24.2	3.7	12.6	12.1	-	-	-	-	-	-	-	-	-
Piscivorous perch	P-PE	-	-	-	-	58.5	9.1	-	-	-	-	-	-	-
Pike perch	PP	-	-	-	-	8.9	1.0	0.1	0.1	-	-	0.1	-	-
Birds														
Herring gull	HG	-	-	-	-	-	0.4	0.5	0.3	-	-	0.4	-	-
Black-headed gull	BHG	-	-	-	-	8.1	1.0	-	-	-	-	1.0	-	-
Greater black-backed gull	GBG	-	-	-	-	-	0.0	0.2	0.2	-	-	0.0	-	-
Little gull	LG	-	-	-	-	0.2	-	-	-	-	-	-	-	-
Common gull	CG	-	-	-	-	0.1	0.0	-	0.0	-	-	0.0	-	-
Common tern	CTE	-	-	-	-	0.6	0.0	-	-	-	-	0.1	-	-
Black tern		-	-	-	-	1.1	0.0	-	-	-	-	0.0	-	-
Great-crested grebe	GR	-	-	-	-	4.6	0.6	0.1	0.1	-	-	0.3	0.1	-
Goosander	GO	-	-	-	-	2.7	0.6	1.5	-	-	-	0.7	0.1	-
Red-breasted merganser	REM	-	-	-	-	0.3	0.0	0.0	-	0.7	-	0.0	-	-
Smew	S	-	-	-	-	0.9	0.1	0.0	-	-	-	-	-	-
Cormorant	COR	-	-	-	-	1.7	8.4	3.1	-	0.1	0.1	7.3	-	-
Fishery		-	-	-	-	9.0	-	1.8	3.9	1.0	3.0	-	3.5	1.0
Total		1,322.2	3.7	12.6	12.1	100.2	21.2	7.2	4.6	1.8	3.1	9.9	3.7	1.0

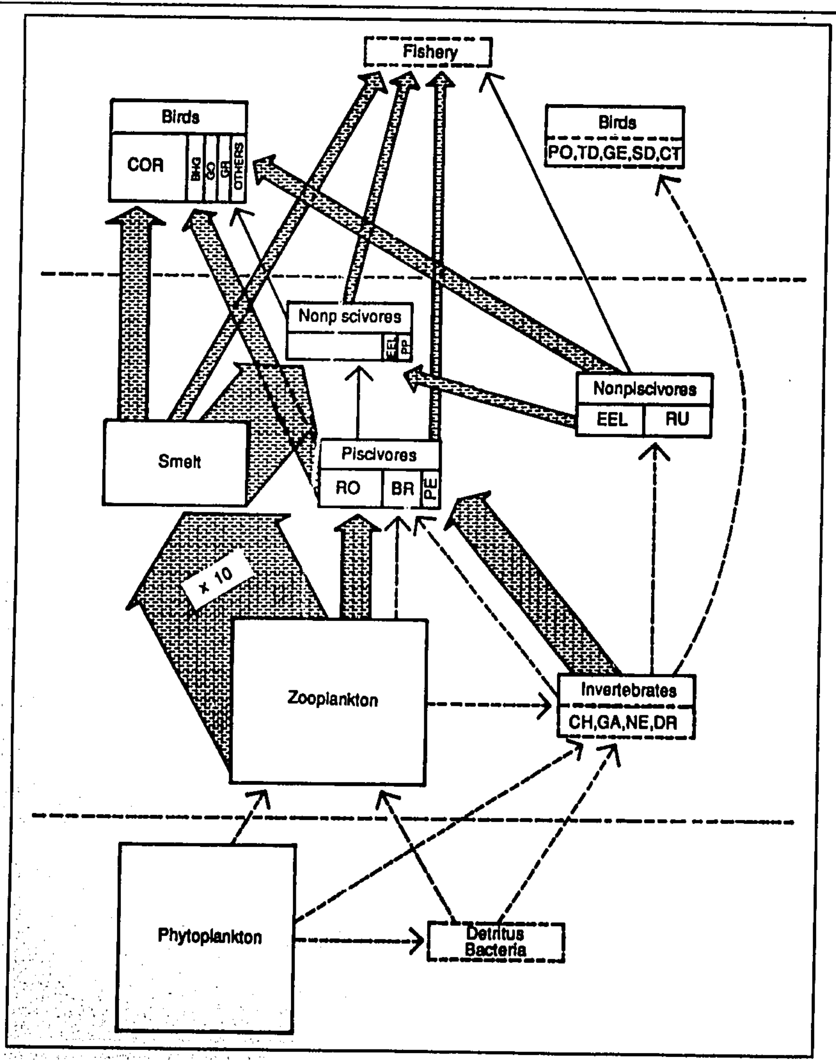

Fig. 2. Biomass and consumption of the major components of the various trophic levels in the IJsselmeer ecosystem. Solid boxes and lines are quantified estimates. The size of the boxes and the thickness of the lines depict the amount of biomass or consumption by a certain component. With the multipliers at the right, biomass can be adjusted to the scale of the middle panel. Dotted boxes are components thought to be important but not quantified. Dotted lines are guesstimated transfer routes (Note that the consumption of invertebrates and zooplankton by perch is quantified, while the consumption by roach and bream is not). See Tables 1 and 2 for codes, also DR = *Dneissena polymorpha*; PO = pochard; TD = tufted duck; GE = goldeneye; SD = scaup duck; and CT = coot.

of minor importance compared to the consumption by perch and birds.

No information is yet available for biomass, production and consumption of macrofauna (*Dreissena polymorpha, Gammarus tigrinus, Neomysis integer*, chironomids and oligochaetes) and macrofauna-eating birds (tufted duck [*Aythya fuligula*], scaup duck [*A. marila*], pochard [*A. ferina*], goldeneye [*Bucephala clangula*] and coot [*Fulica atra*]). These transfer routes, which are thought to be of great importance, will have to be quantified later.

Conclusion

- Smelt is a key species in the IJsselmeer ecosystem: it is the main consumer of zooplankton (1,298 kg ha year^{-1}) and the main food source (42%) for fish-eating birds. Smelt is also the main prey species for the commercially important eel, perch and pikeperch. Management strategies should take this into consideration.
- Perch is the most important piscivorous fish species and cormorants are the most important fish-eating birds, based on the amount of fish consumed.
- Fish biomass may be underestimated, since trawl efficiency was assumed to be 100%. (Comparison of trawl survey indices and cohort analysis of the commercial catch of perch and pikeperch did not show an underestimation by the survey indices. However, this may be due to the fact that sampling is carried out at places where fish biomasses are high).
- This study was meant as an interdisciplinary approach, and quantified production and consumption in the same units (ww·kg·ha^{-1}year^{-1}). This gave an overview of which information is available and what important information is still lacking.
- Although the data presented here did not lead to a detailed, complete foodweb, they nevertheless scaled some problems (cormorants are not the most important predators of eel and the fishery is not the most important cause of smelt mortality) to a level which appears more realistic than previously assumed.

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A Preliminary Ecosystem Model of a Eutrophic Lake (Lake Aydat, France)

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Abstract

An attempt is made to model the eutrophic ecosystem of Lake Aydat in the Massif Central, France, with emphasis on the two dominant fish species, perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). The preliminary model raises interesting questions of trophic efficiencies and food chain structure. A better understanding of the functioning of the ecosystem has been reached with this model, which includes some extraordinarily long food chains (of up to nine trophic levels).

Introduction

In response to the challenge posed and the opportunity offered by the ECOPATH II model of Christensen and Pauly (this vol.), an attempt is presented here to model the Lake Aydat, Massif Central, France.

Lake Aydat is classified as a eutrophic dimictic lake (Millerioux 1976) and is located in the Parc Régional des Volcans d'Auvergne in the Puy de Dôme region in the Massif Central in France. Fig. 1 shows the lake outline and provides various statistics on Lake Aydat.

This lake has been the object of numerous studies, especially by the Freshwater Hydrobiology team of the Zoology-Protistology Laboratory, Université Blaise Pascal, Clermont-Ferrand; the bulk of which focused on estimation of planktonic and bacterioplanktonic biomass. Studies of the fish populations in the lake are scarce. However, a recent study conducted by Jamet et al. (1990) on the diel feeding cycle of roach adults and roach fry population (Reyes-Marchant et al. 1992) in Lake Aydat helped to identify these populations' feeding habits. A recent thesis by Jamet (1991) discusses the ecology and biology of Lake Aydat fishes, but was completed too late to be considered when developing the model presented below (but see Postscript).

There is no continuous fishery in Lake Aydat, only some occasional sports fishers. Their catches remain largely undocumented but can be assumed to be insignificant. No information is available on the benthic populations.

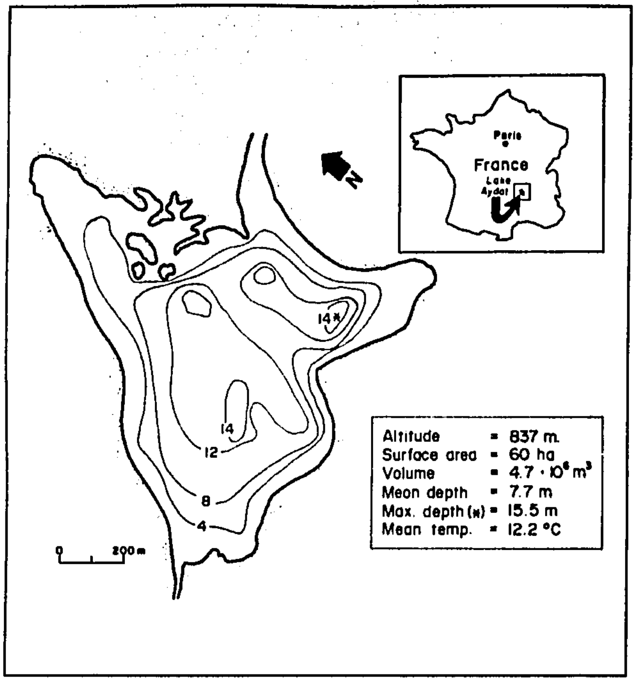

Fig. 1. Lake Aydat, Puy-de-Dôme, Massif Central, France, showing depth isolines, in m (adapted from Aleya et al. 1988).

Materials and Methods

As the ECOPATH II approach is discussed in more detail in Christensen and Pauly (this vol.), only the balanced equation used in ECOPATH II for each "box" is recalled here, i.e.,

$$B_i * P_i/B_i * EE_i = \sum(B_j * Q_j/B_j * DC_{ji}) * EX_i$$

where B_i is the biomass of species i; P_i/B_i its production/biomass ratio; EE_i its ecotrophic efficiency, i.e., the proportion of the production that is used for predation or catches; and where B_j is the biomass of predator j; Q_j/B_j, its relative food consumption and DC_{ji} the fraction of species i in the diet of predator j.

In order to work with this model, an estimate of at least three of the four parameters should be available for each box, along with the diet composition. The following sections describe how these parameters were assembled for Lake Aydat.

Biomass Estimates

PRODUCERS

The phytoplanktonic populations of Lake Aydat are well-studied. Throughout the year, this eutrophic lake experiences three maxima of phytoplanktonic biomass, three of zooplanktonic biomass and three periods of increased water transparency, which follow the increases in zooplanktonic biomass (Aleya and Devaux 1989; Lair and Ayadi 1989). This suggests that grazing by zooplankton controls algal succession in the lake.

Aleya et al. (1988) investigated the 0-4 m zone of the lake and estimated an annual mean phytoplankton production of 78 mg·C·m^{-2}·hour^{-1}. They also gave a mean annual top layer biomass estimate of 6.95 mg·l^{-1} (= 47.8 g·m^{-2}). In a related study, Aleya and Devaux (1989) reported biovolumes for sizes of <12 µm at 0.12 mg·l^{-1} at the surface (1 m) and cholorophyll *a* concentrations of 22.5 µg·l^{-1} at the bottom.

The production of benthic producers is not known. Therefore it is assumed that benthic primary production dominates the 0-1 m zone of the lake and that the production per unit area is similar for phytoplankton and benthic producers. As 37% of the area is in the 0-4 m zone (see Fig. 1), it is estimated that 9.25% is in the 0-1 m zone. Total benthic production can then be estimated as 1,378 g·m^{-2}·year^{-1}.

The benthic producers include larger plants which are hardly used for consumption along with small groups such as diatoms and cyanophytic algae which are important in the diet of fishes (Jamet et al. 1990; Reyes-Marchant et al. 1992). A P/B ratio of 10 is therefore assumed for benthic producers, i.e., is a mean value taking into account the fast turnover rates of small organisms and the relatively lower turnover rates of leafy plants and grasses.

BACTERIOPLANKTON

Lair and Oulad Ali (1990) and Lair (1991, 1992) suggested that, in Lake Aydat, the considerable bacterioplankton biomass (free bacteria plus bacteria attached to detritus) in the 4-7 m zone is an important source of zooplankton food. Moreover, Marvalin et al. (1989) showed that bacterioplankton is not only found in the 4-7 m depth zone and reported (i) 0.08 mg·C·l^{-1} at 2 m, (ii) 0.1 mg·C·l^{-1} at 7 m and (iii) 0.09 mg·C·l^{-1} at 14 m. This leads to a mean biomass of 0.09 mg·C·l^{-1}. If a conversion factor from carbon to wet weight of 12 is assumed, then the mean wet bacterioplanktonic biomass is 1.08 mg·l^{-1} or 7.42 g·m^{-2}.

ZOOPLANKTON

Lair (1990) estimated zooplankton biomasses in 1984-1985. Her data led to annual mean biomasses of (i) rotifer: 2,905 mg·m^{-3} (20 g·m^{-2}), (ii) copepod: 3,250 mg·m^{-3} (22 g·m^{-2}) and (iii) cladoceran: 2,130 mg·m^{-3} (15 g·m^{-2}). If rotifers and cladocerans are considered to be herbivorous/detritivorous feeders and copepods carnivorous feeders (Lair and Hilal 1992), then the total biomass of herbivorous zooplankton in Lake Aydat is 35 g·m^{-2} and that of carnivorous zooplankton is 22 g·m^{-2}.

Relative Production and Food Consumption

PHYTOPLANKTON

Aleya and Devaux (1989) estimated P/B ratios of phytoplankton using different methods. Using cell counts, estimated annual P/B ratios were (i) 0.055 hour^{-1} (482 year^{-1}); (ii) using chlorophyll *a*, 0.035 hour^{-1} (307 year^{-1}). The latter estimate was used in the model presented below.

BACTERIOPLANKTON

The P/B ratio for bacterioplankton was obtained from Jϕrgensen (1979, Table A174) where a mean value of 0.45 day^{-1} (about 160 year^{-1}) was reported for the "southern seas of the USSR". Assuming a gross efficiency of 50%, Q/B was set at 320 year^{-1}.

ZOOPLANKTON

Herbivorous zooplankton P/B values listed in Jϕrgensen (1979, Table A469) were averaged to obtain an annual ratio of 16 year^{-1}. Only one estimate was given for predatory zooplankton (P/B = 5 year^{-1}). A GE value assumed at 25% led to an estimate of Q/B = 20 year^{-1} for the predatory zooplankton. There is no available estimate for herbivorous zooplankton; therefore, a gross efficiency value of 30% was used which sets Q/B at 53 year^{-1}.

INSECTS AND MOLLUSCS

There is no available information in the literature on the benthic populations in Lake Aydat. However, Jϕrgensen (1979, Table A269) lists P/B ratios for several species of invertebrates including some that occur in Lake Aydat. Thus, P/B values for *Asellus*, *Chaoborus*, *Chironomus*, *Gammarus* and miscellaneous annelids, coelenterates and molluscs were averaged to give a mean value of 3 year^{-1}. Assuming a gross efficiency of close to 30%, Q/B can be set at 11 year^{-1}.

FISH POPULATIONS

There is no regular fishery in Lake Aydat and thus, P/B was here set equal to natural mortality (M), as obtained from the empirical formula of Pauly (1980) and the growth parameter estimates listed in Table 1. The M estimates were adjusted downward in cases where the gross efficiency estimates reached 30% or more.

Table 1. Growth parameters, mortality, condition factors, aspect ratios and food types for five fish species considered in the Lake Aydat model. These parameters were averaged for each species and used in the food consumption model of Palomares and Pauly (1989) to obtain estimates of Q/B. Mean environmental temperature used was 12.2°C; "A" is the caudal fin aspect ratio; and "F" refers to the food type used in that model.

Species	Area (sex)	L_∞ (cm TL)	K (year^{-1})	ϕ'	Sources/remarks
Pike (*Esox lucius*)	Windermere (M)	75.0	0.238	3.127	Johnson (1966)
	Windermere (F)	100.0	0.264	3.422	Pauly (1978), based on Nikolsky (1957)
	Wisconsin	93.3	0.310	3.431	
	Aral Lake	80.6	0.204	3.122	
	Peipus Lake (M)	64.4	0.332	3.139	
	Peipus Lake (F)	97.5	0.208	3.296	
	Chany Lake (M)	106.0	0.123	3.141	
	Chany Lake (F)	141.0	0.097	3.285	
	Schlei-Fjord	106.0	0.248	3.445	Nauen (1984)
	MEANS:	96.0	0.201	3.268	t_0 = -0.61; M = 0.312; A = 3.39; F = piscivore; Q/B(year^{-1}) = 1.179; condition factor (a = 0.009276) computed from data in Muus and Dahlström (1973), i.e., 455 g/32.5 cm, 6,500 g/95 cm, b = 3.
Sander (*Lucioperca lucioperca*)	Kuban River	85.6	0.238	3.242	Pauly (1978), based on Nikolsky (1957)
	Don River	86.0	0.168	3.094	
	Aral Lake	79.5	0.204	3.110	
	Il'men Lake	104.0	0.129	3.145	
	Southern Caspian	40.0	0.333	2.727	
	Schlei-Fjord	79.2	0.216	3.132	Nauen (1984)
	MEANS:	79.0	0.190	3.075	t_0 = -0.683; M = 0.317; A = 1.69; F = piscivore; Q/B(year^{-1}) = 0.933; condition factor (a = 0.008957) computed from data in Muus and Dahlström (1973), i.e., 1,000 g/45.5 cm, 12,000 g/120 cm, b = 3.

continued

Table 1 continued

Species	Area (sex)	L_∞ (cm TL)	K (year^{-1})	ϕ'	Sources/remarks
Perch *(Perca fluviatilis)*	Aral Lake	23.3	0.405	2.342	Pauly (1978), based on Nikolsky (1957)
	Petschora	38.0	0.124	2.253	
	Sweden	30.0	0.200	2.255	Alm (1952)
		34.0	0.130	2.177	Alm (1952)
	Orava Reservoir	41.9	0.123	2.334	Pauly (1978), based on Nikolsky (1957)
		36.9	0.119	2.210	
		29.3	0.354	2.483	
	Schlei-Fjord	50.0	0.172	2.633	Nauen (1984)
		50.9	0.120	2.493	
	Lake Aydat	31.8	0.161	2.212	
	MEANS:	36.6	0.163	2.339	t_o = -0.989; M = 0.356; A = 1.69; F = piscivore; Q/B(year^{-1}) = 0.933; length-weight relation W = 0.008618 $L^{3.171}$.
Pope *(Acerina cernua)*	Lake Aydat	15.0	0.306	1.838	Nonlinear fitting, setting $L_{max} = L_\infty$ and using length-at-age data obtained by scale reading
		25.0	0.055	1.535	Nonlinear fitting, setting $L_{max} = L_\infty$ from Terofal (1984) and using length-at-age data from scale readings.
	MEANS:	20.0	0.121	1.687	t_o = -1.592; M = 0.348; A = 0.85; F = omnivore; Q/B(year^{-1}) = 2.578; length-weight relation W = 0.003372 $L^{2.705}$.
Roach *(Rutilus rutilus)*	Tjeukemeer	20.7	0.231	1.993	Nonlinear fitting, using data in Kempe (196 Goldspink (1978, 1979) and Larsson (1980)
	Rostherne Mere	21.8	0.707	2.526	
	Mälaren	31.4	0.146	2.159	
	Sövdeborgssjon	30.8	0.068	1.811	
	Volvi	32.8	0.076	1.913	Nonlinear fitting, using data in Papageorgiou (1979)
	Halmsion	18.9	0.158	1.752	Nonlinear fitting, as cited in Goldspink (1979)
	Petschora	42.5	0.080	2.160	Pauly (1978), based on Nikolsky (1957)
	Il'men Lake	26.2	0.180	2.092	
	Aral Lake	51.3	0.101	2.425	
	Don River	35.5	0.173	2.338	
	Lake Aydat	25.0	0.900	2.750	L/F data analyzed with ELEFAN I.
		53.3	0.128	2.561	Based on L/F data analyzed with Bhattacharya's method.
		30.0	0.147	2.122	Nonlinear fitting of length-at-age data from scale readings.
	MEANS:	32.3	0.152	2.200	t_o = -1.592; M = 0.353; A = 1.48; F = omnivore; Q/B(year^{-1}) = 2.408; mean weights were obtained from three length-weight relationships: A) W = 0.03954$L^{2.883}$ (Pivnicka 1975) B) W = 0.0356$L^{3.405}$, males (Papageorgiou 1979) C) W = 0.0215$L^{3.606}$, females (Papageorgiou 1979)

The Q/B estimates were obtained from the empirical formula of Palomares and Pauly (1989), except for roach. Several estimates of daily ration were obtained from independent sources (Table 2) and turned, using the model of Pauly (1986), into estimates of Q/B. An annual Q/B value of 29.3 was estimated for roach fry by integrating between W_r = 0.001 g and W_{max} = 1.4 g, based on the assumption that 0+ roach can reach a maximum length of 5 cm (about 1.5 g). A value of Q/B = 9.21 $year^{-1}$ was estimated for adult fishes by integrating between W_r = 1 g and W_{max} = 90% of W_∞. The final estimates used in the ECOPATH II model were the means of the estimates obtained as described above and those listed in Table 1 (i.e., based on the empirical formula of Palomares and Pauly (1989)).

Table 2. Daily ration estimates as percentage of body weight for adult roach (natural populations) used in the estimation of Q/B with the integration method of Pauly (1986).

W (g)	Rd % BWD	T (°C)	Source
20	4.00	14	Persson (1982)
46	1.09	-	Persson (1983)
66	1.02	-	Persson (1983)

Ecotrophic Efficiencies and Diet Compositions

Ecotrophic efficiencies were set at 0.95 for perch, roach and benthos. Table 3 presents the diet composition of the different species/groups. This information was mostly obtained from the literature. Note that the diet composition of the top predator box is based on the diet of pike while the perch/pope box is based on the diet of perch.

Table 4 shows input data by group for the Lake Aydat ecosystem.

Results and Discussion

Fig. 2 illustrates the ECOPATH II box model obtained for Lake Aydat in the mid-1980s. Assuming a pike/sander biomass of 1 $g{\cdot}m^{-2}$, the perch/pope biomass could reach 3.3 $g{\cdot}m^{-2}$ and the total roach biomass a level of 0.62 $g{\cdot}m^{-2}$.

The ecotrophic efficiencies estimated by ECOPATH II for pike, zooplankton, bacterioplankton and phytoplankton appear reasonable. The low EE value of 0.037 for the top predator box implies that most of this group's production ends up as detritus when these fishes die of old age. Had the occasional catches taken by anglers been included, the EE would have been higher.

The phytoplankton EE of 0.16 is, as expected, relatively low. Blooms were observed to occur prior to zooplankton biomass maxima (Lair and Ayadi 1989). During these periods, supply exceeds demand. With a fast turnover rate, much of this excess production dies to become detritus. However, the remaining phytoplankton is consumed by the subsequently increasing zooplankton population. As pointed out by Lair and Ayadi (1989), the phytoplankton biomass of Lake Aydat is largely controlled by zooplankton grazing and thus periods of clear waters (i.e., low abundance of phytoplankton) occur after zooplankton blooms. As expected, a very

Table 3. Diet composition (%) of the species/groups considered in the ECOPATH II model of Lake Aydat. Group 9 is benthic producers, 10 phytoplankton and 11 detritus.

	Prey											
Predator	1	2	3	4	5	6	7	8	9	10	11	Sources
1. Pike/sander	1.0	35.9	35.0	20.0	8.1	-	-	-	-	-	-	Bregazzi and Kennedy (1980), Diana (1979)
2. Perch/pope	-	13.0	3.6	7.1	64.3	4.0	3.6	-	-	-	4.4	Persson (1986), Eie and Börgström (1981), Thorpe (1972-1973)
3. Roach adults	-	-	-	0.1	39.3	13.5	3.6	0.4	24.2	7.0	11.9	Weatherly (1987)
4. Roach fry	-	-	-	-	17.0	61.9	10.0	2.0	0.1	9.0	-	Eie and Börgström (1981)
5. Insects/molluscs	-	-	-	-	-	10.0	20.0	40.0	10.0	10.0	10.0	Assumed
6. Predatory zooplankton	-	-	-	-	-	10.0	29.0	20.0	-	40.0	1.0	Assumed
7. Herbivorous zooplankton	-	-	-	-	-	-	-	20.0	-	75.0	5.0	Assumed
8. Bacterioplankton	-	-	-	-	-	-	-	-	-	40.0	60.0	Assumed

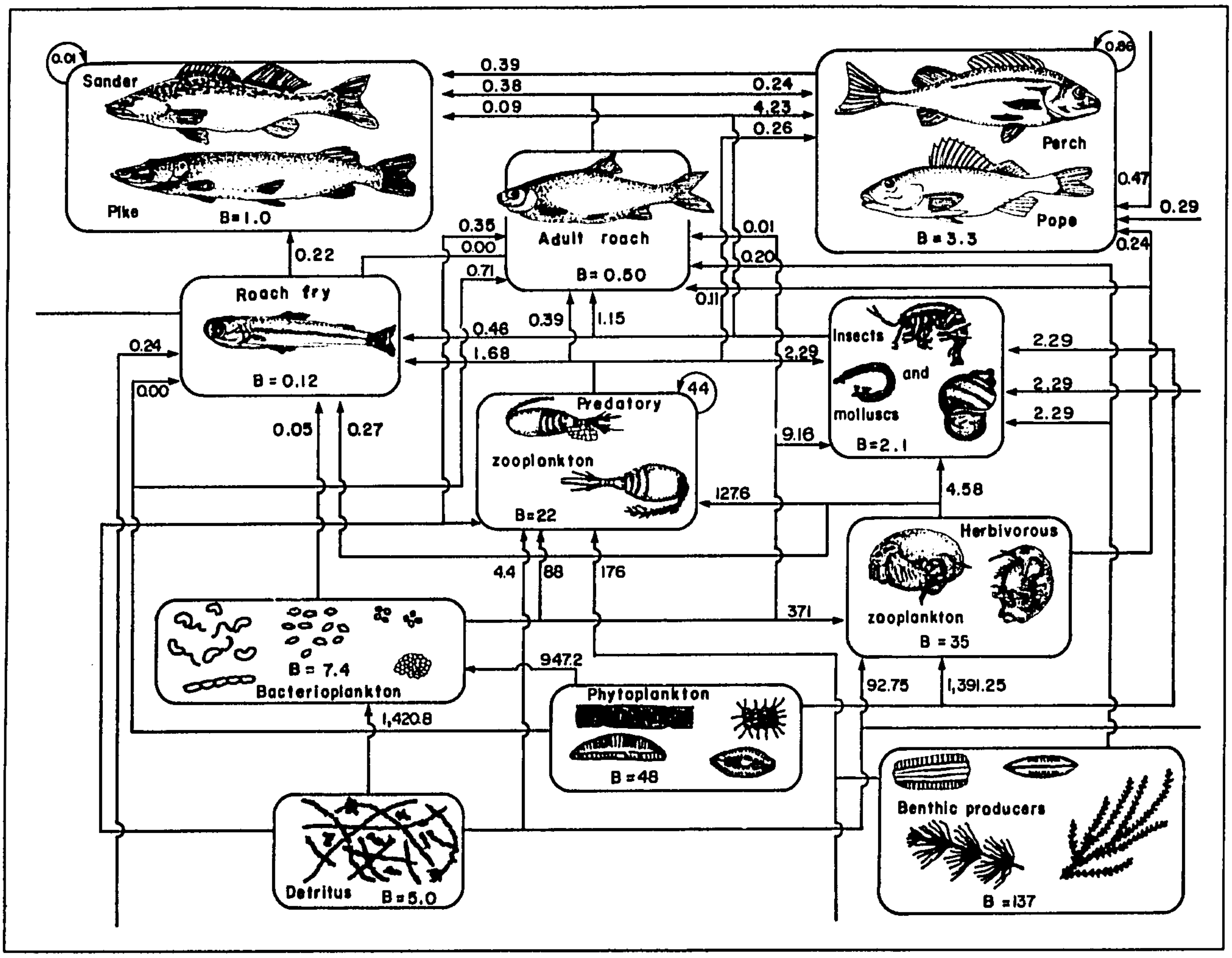

Fig. 2. A quantitative representation of the trophic interaction in Lake Aydat, France. All flows are expressed in g·m^{-2}year^{-1}, while biomasses (B) are in g·m^{-2}.

Table 4. Selected input for (without brackets) and output (with brackets) for data from the steady-state model of Lake Aydat.

Group	Trophic level	Biomass (gm^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE
Pike/sander	(4.4)	1.0	0.3	1.1	(0.04)
Perch/pope	(3.9)	(3.3)	0.4	2.0	0.95
Roach adults	(3.0)	(0.5)	1.3	5.8	0.95
Roach fry	(3.5)	(0.1)	6.0	22.4	0.95
Insects/molluscs	(2.8)	(2.1)	3.0	11.0	0.95
Predatory zooplankton	(2.7)	22.0	5.0	20.0	(0.44)
Herbivorous zooplankton	(2.2)	35.0	16.0	53.0	(0.24)
Bacterioplankton	(2.0)	7.4	160.0	320.0	(0.40)
Phytoplankton	(1.0)	48.0	307.0	0.0	(0.16)
Benthic producers	(1.0)	137.0	10.0	0.0	(0.13)
Detritus	(1.0)	5.0	-	-	(0.10)

low EE was estimated for benthic producers, which are hardly fed upon. Consumption of "live" matter was limited to diatoms and blue-green algae which form a relatively small proportion of the biomass of the benthic producers (although not of their production). This is in accordance with findings for many other systems reported in this volume.

When the food source is depleted, it is possible that zooplankton dies (to become detritus) before they can be exploited by the roach population which builds up around the same time. However, the total roach biomass as estimated by ECOPATH II does not seem large enough to be able to deplete its zooplankton food source. Thus the relatively low EE

Table 5. Result of trophic aggregation of the flows ($g \cdot m^{-2} \cdot year^{-1}$) in the Lake Aydat ecosystem, showing how flows are distributed by trophic levels. The bottom line gives the trophic transfer efficiencies estimated as the percentage of the flows on a trophic level that is either harvested or transferred to the next trophic level.

Group	Absolute flows by trophic level						
	I	II	III	IV	V	VI	VII
Pike/sander	-	-	0.3	0.4	0.43	0.08	0.01
Perch/pope	-	0.3	2.0	3.4	0.76	0.07	0.00
Roach adults	-	1.3	0.6	0.9	0.13	0.01	-
Roach fry	-	0.3	1.2	1.1	0.15	0.00	-
Insects/molluscs	-	6.9	13.9	2.0	0.15	-	-
Predatory zooplankton	-	200	211	28.4	-	-	-
Herbivorous zooplankton	-	1,484	371	-	-	-	-
Bacterioplankton	-	2,368	-	-	-	-	-
Benthic producers	14,736	-	-	-	-	-	-
Phytoplankton	1,370	-	-	-	-	-	-
Detritus	15,731	-	-	-	-	-	-
Total flow	31,837	4,061	600	36.2	1.61	0.16	0.01
Transfer efficiencies (%)	-	14.3	5.7	4.6	9.9	4.5	1.2

values of 0.44 and 0.24 for predatory and herbivorous zooplankton, respectively, are as could be expected.

The diet compositions for the fish species are based on various published sources. Some very long food chains seem to exist in the system, e.g., detritus→ bacterioplankton → herbivorous zooplankton → predatory zooplankton → insects/ molluscs → roach fry → roach adults → perch/pope → pike/sander, including a total of nine trophic levels. Such long food chains are very rare in system descriptions (see other contributions in this volume). One reason for this could be that long food chains are inherently unstable; they often include chain-links with very small flows, and these are probably rather vulnerable. As a result of the long food chains, numerous trophic levels appear when performing a trophic aggregation of the flows in the system using the method described by Christensen and Pauly (1992). The result of the trophic aggregation is shown in Table 5 along with the trophic transfer efficiencies by trophic level. These can be seen to vary considerably without any consistent pattern. Interesting is that the low efficiency on trophic level IV is caused mainly by the low utilization of predatory zooplankton in the system (EE = 0.44).

The present analysis has been initiated in an attempt to gather available information from Lake Aydat and to put this into context. We find that the exercise has been worthwhile; a preliminary model can be used to pinpoint lacking information. In addition, we conclude that the model along with its descriptive diagnostics raises interesting research topics to be addressed in future investigations in order to improve our understanding of the Lake Aydat ecosystem.

Postscript (June 1993)

Following completion of the model presented above, one of us (PRM) constructed a revised model in which the catch samples in Jamet (1991) were used to adjust (= reduce) the biomass of pike and sander relative to that of adult roach. Also, the absolute biomass of juvenile roach was reestimated. As both models of Lake Aydat were constructed from the "top down," this results in a smaller system throughput for the new model and a lower estimated primary production (Reyes-Marchant 1993). The input data for both the original and revised models are included in the files documented in Appendix 4.

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The Ecosystem of Lake Kinneret, Israel

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Abstract

Data collected over more than 20 years at the Kinneret Limnological Laboratory were used in an ECOPATH II model of the Lake Kinneret ecosystem, Israel. For this system, very reliable and detailed estimates were available for the biomass and production of phytoplankton and zooplankton and the diet and catches of the main fish species. Recent studies at the Kinneret Laboratory have produced estimates for biomass and production for bacteria and protozoa, allowing these ecosystem components to be included. Among the most important results: (1) the bacterial loop consumes nearly half of the primary production (as detritus); (2) predatory copepods consume at least 4 times more herbivorous zooplankton than do fish, and (3) about 90% of the zooplankton is consumed, so fish populations cannot be much larger than we have estimated these to be.

Introduction

Lake Kinneret is a warm monomictic lake located in the northern end of the Jordan Valley, an extension of the Great African Rift Valley. The lake is 22 km wide, 14 km long, and has a surface area of 168 km^2. When the lake is full (at 209 m below sea level), it has a volume of 4 x 10^9 m^3, a mean depth of 24 m and a maximum depth of 42 m. The lake is strongly stratified from April-May to December, and completely homothermic between December and February.

Since the lake is Israel's only major freshwater body, it is important for tourism and commercial fishing in addition to its critical importance as a source of drinking water. The Kinneret Limnological Laboratory (KLL) was established in 1968 to provide the scientific information necessary for management of these sometimes conflicting uses. Thus, there exists an extensive data collection which can be used as input for modelling efforts.

Using a box model of the Kinneret ecosystem, Serruya et al. (1980) described the main pathways of carbon flow and emphasized the importance of two distinct food chains: a nanoplankton-zooplankton-lavnun (the cyprinid fish *Mirogrex terraesanctae*, sometimes referred to as the Kinneret sardine) pathway and a *Peridinium*-detritus pathway. Both pathways operate during the winter-spring season when net production of organic carbon is positive. During the summer only the grazing pathway is active, and since respiration costs are high, the organic carbon accumulated during the winter-spring is consumed.

During the 10 years that have passed since the modelling effort of Serruya et al., there have been some major changes in the lake system. For example, fish stocking practices have been changed and tourism has increased. There have also been changes in some of the ecosystem components. Although the structure of the ECOPATH II model is somewhat different from the model used by Serruya et al., comparison of the results of the two models should shed some light on ecosystem changes which may have occurred during the last 10 years. In addition, the application of the ECOPATH II model to a large number of ecosystems provides a unique opportunity for comparison.

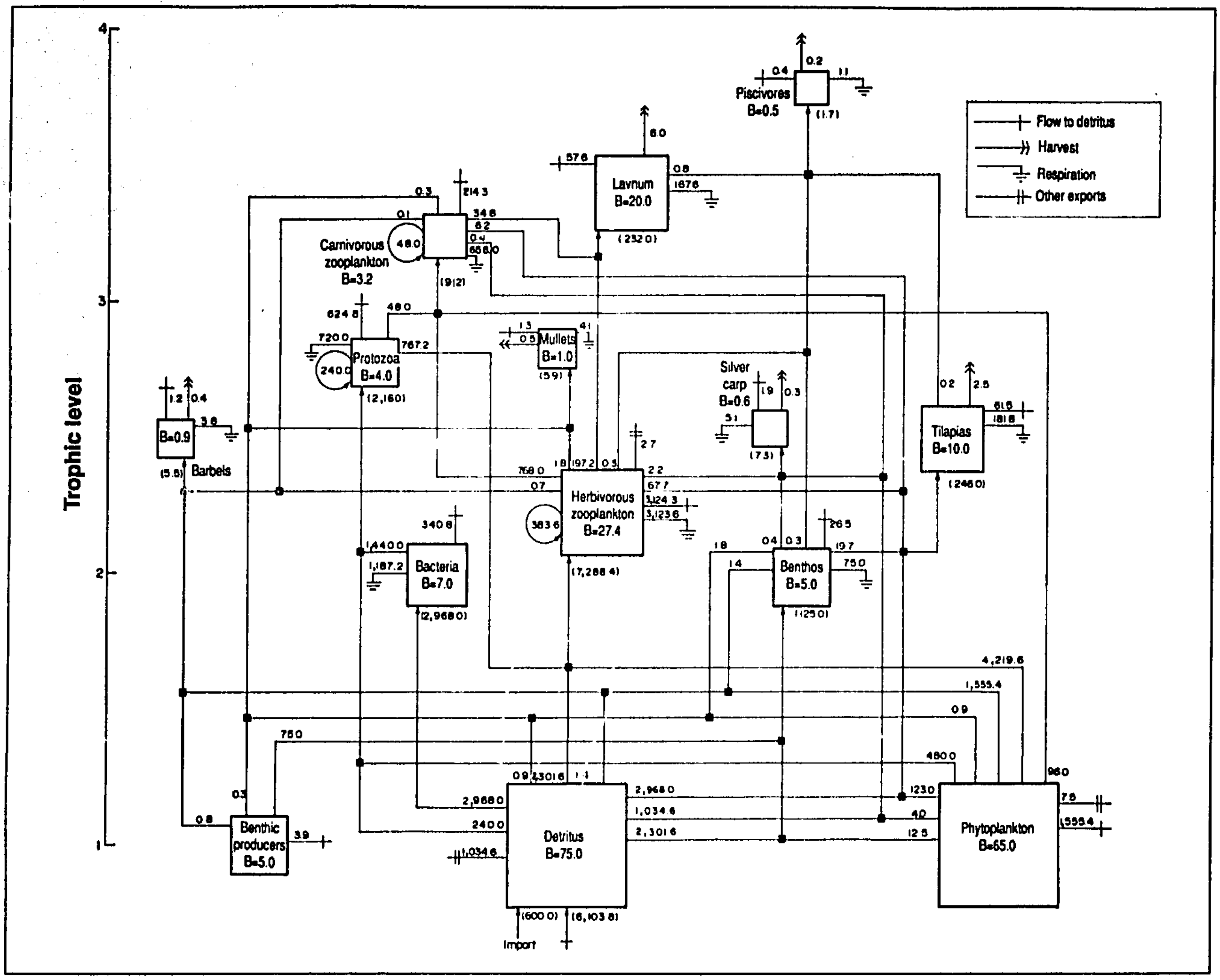

Fig. 1. Food web of Lake Kinneret, Israel. Flows are expressed in g wet weight·m^{-2}year^{-1}. For each ecosystem component the biomass (B) is given in g wet weight·m^{-2}.

Methods

ECOPATH II (version 2.1), a modified version (Christensen and Pauly 1992) of the ECOPATH model of Polovina (1984) was applied to Lake Kinneret. Although there is a strong seasonal effect on the structure of the ecosystem, data were averaged to obtain annual means. This is most problematic with the phytoplankton, as the dynamics of the *Peridinium* population differ completely from those of the nanoplankton species.

Throughout, units of g wet weight·m^{-2} were used for biomasses and g·ww·m^{-2}·year^{-1} for rates. Default values for non-assimulated food (20%) were used for all components except for bacteria, which were assumed to release only 10% of the detritus ingested in a form which could be used by other bacteria, and for herbivorous zooplankton for which a value of 40% was assumed. For bacteria the respiration losses were taken as 40% of ingested food (Cavari et al. 1978). The source of the numbers used for biomass, P/B, Q/B, and gross efficiencies (Table 1) will be discussed below for each ecosystem component.

Phytoplankton

Biomass estimates and P/B ratios were based on microscopically obtained biovolumes and C-14 incubations. Data were taken from annual reports of the KLL. Measured primary production is approximately 6,500 g·m^{-2}·year^{-1}.

Bacterioplankton

Recent studies of this component provide good estimates of biomass and production. Bacteria numbers range from 7 x 10^5 ml^{-1} to 3 x 10^7 ml^{-1} with normal numbers around 1x10^6ml^{-1}. Production rates have been estimated from thymidine uptake. We use a biomass of 7.0 g·m^{-2} and a conservative P/B of 212 year^{-1} (T. Berman, unpublished data). Gross efficiency was assumed to be 50%.

Table 1. Input values and calculated parameters (in brackets) for the ECOPATH II model.

	Group	Export (g·m^{-2}·year^{-1})	Biomass (g·m^{-2})	P/B (year^{-1})	Q/B (year^{-1})	Eff.	EE
1.	Bacteria	-	7.0	212.0	(424.0)	0.50	(0.97)
2.	Protozoa	-	4.0	300.0	(600.0)	0.50	(0.88)
3.	Herb. zooplankton	2.7	27.4	54.0	280.0	0.19	(0.96)
4.	Carn. zooplankton	-	3.2	35.0	300.0	0.12	(0.80)
5.	Lavnun	6.0	20.0	0.9	11.6	(0.08)	(0.38)
6.	Tilapias	2.5	10.0	1.5	24.6	(0.06)	(0.18)
7.	Silver carp	0.3	0.6	(1.2)	12.1	0.10	(0.41)
8.	Mullet	0.5	1.0	(0.6)	5.9	0.10	(0.85)
9.	Barbels	0.4	0.9	(0.6)	6.1	0.10	(0.73)
10.	Piscivores	0.2	0.5	(0.5)	3.3	(0.15)	0.80
11.	Benthos	-	5.0	5.0	(25.0)	0.20	(0.94)
12.	Phytoplankton	7.5	65.0	100.0	0	-	(0.76)
13.	Benthic prod.	-	5.0	16.0	0	-	(0.95)
14.	Detritus	1,034.6	75.0	-	-	-	(0.84)

Protozoans

The abundance and importance of protozoans have been emphasized in recent research at the KLL. Average biomass was estimated as 4 g·m^{-2} and P/B at 300 year^{-1}. Work has also been done on the grazing rates of these organisms, but not enough to obtain a reliable estimate of the relative food consumption by the population, Q/B. Instead, we assumed gross efficiency to be 50%, resulting in a Q/B of 600 year^{-1}.

Zooplankton

Detailed information on the abundance of zooplankton is available from monthly sampling. The zooplankton standing stocks have continuously declined during the past 10 years, reaching levels of less than 50% of those observed in the early 1970s (Gophen et al. 1990). For use in the ECOPATH II model, we chose slightly higher biomasses than those observed in 1989. Q/B ratios were obtained from feeding experiments (for example, Gophen 1981), and P/B ratios were calculated from rates of egg production (for methods, see Gophen 1978).

Benthos

The benthos of Lake Kinneret is not well developed. Benthic flora is restricted to a narrow nearshore strip, in part because the lake has relatively steep sides and few shallows. Development of macrophytes is restricted by unsuitable substrate and vigorous wave action. The anaerobic hypolimnion and unfavorable sedimentation regime prevent development of a large biomass of benthic invertebrates. In the absence of recent work on the benthic populations, we rely on the work of Dor (1970) and Por and Eitan (1970) for estimates of the biomass and P/B ratio for these groups. Gross efficiency (P/Q) was set at 20%.

Fish

Data on the catches of Lake Kinneret fish are published annually by the Fishery Department (Golani 1980-89). However, there are few published estimates of the size of the fish stocks. The biomass of lavnun (*Mirogrex terraesanctae*) was estimated as approximately 2,500 t from hydroacoustic surveys (Walline et al. 1992), but this estimate does not include lavnun too small to be recorded by the acoustic system. We used a value of 3,000 t for the total biomass of lavnun.

Published values on catch and stock size for St. Peter's fish (*Sarotherodon galilaeus*) for the years 1957-81 (Pisanty et al. 1987) were used to estimate the stock from catch in later years. An addition of 50% was added as an estimate of the unknown biomass of noncommercial tilapias. For lack of better data, the relation between catch and stock for St. Peter's fish was applied to the other commercial fish species to obtain biomasses. St. Peter's fish and all other tilapia-like fish were grouped together as "tilapias".

There are few estimates for the basic fisheries statistics or growth parameters which could assist in estimating the P/B and Q/B ratios needed in the model. From catch curve analysis, Landau (1977) estimated total mortalities (Z = P/B; year^{-1}) for lavnun of 0.89 for the years 1974-75 and for St. Peter's fish of 1.22-1.84 for the years 1967-77. Using the equation of Pauly (1980), the natural mortality

(M) for lavnun was estimated at 0.6 year^{-1}. If the biomass of lavnun in the exploited phase is taken as 2,800 t, and the yield is 962 t (the average catch 1986-89), then F=0.3 year^{-1}and Z= M +F = P/B =0.9 year^{-1}. P/B for lavnun was set at 0.9 year^{-1}, for tilapias at 1.5 year^{-1}, while P/B for silver carp, mullet and barbels was calculated based on an assumed gross food conversion efficiency (P/Q) of 0.10. For piscivores an assumed ecotrophic efficiency (EE) of 0.80 was used.

The food consumption of lavnun was experimentally determined to be 4% of body weight per day for adults (Gophen and Threlkeld 1989), equivalent to a Q/B of 15 year^{-1} and a gross efficiency of 6.6%. Zooplankton densities were higher in the experimental tanks than in the lake, as fresh zooplankton was added daily. Thus, the consumption was probably higher than the yearly average. For lavnun, Q/B can be calculated to be 11.6 year^{-1} (see Table 2). This is slightly lower than the experimental estimates and probably more realistic and we have opted to use it for these analyses. Details of estimation of Q/B for the various fish group are given in Table 2.

The diets of the main fish species are relatively well studied (see for example, Gophen and Landau 1977; Spataru and Gophen 1985a, 1985b; Gophen and Spataru 1989). All fish consume at least some zooplankton, especially in the summer when phytoplankton production is low (Table 3).

Results and Discussion

As in the model of Serruya et al. (1980), the ECOPATH II model of the food web of Lake Kinneret is characterized by two important pathways: the phytoplankton-detritus-protozoa pathway and the phytoplankton-herbivorous-zooplankton-carnivorous zooplankton pathway (Fig. 1). Thus, in a sense the bacterial loop "competes" with higher trophic levels for primary production.

Import of detritus was set at 600 g·m^{-2}·year^{-1} (from Serruya et al. 1980). The export of detritus (the difference in flow into and out of the detritus box) was calculated to be 1,035 g·m^{-2}·year^{-1}, reasonable for losses to the sediment (which are thought to be approximately equal to the import of organic material) and losses through the removal of water by the pumps of the National Water Carrier. It seems that the measured production is sufficient to support the ecosystem.

Carnivorous zooplankton (mainly copepods) are the main consumers of herbivorous zooplankton (mainly Cladocera). Fish consume about 12% of the herbivorous zooplankton production (Table 3). The results are very sensitive to any cannibalism by herbivorous zooplankton.

More than 90% of the zooplankton is consumed, so fish populations cannot be much larger than the estimates used here. Zooplankton population size in recent years has been less than that used in our

Table 2. Input data for calculation of consumption/biomass (Q/B) ratio for fish in Lake Kinneret using the empirical equation of Palomares and Pauly (1989). A is the caudal fin aspect ratio, F is the food type (0 for predators, 1 for herbivores/detritivores). Q/B is expressed on an annual basis. Temperature is 23°C.

Group	Main species	A	W_∞(g)	F	Q/B	Comments
Lavnun	*Mirogrex terraesanctae*	2.3	150	0	11.6	A based on Ben-Tuvia (1978)
Tilapias	*Sarotherodon galilaeus* *Sarotherodon aureus* *Tilapia zillii* *Tistramella* spp.	1.6	750	1	24.6	A based on Ben-Tuvia (1978)
Silver carp	*Hypophthalmichthys molitrix*	-	-	-	12.1	From Ruddle and Christensen (this vol.)
Mullet	*Mugil cephalus* *Mugil capito*	2.55	5,877	0	5.9	A and W_∞ from Palomares (1991)
Barbels	*Barbus longiceps* *Barbus canis*	1.39	1,000	0	6.1	Ben-Tuvia (1978) W_∞ assumed
Piscivores	*Clarias lazera*	1.26	16,000	0	3.3	A from Palomares (1991, for *Clarias gariepinus*), W_∞ from Ben-Tuvia (1978)

Table 3. Diet composition of the species considered in the ECOPATH II model of Lake Kinneret. Units are in g·ww·m^{-2}·year^{-1}. Items 7, 8, 9 and 10 have no significant predators, and thus do not appear as prey items; 12 is phytoplankton; 13, benthic producers; and 14, detritus.

	Predator	Prey 1	2	3	4	5	6	11	12	13	14
1.	Bacteria	-	-	-	-	-	-	-	-	-	2,968.0
2.	Protozoa	1,440.0	240.0	-	-	-	-	-	480.0	-	240.0
3.	Herb. zooplankton	-	767.2	383.6	-	-	-	-	4,219.6	-	2,301.6
4.	Carn. zooplankton	-	48.0	768.0	48.0	-	-	-	96.0	-	-
5.	Lavnun	-	-	197.2	34.8	-	-	-	-	-	-
6.	Tilapias	-	-	67.7	6.2	-	-	19.7	123.0	-	29.5
7.	Silver carp	-	-	2.2	0.4	-	-	0.4	4.0	-	0.4
8.	Mullet	-	-	1.8	0.3	-	-	1.8	0.9	0.3	0.9
9.	Barbels	-	-	0.7	0.1	-	-	1.4	1.1	0.8	1.4
10.	Piscivores	-	-	0.3	-	0.8	0.2	0.3	-	-	-
11.	Benthos	-	-	-	-	-	-	-	12.5	75.0	37.5

model. In addition, a large increase in any component immediately causes a decrease in the detritus component (due to the respiration costs) forcing a further increase in primary production or import of detritus to balance the model.

The most uncertain values used in the model are those for Q/B. So little is known about the food requirements of fish in Lake Kinneret that the model can be of little use in estimating the population size of those fish that are not well studied.

Summary Statistics

The summary statistics (Table 4) are strongly affected by two characteristics of the Kinneret model: the lack of piscivory and the inclusion of bacteria in the model. Because piscivory is unimportant, the fisheries has a low "mean trophic level" and is efficient, compared, e.g., to the fisheries in the South China Sea model (Pauly and Christensen 1993). Inclusion of bacteria and use of the input primary production to balance the model results in a total primary production (P_p) to total respiration ratio of 1. A ratio of 1 is consistent with the reported balance between the input of organic material by the Jordan River and the loss to the sediments (Serruya et al. 1980). Without inclusion of the bacterial loop, this ratio would increase to 1.3-1.4, similar to that for the French Frigate Shoals system, but still lower than that reported for the South China Sea model (Pauly and Christensen 1993). Thus, the Kinneret ecosystem seems to be relatively mature *sensu* Odum (1971).

Table 4. Summary statistics for ECOPATH II (Version 2) model of Lake Kinneret. Flows are in g·m^{-2}·year^{-1}, while trophic levels and gross efficiency are dimensionless.

Sum of all consumption	14,623.3
Sum of all exports	1,054.7
Sum of all respiratory flows	6,125.3
Sum of all flows to detritus	6,613.8
Total system throughput	28,417.1
Sum of all production	10,915.7
The fishery has a mean trophic level	4.07
Its gross efficiency (catch/primary production) is	0.0015

By contrast, the ratio between P_p and total biomass is high (44) compared with other systems. This might be explained by the low biomass of benthic organisms, which are relatively slow-growing, and the inclusion of fast-growing bacteria and protozoa, rather than by lack of system maturity.

Trophic Aggregation Analysis

The flows in the Lake Kinneret ecosystem can be distributed on discrete trophic levels using the routine described by Christensen and Pauly (1992). The results of this analysis are shown in Table 5 from which the importance of detritus is apparent. The sinking of a large portion of the *Peridinium* bloom and its consumption as detritus by bacteria is reflected in the high proportion of total flow originating from detritus. The table also shows the trophic transfer efficiencies in the system. These are fairly high (22%) for trophic levels II and III mainly due to the high efficiencies of bacteria and protozoa. The efficiencies seem to decrease gradually as one goes up the trophic levels.

Mixed Trophic Impacts

The trophic impact any of the groups in a system have on the other groups can be quantified using an ECOPATH II routine based on input-output analysis (see Fig. 2). The figure shows some interesting aspects of the interactions. It appears,

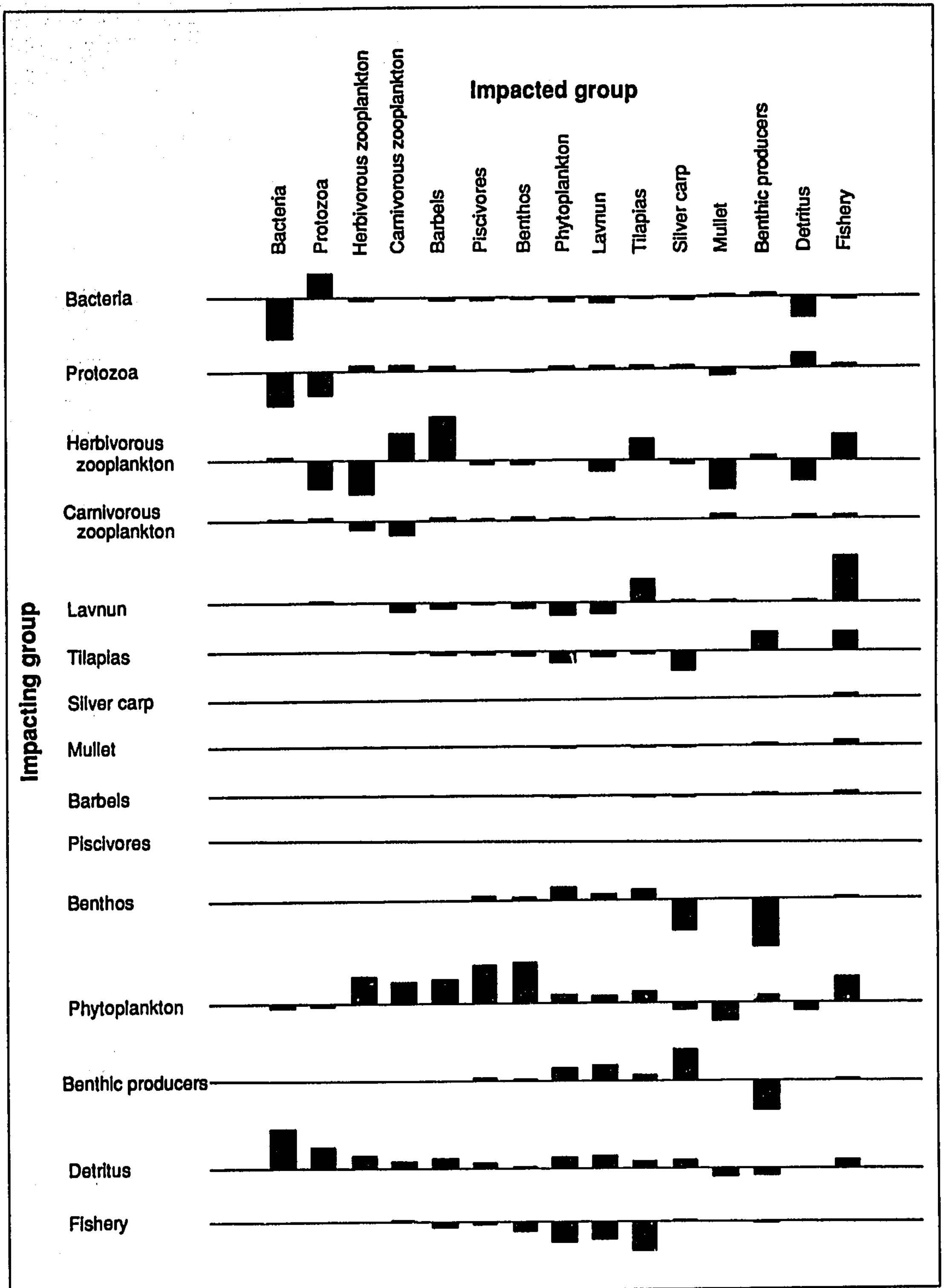

Fig. 2. Mixed trophic impacts in the Lake Kinneret food web. Positive impacts are shown above the baseline, negative below. The impacts are relative and comparable between groups.

for instance, that the bacteria have a negative impact on the fishery. This is because the detritus-bacteria-protozoa is seen as a competitor to the pathways leading to the fishes. This is, however, an artifact as it does not take into account that the bacteria are fundamental for the other pathways, not a competitor to them. Interestingly, bacteria is the only group which is found to have a negative impact on the fishery. This indicates that there are no obvious ways to improve catches based on trophic, multispecies considerations.

The results emphasize the importance of carnivorous zooplankton in controlling the population of herbivorous zooplankton. The effect

Table 5. Trophic aggregation of flows in the Lake Kinneret ecosystem showing flows ($g \cdot m^{-2} \cdot year^{-1}$) by group and trophic levels. The bottom line gives trophic transfer efficiencies estimated as the percentage of the flows on a trophic level that is either harvested or transferred to the next trophic levels. The groups are shown in descending order of trophic level.

Group	I	II	III	IV	V	VI	VII
Piscivores	-	-	0.73	0.71	0.15	0.06	0.01
Lavnun	-	-	180	33.8	16.1	2.06	-
Carn. zooplankton	-	101	740	62.0	56.7	-	-
Mullet	-	2.06	3.38	0.29	0.14	0.02	-
Protozoa	-	800	1,600	-	-	-	-
Silver carp	-	4.36	2.35	0.36	0.18	0.02	-
Tilapias	-	153	80.9	7.12	5.14	0.36	-
Barbels	-	5.40	2.00	0.13	0.06	0.01	-
Herb. zooplankton	-	6,864	269	538	-	-	-
Bacteria	-	2,968	-	-	-	-	-
Benthos		125	-	-	-	-	-
Phytoplankton	6,500	-	-	-	-	-	-
Benthic prod.	80.0	-	-	-	-	-	-
Detritus	6,614	-	-	-	-	-	-
Total	13,194	11,021	2,879	643	78.5	2.53	0.01
Transfer efficiency(%)	-	25.2	23.3	12.2	3.6	4.5	4.0

of fish may be mediated through their effect on the ratio between carnivorous and herbivorous zooplankton. Changes in the diet composition of fish are probably of crucial importance in explaining the decline in zooplankton biomass and these are not considered in the mixed trophic impact analysis. This remains a tool for describing the direct and indirect impacts in a system in steady state.

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The Pelagic Zone of Central Lake Malaŵi - A Trophic Box Model

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DEGNBOL, P. 1993. The pelagic zone of central Lake Malaŵi - a trophic box model, p. 110-115. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Abstract

Lake Malaŵi contains a pelagic ecosystem which is based on a deep euphotic zone (up to 60 m) and medium primary production (0.7 $g \cdot C \cdot m^{-2} \cdot day^{-1}$). A trophic box model has been implemented based mainly on investigations conducted from 1977 to 1981. The grazer chain in the pelagic system is dominated by one major pathway: via crustacean zooplankton to a larvae of the lake fly, *Chaoborus edulis*. Nearly all the primary production is estimated to pass through this pathway. Minor pathways pass through zooplanktivorous fish of which the most important are the cyprinid *Rastrineobola sardella* and a group of haplochromine cichlid species (Cichlidae). The top predators constitute a small group of species which feed on fish as well as on *Chaoborus* larvae. The majority of the *Chaoborus* production is exported from the lake.

Introduction

Lake Malaŵi (East-Central Africa, 10-14°S, 471 m above sea level, surface area 30,800 km^2, mean depth 426 m, maximum depth 758 m, Fig. 1) contains an extensive pelagic ecosystem which in the central and northern part of the lake is limited by steep shores and a permanent thermocline at approximately 250 m depth (Eccles 1974). The euphotic zone of the pelagic ecosystem of Lake Malaŵi is deep, up to 60 m, and the primary production has been measured to average 0.74 $g \cdot C \cdot m^{-2} \cdot day^{-1}$ or 2,710 $g \cdot wet\ weight \cdot m^{-2} \cdot year^{-1}$. A sample production profile is presented in Fig. 2. The system is subject to an annual cycle of stratification and a mixing period of 2-3 months duration. The FAO Fisheries Expansion Project 1977-82, based in Nkhata Bay, Malaŵi, included studies on the trophic structure of the pelagic ecosystem of the central lake. The majority of these studies have been assembled in one volume (Turner 1982a), and supplementary studies on feeding in the pelagic ecosystem have been reported separately (Degnbol 1982; Walczak 1982). Data from these studies have been analyzed using the ECOPATH II system to prepare a preliminary model of the trophic structure of the pelagic part of central Lake Malaŵi.

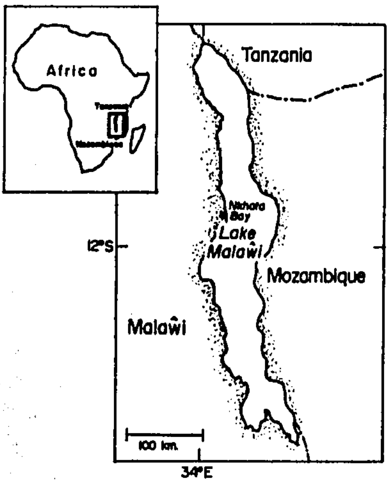

Fig. 1. Lake Malaŵi. (• Nkhata Bay)

Materials and Methods

The present study is mainly based on data collected by the FAO Fisheries Expansion Project in 1979-81 (Degnbol 1982; Degnbol and Mapila 1982; Rufli and Vitullo 1982; Turner 1982b, 1982c; Walczak 1982). Phytoplankton samples were analyzed by the Freshwater Institute, Winnipeg (Hecky and Kling 1987). Detailed descriptions of materials and methods are found in these references.

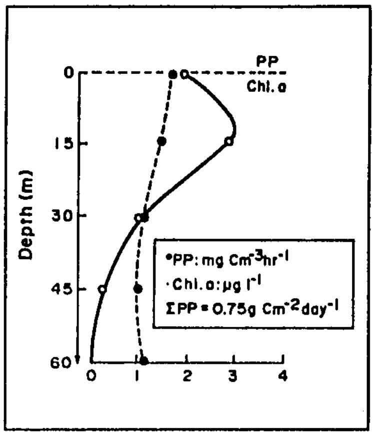

Fig. 2. Sample primary production and chlorophyll a profile from the pelagic zone of central Lake Malaŵi (Degnbol and Mapila 1982). The integrated primary production was 0.75 $g \cdot m^{-2} \cdot day^{-1}$.

Data covering the seasonal cycle are available from a standard station at 360 m depth in the central lake and from two lakewide surveys.

Primary production was measured using *in situ* C-14 incubation in dark and light bottles (Degnbol and Mapila 1982). Phytoplankton biomass was obtained from counts and volume estimates (Hecky and Kling 1987).

Zooplankton was sampled with a 112 micron 30 cm diameter net, with pump and with a 200-l Schindler trap. Only counts are available, no consumption or production measurements were made (Degnbol and Mapila 1982).

Larval *Chaoborus edulis* (phantom midge larvae; Fig. 3) were sampled with a 150 micron 70 cm diameter net. Instars were weighed and counted and stomachs analyzed for composition of contents and volume. Food consumption was estimated on basis of mean stomach contents and stomach evacuation rates. These were measured through *in situ* estimation based on decrease in stomach contents after cessation of feeding and by experiments. The analysis was done separately for the four instars (Degnbol 1982).

The present study includes five fish groups. Two common fish species from the system are shown on Fig. 3. Fish biomass and composition were estimated from purse seine catches applying area fished by seine to raise samples to area (Turner 1982b; Walczak 1982). The seine only covered the top 60 m of the water column which resulted in some underestimation of the fish abundances as fish were found distributed down to the limits of dissolved oxygen, 220-240 m (Turner 1982).

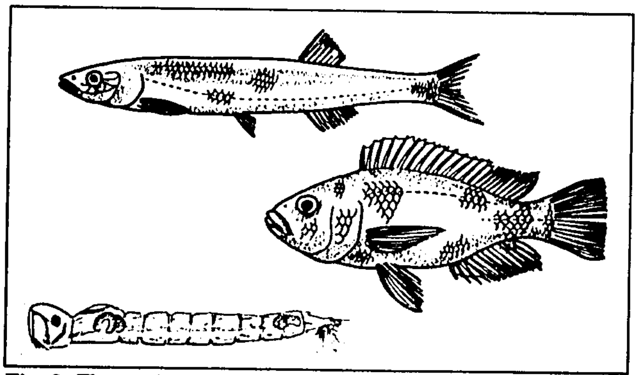

Fig. 3. Three of the main actors in the Lake Malaŵi food web, *Rastrineobola sardella* (top), a haplochromine cichlid (below) and a *Chaoborus* larvae.

Food consumption/biomass ratio (Q/B) for fish was estimated from mean stomach contents and stomach evacuation rates as estimated *in situ* from decrease in stomach contents after cessation of feeding. This analysis was done by species and size group (Walczak 1982). The consumption rate estimate for haplochromine cichlids obtained through this analysis seems unrealistically low (Q/B = 1 year^{-1}) and was not used in the present model. Instead Q/B was estimated based on an assumed gross food conversion efficiency (i.e., production/biomass ratio) of 20%. The Q/B for *Diplotaxodon* is probably too low (0.4 year^{-1}) but it is used here as no better estimate is available, and as it cannot be estimated along with P/B for this group.

Fish catches from the pelagic zone proper are very small on an area basis as only the nearshore environment is exploited. There are no fishing operations in the major parts of the lake which is more than a couple of kilometers offshore outside the southern area. Statistics on the landings from the pelagic proper are incomplete due to the nature of the fishery, but it can be assumed that less than one percent of the overall landings of less than 1 g ww·m^{-2}·year^{-1} are from truly pelagic stocks. The order of magnitude of catches from the pelagic areas proper can thus be assumed to be less than 0.01 g ww·m^{-2}·year^{-1}. Due to this insignificant size no catches have been incorporated in the model.

The ECOPATH II model (Christensen and Pauly 1992) was used on data from Lake Malaŵi supplemented with literature estimates or assumed values where needed. The model was made on a wet weight per area basis, and a wet weight to carbon ratio of 10 was used throughout when data were on a carbon basis. A value for the production/biomass ratio (P/B) of zooplankton of 30 year^{-1} was used based on data on a related species of similar size at similar temperatures (Banse and Mosher 1980). Ecotrophic efficiency was set at 0.95 for *Rastrineobola sardella* and haplochromine cichlids (the primary zooplankton grazers, subject to predation). A gross food conversion efficiency of 0.1 has been assumed for the top predators.

The Q/B ratio for zooplankton has been calculated to match primary production (EE of phytoplankton assumed to be 0.95). The diet composition of zooplankton was not investigated. As zooplankton are known to consume some dead organic material, it was arbitrarily assumed that 10% of the diet consisted of detritus, the rest of phytoplankton. Input parameters except food composition data are presented in Table 1. Food composition input data can be extracted from the flowchart in Fig. 4.

A crustacean zooplankton community dominated by *Diaptomus kraepelini, Mesocyclops leuckarti, Diaphanosoma exisum* and *Bosmina longirostris* grazes this production. Predation within the crustacean zooplankton community has not been measured and the community is in this context taken as one ecological entity. The zooplanktivores are (in sequence of decreasing importance) *Chaoborus edulis* larvae, mainly instars 3 and 4, *Engraulicypris edulis* (a small cyprinid, now *Rastrineobola*), young *Rhamphochromis longiceps*, young *Opsaridium microcephalus, Diplotaxodon pallidorsalis* and various species of haplochromine cichlids. *Chaoborus* larvae are preyed upon by several fish species, mainly *O. microcephalus*. The main piscivore predators are *O. microcephalus* and *R. longiceps*.

Chaoborus larvae are removed from the system by predation and by hatching into adult airborne midges. Some of these are recycled into the system as they fall back into the water, others are exported as they land on shores. The export of *Chaoborus* has not been quantified, therefore it is estimated indirectly in the present model. The ecotrophic efficiency for *Chaoborus* is assumed to be around 0.75, indicating that 75% of the production is either consumed within or exported from the system. This efficiency was assumed to reflect mortality during the three larval stages and the metamorphosis. To obtain an EE = 0.75 the model was run iteratively with varying values for export. A resulting export of 44 g·m^{-2}·year^{-1} was obtained and this estimate was used in the analysis. Although high, this estimate does not seem unrealistic noting that sightings of large clouds of *Chaoborus* over Lake Malaŵi are quite common. Not all of the airborne *Chaoborus* exports actually leave the lake area, some reenter and are consumed or enter the detritus box. This "import" has not been quantified. It is emphasized that the estimate for *Chaoborus* production only refers to the central part of Lake Malaŵi, and that it cannot be extrapolated to the whole lake.

Default values of 80% assimilation rate are assumed for all groups. Trophic transfer efficiencies are estimated using a routine of ECOPATH II.

Results

Some results of the ECOPATH modelling are presented in Table 1 and Fig. 3. The P/B ratio of phytoplankton is high, 502 year^{-1}. Cell counts and volumetric measurements from samples taken independently of primary production measurements have been used for biomass. If chlorophyll *a* measurements made simultaneously with the primary production estimates are used as a guide (assuming approximately 0.05 mg chlorophyll *a* per mg·C), the P/B ratio is estimated to be approximately 300 year^{-1}. The main point here is that the estimate of biomass and thus of the P/B ratio is inaccurate in either case. This is however of little importance as the parameter that is directly related to the remaining part of the system - production - has been measured directly.

Table 1. Input values and results of ECOPATH II modelling. The P/B and Q/B gives production/biomass ratio and consumption/biomass ratio, respectively, both in year^{-1}. EE is the ecotrophic efficiency, i.e., the proportion of the production that is consumed by predators or exported, while GE is the gross food conversion efficiency (P/Q). Flows are g ww·m^{-2}·year^{-1} and biomass g·m^{-2}. Input values are without brackets, while computed estimates biomasses are in brackets.

	Biomass	P/B	Q/B	EE	GE
Phytoplankton	5.4	501.9	0.0	0.95	-
Zooplankton	18.0	30.0	(159.0)	0.89	(0.19)
Chaoborus larvae	2.2	(32.0)	213.0	0.75	0.15
Engraulicypris	0.9	(3.4)	9.6	0.95	(0.36)
Haplochromine cichlids	0.7	0.0	(3.9)	0.95	0.20
Opsaridium	1.2	(0.7)	6.6	0.00	0.10
Diplotaxodon	0.9	(0.04)	0.4	0.00	0.10
Rhamphochromis	3.3	(0.2)	2.0	0.00	0.10
Detritus	-	-	-	0.33	-

The Q/B value for zooplankton that is estimated to give an ecotrophic efficiency for phytoplankton of 0.95 is seen to result in a gross food conversion efficiency for zooplankton of 0.19 (Table 1). This estimate seems acceptable.

The system possesses one major grazing pathway: via zooplankton to *Chaoborus* larvae. Nearly all (98%) of the primary production passes through this pathway. Of the total *Chaoborus* production only some 6 g·ww·m^{-2}·year^{-1} is grazed by fish, mainly by *Opsaridium*. The remainder (here estimated to 7 times *Opsaridium* consumption) is exported with the adult *Chaoborus*.

The total production of fish biomass estimated amounts to 5 g·m^{-2}·year^{-1}. The major part (3.6 g·m^{-2}·year^{-1}) is composed of the two zooplanktivores *Rastrineobola sardella* (Cyprinidae) and haplochromine cichlids (belonging to the Cichlidae, a species flock locally called *utaka*) for which the production is estimated from predation data. For the remaining fish species, production is based on an input guess of gross efficiency. Production may well be double the amount estimated in the model.

Discussion

The model presented gives a coarse synthesis of some of the data available on the Lake Malaŵi. The shortcomings of the analysis are due to both lack of data and the limitations of the model used.

The limitations in data are: measurements on the production dynamics of zooplankton are not available, the role of detritus is not clear, nothing is known on the importance and role of dissolved organic matter and the production of *Chaoborus* is not measured. In addition, data on fish mortalities (P/B) and consumption rates (Q/B) are lacking.

The key model limitation is that the model does not include any size or stage structure. Data on Lake

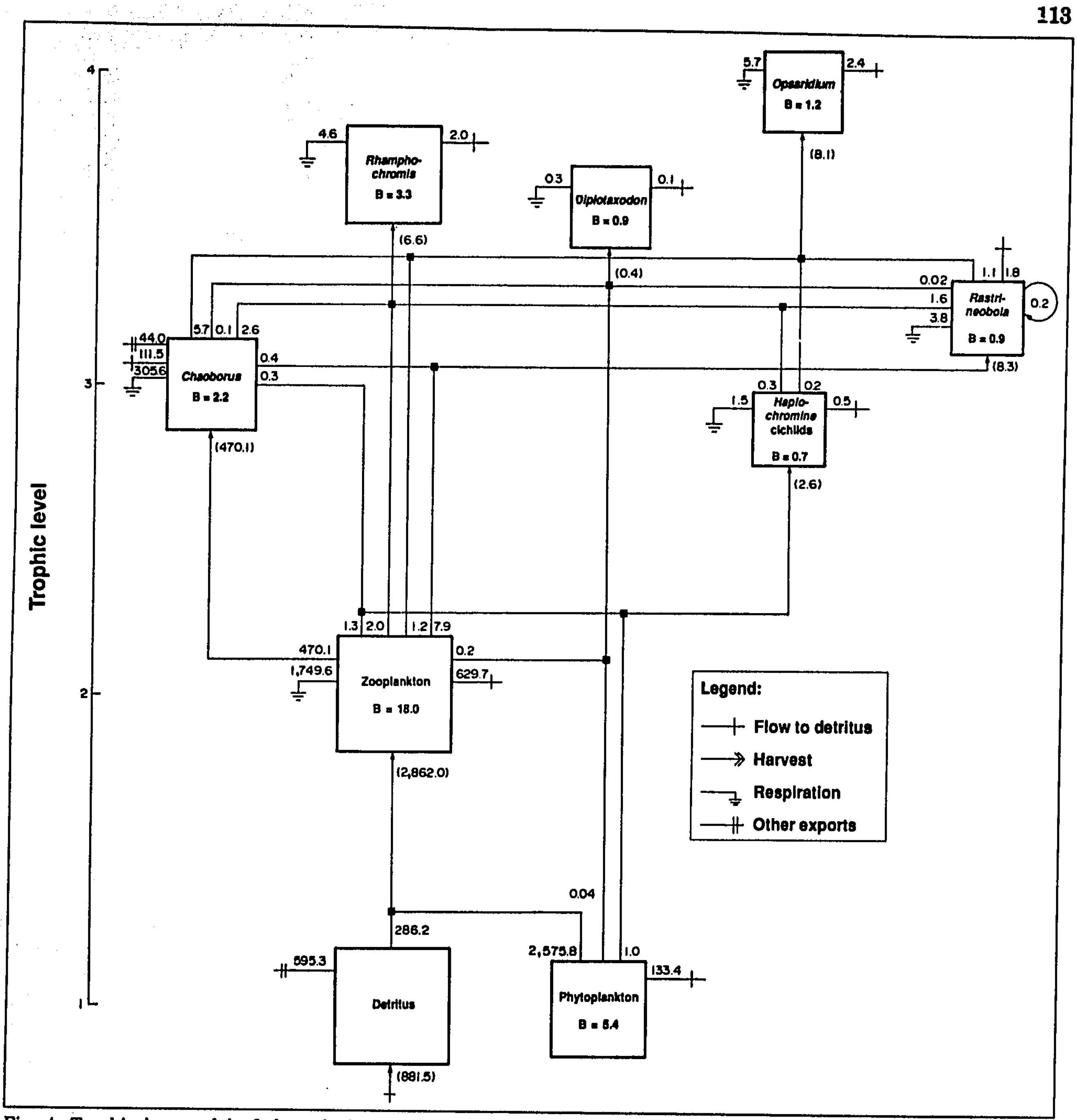

Fig. 4. Trophic box model of the pelagic ecosystem of the central part of Lake Malaŵi. Biomass is given inside boxes. Units: g·ww·m^{-2}·year^{-1} (flows) and g·m^{-2} (biomass).

Malaŵi key species (biomasses, food composition and consumption rates) are available on a size basis, but this information could not be utilized in the present model. Inclusion of a size or stage structure would facilitate inclusion of phytoplanktivory by 1st and 2nd lake-fly instars (Degnbol 1992).

The trophic structure of the pelagic part of the central Lake Malaŵi ecosystem is presented in Table 2. Here the distribution of flows by group and trophic levels are given along with trophic transfer efficiencies. It is apparent that the trophic transfer efficiency on trophic level II (herbivores and detritivores) is rather high (16.9%). One explanation for this could be heterotrophic production (not considered here), as already suggested by Hecky et al. (1981), who found that heterotrophic production might account for the observed high transfer efficiency in Lake Tanganyika. Since then, the production and pathway of dissolved organic matter have come into focus as an important component in the trophic ecology of lakes.

For the higher trophic levels the trophic transfer efficiencies are very low. This can be attributed to the loss of *Chaoborus* from the system along with the lack of exploitation of the fish in the system.

The production estimate of fish biomass (5

Table 2. Trophic transformation matrix for the central pelagic part of the Lake Malaŵi ecosystem. The table shows how flows (g·m^{-2}·year^{-1}) are distributed on groups and trophic levels. Mean trophic level by groups and trophic transfer efficiencies are also given.

Group	Mean trophic level	I	II	III	IV	V
Opsaridium	3.9	-	-	1.3	6.7	0.07
Rhamphochromis	3.7	-	-	2.1	4.3	0.12
Diplotaxodon	3.3	-	0	0.2	0.1	0.00
Engraulicypris	3.1	-	-	8.1	0.4	-
Chaoborus	3.0	-	-	470.0	-	-
Haplochromine cichlids	2.7	-	1	1.3	0.3	-
Zooplankton	2.0	-	2,862	-	-	-
Phytoplankton	1.0	2,710	-	-	-	-
Detritus	1.0	881	-	-	-	-
Total	-	3,592	2,863	483.0	11.9	0.19
Trophic transfer efficiency (%)	-	-	16.9	2.5	1.6	-

g·m^{-2}·year^{-1}) indicates potential yields of some 2.5 g·m^{-2}·year^{-1} or around 0.1% of primary production. The P/B estimate of *Engraulicypris* of 3.4 is in the range of 2.2-5.0 (mean 3.4) estimated for *Engraulicypris* in the southern end of Lake Malaŵi (Turner 1982c). The mortality estimate is also close to the value of 3.6 year^{-1} obtained from the growth parameters of Rufli and Vitullo (1982) and the empirical formula of Pauly (1980). Yet the gross food conversion efficiency is rather high for the group (0.36), indicating that the food consumption rate may be an underestimate.

The fish biomass used in the present model (based on purse seine nets used for stomach analysis) is equivalent to 7 g·m^{-2}. This is comparable to the 9 g·m^{-2} found by Rufli and Vitullo (1982) based on lakewide data and using a combination of echo integration and purse seining and to 7.5 g·m^{-2} estimated from another set of purse seine catches by Turner (1982b).

Rufli and Vitullo (1982) estimated potential fish yield from the pelagic zone to be 4.5 g·m^{-2}·year^{-1} on the basis of their biomass estimate, an average natural mortality based on growth data and the empirical formula of Pauly (1980) and Gulland's (1971) formula with a factor of 0.5. This estimate is in good accordance with the estimate from the present model which is based on independent data and a different approach. It has been suggested that primary production was unusually high at the time and in the area from which the primary data for the present study were sampled. This suggestion is based on unpublished data from sediment cones (Magasa 1988, referring to R. Crossley, pers. comm.). The significance of this possibility cannot be assessed as a basis of the information available.

The general pattern emerging is that this pelagic ecosystem of central Lake Malaŵi produces midge larvae and midges, not fish - at least at the time of this investigation. One conclusion which could be drawn is that it takes more than the age of Lake Malaŵi (approximately 10 mio. years) for a cyprinid to accumulate the skills needed for competitive zooplankton grazing. Considerations along these lines coupled with a discussion on the possible introduction of Lake Tanganyika clupeids (Turner 1982d) has triggered a heated debate on the introduction of exotic species in Lake Malaŵi. The present paper is - just as Turner's original discussion - not intended to support a certain standpoint in this debate. It is just another example of the dilemma that the presentation of research results may prove to be equivalent to opening the box of Pandora. Consequences may pop out which are beyond further control. But keeping the box closed may also be questionable.

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Trophic Interrelationships and Community Structure at Two Different Periods of Lake Turkana, Kenya: a Comparison Using the ECOPATH II Box Model

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Abstract

The ecotrophic community structure in the open Lake Turkana, Kenya, has changed since the early 1970s when the system appeared limited by zooplankton production and energy was accumulated in stocks of small pelagic species. Later, the slower growing predator stocks of *Lates* spp. have proliferated and in the late 1980s energy has accumulated at the top predator level. The result is a strong increase (250%) in predation mortality on small pelagic species. This may explain the fivefold decrease in their biomass which is much more than can be expected from the relative decrease in secondary and primary productivity between the two periods. The regulatory mechanisms in the open lake ecosystem structure seem to have shifted from bottom-up to top-down "control" between 1973 and 1987. Fishing effort should be directed at the *Lates* spp. and *Synodontis* stocks and sustainable yields under the present conditions could be strongly increased.

Introduction

Lake Turkana, in the arid northwest part of the Kenya Rift Valley, 2°27'-4°40'N, is a large holomictic closed basin lake. The lake is 257 km long with a mean width of 31 km and a mean depth of 31 m at 0 m lake level (Fig. 1). By volume it is the fourth largest lake on the African continent, after Lake Victoria, Lake Tanganyika and Lake Malawi. The most comprehensive accounts of its limnology and fisheries are given in Hopson (1982), Källqvist et al. (1988) and Kolding (1989). A general summary and comparison with other systems is given in Kolding (1992).

The climate is very hot and dry. More than 90% of the water influx comes from the southern Ethiopian highlands via the Omo river drainage. The great irregularity of rainfall results in large fluctuations of the water level which have changed more than 20 m during the last century (Butzer 1971) (Fig. 1). At present, the lake level is low and the surface area covers about 6,750 km^2 compared with 7,560 km^2 in 1973 with 3.5 m higher level. The water temperature varies little, with a mean of 27.1°C and a range of 2.2°C (Hopson 1982). An estimated mean evaporation rate of 2.5 m·year^{-1} (Kolding 1989) requires an inflow compensation of about 600 m^3·s^{-1} or 19 km^3·year^{-1} to maintain balance. This is consistent with Beadle (1981) who reports a mean annual discharge for the Omo River of 18.6 km^3·year^{-1}. With no outlet, saline conditions are created and the present concentration of 2.44 g·l^{-1} dissolved solids is moving toward the limit of 3 g·l^{-1} defining true saline lakes (Williams 1964). Sodium, chloride and bicarbonate dominate the water chemistry and most plant nutrients are in surplus except nitrogen which, together with light in the turbid water, is considered the limiting factor for primary production (Harbott 1982; Källqvist et al. 1988). Nitrogen in the open lake is mainly supplied by river inflow, as evidenced by a strong seasonality in the phytoplankton densities coinciding with the flooding cycles of the Omo River. There is also a strong diminishing gradient with distance to the Omo River mouth in the north. Primary productivity in the south of the lake is on average less than 10% of the northern part (Hopson 1982). The phytoplankton diversity of the open lake is low (eight species) and mostly dominated by *Microcystis aeruginosa*. This large colonial blue-green algae is only slightly cropped by fish or crustaceans and

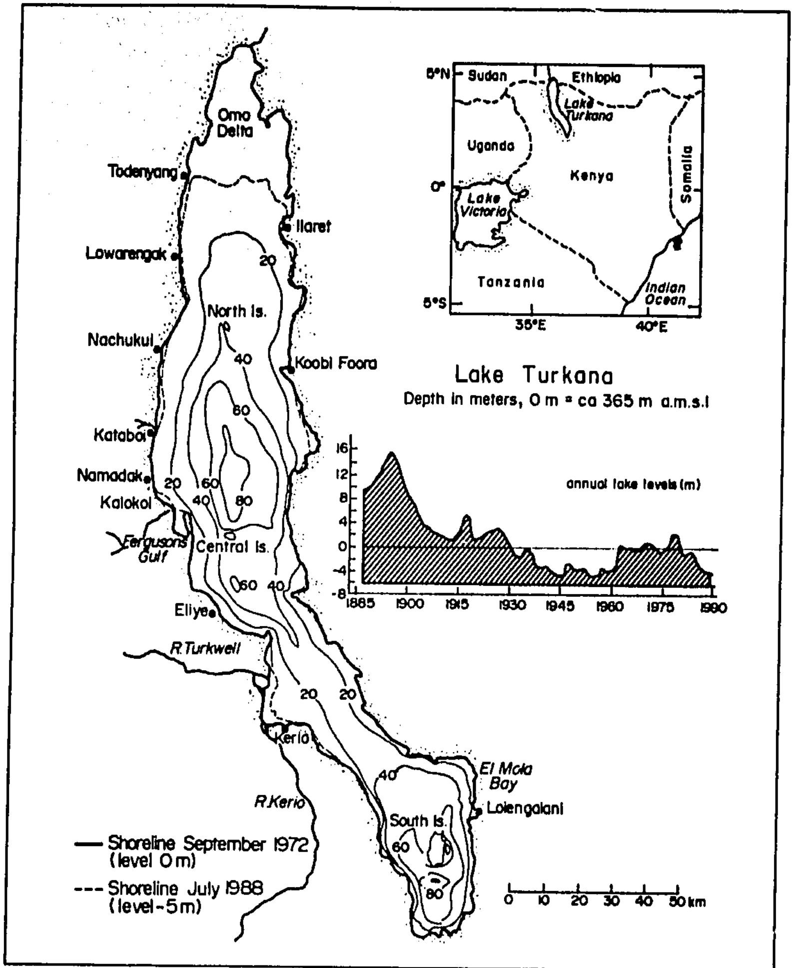

Fig. 1. Topography and bathymetry of Lake Turkana. Depth contours refer to 0 m lake level (September 1972 level). The insert shows the mean annual lake levels over the last century (from Kolding 1989).

most of the primary production passes through bacterial decomposition before it becomes available to the zooplankton as detritus (Hopson 1982). Large amounts of suspended particulate material are also supplied by the rivers with an organic content of 4.25 mg·(dw)·l^{-1}. With a mean influx of 600 m^3·s^{-1}, the annual load of organic allochtonous matter is ca 10 t·(dw)·km^{-2}. The mean standing suspended organic content of the lake water is 1.4 mg·l^{-1} (Källqvist et al. 1988). This, together with the unusually poor organic carbon content in deepwater sediments (Yuretich 1976; Cohen 1984, 1986), suggest that recycling processes might be predominant and that a relatively high proportion of the primary production, or imported carbon, is lost to respiration before it can contribute to fish production.

The importance of a detritus-based foodweb in Lake Turkana is indicated by: (1) the high abundance of planktonic ciliates feeding on bacteria; (2) the composition of the zooplankton where the detritivore *Trophodiaptomus banforanus* contributes ca 60% of the biomass; (3) large concentrations of the small detritus feeding prawns *Macrobrachium niloticum* and *Caridinia nilotica;* and (4) the relative large community of big mud-sifting/benthic feeding fish (*Labeo horie, Barbus bynni, Citharinus citharis* and *Distichodus niloticus*) which form an important part of the fishery.

The zooplanktivorous pelagic fish consist of *Alestes baremoze* and a unique midwater scattering layer composed chiefly of two small endemic characids: *Alestes minutus* (maximum size 3.7 cm FL) and the larger *A. ferox* (6-8 cm FL). These two small species form the main biomass of fish in the lake and are the most important link between zooplankton and the piscivorous species: tigerfish (*Hydrocynus forskalii*), Nile perch (*Lates niloticus*) and the smaller endemic dwarf perch (*L. longispinis*). The second largest stock is the omnivorous mochokid catfish *Synodontis schall* which, unlike elsewhere, is mainly pelagic in Lake Turkana. This species is not much predated upon (Hopson 1982), possibly due to its long sharp pectoral and dorsal spines which can be locked in erect positions. Lake Turkana also has an inshore littoral community in sheltered localities characterized by abundant ostracods, tilapias, birds and crocodiles. This system, however, is nearly totally separated from the open lake system. More than 700 gillnet settings over a one-year period between the 10 and 25 m depth contour only caught two tilapia (Kolding 1989) and only *L. niloticus* regularly enter the littoral system from the open lake to forage on tilapia (ca 20% of consumption).

There is a strong correlation between nutrient input and production in Lake Turkana. A linear regression between annual lake levels (proportional to water influx, i.e., nitrogen and allochtonous organic matter) and the commercial fish catch rates (ranging from 31 to 5 t·(ww)·boat^{-1}·year^{-1}) over the period 1972-1988 explained 88% of the variation of the catches (Kolding 1989, 1992). Between 1979 and 1987, the lake level receded almost linearly by 6 m and commercial catches went down 80%. Between 1973 and 1987, overall experimental catch rates (on commercial species) went down by 46%, but smaller species from the pelagic community (*Alestes* spp. and *Hydrocynus*) had been reduced by 80-98%, although fishing mortality (F) is practically zero for these species. Only the two perch species had increased, with experimental catch rates going up, while *Synodontis* had remained stable (Table 1). However, all species in the experimental fishery seemed under increased stress as indicated by overall decrease in mean sizes compared with a similar survey in 1973 (Hopson 1982). For some, such as *Labeo horie* and *Barbus bynni*, there was also clear indication that the median size at maturity had decreased. Thus, while the basis of production in Lake Turkana is certainly not steady, the trophic system up to the fishable biomass appears to track the fluctuations in production with little delay. This indicates resilience and that self-regulatory mechanisms, such as predator-prey relations maintain a natural balance in the medium term (Kolding 1989, 1992).

This paper is an attempt to quantitatively simulate and describe the ecotrophic community structure in the open Lake Turkana and to compare the large changes in the biomass and production of different trophic groups which have occurred during the last decade of lowering lake levels. Despite the limitations of ECOPATH II as a steady-state model (Christensen and Pauly 1992), such changes can be explored by narrowing the state parameters and rates to one-year periods.

Materials and Methods

The ECOPATH II (version 2.1) box model was applied to the Lake Turkana openwater ecosystem for the two annual periods 1973 and 1987 (the only two periods for which somewhat detailed data exist). Only the important openwater fish species are included. Some have been grouped together when their biology was very similar, when detailed information were not available, or when they are not differentiated in the commercial landings (Table 1). The model assumes that net production during the period under investigation is zero. That is, the total production P(i) of all components (i) (ecotrophic groups) equals losses (predator consumption, other mortality and catches) so that the standing mean biomass is constant. Under these very constraining, and seldom met conditions, the production to mean biomass ratio (P/B) equals the total mortality rate (Z) (Allen 1971). This can be used to estimate total production. Production is also defined as the consumption (Q) multiplied by the gross food conversion efficiency coefficient (GE).

All data for 1973 are from Bayley (1977) and Hopson (1982). All data for 1987 are from Källqvist et al. (1988) and Kolding (1989). Phytoplankton production and zooplankton biomass figures are available for both periods. Their P/B ratios were estimated from comparable systems (Le Cren and Lowe-McConnell 1980; Payne 1986; Källqvist et al. 1988). Allochtonous organic input is calculated from the load of 4.25 $mg \cdot l^{-1}$ in the river water times 600

Table 1. Input values (underlined) and results from ECOPATH II modelling of the open Lake Turkana ecosystem. The last two columns (W_{max} and C/f) are not used in the model itself. Biomasses are in $t \cdot km^{-2}$, catches in $t \cdot km^{-2} \cdot year^{-1}$, while P/B and Q/B are annual rates.

Group	Year	Biomass	Catch	P/B	Q/B	EE	GE	TL[g]	Wmax[h]	C/f[i]
1. *Lates* spp.[a]	1973	2.94	0.057	0.49	2.45	0.29	0.20	3.39	48.820	0.29
	1987	3.68	0.070	0.57	2.86	0.51	0.20	3.35	19.513	0.36
2. Tigerfish[b]	1973	1.13	0.041	1.18	5.91	0.30	0.20	4.00	0.903	1.88
	1987	0.06	0.002	1.24	6.21	0.45	0.20	4.00	0.663	0.10
3. Small pelagic[c]	1973	29.85	-	5.20	34.67	0.18	0.15	3.01	-	-
	1987	5.97	-	5.25	35.00	0.46	0.15	3.01	-	-
4. Benthic fish[d]	1973	1.24	0.237	0.50	3.33	0.50	0.15	2.20	4.494	0.69
	1987	0.71	0.125	0.67	4.47	0.48	0.15	2.25	3.487	0.39
5. *Synodontis schall*	1973	3.31	0.041	1.37	9.13	0.03	0.15	3.00	0.715	1.32
	1987	2.98	0.025	1.41	9.40	0.03	0.15	3.00	0.595	1.19
6. Zooplankton[e]	1973	60.00	-	30.00	200.00	0.58	0.15	2.00	-	-
	1987	26.00	-	30.00	200.00	0.29	0.15	2.00	-	-
7. Phytoplankton	1973	21.75	-	365.00	0.00	0.37	-	1.00	-	-
	1987	15.25	-	365.00	0.00	0.23	-	1.00	-	-
8. Detritus[f]	1973	438.90	-	-	-	-	-	1.00	-	-
	1987	391.80	-	-	-	-	-	1.00	-	-

[a] Includes *L. niloticus* and *L. longispinis* in the ratio 2:1 (Hopson 1982; Kolding 1989).

[b] Biomass in 1973 calculated from: *C/f (Hydrocynus) / C/f (A. baremoze)* · biomass (*A. baremoze*).

[c] Includes mainly *A. minutus* and *A. ferox* in the ratio 10:1 (Hopson 1982). The decrease in biomass of 80% is estimated from Kolding (1989).

[d] Includes *Labeo horie, Barbus bynni, Citharinus citharis* and *Distichodus niloticus* in the ratios 26:10:13:9 (1973) and 60:8:1:4 (1987).

[e] 1973 figures estimated from Hopson (1982) and 1987 figures from Källqvist et al. (1988). The 1973 zooplankton biomass is a compromise between two very different figures of about 10 $t \cdot ww \cdot km^{-2}$ (Ferguson 1982) and 120 $t \cdot ww \cdot km^{-2}$ (Hopson 1982).

[f] Calculated from mean organic content in lake water of 1.4 $g \cdot dw \cdot l^{-1}$ and volume/surface figures.

[g] TL is mean trophic level.

[h] Weighted mean (kg·ww) in groups consisting of several species (Hopson 1982; Kolding 1989).

[i] Experimental C/f in kg·ww per standard net per setting (Bayley 1982; Kolding 1989).

and 500 $m^3 \cdot s^{-1}$ in 1973 and 1988, respectively. A wet weight/dry weight ratio of 10 has been used throughout when data are given in dry weight only. Quantitative biomass figures of the fish stocks, based on extensive acoustics and trawl surveys, total mortality estimates and food composition tables only exist for the 1973 period. Fish biomass estimates for 1987 are calculated by multiplying the 1973 figures by the ratio of the mean experimental catch per effort (C/f) (1973) to mean experimental C/f (1987) (Kolding 1989). Total landings are from Kolding (1989). P/B values of fish for 1973 are given or calculated from Hopson (1982). In case of unknown P/B value in 1973 (tigerfish) or unknown biomass (benthic fish), the ecotrophic efficiency (EE), defined as the fraction of total production which is consumed by higher trophic levels (Dickie 1972), has been assumed. Diet compositions of fish in 1973 are from tables in Hopson (1982). They are presumed unchanged for all groups in 1987 except for *Lates* spp., which with the large decrease in prey densities and increase in own biomass, are assumed to have become more cannibalistic, as observed in Lake Victoria (Ogari and Dadzie 1988). GE values are estimated from literature (Dickie 1972; Payne 1986) and considered constant in a stable physical environment as Lake Turkana. Unassimilated food for all groups is given the default value of 20%. As P/B values were given as input (1973), then Q/B values were output since their coefficient (GE) is constant. Given the knowledge of significant changes in maximum weight (W_{max}) for each fish group between the two periods (Table 1), conversion factors for Q/B between 1973 and 1987 were calculated using an empirical relationship between Q/B, temperature and W_{max} (Christensen and Pauly 1991). From these ratios the Q/B values of 1987 were estimated and P/B values were model output. All units are $t \cdot (\text{wet weight}) \cdot km^{-2}$ (=$g \cdot (\text{wet weight}) \cdot m^{-2}$) averaged over the whole lake surface area and flow rates are per year.

Results and Discussion

All input parameters are presented in Tables 1 (underlined) and 2. All other parameters are estimated by ECOPATH II. The balanced energy flow diagram for the two time periods is given in Figs. 2 and 3, respectively. Table 1 shows a remarkably good overall correspondence between relative changes in biomass of the fish groups from 1973 to 1987 (calculated from experimental C/fs, Table 1 last column) and relative changes in commercial landings. As the two datasets on experimental and commercial catches are totally independent, this indicates that the changes in biomass data are probably realistic and that the F values (Table 3) can be considered reliable. These are nearly identical in the two periods which also appears reasonable since the fishing equipment (passive gear only) and fishing pattern have not changed and the total effort at the two periods is quite similar (Kolding 1989).

From these conclusions, and considering the relatively small changes in the Q/B ratios (ranging from 1.03 to 1.17), it can be deduced, still assuming that the diet compositions have not changed - except for *Lates* spp. (Table 2) - that the large increases in predation mortalities (M2) of the fish groups between the two periods are also real. However, predation pressure (M2), and thus ecotrophic efficiency (EE), on zooplankton and phytoplankton have decreased according to this model, although their productivities have also decreased (Table 1). This indicates that the relative decline (80%) in the small pelagic fish biomass is larger than can be explained from the decrease (56%) in food (zooplankton) availability alone and that the system in 1987 can be assumed to be top-down controlled in contrast to 1973 where zooplankton appeared to be the limiting factor. This switch is consistent with the increase in top-predator biomass (except tigerfish which has crashed for

Table 2. Input diet compositions (%) from two models of the open Lake Turkana ecosystem. For consumers 2-6 the diets pertain to both the 1973 and 1987 models.

Prey/food	1		2	3	4	5	6
	1973	1987					
1. *Lates* spp.	5.0	9.5	-	-	-	-	-
2. Tigerfish	5.0	0.3	-	-	-	-	-
3. Small pelagic	60.0	60.0	99.0	1.0	-	20.0	-
4. Benthic fish	1.0	1.0	-	-	-	-	-
5. *Synodontis schall*	1.0	1.0	-	-	-	-	-
6. Zooplankton	8.0	8.2	1.0	99.0	20.0	70.0	-
7. Phytoplankton	-	-	-	-	-	-	25.0
8. Detritus	-	-	-	-	80.0	10.0	75.0
9. Import[a]	20.0	20.0	-	-	-	-	-

[a] Import is tilapia from the littoral community.

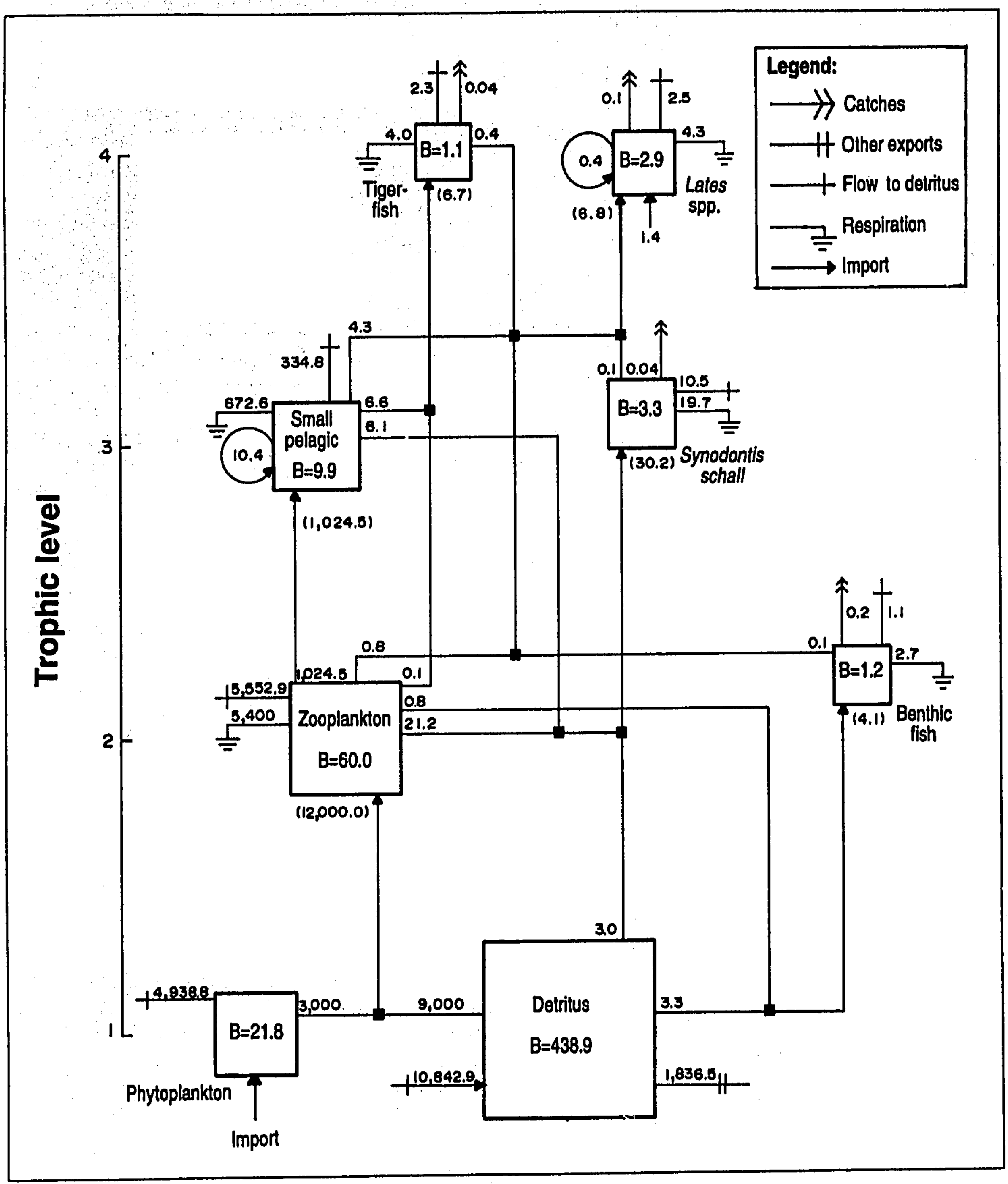

Fig. 2. Flow diagram for the open Lake Turkana 1973-model. All flows are in t·km^{-2}year^{-1}.

unknown reasons) and the subsequent increase in predation mortality on small pelagics, of more than 250% (Table 3). Such regulatory effects of predators and the inherent tendency for predator-prey interactions to generate coupled time-delayed oscillations is a general tenet in system ecology (e.g., Begon et al. 1990) although cause and effect are often difficult to determine.

The production and consumption rates of organisms are dependent on their size (Allen 1971; Dickie 1972; Sissenwine 1986). The size composition of individual populations varies as a result of exploitation/predation and fluctuations in recruitment. Therefore the interdependent P/B and Q/B ratios also vary. Although the increase in total mortalities (Z) in this simulation is a result of the observed decrease in W_{max} for all fish groups between 1973 and 1987 (Table 1), the observed changes would not be meaningful unless mortality had risen. In spite of the lack of conclusive evidence for top-down control by *Lates*, it must be noted that the relative predation mortality (M2/Z, Table 3) has

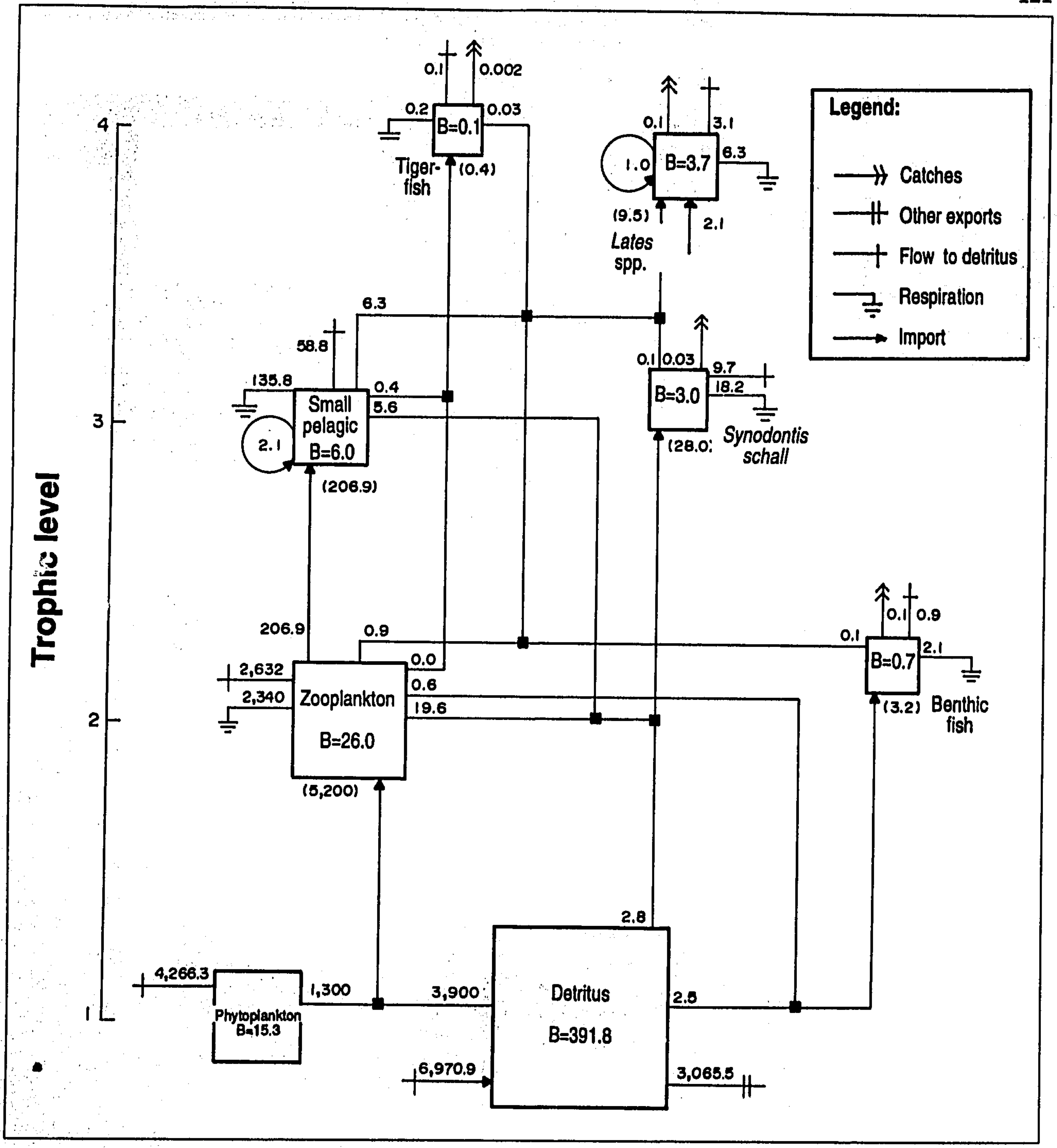

Fig. 3. Flow diagram for the open Lake Turkana 1987-model. All flows are in t·km^{-2}·year^{-1}.

approximately doubled for all fish groups from 1973 to 1987, while it was approximately halved for phytoplankton and zooplankton. This indicates that the system has changed character from a bottom-up controlled system to a top-down controlled system.

The greatly increased predation mortality has caused the EE values of all fish groups to increase but it is interesting to note that they do not exceed about 0.5 in any one group. This is in accordance with Dickie (1972) who deduced, based on theoretical considerations, that "the ecotrophic coefficient [= efficiency] in nature is unlikely to exceed a value of about 0.5". As the EE determines the fraction of total production of a trophic level which can be passed on to higher trophic levels, this has important theoretical consequences for calculations of sustainable yields from single-species production models used in fisheries where EE is called the exploitation rate (E = Y/P) defined as F/Z. In a multispecies situation, however, EE is the fraction

Table 3. Predation mortality (M2) breakdown showing how the M2's can be attributed to predators, fishing mortalities (F), other mortalities (M0) and total mortality (Z=P/B) for the living groups in the open Lake Turkana ecosystem as estimated in the 1973 and 1987 models. All mortalities are on an annual basis.

Group	Year	M2							F	M0	Z	M2/Z
		1	2	3	4	5	6	Total				
1. *Lates* spp.	1973	0.12	-	-	-	-	-	0.12	0.02	0.35	0.49	0.24
	1987	0.27	-	-	-	-	-	0.27	0.02	0.28	0.57	0.47
2. Tigerfish	1973	0.32	-	-	-	-	-	0.32	0.04	0.83	1.18	0.27
	1987	0.55	-	-	-	-	-	0.53	0.03	0.68	1.24	0.42
3. Small pelagic	1973	0.14	0.22	0.35	-	0.20	-	0.92	-	4.28	5.20	0.18
	1987	1.06	0.06	0.35	-	0.94	-	2.41	-	2.84	5.25	0.46
4. Benthic fish	1973	0.06	-	-	-	-	-	0.06	0.19	0.25	0.50	0.12
	1987	0.15	-	-	-	-	-	0.15	0.18	0.35	0.67	0.22
5. *Synodontis schall*	1973	0.02	-	-	-	-	-	0.02	0.01	1.34	1.37	0.01
	1987	0.04	-	-	-	-	-	0.04	0.01	1.37	1.41	0.03
6. Zooplankton	1973	0.01	0.00	17.07	0.01	0.35	-	17.45	-	12.55	30.00	0.58
	1987	0.03	0.00	7.96	0.02	0.75	-	8.77	-	21.23	30.00	0.29
7. Phytoplankton	1973	-	-	-	-	-	137.93	137.9	-	227.07	365.00	0.38
	1987	-	-	-	-	-	85.25	85.2	-	279.75	365.00	0.23

which should be shared between fishers and the fish predators, implying that $E \leq EE$.

Table 3 shows that the relatively large stocks of *Lates* spp. and *Synodontis* are very lightly exploited ($E = 0.03$ and 0.007) and from the table it appears that these two groups together contribute more than 80% of the high M2 on the small pelagic fish. Clearly these two predator resources are underutilized and a fishery might perhaps induce the ecosystem to move away from its present "top-heavy" state. Applying the above principles of the EE and E values on the present total production rate (BZ) of the two stocks the sustainable yield rates (SY) can be calculated from

$$SY = E \cdot BZ$$

which is a modification of the so-called "Cadima estimator" (in Troadec 1977) where E replaces a constant of 0.5. E can be estimated as approximately 0.5-M2/Z, unless one wants to influence on M2 as, for example, in case of cannibalism. For *Lates* spp. in Lake Turkana, M2/Z has risen from 0.24 to 0.47 (Table 3) over the studied period as a result of assumed increased cannibalism. Whether this is the case or not, E can be set at 0.25 which means: (1) sharing the theoretical maximum net production equally between man and other predators (the 1973 situation), or (2) the same plus inducing a decrease in the present stock, which will reduce predation mortalities and cannibalism (the 1987 situation). For *Synodontis*, the M2/Z is only 0.03 (Table 3) which means that we can set E to 0.45. Using the modified Cadima estimator on the stocks of *Lates* spp. and *Synodontis* the sustainable yields would be:

SY (*Lates* spp.) = 0.5 $t \cdot km^{-2} \cdot year^{-1}$ ($E = 0.25$)

SY (*Synodontis*) = 1.9 $t \cdot km^{-2} \cdot year^{-1}$ ($E = 0.45$)

These potential yields are equivalent to a tenfold increase of the present commercial landings of about 0.22 $t \cdot km^{-2} \cdot year^{-1}$ (Kolding 1992).

The models presented here of the open Lake Turkana ecosystem are crude simplifications of reality not only at the species groupings level, but also because they do not allow for variation in the biomass. Also, the models require that the total production is "utilized" within the boxes defined, ignoring unknown/unaccounted pathways or size-dependent interactions.

The fraction of the production which is not explicitly determined as M2 or F (i.e., 1-EE) goes directly to the detritus box which is very large. Recycling processes via bacteria and protozoans are not included due to lack of data although they probably are responsible for the largest turnover of energy in Lake Turkana. The problem of size-dependent interactions of flows is particularly prominent for the juvenile components of the populations where predator-prey interrelations and trophic levels are very different. Sissenwine (1986) found that while prerecruitment fish are only 10% of the biomass of the exploitable part of the population, their consumption is nearly as great and their production is two and a half times as high. However, Allen (1971) and Dickie (1972) indicated that the calculations of production from P/B ratios over particular periods of the life history, that is over specified sizes, are meaningful within this range under conditions of steady state and if mortality is well described by a constant negative exponential term.

Conclusion

Based on the limited data and underlying assumptions of the model, the conclusions drawn from this study can only be conjectures. As "snapshots", the two models only provide a framework for identification of the interacting factors regulating energy flow in the open Lake Turkana ecosystem. Nevertheless, there seems to be some consistency in the parameters and overall outcome. In addition, the results appear to sustain the general conclusions of Kolding (1989): (1) It is doubtful that overfishing has ever been a problem in Lake Turkana as has otherwise been indicated in most reports since the Hopson survey. (2) A more flexible and diversified fishing pattern should be considered and especially encouragement for a high fishing effort on top predators by promoting longlines and large mesh sized gillnets. (3) Some of the open Lake Turkana resources are underutilized and a surface offshore 3" mesh (minimum legal mesh size in Lake Turkana is 5") pelagic gillnet fishery for *Synodontis schall* should be seriously considered to alleviate needs in this often hunger-stricken region of Africa.

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A Trophic Ecosystem Model of Lake George, Uganda

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Abstract

A trophic model of Lake George, Uganda, Central Africa, was constructed using published quantitative and qualitative information on the various biotic components of the lake and the ECOPATH II approach and software. It is shown that the available production and biomass estimates for the various groups in the system are consistent with each other, and that it is possible to make a balanced model of the major trophic interactions in Lake George.

Introduction

In this contribution, a trophic ecosystem model of Lake George in Uganda is presented, based on an approach already used to construct models of a number of other African lakes and ecosystems (see Degnbol this vol., Kolding this vol., Moreau et al., this vol.).

This paper aims:

1. to add Lake George, which has been well studied in terms of its ecology and constituent fauna and flora, to the series of lakes that have been described using the trophic modelling approach; and
2. to demonstrate further the utility and versatility of the ECOPATH II approach and software; and its use in integrating the work of different researchers.

Lake George is relatively small, 250 km^2, and has a mean depth of 2.4 m, with a maximum of 4 m. Although connected via the Kazinga Channel with Lake Edward (formerly Lake Idi Amin), Lake George can be considered a self-sufficient ecosystem, given the restricted nature of its connection with Lake Edward (Fig. 1).

Lake George has been studied rather extensively, both in terms of its fish fauna (Greenwood 1973) and in the context of the International Biological Program (IBP). Burgis and Dunn (1978), Beadle (1981) and Burgis and Symoens (1988) present reviews of the relevant works, which are considered below.

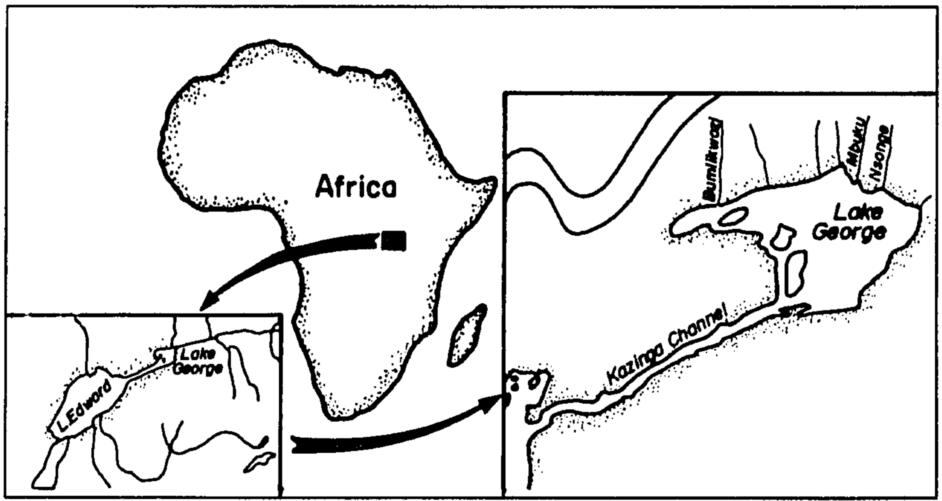

Fig. 1. Map of Lake George, showing its connection, via the Kazinga Channel, with Lake Edward, and their location in Africa.

Materials and Methods

The model of Lake George was constructed by applying the ECOPATH II approach and software of Christensen and Pauly (1992a, 1992b) to data collected by various authors in Lake George, and standardized by this paper's authors.

The basic equation of ECOPATH II expresses that for each group (i) in the model,

$$B_i (P/B)_i EE_i = Y_i + \Sigma_j (B_j (Q/B)_j DC_{ji}) \qquad ...1)$$

where B_i is the biomass of i, $(P/B)_i$ its production/biomass ratio, EE_i its ecotrophic efficiency, Y_i its yield (= fisheries catch), B_j the biomass of its k predators j, $(Q/B)_j$, the food consumption per unit biomass of j and DC_{ji} the fraction of i in the diet of predator j.

This equation implies equilibrium, i.e., input to a group is assumed to equal output from the group over the period considered. This assumption appears unavoidable in view of the scattered nature of the dataset considered here. It is justified, on the other hand, by the between-year consistency of phytoplankton biomass reported by Ganf and Viner (1973).

Table 1 presents the groups used to describe Lake George, along with some of their characteristics.

Except for the birds and the phytoplankton, all biomasses were estimated using ECOPATH II. Estimates of parameters were provided as follows.

Table 1. Basic information on elements ("boxes") of trophic model of Lake George.[a]

1.	Fish-eating birds	:	Fishing eagles, kingfishers, cormorants, pelicans
2.	*Bagrus docmac*	:	Catfish (85)
3.	*Clarias gariepinus*	:	Catfish (85)
4.	*Protopterus aethiopicus*	:	Lungfish (75)
5.	*Haplochromis squamipinnis*	:	Predatory dwarf bream (20)
6.	*H. angustifrons*	:	Benthophagous dwarf bream (12)
7.	*H. nigripinnis*	:	Phytoplanktophagous dwarf bream (10)
8.	*Oreochromis niloticus*	:	Nile tilapia (40)
9.	*O. leucostictus*	:	Tilapia (35)
10.	Zooplankton	:	*Thermocyclops hyalinus* + *Mesocyclops leuckarti*
11.	Zoobenthos	:	*Chaoborus* spp., Copepods, Oligochaetes, Ostracods (*Cyprinotus* spp.), *Chironomus* spp.
12.	Phytoplankton	:	Blue-green algae (*Anabaena, Microcystis, Lingbya*) (70% of biomass); Diatoms (*Melosira, Nitzschia, Synedra*); Chlorophytes (*Pediastrum* and *Scenedesmus*)
13.	Benthic producers	:	-
14.	Detritus	:	-

[a] Numbers in brackets refer to maximum length, in cm.

Fisheries Catches (Y)

Catch estimates pertaining to the 1970s were obtained for the fish groups in Table 1 from records of the Uganda Department of Fisheries (Gwahaba 1973; Dunn 1973, 1975, 1989). They are expressed here, like all other flows, in $t \cdot ww \cdot km^{-2} \cdot year^{-1}$.

Production/Biomass Ratio (P/B)

As shown by Allen (1971), under an equilibrium assumption, when von Bertalanffy growth can be assumed (as is here the case), P/B is equal to Z as defined in fisheries science. Hence we have estimated this parameter for the fishes from length-frequency data as outlined in Gayanilo et al. (1989). For the other groups, literature values were taken mainly from Winberg (1971) and Payne (1986). All values of P/B presented here are annual.

Diet Composition (DC)

The average composition of the food of each consumer organism is presented in Table 3. The table is on a weight basis, and was assembled from published information.

Food Consumption (Q/B)

This parameter expresses the food consumption (Q) of an age-structured population in fishes relative to its biomass (B), on an annual basis. Except for *O. niloticus* and *H. nigripinnis*, the estimate of Q/B used here was obtained via the empirical model of Palomares (1991) who also showed that freshwater and marine fishes have similar Q/B values when their shapes, size, food type and environmental temperature are equal, thus justifying the use of a model based on both marine and freshwater fishes.

The Q/B estimated for *O. niloticus* and *H. nigripinnis* were taken from Palomares (1991), who based her computations on stomach contents data from Moriarty and Moriarty (1973).

Ecotrophic Efficiency (EE)

This is the fraction of the production of any group that is consumed within the system, or caught by the fishery. This parameter is difficult to estimate and is usually assumed to range from low values (in apex predators) to 0.95 (Ricker 1969). Note that ECOPATH II directs the fraction (1-EE) of production toward the detritus, a feature that is of relevance when attempts are made to equilibrate an ECOPATH II model. Note also that the EE values differ from gross efficiency, GE = (P/B)/(Q/B), used here to check the inputs in Table 2, but not further discussed.

Balancing of the Model

The equilibrium assumption implicit to equation (1) is important in that it strongly constrains the possible solution, i.e., the range of parameters that will satisfy a set of simultaneous equations such as (1). Thus, the solution accepted as realistic is that which required the least modifications of the initial inputs (including the diet matrix), and yet generated biologically and thermodynamically possible outputs (i.e., all GE and EE < 1).

Results

Tables 2 and 3 present the key features of our model of Lake George, which is also illustrated in Fig. 2. The estimated biomasses are either within the ranges, or close to the biomasses so far published and, therefore, Fig. 2 represents a "possible" Lake George situation. The fish biomass is dominated by *O. niloticus*, an herbivore, whose central role in Lake George was previously emphasized by Gwahaba (1973), and by Moriarty and Moriarty (1973) and by *H. nigripinnis* and *H. angustifrons*, small phytoplanktivores (Moriarty and Moriarty 1973) and zoobenthivores, respectively (Gwahaba 1975). The major predators in the system are the lungfish *P. aethiopicus* and the catfish *C. gariepinus*, with consumptions of 7.3 and 6.2 t·km^{-2}·year^{-1}, respectively.

The predatory fishes are caught by fishers and by birds (Sumba 1983) and their EE (0.95) was assumed to be high. It is noted that the total consumption by birds (1.28 t·km^{-2}·year^{-1}) is far from negligible. It amounts to 8.5% of the actual catch (14.3 t·km^{-2}·year^{-1}). EE is also high for *Oreochromis* species which constitutes the bulk of the actual catch and of the food of the birds. In contrast, EE values are considerably lower for *H. angustifrons* and *H. nigripinnis*. These two groups are very poorly exploited and do not appear to suffer any severe predation (Moriarty et al. 1973; Dunn 1975).

Among the food sources, e.g., zooplankton, benthos, phytoplankton and benthic producers, only the last one has been expected to be heavily predated upon. The huge primary production of Lake George is not fully exploited (EE=0.95) and, to some extent, this is also true for zooplankton (Burgis and Dunn 1978). EE (=0.8) is quite high for zoobenthos which is an important source of food for several fish species even if its biomass (10.8 t·km^{-2}) is low when compared to other

Table 2. Input values for the required parameters for ECOPATH modelling of Lake George ecosystem (see also Tables 1 and 3). Computed and observed biomasses are also shown. Values of EE are guesses based on the known level of exploitation and/or predation of the group under consideration. Catches come from several sources: Gwahaba (1973), Dunn (1973, 1989), Burgis (1978), G.W. Ssentongo (pers. comm.). They refer to the early 1970s. Gross efficiency is computed as (P/B)/(Q/B) and is usually between 0.1 and 0.3.

	Group	Catches (t·km^{-2} year^{-1})	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	Computed biomass (t·km^{-2})	Observed biomasses (t·km^{-2})
1.	Birds	0.0	0.022[a]	0.25[a]	58.00[a]	-	-	(0.022)[a]
2.	*B. docmac*	0.3	-	0.90[b]	5.45[b]	0.95	0.50	(0.4-0.5)[f]
3.	*C. gariepinus*	0.8	-	0.90[b]	5.33[b]	0.95	1.16	(0.7-1.2)[f]
4.	*P. aethiopicus*	0.6	-	0.50[b]	4.85[b]	0.95	1.50	(1.4-1.6)[f]
5.	*H. squamipinnis*	0.8	-	1.70[c]	8.80[c]	0.95	0.62	(0.4-0.7)[f]
6.	*H. angustifrons*	0.4	-	2.50[c]	16.00[c]	0.30	2.55	(2.1-2.9)[f]
7.	*H. nigripinnis*	0.5	-	3.10[d]	17.50[e]	0.25	6.61	(5.2-6.9)[f]
8.	*O. niloticus*	10.5	-	1.30[f]	12.80[e]	0.95	9.89	(8.5-12.1)[f]
9.	*O. leucostictus*	0.4	-	1.10[f]	12.50[e]	0.95	0.59	(0.4-0.6)[f]
10.	Zooplankton	0.0	-	26.00[g]	140.00[i]	0.60	4.47	(2.7-5.8)[g]
11.	Zoobenthos	0.0	-	4.50[h]	26.00[i]	0.80	10.80	(9.8-11.4)[k]
12.	Phytoplankton	0.0	30.0[j]	66.00[j]	0.00	-	-	(30)[j]
13.	Benthic producers	0.0	-	5.00[h]	0.00	0.95	19.81	-

[a] Sumba (1983).

[b] Moreau et al. (this vol.).

[c] Guessed values based on the maximum observed length for P/B (see Moreau et al., this vol.) and on the gross efficiency for Q/B.

[d] Computed from an estimate of natural mortality M = 2.9 year^{-1} by Palomares (1991), assuming F = 0.2 year^{-1} in a population which is lightly exploited.

[e] Moriarty and Moriarty (1973).

[f] Gwahaba (1973). The observed biomass for *O. niloticus* pertains only to the inshore waters.

[g] Burgis (1974).

[h] Payne (1986), Winberg (1971).

[i] Guessed values, based on the gross efficiency for these groups and estimates from Polovina (1984) and Polovina and Ow (1985).

[j] Ganf (1972, 1974, 1975), Burgis and Dunn (1978).

[k] Darlington (1977).

Table 3. Diet composition (in % of weight of stomach contents) of consumers in the Lake George ECOPATH II model. Groups 12, 13 and 14, respectively : phytoplankton, benthic producers and detritus. Estimates are from: Sumba (1983) for group 1; Moreau et al. (this vol.) for groups 2, 3, 4; Dunn (1975) for groups 5, 6, 7; Moriarty and Moriarty (1973) for groups 7, 8, 9; Trewavas (1983) for group 9; Burgis and Dunn (1978), Moriarty et al. (1973) for group 10; Payne (1986) and Palomares (1991) for group 11.

	Prey													
Consumer	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. Fish-eating birds	-	6	9	-	1	-	-	76	8	-	-	-	-	-
2. *B. docmac*	-	0.5	0.5	0.5	0.5	4	20	3	1	5	50	-	2	13
3. *C. gariepinus*	-	-	0.5	1	0.5	5	10	3	0.5	5	48.5	1	5	20
4. *P. aethiopicus*	-	0.5	0.5	0.5	0.5	3	10	2	-	5	60	2	5	11
5. *H. squamipinnis*	-	-	-	-	2	16	50	6	1	10	10	-	-	5
6. *H. angustifrons*	-	-	-	-	-	-	-	-	-	10	50	10	10	20
7. *H. nigripinnis*	-	-	-	-	-	-	-	-	-	2	-	90	3	5
8. *O. niloticus*	-	-	-	-	-	-	-	-	-	2	-	90	4	4
9. *O. leucostictus*	-	-	-	-	-	-	-	-	-	1	-	80	5	14
10. Zooplankton	-	-	-	-	-	-	-	-	-	5	-	95	-	-
11. Zoobenthos	-	-	-	-	-	-	-	-	-	10	5	5	30	50

African lakes (Beadle 1981; Payne 1986; Burgis and Symoens 1988).

To some extent, this ECOPATH II model of Lake George confirms the frequently mentioned assumption (Burgis 1978; Burgis and Dunn 1978; Beadle 1981) that this ecosystem has a low ecological efficiency as compared to other African lakes such as Lake Victoria (Moreau et al., this vol.). The gross efficiency of the fisheries (actual catch/primary production) is 0.0057 in Lake George, between that of Lake Victoria prior to (0.0016) and after the introduction of Nile perch (0.0082).

Discussion

Interactions between Organisms

The Lake George ecosystem is quite well studied, and it is comforting to see that ECOPATH II could describe it properly in terms of biomasses and ecological production.

For instance, the observed catch (14.3 t·km^{-2}·year^{-1}) is realistic if extracted from an average total fish biomass of 23.4 t·km^{-2}. The latter figure is in agreement with the evaluations of Gwahaba (1975): 16.4 and 29 t·km^{-2}, depending on how one raises to the whole lake area figures initially estimated only for some biotas and/or stations. The difference between the two figures given by Gwahaba seems to stem mainly from the method of taking into account the important inshore biomass of exploited *O. niloticus*. Furthermore, the low values of EE for food sources, and also for the haplochromine cichlids, contribute to explain the low ecological efficiency of the system (Burgis and Dunn 1978; Payne 1986). A significant amount of the primary production is sedimented and exported through the Kazinga Channel, the main outflow to Lake Edward (Fig. 1).

The assumed low ecotrophic efficiencies for the two haplochromines (No. 6 and 7) indicate that these species are incompletely utilized. It is estimated that a production of around 20 t·km^{-2}·year^{-1}, or more than the total present catches is unutilized. It is however not clear if this is an artefact caused by erroneous assumptions in the model or if the fishery on these groups could in fact be increased considerably.

As already mentioned, the ECOPATH model was developed for static situations under general equilibrium conditions. However, we know little on the states of tropical fish communities. Also, little is known of the sensitivity of the model to perturbations caused by fishing or ecological stresses.

The mixed trophic impacts (Fig. 3; see Christensen and Pauly 1992a and 1992b for description) suggest that the fishing pressure that is operating now has a negative impact on all fish groups except *Haplochromis angustifrons* and *H. nigripinnis*, which show slightly positive impacts. This indicates that the fisheries presently has, relative to predation and competition, limited impact on those two species.

Interaction among Scientists

During the IBP study of Lake George, specialists of different groups were associated with a team supported by IBP which provided opportunities to interact and to exchange informations on a qualitative basis. This has made possible the publication of several synthesis papers (see Burgis and Symoens 1988 for review). ECOPATH II shows how the quantitative data on each group can be used to describe the ecosystem as a whole. Thus, we could verify that the estimates of biomasses and production of each main group provided by the IBP team were largely consistent with each other. We could also show the gaps in knowledge of this lake, at the end of the IBP project. To some extent, these gaps have forced the authors of

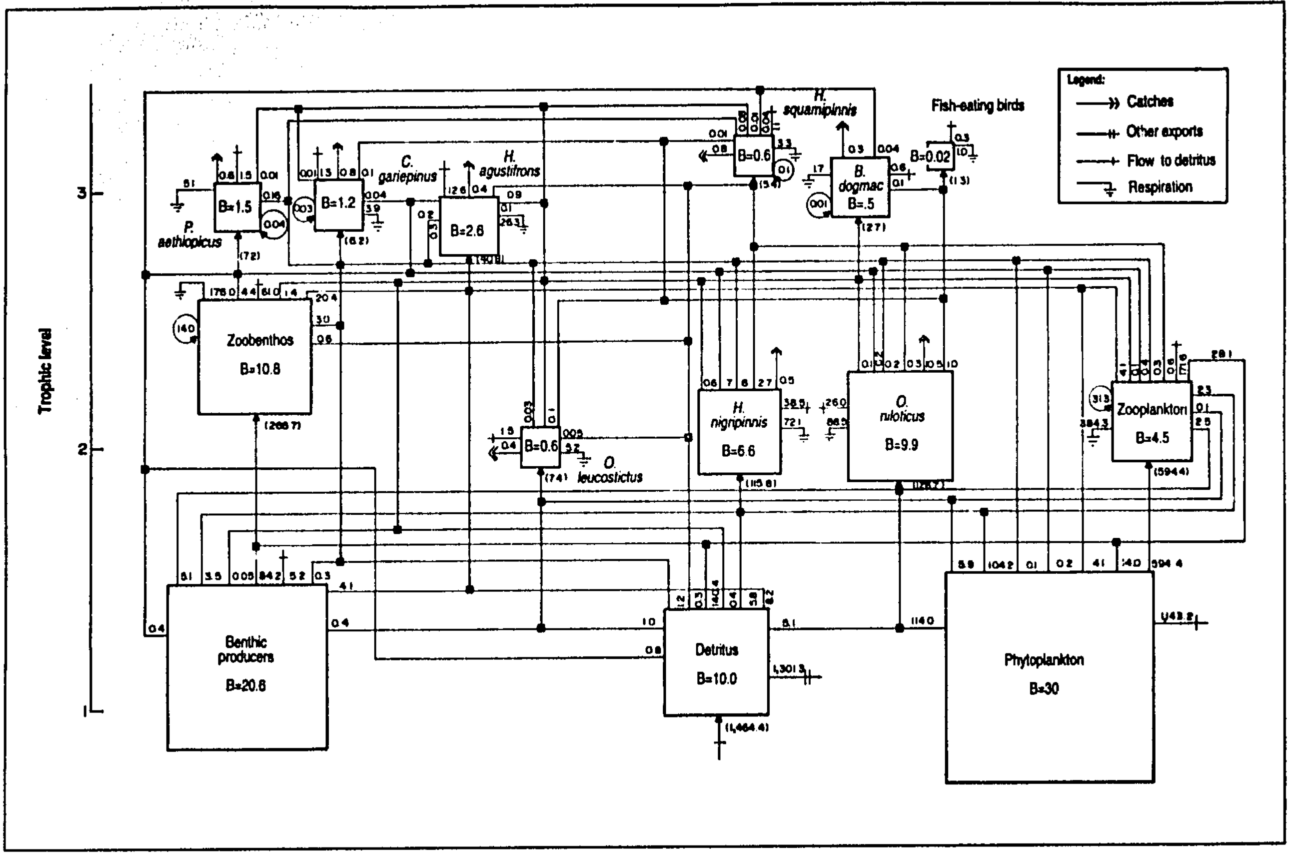

Fig. 2. ECOPATH II model of Lake George, indicating the biomasses (B in t·km^{-2}) of the groups used for description of the ecosystem and the flows connecting these (t·km^{-2}·year^{-1}).

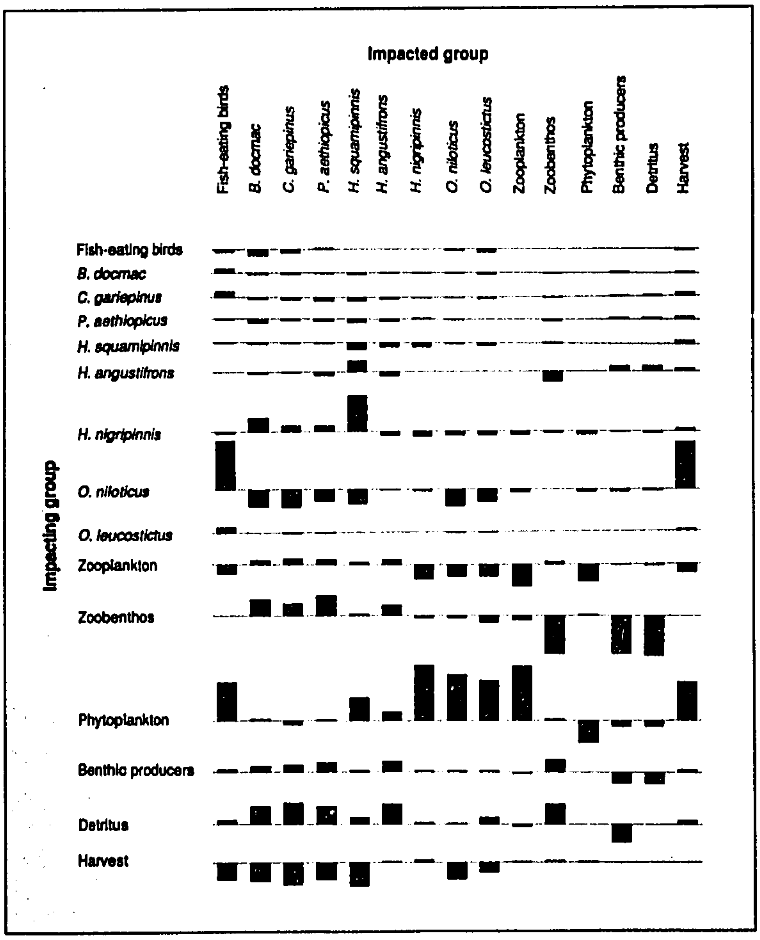

Fig. 3. Mixed trophic impacts of the groups included in the Lake George ecosystem model. The figure shows the direct and indirect trophic impacts on the groups mentioned on top from the groups given on the left. Positive impacts are shown above the baseline, negative below; the impacts are relative, but comparable between groups.

synthesis papers to make arbitrary assumptions on the relative importance of transfers of energy and biomass between the successive trophic levels (Burgis and Dunn 1978).

A short, and not exhaustive list of gaps in knowledge of Lake George includes:

- impact of predation by fish-eating birds;
- dynamics and ecological production of predatory fishes, haplochromines and zoobenthos;
- diet composition and food consumption of zoobenthos and benthophagous fishes;
- actual catch and its range of variations for each group of fishes;
- identification of the reason(s) why a large part of the primary production is not channelled into secondary production (as mentioned by several authors and confirmed by our low EE value for phytoplankton); and
- extent of the predation on zooplankton by young fishes (all species considered) in inshore areas.

Conclusion

ECOPATH II has allowed the authors to balance the biomass and production of several interacting groups in Lake George, based on data from the literature on the lake itself, or adapted from information from other lakes. The accuracy of several previous biomass and production estimates for major groups was demonstrated and the underutilization of some sources of food by fishes (especially phytoplankton) was confirmed. However, some gaps in our knowledge of the transfers of biomass between the groups have also been pointed out.

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A Preliminary Assessment of the Trophic Structure of Lake Kariba, Africa

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Abstract

Nine major trophic groups (*Hydrocynus vittatus*, *Synodontis zambezensis*, cichlids, *Limnothrissa miodon*, mussels, zooplankton, phytoplankton, macrophytes and periphyton) were analyzed using the ECOPATH II model to assess the trophic interrelationships and community structure of Lake Kariba, Zimbabwe. The utilization of energy flows, represented by the ecotrophic efficiencies vary widely among the various groups. The production of *S. zambezensis*, of macrophytes and of periphyton is apparently little utilized within the system and thus *S. zambezensis* represents a potentially important resource. The utilization of *H. vittatus* and of the cichlids is moderate, but this inference depends on the reliability of the catch data. The small pelagic *Limnothrissa miodon* is fairly heavily harvested, although the analysis indicates that fishing mortality could be increased. This, however, depends on the reliability of the P/B ratio. The pelagic food chain appears fully utilized whereas there is room for herbivorous species in the vegetated littoral zone. These two habitats are new to the original riverine fish fauna and only the former has become productive after the introduction of the pelagic *L. miodon*.

Introduction

Lake Kariba (277 km long; about 5,364 km^2, 29 m mean depth and 120 m maximum depth) was dammed in 1958 and filled in 1963; at that time it was the largest artificial lake in the world.

A number of ecological characteristics make this water body fairly different from the great lakes on the African continent. The mean retention time of water in Lake Kariba is only about 3-4 years and the bulk of this water is lost through the hydroelectric turbines. Being located in a tropical area with seasonal rainfall, the lake usually experiences annual drawdowns of about 3 m, although this is exceeded during periods of drought (Fig. 1). The lake lies over an infertile bedrock and overall productivity is dependent on nutrient inflow from the catchment (Marshall 1982). Thus in periods of drought, productivity declines. The Zambezi River contributes about 70% of the water inflow. Next in importance is the Sanyati River which discharges its water into the lake close to the dam (Fig. 1). The wide seasonal fluctuations in water temperature (between 20° and 30° at the surface) and the turnover in July-August, with a period of maximum stability between December and April, are important in relation to seasonal fluctuations in productivity.

These factors and others not discussed here combine to give the lake a very peculiar ecological character. For example, the drawdowns create unstable littoral habitats which can only be colonized by few benthic species with broad tolerance limits (Machena 1989a). On the other hand, the alternations in flooding and drying along the stretches of gently sloping shorelines with the subsequent growth and decomposition of ephemeral vegetation, especially grasses, are a source of nutrients and a favorable environment for growth and reproduction of some fish species, particularly tilapias (Donnelly 1969; McLachlan 1970).

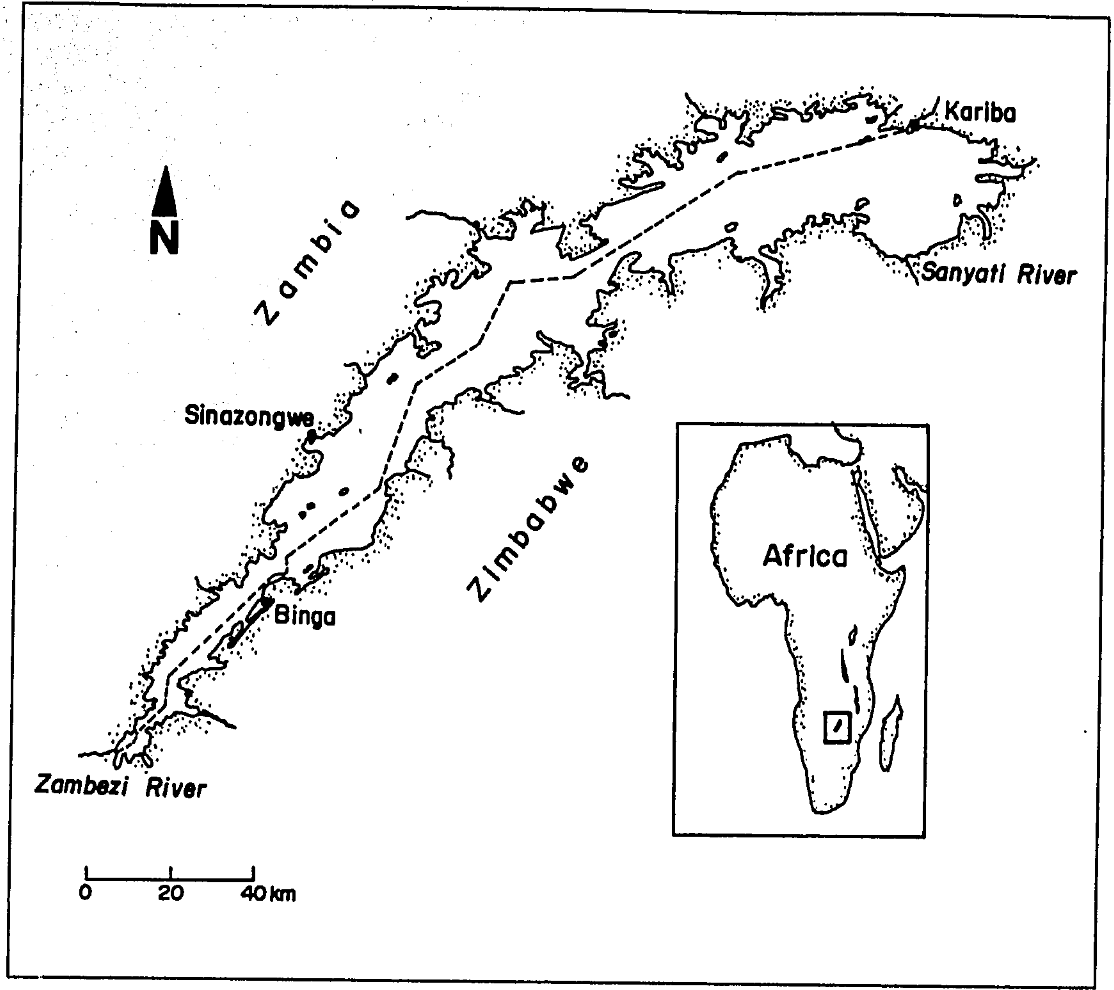

Fig. 1. Lake Kariba, one of the largest artificial lakes in Africa.

The lake has undergone changes in its physical and chemical characteristics with marked succession in the development of plant and animal communities (Coche 1968; Magadza 1970; McLachlan and McLachlan 1971; Balon and Coche 1974; Balon 1978; Marshall and Junor 1981). In the early filling phase of the lake, nutrient input from the flooded terrestrial habitats was high and total dissolved solids (TDS) rose from 55 $mg \cdot l^{-1}$ (in the former Zambezi River) to 65 $mg \cdot l^{-1}$ in the lake by 1960. Fish populations were very large while the lake was still rich in nutrient and very good catches were made in the inshore fishery. These however declined steadily from 1965 as the nutrient levels decreased and stabilized at a lower level around 1973. There was also an explosive growth of the floating fern *Salvinia molesta*, which covered 22% of the lake in 1962 and locked up large quantities of nutrients (Mitchell 1973). From around 1972 it shrank considerably (Marshall and Junor 1981) and is now practically absent.

There are about 40 fish species in the lake (Bell-Cross and Minshull 1988), of which about 20 are fairly common, but marked fish population changes have occurred since the lake was created (Donnelly 1970, 1971; Kenmuir 1984). Before impoundment, the most numerous fish in the Zambezi River were typical riverine species, notably cyprinids, distichodontids and characids. Small species were relatively scarce because there was little cover in the sandbank river and heavy predation from the tigerfish (*Hydrocynus vittatus*) (Jackson 1961). Larger cichlids were also uncommon. Cichlid populations have increased following the establishment of a lacustrine environment whilst the populations of cyprinids and distichodontids have decreased. The change from riverine to lacustrine conditions has also produced several new habitats, to which the Zambezi River fish were not pre-adapted. In particular ca. 70% of the lake area constituting the open pelagic region, with depth of more than 15 m, was not utilized. In 1967-1968 the small pelagic clupeid, *Limnothrissa miodon,* was introduced from Lake Tanganyika to fill the vacant niche in the open pelagic (Bell-Cross and Bell-Cross 1971). This introduction was highly successful and today this species is the most important commercially, with an annual Zambian and Zimbabwean yield of about 32,000 t (Anon. 1992). The pelagic fishery is fairly industrialized, whereas the inshore demersal species are cropped by an artisanal gillnet fishery. Lake Kariba is also a holiday resort and supports a popular recreational fishery, relying predominantly on tigerfish *H. vittatus*.

The importance of some ecotrophic groups in different aquatic systems will vary due to ecological characteristics. Hence a comparison of the energy flows in different lakes will reveal the different ecological forces shaping up the different systems. Trophic analysis is a widely accepted way to compare ecosystems (Hecky 1984). Quantitative assessment of trophic interactions in an aquatic ecosystem is not only of academic interest, but has important implications for the understanding and management of a multispecies fishery - fish yields are the results of energy flows.

This paper is an attempt to summarize our perception of the present trophic relationships among the most important ecotrophic groups in Lake Kariba, based on the available literature.

Materials and Methods

The ECOPATH II model (Christensen and Pauly 1992) was used to quantify the present trophic relationships and community structure in Lake Kariba. The ECOPATH box model assumes that each ecotrophic group is in steady state, where total gross production ($P = Z \cdot B$) is balanced by total mortality (Z) so that the average biomass (B) remains constant. This is a rigid assumption, especially in a young ecosystem such as Lake Kariba which is known for its successive changes in plant and animal populations. On a short-term scale, however, the assumption of steady state can be considered to have been reasonably fulfilled and the model can serve as a useful tool for exploring and evaluating the consistency of collected data and population statistics from the various groups.

Only nine trophic groups were selected in Lake Kariba on the basis of their known importance and availability of data from the literature. Some groups were left out (e.g., benthic mormyrids) because of their perceived minor importance for the overall trophic flows. Some fish species, e.g., the cichlids, were grouped both because commercial landing statistics do not separate individual species and also because their biology is similar. For each selected group values of

(i) the diet (% weight or volumetric composition);
(ii) average biomass ($t \cdot km^{-2}$);
(iii) catches or export ($t \cdot km^{-2}$); and
(iv) production to biomass ratios (P/B) and gross growth efficiencies (GE);

were determined. These values are shown in Tables 1 and 2. All units are averaged over the whole lake surface area, and the flow rates on an annual basis. From these input parameters, the ECOPATH II program computes an array of output parameters (Christensen and Pauly 1992), of which the most important for the purpose of this study are shown in Table 2. Q/B is the ratio of food consumption to biomass, where the consumption (Q) is defined as total production divided by the gross growth efficiency (GE). EE is the ecotrophic efficiency and expresses the fraction of the total production which is either consumed by predators included in the system (M2) or caught by the fishery (F).

Biomass estimates of tigerfish, *Hydrocynus vittatus*, and four cichlids (*Tilapia rendalli*, *Serranochromis codringtoni*, *Serranochromis macrocephalus* and *Oreochromis mortimeri*, the dominant cichlids in terms of catches) were obtained from Machena (1988, Table 7 based on Langerman 1984, which gives the most recent estimates). For the squeeker, *Synodontis zambezensis*, the biomass value of 21 $kg \cdot ha^{-1}$ in Mitchell (1976) was adjusted by the 1989 catch/effort (≈ 8 times higher; L.P.Karenge and J. Kolding, unpubl. data) as this species seems to have greatly increased in abundance (Sanyanga 1990, in press). The biomass of the pelagic sardine, *Limnothrissa miodon*, seem to fluctuate widely and various estimates are given (Marshall 1988). We have chosen the value of 37 $kg \cdot ha^{-1}$ obtained from acoustic surveys in 1988 (Lindem 1988), partly because we consider the acoustic estimate more accurate than others based on catch/effort and partly to match the estimate closest in time with the zooplankton data used here.

Three different biomass values of zooplankton were available. One of these values was based on data collected in 1967 and 1968 at a river mouth (Bowmaker 1973), the other in 1980 over a seven-day sampling period (Magadza 1980). Neither of these values were considered representative of the annual mean standing stock. Therefore, the biomass value used here was back-calculated from the mean daily production rate over a one-year sampling period (≈ 3 $mg \cdot dry\ weight \cdot m^{-3} \cdot day^{-1}$) obtained from Masundire (1992) and integrated over the mean lake depth of 29 m (H. Masundire, pers. comm.). Also, we used Masundire's estimate of mean replacement time of 10 days (i.e., $Z = 36.5\ year^{-1}$). This mortality estimate for zooplankton corresponds closely with the average value of 10% per day given in Gliwicz (1986, Table 2) from the Cahora Bassa reservoir on the lower Zambezi.

The yearly mean biomass of phytoplankton was 310 $mg \cdot wet\ weight \cdot m^{-3}$ (Ramberg et al. 1987) which equals 3.70 $t \cdot km^{-2}$ when integrated over the average euphotic depth zone of 12 m (Balon and Coche 1974).

Ramberg et al.'s figure was obtained during a dry period (1982-1984) with little nutrient inflow into the lake. The biomass of submerged vegetation and mussels was obtained from Machena and Kautsky (1988) and the biomass of periphyton was obtained from Ramberg et al. (1987).

Estimates of the catches of cichlids of *Hydrocynus vittatus* and of *L. miodon*, were available from Sanyanga et al. (1991). Commercial catches of *S. zambezensis* are low and a value of 0.1 kg·ha^{-1} was used. Catches of the inshore species were raised by a factor of 3 partly to accommodate the yields from the Zambian side, and partly because of problems of underreporting (Sanyanga et al. 1991).

The P/B ratios of *S. zambezensis* and the cichlids (a mean of four species) were obtained from Balon and Coche (1974) and of *H. vittatus* from Langerman (1984). As Marshall's (1985, 1987) estimate of Z ($\approx$ 12 year^{-1}) for *Limnothrissa miodon* is considered too high (Pearce 1989; Anon. 1992), a conservative value of 6 year^{-1} was used.

The P/B ratios (Kenmuir 1980) of the four mussel species in the lake were weighted by the biomass of each mussel and then averaged. The P/B ratio of submerged vegetation was obtained from Machena et al. (1990). The P/B ratios of zooplankton and phytoplankton were obtained from Masundire (1992) and Brylinsky (1980), respectively. The P/B ratio of periphyton was estimated.

The diet of *Hydrocynus vittatus* has shifted from predominantly cichlids and is now largely based on *Limnothrissa miodon* (Begg 1974; Kenmuir 1975; Mitchell 1976; Langerman 1984). The composition of the diet of four cichlid species was expressed as a mean of the values (weighted by biomass) given in Mitchell (1976).

The diet of *Limnothrissa miodon* was obtained from Begg (1974) and Cochrane (1984), and thus refers to data collected before 1975/76. The diet composition of *Synodontis zambezensis* was obtained from Mitchell (1976). A large proportion of their diet was from items imported from outside of the Lake Kariba system as defined here. This applies especially to the adult insects and to their larvae, which could not be included as separate groups because data on their biology were too scanty.

Mussels are predominantly filter feeders and it was assumed that they eat mostly detrital matter and phytoplankton. Zooplankton were assumed to feed on phytoplankton, and, to a large extent, on suspended detritus and nanoplankton and bacteria (H. Masundire, pers. comm.).

Dry weight values were converted to wet weight by multiplication with a factor of 10. The biomasses of vegetation, mussels and fish which only colonize littoral areas were averaged over the whole lake area by using the relationship of area colonized to total area of the lake. The average bottom area per 1 m depth interval between 0 and 15 m is 105.22 km^2·m^{-1} (Machena and Kautsky 1988). Vegetation only extends to a maximum depth of 6 m (Machena 1989a) while fish, except *Limnothrissa miodon*, and mussels are mainly found in the 0 to 15 m depth zone (Coke 1968; Balon and Coche 1974; Langerman 1984).

Gross growth efficiency coefficients (GE), defined as the proportion of ingested food that is used for tissue production, were estimated from the literature (Dickie 1972; Payne 1986), and the ECOPATH II default value of 20% nonassimilated food was used for all consumers.

Results and Discussion

An overview of the trophic flows in Lake Kariba is presented in the flowchart in Fig. 2. The groups are here placed on the Y-axis after trophic level as estimated with ECOPATH II.

The ecotrophic efficiencies (EE), which represent the proportions of the total gross production that is exported is consumed by predators defined in the system, vary considerably (Table 2). Energy flows to higher trophic levels are low from *S. zambezensis* and from the macrophytes, periphyton and detritus. They are medium for *H. vittatus*, cichlids, *L. miodon*, zooplankton and phytoplankton but relatively high for mussels. In comparison the energy flows to detritus appear high (Table 2) but this is because they represent both the proportion (20%) of unassimilated ingested food of the heterotrophs and the fraction of the total production (1 - EE) which is not consumed by higher trophic levels.

In Lake Kariba, *H. vittatus* is the top fish predator and only fishing and cannibalism contribute to its EE value. If the figures presented here are correct, there is no indication of overfishing on this species. On the contrary, fishing mortality (F) could be doubled without affecting the productivity assuming that maximum productivity is obtained with an EE of $\approx$ 0.5 (Dickie 1972). This, however, would certainly affect the recreational fishery as the number of large trophy-specimens would probably become very scarce. An increase of this fishery might therefore not be advisable, as the recreational fisheries make a valuable economic contribution to the area (Langerman 1981; Machena 1989b).

The cichlids, which are the most important commercial inshore species, also appear to be lightly exploited on a lake-wide basis. This might not be so in reality, as the yield statistics are based on extrapolation from data collected at a few landing sites. There are also problems with illegal fishing. The data used in this analysis were averaged over the whole lake area, and includes the protected areas. On the Zimbabwean side of the lake, about 40% of the shoreline are wildlife

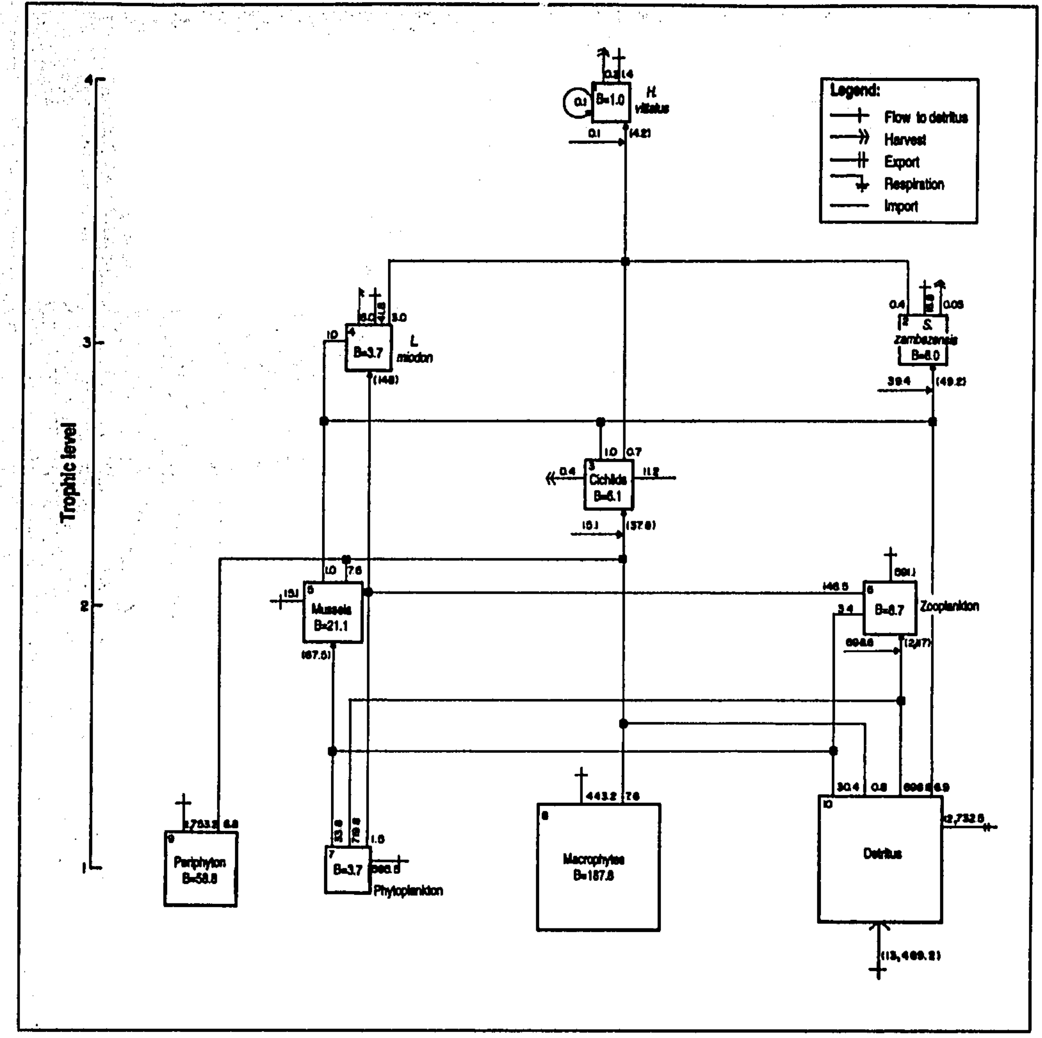

Fig. 2. Flowchart summarizing trophic flows (t·km^{-2}year^{-1}) in Lake Kariba, Africa.

Table 1. Input diet compositions of each group in percent for various ecotrophic groups in Lake Kariba.

No.	Consumer	Food 1	2	3	4	5	6	Phyto-plankton	Macro-phytes	Peri-phyton	Detritus	Import
1.	*Hydrocynus vittatus*	3	10	15	70	-	-	-	-	-	-	2[a]
2.	*Synodontis zambezensis*	-	-	2	2	2	-	-	-	-	14	80[b]
3.	Cichlids	-	-	-	-	20	-	-	20	18	2	40[b]
4.	*Limnothrissa miodon*	-	-	-	-	-	99	1	-	-	-	-
5.	Mussels	-	-	-	-	-	5	50	-	-	45	-
6.	Zooplankton	-	-	-	-	-	-	34	-	-	33	33[c]

[a] Includes aquatic and terrestrial insects that fall into the water.
[b] Includes largely aquatic insects and gastropods.
[c] Includes nanoplankton and bacteria.

Table 2. Input values (underlined) and results from the ECOPATH II modelling of the artificial Lake Kariba ecosystem. Export includes catches.

	Group	Biomass (t·km^{-2})	Export (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	Gross efficiency	Trophic level	M0 (year^{-1})	M2 (year^{-1})	F (year^{-1})
1.	*Hydrocynus vittatus*	1.0	0.15	0.86	4.3	0.32	0.20	3.9	0.58	0.13	0.15
2.	*Synodontis zambezensis*	6.0	0.03	1.23	8.2	0.06	0.15	2.4	1.15	0.07	0.00
3.	Cichlids	6.1	0.42	0.93	6.2	0.36	0.15	2.4	0.59	0.27	0.07
4.	*Limnothrissa miodon*	3.7	6.00	6.00	40.0	0.45	0.15	3.0	3.30	1.08	1.62
5.	Mussels	21.1	-	0.48	3.2	0.84	0.15	2.1	0.07	0.41	0
6.	Zooplankton	8.7	-	36.5	243.3	0.47	0.15	2.0	19.27	17.23	0
7.	Phytoplankton	3.7	-	365	-	0.56	-	1.0	160.94	204.06	0
8.	Macrophytes	187.8	-	2.4	-	0.02	-	1.0	2.36	0.04	0
9.	Periphyton	58.8	-	200	-	0.00	-	1.0	199.88	0.12	0
10.	Detritus	-	12,733	-	-	0.06	-	-	1.0	-	-

areas where fishing generally is prohibited. Large areas in the lake were not bush-cleared before inundation and this makes gillnet fishing difficult. Although the inshore commercial species are heavily cropped locally, the results of this study indicate that they are not in immediate danger of being overfished.

S. zambezensis has been steadily increasing in abundance in the lake (Kenmuir 1984; Sanyanga, in press) but is hardly utilized in the system. It is lightly cropped commercially because it has a narrow girth and is seldom caught in commercial gillnets, which have an (enforced) minimum mesh size of 100 mm. It is also very lightly preyed upon as is the case with *S. schall* in Lake Turkana (Kolding, this vol.). These species have evolved effective antipredator mechanisms by their long, sharp, locking serrated pectoral and dorsal spines (Lowe-McConnell 1987). *S. zambezensis* could therefore be utilized commercially if an appropriate cropping gear is designed. This is presently being investigated by the Lake Kariba Fisheries Research Institute. The present data suggest that sustainable yields could be some 15,000 t·year^{-1} with an exploitation rate (F/Z) of 0.4.

Limnothrissa miodon is fairly heavily exploited although there might still be room for expanding the fisheries. This, however, will depend on the true value of the P/B ratio. Literature estimates vary widely and have been the object of much discussion. Applying traditional length-based methods to this species to estimate mortality has proven very difficult, especially as it appears to have continuous recruitment (Begg 1974) and as the distribution of modes in length-frequency samples are very erratic, which makes growth curves a matter of belief (Pearce 1989; Anon. 1992). There is a strong need for reassessing growth and mortality for this species in Lake Kariba. It should be noted that if Marshall's (1985) estimates of total mortality ($Z \approx 12$ year^{-1}) were used under the present conditions, then the EE value of zooplankton would be very close to 1 which, according to Dickie (1972), is unsustainable.

The EE value of zooplankton indicates that it is fully utilized by higher trophic levels. Since *L. miodon* is an efficient zooplankton predator (Green 1985; Gliwicz 1986) it is clear that fluctuations in the sardine biomass will follow the biomass of the zooplankton which again is a function of the nutrient inflows to the lake.

The EE of mussels suggests that this ecotrophic group is heavily utilized. Mussels, however, have a very high biomass, consisting largely of adult animals with a relatively low P/B ratio, and this part of the population is at equilibrium (Kenmuir 1980). These animals are therefore chiefly preyed upon in their young stages, mainly by the cichlids (Table 1). As the relatively low mortality value of 0.48 year^{-1} refers to the adult population, with no significant predators, the EE value of 0.83 might be strongly misleading. Mortality data are not available for the juvenile part of the population, but can be assumed to be much higher than for the adult.

The EE values of macrophytes, and especially of periphyton, appear very low and they add considerable amounts to the detritus box in this model (Table 2). Herbivorous fish species in Lake Kariba are few and the major herbivore is *Tilapia rendalli*. This species prefers *Vallisneria aethiopica* (Chifamba 1990) which, according to Machena and Kautsky (1988), comprised only 10% of the submerged macrophyte biomass. *Lagarosiphon ilicifolius* and *Najas pectinata*, which comprised 52% and 33% of the macrophyte biomass, constituted less than 50% of the diet of *Tilapia rendalli*. According to Machena et al. (1990), the net community production of *Lagarosiphon* was only 1.16 mg·C·gm^{-2}·year^{-1}. This indicates a high degree of self-maintenance and little utilization by herbivores.

It is questionable if the periphyton is as little utilized as indicated here. Small omnivorous cichlids, which are relatively numerous in vegetated areas (Hustler and Marshall 1990), as well as various invertebrates are presumably grazing on the periphyton and associated "aufwuchs".

The biomass of phytoplankton, 3.72 t·km^{-2} (Ramberg et al. 1987), is low compared to the biomass of zooplankton. The ratio of total annual production of phytoplankton to zooplankton is only about 3 and although it is intensively grazed it was estimated that phytoplankton only constituted about one-third of the zooplankton diet. This finding corresponds with those of Gliwicz (1984) in the Cahora Bassa reservoir 400 km further down the Zambezi River. Here the annual production of phytoplankton was only about three times higher than that of zooplankton, which Gliwicz considered was acceptable if it is assumed that the zooplankton feeds extensively on bacteria and suspended organic aggregates.

Conclusion

The nine ecotrophic groups that were used in this study are not the only important ones in Lake Kariba. The larger benthic feeding mormyrids and cyprinids are important commercially, and small species of characids, cichlids and cyprinids contribute notably to the ichthyomass of the lake (Balon and Coche 1974). Mitchell (1976) showed that insects contribute significantly to the diets of juvenile fish and most benthic fish species. The population dynamics of these insects - treated here only as imports - need to be quantified and their production rates evaluated. Sources and production rates of phytoplankton need to be evaluated as well. From a fisheries point of view, it is particularly important that reliable estimates of the growth and P/B ratio of *Limnothrissa miodon* are established.

Although we provide a first impression of the trophic setup of Lake Kariba for the most important groups, there are good reasons why this should only be taken as a preliminary assessment. The data that were used cover different periods of time, although most were collected during the 1980s. As the lake has experienced a marked succession of both flora and fauna, as well as fluctuations in their population densities, data collected at an earlier date may not be comparable with data collected later. In addition, some of the parameters are associated with large uncertainties, while others have been indirectly estimated. For further analysis it will be necessary to collect data covering all important ecotrophic groups, over the same period of time.

Acknowledgements

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Trophic Relationships in the Pelagic Zone of Lake Tanganyika (Burundi Sector)

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Abstract

An update of previous estimates of production by the pelagic fish and invertebrate populations of Lake Tanganyika (Burundi sector) of Africa, is presented, along with a revised quantification of their trophic interactions. Two models are provided, pertaining to the periods 1974-1976 (high biomasses) and 1980-1983 (low biomasses). Some implications for research on the living resources of Lake Tanganyika are also presented.

Introduction

This contribution follows up a previous attempt to model quantitatively the food web of the Burundi sector of Lake Tanganyika (see Fig. 1), henceforth "Lake Tanganyika". The previous effort is documented in Moreau and Nyakageni (1989), and was based on the original version of the ECOPATH program (Polovina and Ow 1983; Polovina 1984).

The following information, not previously available, has made the present update of the Lake Tanganyika model possible:

1. the population dynamics of the pelagic clupeids and of their predators have been quantified for the periods 1974-1976 (Moreau et al., 1991) and 1980-1983 (Moreau and Nyakageni 1992),
2. the food consumption of *Luciolates stappersii* has been quantified (Pearce, unpubl.);
3. a time series of catch data has been generated which is free from the known biases of the earlier series (Petit 1990; Petit et al. 1990);
4. Roest (1988) defined predator-prey relationships for Lake Tanganyika.

These points, the fact that much of our previous work was published in French and the availability of the ECOPATH II software, appear to justify the present contribution. Additionally, the authors expanded on the previous work by constructing and comparing two models, pertaining to two different periods, 1974-1976 and 1980-1983, during which the pelagic stocks of Lake Tanganyika differed markedly in their structure.

Materials and Methods

The data used here followed the requirements of the ECOPATH II program (Christensen and Pauly, this vol.) for a model with seven boxes:

1. *capitaines*, i.e., large predators of the genus *Lates* (*L. mariae, L. microlepis* and *L. angustifrons*), previously abundant, but now much reduced by fishing;
2. small predators, especially the *mukeke, Luciolates stappersii*, presently subjected to an intense exploitation;
3. the *ndagala, Stolothrissa tanganyicae,* a strictly pelagic zooplanktivorous clupeid, presently dominant and characterized by a short life span of about one year;
4. *Limnothrissa miodon*, another *ndagala* (clupeid), of lesser importance and

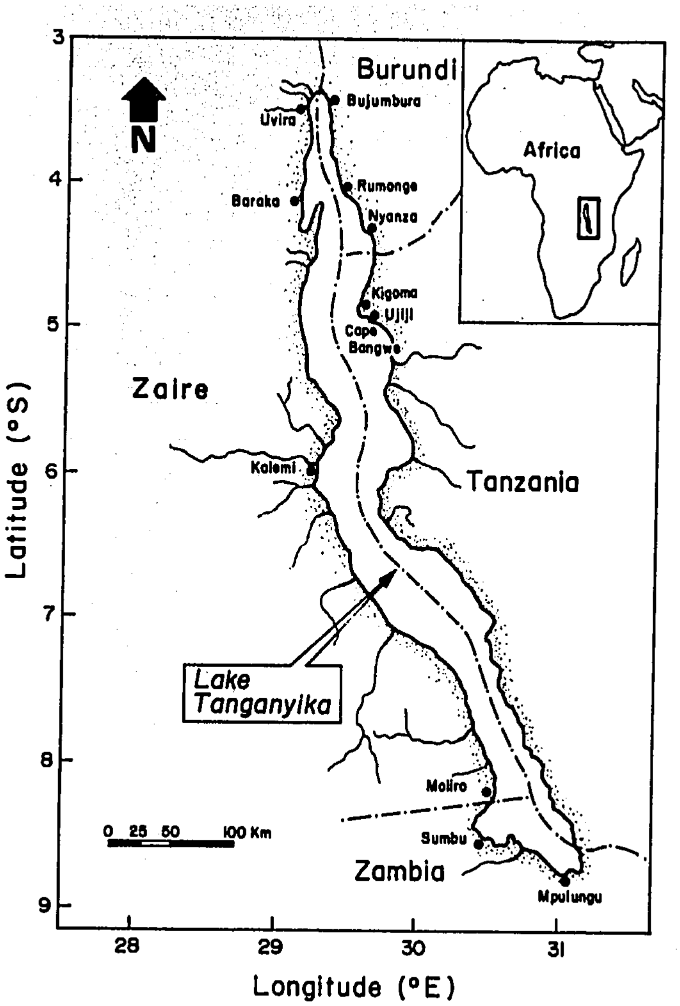

Fig. 1. Chart showing Lake Tanganyika, Africa. The models presented here describe the Burundi sector of the lake.

characterized by a higher longevity and a slight tendency towards ichthyophagy;

5. zooplankton;
6. phytoplankton; and
7. detritus, a box to which all boxes are connected via production of feces and/or dead material.

Tables 1, 2 and 3 document the values and sources of the input parameters used for the 1974-1976 and 1980-1983 models.

For the analysis, it has been assumed that the ecotrophic efficiency (EE, i.e., the proportion of the production that is either harvested or consumed within the system) was 0.95 for all groups in 1975. This implies that only a minor part (5%) of the production is assumed to die off and flow to the detritus box. The same EE of 0.95 is used for all consumer groups in the 1980-1983 model, except phytoplankton.

The observed reduction in the biomasses of the planktivorous fish in the time period between the two models should lead to a decreased predation on the zooplankton. This in turn will change the size structure of the zooplankton group and lead to an increased predation by copepodites on nauplii. We assume the increase to be from 5% to 10% of the diet (Gophen et al. 1990).

The effect the changes in the upper part of the ecosystem have on the phytoplankton is unknown. We therefore assume that the biomass and production of phytoplankton did not change between the two time periods.

Results and Discussion

Figs. 2 and 3 present our key results, i.e, graphical representations of the models for 1974-1976 and 1980-1983, respectively. A summary of the main results is given in Table 4.

For the 1974-1976 period, our biomass estimates for the predators (10 t·km^{-2}) and clupeids (18 t·km^{-2}) are very close to the estimates of Herman (1978) and Coulter (1981), who reported total pelagic stock biomasses of 25-30 t·km^{-2}, (i.e.,

Table 1. Input parameters used in ECOPATH II for the periods 1974-1976 and 1980-1983. Note names as used in Figs. 2 and 3. Catches are in t·km^{-2}·year, while P/B is year^{-1}.

Species/group	Catch[a] 1974-1976	Catch[a] 1980-1983	P/B 1974-1976	P/B 1980-1983
Lates spp.	0.6	0.05	0.45[b]	0.55[d]
Luciolates stappersii	3.5	1.81	0.75[c]	0.90[d]
Limnothrissa miodon	1.4	0.81	3.00[d]	4.00[e]
Stolothrissa tanganyicae	6.5	3.10	5.00[d]	5.50[e]
Zooplankton	0.0	0.0	26.00[f]	26.00[f]
Phytoplankton	0.0	0.0	450.00[g]	450.00[g]

[a] 1974-1976 data from Coulter (1977, 1981); 1980-1983 data from Roest (1988) and Petit (1989, 1990).
[b] Method of Lévêque et al. (1977).
[c] Nyakageni (1985).
[d] Roest (1988); Moreau and Nyakageni (1992).
[e] Moreau et al. (1991).
[f] Burgis (1983).
[g] Hecky and Fee (1981).

Table 2. Food consumption per unit biomass (Q/B) and related statistics of the main consumer groups in Lake Tanganyika.

Species/group	Period	W_∞ (g·ww)	K (year^{-1})	K_1	Q/B[a] (year^{-1})	Sources
Lates spp.	1974-1976	6,000.0	0.17	3.5	1.80	VBGF from Coulter (1976), K_1 from Lauzanne (1978) for "predators"
Luciolates stappersii	1974-1976	1,250.0	0.35	4.5	4.75	VBGF from Moreau and Nyakageni (1992), K_1 from M. Pearce (unpubl.)
	1980-1983	1,150.0	0.40	4.5	5.50	
Limnothrissa miodon	1974-1976	22.8	1.22	9.0	17.70	VBGF from Moreau et al. (1991), K_1 from Lauzanne (1978)
	1980-1983	25.0	1.20	9.0	21.00	
Stolothrissa tanganyicae	1974-1976	9.0	3.50	11.0	44.40	VBGF from Moreau et al. (1991), K_1 from Lauzanne (1978)
	1980-1983	11.2	2.50	11.0	38.40	
Zooplankton	1974-1983	-	-	-	110.00	assumed[b]

[a] The Q/B estimates for fishes are based on the parameters W_∞ and K of the von Bertalanffy growth function (VBGF), estimates of food conversion efficiency (K_1) and the empirical food consumption model of Pauly (1986), as implemented in Jarre et al.(1990). Egestion and excretion rates used (for all groups) were 20% of Q/B, totally, which probably represent an underestimate for zooplankton.

[b] This value divided by the corresponding P/B ratio in Table 1 leads to a gross food conversion efficiency of 0.24, an acceptable value (Payne 1986).

Table 3. Diet composition (in % of weight) of the major trophic groups in Lake Tanganyika for both 1974-1976 and 1980-1983 (except for zooplankton, for which two sets of values are provided). Prey (6) is phytoplankton and (7) is detritus.

	Predator	Prey							Sources
		1	2	3	4	5	6	7	
1.	*Lates* spp.	1	5	18	72	4	-	-	Coulter (1976)
2.	*Luciolates stappersii*	1	5	10	80	3	1	-	Nyakageni (1985) Coulter (1976)
3.	*Limnothrissa miodon*	-	-	4	16	78	2	-	Henderson (1976) Coulter (1977)
4.	*Stolothrissa tanganyicae*	-	-	1	1	95	3	-	Chapman and van Well (1978)
5.	Zooplankton	-	-	-	-	5	90	5	1974-1976[a]
		-	-	-	-	10	85	5	1980-1983[b]

[a] Modified from Burgis (1983) and Hecky and Kling (1981).

[b] Modified from Gophen et al. (1990).

Table 4. Summary of 1974-1976 and 1980-1983 models of the Burundi sector of Lake Tanganyika.

Group	Production (t·km^{-2}·year^{-1})		Biomass (t·km^{-2})		Food intake (t·km^{-2}·year^{-1})		Trophic[a] level
	1974-1976	1980-1983	1974-1976	1980-1983	1974-1976	1980-1983	
Lates spp.	1.1	0.2	2.4	0.5	4.3	1.0	4.1
Luciolates stappersii	5.9	2.9	7.8	3.2	37.1	17.6	4.1
Limnothrissa miodon	16.1	6.2	5.4	1.5	95.0	32.5	3.2
Stolothrissa tanganyicae	63.3	26.2	12.7	4.8	561.8	183.2	3.0
Zooplankton	824.9	379.5	31.7	14.6	3,489.9	1,605.5	2.1
Phytoplankton	3,330.0	2,880.0	7.4	6.4	-	-	1.0

[a] Values applying to both periods.

10 t·km^{-2} of predators and 15-20 t·km^{-2} of clupeids). The zooplankton biomass estimates (31.7 t·km^{-2}) are within the range proposed by Burgis (1983).

For 1980-1983, the computed biomass of fishes was almost three times lower than in 1974-1976 (10.1 t·km^{-2} against 28 t·km^{-2} previously). This is true for both predators and clupeids. This considerable decrease of fish biomass is in agreement with the finding of Roest (1978) and Herman (1978), who noted that in the northern and southern part of Lake Tanganyika, fish biomass dropped to about 12.2 t·km^{-2}, a very low level.

The change in the total production of zooplankton (from 813 to 379 t·km^{-2}·year^{-1}) is remarkable even if the

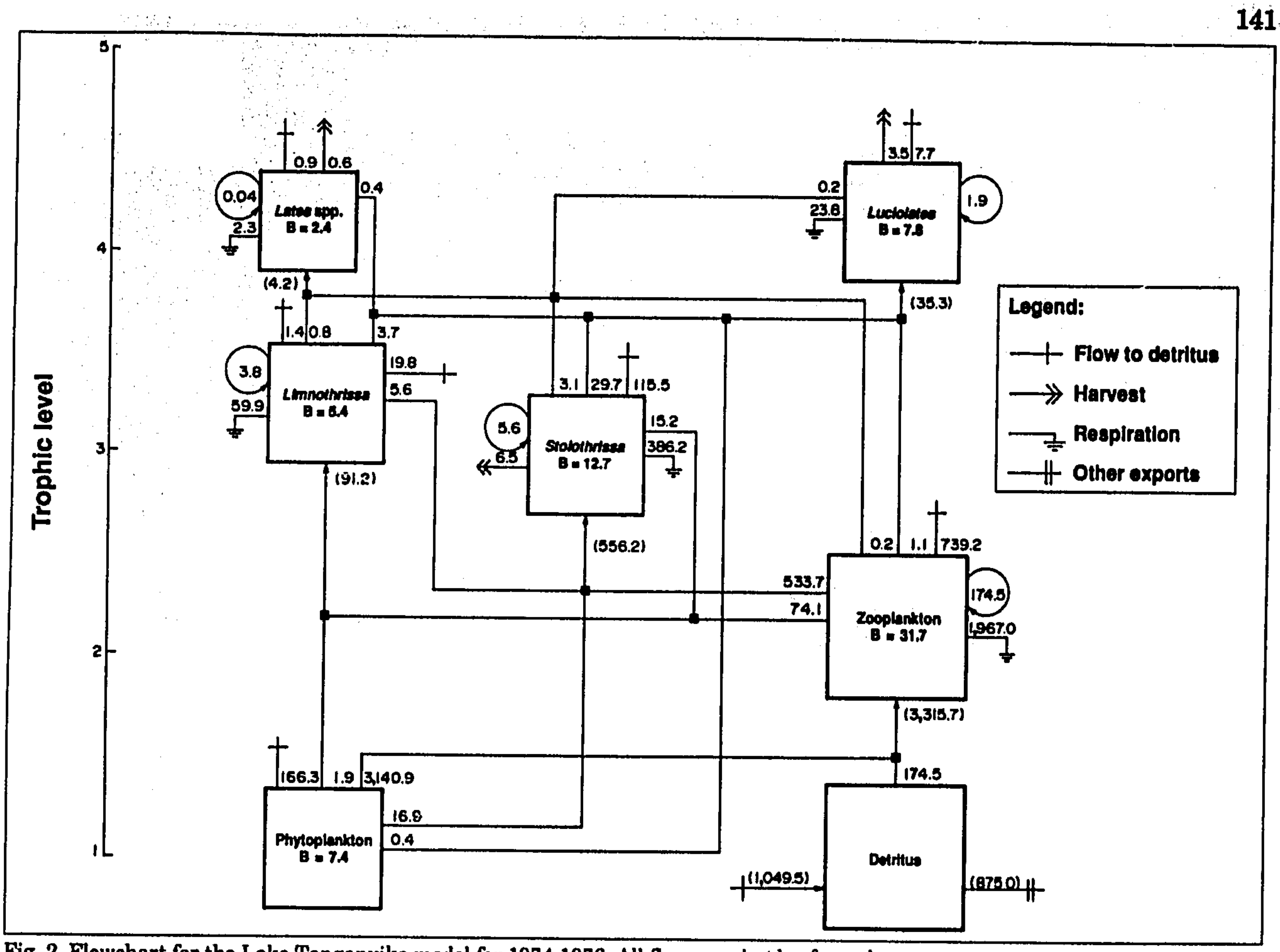

Fig. 2. Flowchart for the Lake Tanganyika model for 1974-1976. All flows are in t·km^{-2}year^{-1}.

lower value is still in the range proposed by Burgis (1983). Studies in other ecosystems have shown a similar pattern, with zooplankton production decreasing following collapse of stocks of planktivorous fish, e.g., in the Peruvian upwelling system (Carrasco and Lozano 1989). This reduction may be attributed to a changed size structure of the group and increased within-group predation, as previously discussed (Gophen et al. 1990).

This paper's estimate of phytoplankton biomass for 1975 is slightly higher than those of Ferro (1975) and of Hecky and Kling (1981) who published values of 4.9 and 6.4 t·km^{-2}, respectively. These estimates (like the authors') are, however, rather uncertain given the known seasonal variability of phytoplankton biomass in Lake Tanganyika (Payne 1986), as they were based on extrapolation of seasonal values to an entire year. However, for the 1980-1983 model, the authors assumed the phytoplankton biomass to be 6.4 t·km^{-2} (Hecky and Kling 1981). A noteworthy feature of the 1980-1983 model is that the ecotrophic efficiency for phytoplankton is estimated to be 0.48, which indicates that a major part of the phytoplankton production dies off due to reduced predation pressure from the zooplankton.

For the northern part of the lake, the Burundi sector, the biomasses of the pelagic fishes in the mid-1970s were estimated to be 28 t·km^{-2} which exceeded those in the early 1970s, 21 t·km^{-2}, the average for the lake as a whole, as reported by Mathisen (1976). The 1974-1976 period appears to have corresponded to an increased activity of the fisheries, following a local civil war, and it is tempting to propose that, during this period, the fish catches roughly corresponded to "maximum sustainable yield". This was first proposed by Coulter (1981), who, moreover, pointed out the strong variability of pelagic fish biomasses in Lake Tanganyika.

These biomass changes are largely due to the variable recruitment of clupeids, which appears to be linked to changes in intensity and duration of the rains leading, via terrigenic nutrients, to changes of plankton biomasses. An alternative interpretation of these changes of biomass is the possible influence of rains and upwelling (Coulter 1981; B. Nyakageni, unpubl.). These changes in clupeid biomasses are then tracked, with some lag time, by changes in the recruitment and biomass of *Luciolates stappersii* (Roest 1988).

The fishery catches for 1980-1983 are about 50% lower than for 1974-1976 and the biomasses are reduced by a similar factor (see Tables 1 and 4). This is

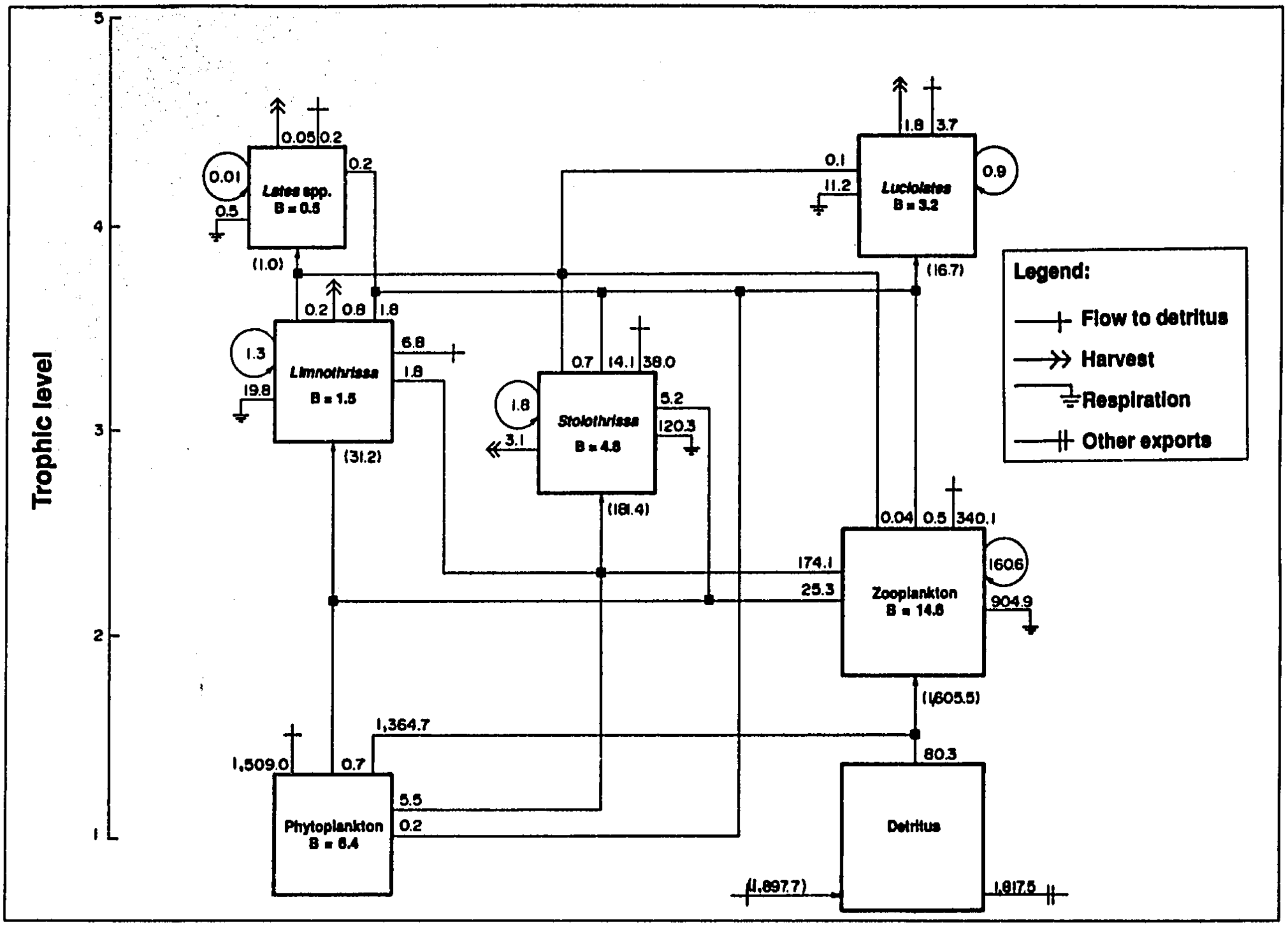

Fig. 3. Flowchart for the Lake Tanganyika model for 1980-1983. All flows are in t·km^{-2}year^{-1}.

supported by a reduction of about 40% from 1974-1976 to 1980-1983 of the catch/effort based on official catch statistics of Burundi (Petit 1989).

There are several explanations for the changes in the fish biomasses over the time period studied here. One may be based on the observation that the decline of the larger predators was relatively steeper than that of the clupeids (Table 4), leading to a decrease of the predatory impact of *Lates* spp. This again may have led to an increased longevity of the clupeids (Moreau et al. 1991). Given a continued high plankton production (Burgis 1983 and see Table 4), these changes may have led, finally, to an increased production of nonrecycled detritus, as the lake is too deep to allow recycling of detrital aggregates. Thus, seen from a fishery-oriented perspective, the ecosystem now functions less optimally than previously.

This hypothesis, although plausible, cannot be substantiated through a closer examination of the data. The mixed trophic impacts for the two periods are shown in Table 5. As can be seen, the large predators do not have any noteworthy trophic impact on the *Stolothrissa* in either of the models. The major predators are, in both models, the small predators and *Limnothrissa*. This suggests that the changes were not likely to be caused by top-down control; it could easily be that other mechanisms cause fluctuations in *Stolothrissa* recruitment.

Table 5. Mixed trophic impact of the groups in Lake Tanganyika (Burundi sector) on the clupeid, *Stolothrissa tanganyicae*. See Christensen and Pauly (this vol.) for a definition of trophic impact.

Group	Period 1974-1976	1980-1983
Large predator	-.01	-.01
Small predator	-.11	-.14
Limnothrissa	-.08	-.08
Zooplankton	0.33	0.41
Phytoplankton	0.32	0.37
Detritus	0.02	0.02
Fishery	0.01	0.01

Finally, this paper deals with the northern part of Lake Tanganyika and it cannot be directly extrapolated to all the lake. In the southern part (M. Pierce, unpubl.), the feeding habits of *Luciolates* are quite different (up to 50% of the bulk of the food of the adults consists of plankton and shrimps); more generally, fishing activity, growth rate and demography of the pelagic fishes are different and the plankton productivity of the lake as well. This means that a comparative study of northern and southern part of

Lake Tanganyika would probably give results indicating significant differences between the two pelagic communities.

Conclusion

ECOPATH II turned out quite helpful for analysis of the relatively simple pelagic zone of the northern part of Lake Tanganyika, especially with regard to the estimation of biomasses.

The problems encountered in those analyses were:

1. imprecise catch data (Petit 1990);
2. insufficient knowledge of the biology and population dynamics of the clupeids, especially *L. miodon*; and
3. problems with the estimations of vital statistics from length-frequency data on the clupeids, due to changes of their spawning seasons and longevity (Moreau et al. 1991).

Therefore, future research on the pelagic zone of Lake Tanganyika should emphasize:

- reliable methods for the estimation of age and growth for the clupeids;
- improved sampling schemes from length-frequency data leading to unbiased samples;
- a sampling scheme for fisheries data which would avoid underestimation of catch and landing;
- studies on diet composition and food consumption by the major consumers; and
- the collection of environmental data (especially on the rains and the winds) likely to contribute to the establishment of a model explaining the recruitment fluctuations of the clupeids.

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Trophic Relationship in the Fish Community of Lake Victoria, Kenya, with Emphasis on the Impact of Nile Perch (*Lates niloticus*)

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Abstract

The ECOPATH II approach and software were used to construct a box model of the fish community of the Kenyan sector of Lake Victoria before and after the introduction of Nile perch (*Lates niloticus*) to document how this introduction affected the dynamics of the lake. We demonstrate a change in ecosystem structure and an increase in ecotrophic efficiencies of most components of the ecosystem, following the introduction of Nile perch.

Introduction

During the first two decades after its introduction in the late 1960s in Lake Victoria, the Nile perch (*Lates niloticus*) population remained at low levels of abundance. In 1969-1970, the catch rate in open waters did not exceed 2 kg·hour^{-1} (Kudhongania and Cordone 1974). However, the end of the 1970s saw a sudden increase of the Nile perch population, with trawl catches reaching a high of 169 kg·hour^{-1} in Nyanza Gulf (former Kavirondo Gulf), Kenya.

During this latter period, Nile perch represented 90% of the total catch by weight of the Lake Victoria fisheries. Furthermore, the rich variety of catfish (*Bagrus* sp.), *Clarias* sp., *Oreochromis esculentus*, *Protopterus aethiopicus* and especially of haplochromines (Cichlidae) represented in the fishery catches were reduced to three dominant species, i.e., *Lates niloticus*, *Rastrineobola argentea* and *Oreochromis niloticus*.

The introduction of the Nile perch had an immense impact on the structure of the Lake Victoria ecosystem. To assess the strength of this impact, Ssentongo and Welcomme (1985) constructed a general model of trophic exchanges within the lake. They concluded that if the Nile perch biomass amounted to 120,000 t in 1980, it would consume about 650,000 t of fishes, 85% of which would consist of haplochromines. One problem with this model was the assumption that Nile perch preys exclusively on fish, irrespective of their size and age.

Another model proposed by Ligtvoet (1989) stressed the trophic importance of haplochromines in earlier times and the recent increase of *Caridina nilotica*, *Rastrineobola argentea* and juvenile Nile perch in the diet of *Lates niloticus*.

As a follow-up of these studies, this contribution presents quantitative box models for two different periods in the history of Lake Victoria. The first of these, describing the late 1960s and early 1970s, emphasizes the role of haplochromine species in the Lake Victoria food web. The second pertains to the late 1970s onwards and shows the ecological importance of Nile perch as it became the dominant predator.

It should be noted that the records available for use in this modelling effort describe only the shallow and intensively exploited Kenyan sector of the lake (Fig. 1). Thus, these models do not apply to the lake as a whole.

Materials and Methods

The ECOPATH II model of Christensen and Pauly (1992), a modified version of the ECOPATH model proposed by Polovina (1984), was used to describe the Lake Victoria ecosystem. This model is based on a budget equation of the form

$$P_i - M2_i - M0_i - C_i = 0$$

where P_i is the production of species i, $M2_i$ its predation mortality, $M0_i$ its nonpredation mortality and C_i the fisheries catch consisting of species i.

The first step in this modelling attempt was to determine the feeding network of the main component groups in the Lake Victoria ecosystem using diagrams as presented in Figs. 2 and 3. Then, the data inputs required by ECOPATH II were assembled and standardized (to $t{\cdot}km^{-2}{\cdot}year^{-1}$) for each component group. The following paragraphs describe the input parameters.

Fisheries Catches

Information on the fisheries catches in Lake Victoria was obtained from records available for the Kenyan sector. In 1970-1978, *Lates niloticus* became an important component of the commercial catch landed in Kenya (Ogari 1985). At about this time, *Rastrineobola argentea* and *Caridina nilotica* had already replaced the haplochromines in the diet of Nile perch (see portion on diet composition and Table 3) (Hughes 1986; Ogari and Dadzie 1988). Fishing effort increased from 90,000 nets (mesh size of 0.5-4 inches knot to knot) in 1971-1972 to a maximum of 415,000 in 1976 and decreased to 250,000 in 1978.

Annual fisheries catches for the main exploited species in Kenyan waters for 1971-1972 and 1985-1986 were adapted from Benda (1979) and Reynolds and Greboval (1988) and assembled in Table 1. The total catches increased fivefold, from 3.3 to 16.5 $t{\cdot}km^{-2}{\cdot}year^{-1}$ between the study periods.

Production-Biomass Ratio

Table 1 presents the production/biomass ratios (P/B) used in ECOPATH II. For fish groups whose growth can be described by the von Bertalanffy growth function (VBGF), this parameter was obtained from estimates of total mortality (Z). Values of Z were either obtained from available data in the literature or estimated from length-frequency distributions. For the components whose growth is usually not described by the VBGF (e.g., plankton, benthos and benthic producers), P/B estimates were obtained from the literature cited in Table 1.

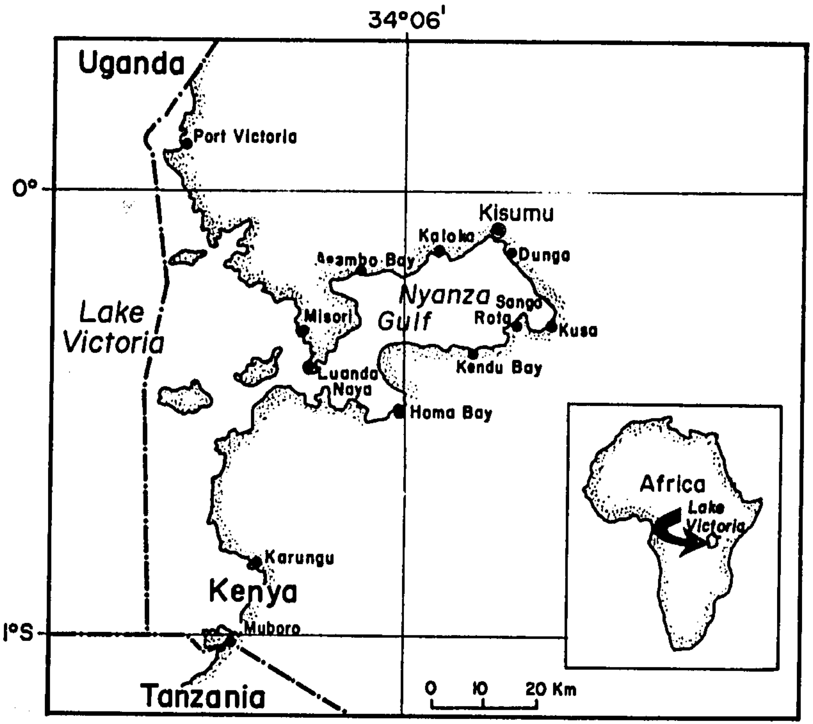

Fig. 1. The present study describes the trophic interactions in the shallow and intensively exploited Kenyan sector of Lake Victoria.

The P/B values for Nile perch were roughly constant between 1969 and 1975 (Hughes 1983; Acere 1985) and increased slightly after that period. Similar increases of P/B values have been observed for *Bagrus* and *Clarias*, and for haplochromines and tilapiine fishes (Ssentongo 1985; Getabu 1987; Witte 1987).

No recent information was available for P/B ratios for the other fish groups of minor importance in the fisheries (e.g., *Protopterus, Mormyrops* and *Synodontis*). Therefore, assuming that for these fishes the P/B ratios did not markedly increase over the past 15 years, the same values were used for both models.

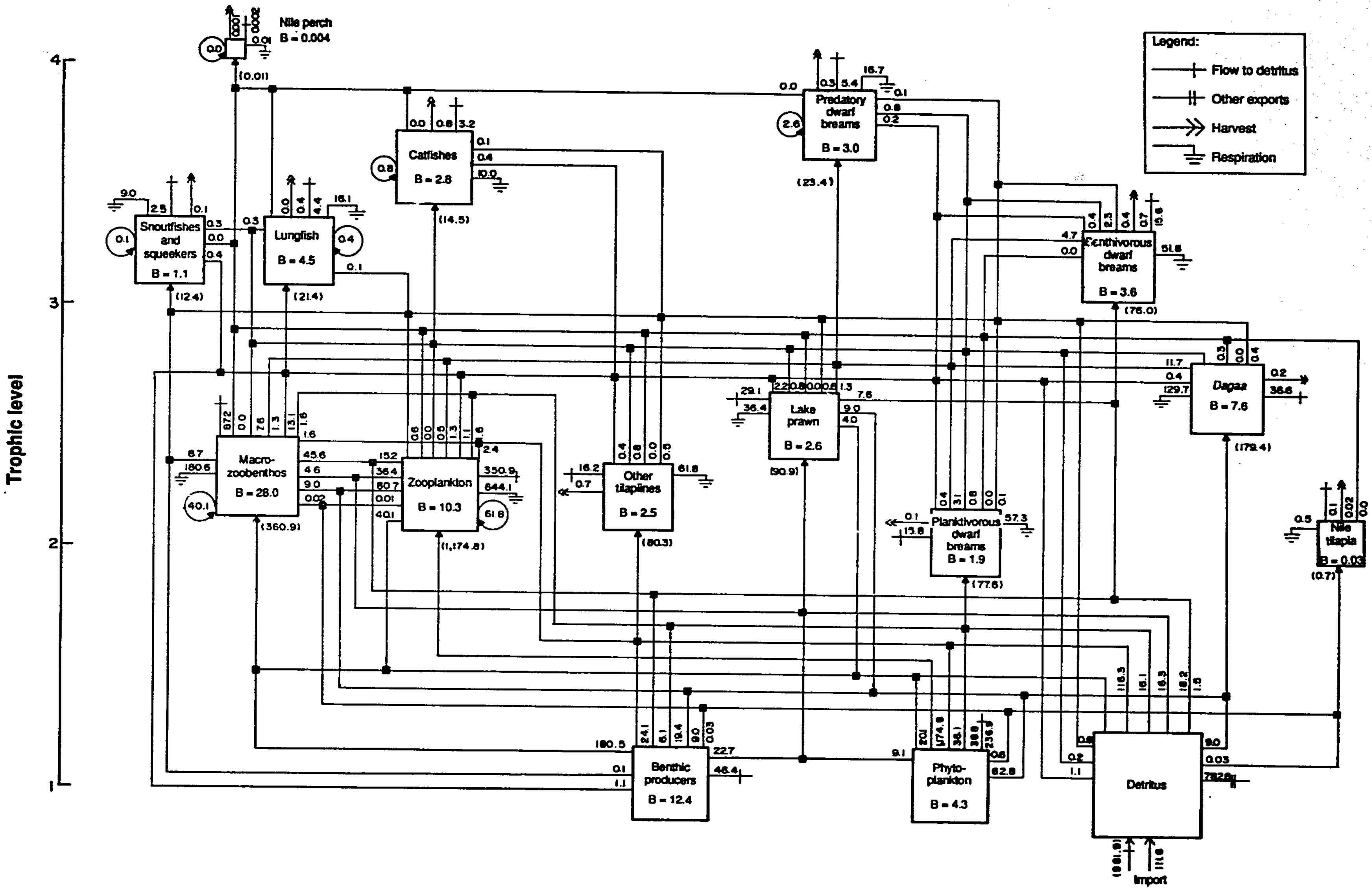

Fig. 2. ECOPATH II model of the Lake Victoria system, Kenya, for the period 1971-1972. Scientific names of species groups are included in Table 1. Biomasses (B) are in t·km⁻², flows in t·km⁻²·year⁻¹.

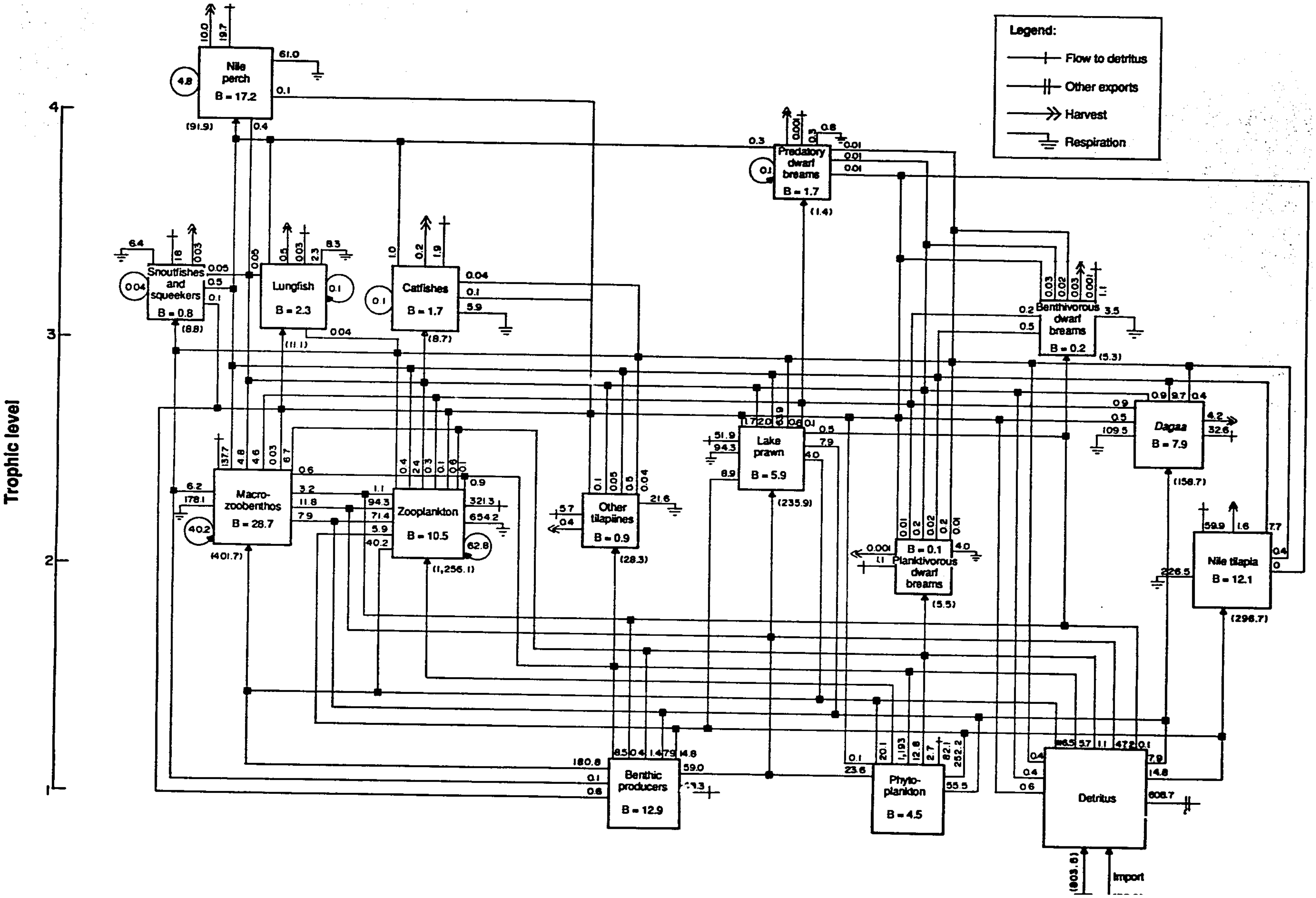

Fig. 3. ECOPATH II model of the Lake Victoria system, Kenya, for the period 1985-1986 (see Table 1 for scientific names of species groups). Biomasses (B) are in t·km^{-2}, flows in t·km^{-2}·year^{-1}.

Table 1. Input parameters used in ECOPATH II for the periods 1971-1972 and 1985-1986. Note common names as used in Figs. 2 and 3. The "Source" column pertains only to references used to obtain P/B values.

Common name	Scientific name	Annual catch ($t\cdot km^{-2}\cdot year^{-1}$)[a]		EE[h]		P/B ($year^{-1}$)		Source of P/B estimates
		1971-1972[b]	1985-1986[b]	1971-1972	1985-1986	1971-1972	1985-1986	
Nile perch	*Lates niloticus*	0.001	10.000	0.75	0.95	0.39	0.98	Hughes (1983), Asila and Ogari (1987)
Catfishes	*Bagrus* and *Clarias*	0.770[c]	0.176[c]	0.95	0.95	0.79	0.85	Chilvers (1969), Marten (1978)[i]
Lungfish	*Protopterus aethiopicus*	0.420[d]	0.030[d]	0.95	0.95	0.30	0.30	Lévêque et al. (1977), Merona (1983)
Snoutfishes and squeekers	*Synodontis* and mormyrids	0.060	0.030	0.95	0.95	0.90	0.90	Okedi (1969), Lévêque et al. (1977)[j]
Predatory dwarf breams	Predatory haplochromines	0.280[e]	0.001[e]	0.95	0.95	1.40	2.50	Maximum observed length from Fryer and Iles (1972); longevity and P/B values from Lévêque et al. (1977) and Witte (1987)
Planktivorous dwarf breams	Planktivorous haplochromines	0.110[e]	0.001[e]	0.95	0.95	2.50	3.00	
Benthivorous dwarf breams	Benthivorous haplochromines	0.730[e]	0.001[e]	0.95	0.95	2.50	3.00	
Dagaa	*Rastrineobola argentea*	0.240	4.230	0.95	0.95	1.80	2.20	Lévêque et al. (1977), Wanjala (1978)[k]
Nile tilapia	*Oreochromis niloticus*	0.020	1.630	0.90	0.95	0.65	0.90	Getabu (1987)
Other tilapiines	Other *Oreochromis* spp.	0.660[f] -	0.380[g] -	0.95	0.95	1.00	1.20	Rinne (1975), Lévêque et al. (1977)
Zooplankton		-	-	0.70	0.80	33.50	33.50	Lévêque (1979)
Lake prawn	*Caridina nilotica*	-	-	0.70	0.95	14.00	16.00	Winberg (1971), Hart and Allanson (1981)
Macro-zoobenthos		-	-	0.95	0.60	5.00	5.00	Symoens et al. (1980) Lévêque et al. (1983)
Phytoplankton		-	-	0.85	0.95	365.00	365.00	Computed from data in Payne (1986) and Burgis and Symoens (1988)
Benthic producers		-	-	0.85	0.85	25.00	25.00	

[a] Annual catch of the main species during different periods in Lake Victoria, Kenya, waters (4,200 km^2) (Benda [1979]; Barlow and Lisle [1987] and Reynolds and Greboval [1988]).

[b] Average value for the periods considered.

[c] 1/4 *Bagrus* and 3/4 *Clarias*.

[d] 1/3 *Mormyrus* and 2/3 *Synodontis*.

[e] Partitioned as: 25% predators, 10% phytoplanktivores, 65% benthivores (Greenwood 1974).

[f] Consisted of 80% *O. esculentus*.

[g] *O. esculentus* replaced by *O. leucostictus*, and *T. zillii* recently introduced (Welcomme 1988).

[h] Assumed values.

[i] P/B (=Z) ratios given here refer only to *Bagrus docmac* which were obtained using the compleat ELEFAN software (Gayanilo et al. 1987), based on length-frequency data available from these two sources. Note that the ratios are assumed to be true for *Clarias* spp. since these two species have similar longevities.

[j] P/B was computed based on the method of Lévêque et al. (1977), using the maximum observed longevity of four years.

[k] Wanjala (1978) records t_{max} = 2 to 2.5 years (P/B = 1.8 to 2.2 from methods of Lévêque et al. [1977]). Slight increase in P/B was due to increased fishing pressure and predation by *Lates niloticus*.

Diet Composition

Diet composition of each (group of) species is defined as the fraction of each prey species consumed to the total consumption. This diet matrix is obtained from results of stomach contents analyses available in the literature. Table 2 presents the diet matrixes used for the pre- and post-*Lates niloticus* periods in Lake Victoria.

Note that haplochromines in the early 1970s constituted the bulk of the diet of Nile perch (Moreau 1982). In 1979-1985, the diet of the Nile perch shifted to *Rastrineobola argentea, Caridina nilotica* (Hughes 1983, 1986) and juvenile Nile perch. This autopredation is an important phenomenon (Ogari 1988).

Ecotrophic Efficiency

Table 1 also presents ecotrophic efficiency (EE) values defined as the fraction of total production consumed by predators and/or the fishery. This parameter is very difficult to measure, but is often assumed to range from 0.65 to 0.95 (Ricker 1969). Given that the fraction (1-EE) of production is directed toward the detritus box, reasonable guesses of EE can be assigned to the components of the Lake Victoria ecosystem.

Table 2. Diet composition (%) of the groups of species in the Kenyan waters of Lake Victoria. Where no years are given, the same estimates are used for both periods.

Predator	Years	Prey 1	2	3	4	5	6	7	8	9	10	11	12	13	Phyto-plankton	Benthic producers	Detritus	Source
1. Nile perch	1971-72	1.0	8.0	2.0	2.0	35.0	10.0	25.0	2.0	1,0	10.0	1.0	1.0	2.0	-	-	-	Moreau (1982)
	1985-86	5.0	1.0	0.5	0.5	0.3	0.2	0.5	10.0	8.0	0.5	2.5	66.0	5.0	-	-	-	Ogari and Dadzie (1988)
2. Catfishes	1971-72	-	5.0	2.0	2.0	5.0	5.0	15.0	2.0		5.0	3.0	5.0	50.0	-	-	1.0	Greenwood (1966)
	1985-86	4.0	1.0	0.5	0.5	0.1	0.2	0.2	10.0	4.0	0.5	3.0	22.0	50.0	-	-	4.0	
3. Lungfish	1971-72		2.0	2.0	2.0	1.0	2.0	2.0	2.0		2.0	5.0	10.0	60.0	-	5.0	5.0	Ssentongo and
	1985-86	0.5	0.5	0.5	0.5	0.1	0.1	0.3	4.0	2.0	0.5	5.0	15.0	60.0	1.0	5.0	5.0	Welcomme (1985)
4. Snoutfishes	1971-72	-	1.0	1.0	1.0	0.5	0.5	3.0	3.0		4.0	5.0	70.0	-	-	1.0	5.0	Ssentongo and
and squeekers	1985-86	-	0.5	0.5	0.5	0.1	0.1	0.3	5.0	4.0	0.5	5.0	7.0	70.0	-	1.5	5.0	Welcomme (1985)
5. Predatory	1971-72					10.0	12.0	18.0	45.0	-	-	5.0	5.0	5.0	-	-	-	Fryer and Iles(1972)
dwarf breams	1985-86	-	-	-	-	5.0	10.0	10.0	60.0	-	-	8.0	5.0	2.0				
6. Planktivorous dwarf breams	-	-	-	-	-	-	-	-	-	-	-	2.0	-	2.0	50.0	25.0	21.0	Greenwood (1974)
7. Benthivorous dwarf breams	-	-	-	-	-	-	-	-	-	-	-	20.0	10.0	60.0	-	8.0	2.0	Greenwood (1974)
8. *Dagaa*	-	-	-	-	-	-	-	-	-	-	-	45.0	5.0	5.0	35.0	5.0	5.0	Ssentongo and Welcomme (1985)
9. Nile tilapia	-	-	-	-	-	-	-	-	-	-	-	2.0	3.0	-	85.0	5.0	5.0	Trewavas (1983)
10. Other tilapiines	-	-	-	-	-	-	-	-	-	-	-	3.0	2.0	-	45.0	30.0	20.0	Payne (1986)
11. Zooplankton	-	-	-	-	-	-	-	-	-	-	-	5.0	-	-	95.0	-	-	Lévêque (1979)
12. Lake prawn	-	-	-	-	-	-	-	-	-	-	-	40.0	-	5.0	10.0	25.0	20.0	Hart and Allanson (1981)
13. Macrozoobenthos	-	-	-	-	-	-	-	-	-	-	-	10.0	1.0	10.0	5.0	45.0	29.0	Lévêque et al. (1983)

Food Consumption per Unit Biomass

Food consumption per unit biomass (Q/B) values are presented in Table 3. This parameter refers to an age-structured population and considers the fact that in natural steady-state populations, there are more young than old fish and that, per unit weight, young fish eat more than old fish. The Q/B estimates presented here were obtained using the method proposed by Pauly and Palomares (1987, see also Pauly 1986).

Other (Missing) Parameters

The percentage of ingestion that is not assimilated was assumed to be 20% (Winberg 1971). The rest of the parameters, e.g., biomass, gross conversion efficiency, net conversion efficiency and mean trophic level were estimated by ECOPATH II.

Results and Discussion

Estimates of biomass and gross conversion efficiency obtained from the above-mentioned input parameters are presented in Table 4. Total fish biomass increased from 27 t·km^{-2} in the early 1970s to 43 t·km^{-2} in the mid-1980s. This is mainly due to the increased biomasses of Nile perch and Nile tilapia after their introduction into the lake.

Another important change is the consistent decrease in the biomass of the three haplochromine groups. Total haplochromine biomass declined from 8-9 t·km^{-2} (see also Reynolds and Greboval 1988) in the early 1970s to about 0.5 t·km^{-2} in mid-1980s.

Similar decreases in biomass are recorded for the boxes representing *Bagrus* / *Clarias*, *Protopterus aethiopicus*, mormyrids/synodontids and other *Oreochromis*. The only group that maintained its biomass over the period of study is *Rastrineobola argentea*.

The estimates of gross efficiency for the different fished groups are more or less similar, with the exception of the three haplochromine boxes, and that of *Rastrineobola argentea,* which show an increasing trend. However, there is some uncertainty about the validity of the P/B and Q/B values used as inputs. It is interesting to note, though that the maximum size of the haplochromines probably did not decrease as it did in Lake Malawi, due to overfishing (Turner 1977a, 1977b). Thus, it may be justifiable to expect an increase in gross efficiency.

The introduction of *Lates niloticus* and, to a minor extent, *Oreochromis niloticus* in the early 1970s precipitated a change in the structure of the Lake Victorian ecosystem. During the early 1970s, the fisheries (in the Kenyan sector) were poorly exploited, and the dominant species in the fisheries catch were *Haplochromis* spp., *Bagrus* and *Clarias.* Later in the mid-1980s, the haplochromines completely disappeared from the fisheries and *Lates niloticus* became dominant in the catch. This is illustrated in the ECOPATH II models for Lake Victoria in the early 1970s (Fig. 2) and in the mid-1980s (Fig. 3).

Table 3. Food consumption per unit biomass estimated from the relationship between asymptotic body weight (W_∞) and gross food conversion efficiency (K_1) presented in Pauly (1986) and Pauly and Palomares (1987). Note that estimates of mortality required for the model of Pauly (1986) model were obtained from P/B values given in Table 1.

Species group	Period	W_∞ g	K year	K_1 year	Q/B year	Source
Lates niloticus	1971-72	200,000	0.08	4.0	2.34	W_∞ & K from Hughes (1983), K_1 from Lauzanne (1977)
	1985-86	75,356	0.36	4.5	5.61	W_∞ & K from Asila and Ogari (1987) K_1 in agreement with Hughes (1983)
Bagrus dogmac	1971-72	3,520	0.25	5.0	5.47	W_∞ & K from Marten (1979) obtained using ELEFAN I (Gayanilo et al. 1987)
	1985-86	5,785	0.09	5.0	5.56	K_1 consistent with results of Chilvers and Gee (1974)
Clarias sp.		9,500	0.10	5.0	5.33	W_∞ & K from Willoughby and Tweddle (1977), refer to benthic feeding habits, L. Lauzanne (pers. comm.)
Protopterus aethiopicus	-	13,600	0.10	5.0	4.84	W_∞ & K from Merona (1983), K_1 L. Lauzanne (pers. comm.)
Mormyrid fishes	-	400	0.50	10.0	11.00	W_∞ & K from maximum size recorded in Merona (1983)
Synodontis sp.	-	650	0.50	10.0	11.62	W_∞ & K suggested in Merona (1983), K_1 from L. Lauzanne (1977)
Haplochromis sp.						
Predators	-	205	0.90	7.0	8.80	W_∞ & K suggested in Merona (1983)
Phytoplanktivores	-	35	1.50	20.0	41.00	K_1 from Moriarty and Moriarty (1973a, 1973b), Q/B obtained by Moriarty and Moriarty (1973a, 1973b)
Benthivores	-	40	1.50	12.0	21.20	$\ln Q/B = -0.1775 - 0.2018 \ln W_\infty + 0.6121 \ln T + 0.5156 \ln A + 1.26F$ (Palomares and Pauly 1989), (T = annual temperature °C, A = aspect ratio, F = food type)
Oreochromis niloticus	1971-72	2,000	0.29	20.0	18.90	W_∞ & K from Rinne (1975), K_1 averaged from results in Moriarty and Moriarty (1973a, 1973b), Harbott (1975) and Lauzanne (1977)
	1985-86	13,000	0.25	20.0	24.60	W_∞ & K from Getabu (1987) using ELEFAN I, K_1 averaged from Moriarty and Moriarty (1973a, 1973b), Harbott (1975) and Lauzanne (1977)
Other *Oreochromis* spp.	1971-72	745	0.37	20.0	32.30	W_∞ & K obtained for *O. esculentus* (dominant species) from Ssentongo (1985), K_1 from Moriarty and Moriarty (1973a, 1973b), Harbott (1975) and Lauzanne (1977)
	1985-86	535	0.80	20.0	32.00	W_∞ & K obtained for *O. leucostictus* from Rinne (1975), K_1 from Moriarty and Moriarty (1973a, 1973b), Harbott (1975) and Lauzanne (1977)
Rastrineobola argentea	1971-72	6	1.30	11.0	23.50	W_∞ & K obtained from method of Merona (1983), K_1 from Lauzanne (1977) and also from estimates obtained for zooplanktivores in Lake Tanganyika (Moreau and Nyakageni 1988)
	1985-86	5	1.50	11.0	20.00	

This decline in the haplochromine biomass can be attributed to the increasing fishing effort in the lake coupled with the high consumption of haplochromines by Nile perch. Furthermore, the success of introduced *Oreochromis niloticus* in 1981 (which was restricted to very shallow littoral waters) in the lake presented a strong competition for food to the phytoplanktivorous haplochromines.

The increase in *Lates niloticus* biomass in the mid-1980s coupled with the steady decline of the haplochromines prompts the expectation of a huge shift in the trophic level of the fisheries. However, ECOPATH II estimated similar values of the trophic levels of the fisheries, i.e., 3.98 in the early 1970s and 4.10 in the mid-1980s, respectively. This implies that although there has been a shift in dominance from the haplochromines (a moderately sized species group) to *Lates niloticus* (a large, single predatory species), this has not affected the trophic level at which the fisheries operate. Yet, overall catches

Table 4. Biomass, gross efficiencies (i.e., production/consumption) and food intake for all groups of the Lake Victoria system for the two periods 1971-1972 and 1985-1986.

Group	Biomass ($t \cdot km^{-2}$) 1971	Biomass ($t \cdot km^{-2}$) 1985	Gross efficiency 1971	Gross efficiency 1985	Food intake ($t \cdot km^{-2} \cdot year^{-1}$) 1971	Food intake ($t \cdot km^{-2} \cdot year^{-1}$) 1985
Nile perch	0.0	17.2	0.17	0.17	0.0	96.8
Catfishes	2.8	1.7	0.14	0.16	15.3	9.1
Lungfishes	4.5	2.3	0.06	0.06	21.9	11.2
Snoutfishes and squeekers	1.1	0.8	0.08	0.08	12.5	8.9
Predatory dwarf breams	3.0	0.2	0.16	0.28	26.0	1.5
Planktivorous dwarf breams	1.9	0.1	0.06	0.07	77.6	5.5
Benthivorous dwarf breams	3.6	0.2	0.12	0.14	76.0	5.3
Dagaa	7.6	7.9	0.08	0.11	179.4	158.7
Nile tilapia	0.0	12.1	0.03	0.04	0.7	296.7
Other tilapiines	2.5	0.9	0.03	0.04	80.3	28.3
Zooplankton	10.3	10.5	0.28	0.28	1,236.6	1,255.8
Lake prawn	2.6	5.9	0.40	0.40	90.9	235.9
Macrozoobenthos	28.0	28.7	0.35	0.36	401.0	401.7
Phytoplankton	4.3	4.5	-	-	-	-
Benthic producers	12.4	12.9	-	-	-	-
Total	84.6	105.9			2,218.2	2,515.4

Table 5. Trophic transfer efficiencies (%) for the Kenyan sector of Lake Victoria estimated using ECOPATH II.

Trophic level	Model 1970-1971	Model 1985-1986
VI	4.9	10.7
V	5.4	10.8
IV	7.0	10.5
III	12.3	18.6
II	16.0	15.9

from the system have increased considerably as also reflected in the increase in the gross efficiency (relative to primary production) of the fisheries, from 0.0016 in the early 1970s to 0.0082 in the mid-1980s.

The change in exploitation pattern in the lake is to some extent also reflected in the trophic transfer efficiencies in the system (Table 5). These show the proportion of the energy flow entering a trophic level that is transferred to the next trophic level or to the fisheries. As expected, the transfer efficiencies are similar for the herbivores (trophic level II) in the two models, while they are much higher in the upper part of the food web in the more recent time period. This illustrates how the fish resources of the lake are now more utilized for human consumption.

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An ECOPATH II Model of the Lake Chad System*

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Abstract

The trophic ecosystem modelling software, ECOPATH II, was used to analyze the Lake Chad system, Africa, during its "normal" phase, the period between 1969 and 1972. Reasonable estimates of population-related parameters for fish and invertebrate stocks were obtained, and an energy flow diagram for the whole lake is presented.

Introduction

Lake Chad (Fig. 1) is located between 12° and 14°20 N and 13° and 15°20 E, and occupies a 25,000-km^2 enclosed basin (Carmouze and Lemoalle 1983). The lake is supplied by two large river systems, the Shari-Logone in the south and the Yobe in the north; and has one outlet, the Chad Bahr-el-Ghazal in the southeast. The south basin of the lake sits at a higher altitude, 280-278.5 m, than the north basin, whose altitude varies between 277.5 and 275.5 m. Carmouze and Lemoalle (1983) explained how this difference in bottom basin altitudes affects the rise and fall of water level. The north basin completely dries up during extended dry periods and is filled only after several successive high river floods (from the Shari delta). High-water periods were recorded in the second half of the 19th century and in 1963-1964 when the entire basin was filled with floodwater. Dry periods so far recorded date back to the beginning of the century and to 1973-1976 (Carmouze and Lemoalle 1983) when the area occupied by lake waters was reduced to 9,000 km^2.

Carmouze and Lemoalle (1983) described Lake Chad as "unstable in time and heterogenous in space". The lake has a mean depth of 4 m, with a high variance due to the irregular seasonal flow of the Shari and the other rivers, evaporation (which is responsible for 20% of water losses) and infiltration (responsible for 10% of losses). The resulting fluctuations of mean water depth lead to radical changes in the structure of the lake.

The nature of the lake bottom varies from zone to zone mainly as a function of the suspended particles brought by the inflowing waters of the Chari-Logone, by water movement within the lake itself and by the presence of aquatic vegetation. Thus, the open water of the lake is characterized by clay substrates, the zones around the archipelago with clay-muddy substrates. This results in very variable amounts of

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*ICLARM Contribution No. 917.

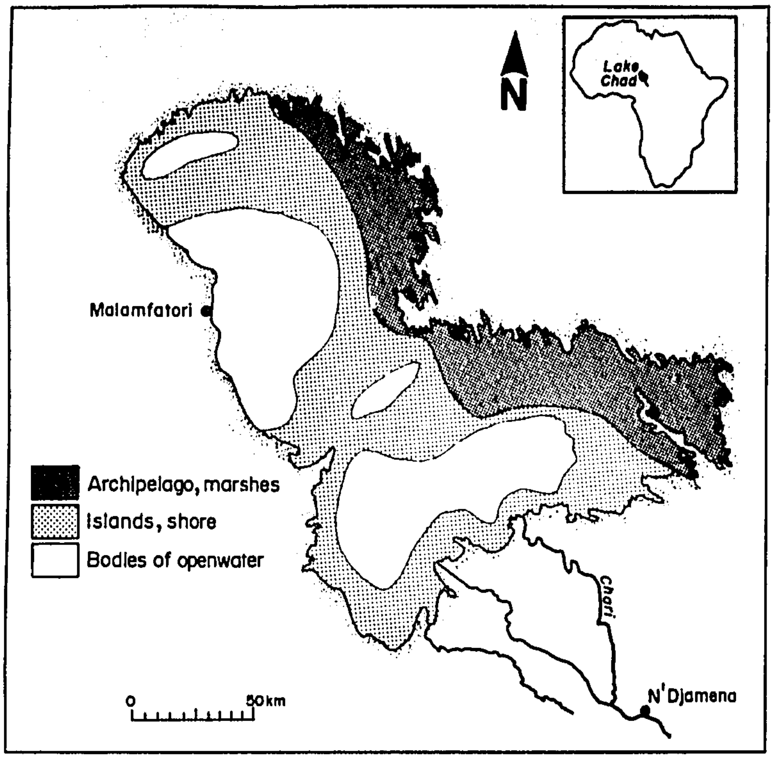

Fig. 1. The Lake Chad system in an intermediate phase, modified from Carmouze et al. (1983).

sediments being deposited on the lake bottom and in a spatially very heterogenous environment (Carmouze and Lemoalle 1983).

Macrophytic and Phytoplanktonic Populations

The differences in bottom sediments together with the mean lake water level influence the nature of populations dominant in each zone. For example, during what is termed the "normal" Chad period around 1969-1972 when lake waters covered a total area ranging from 18,000 and 21,000 km^2, with a water level of 281 m, the bulk of the aquatic vegetation was concentrated in the deltaic zones, around the borders of the archipelago and floating islands that detach from it, and in the shallower areas of the eastern part of the lake (Iltis and Lemoalle 1983). These emergent and semisubmerged macrophytes then covered an area of about 2,400 km^2 or 12% of the total lake area (Carmouze et al. 1983) representing a total macrophyte biomass of 400 t·km^{-2} dw (or 2,000 t·km^{-2} ww assuming a 1 to 5 dry to wet weight conversion ratio).

During the drought of 1973, the north basin was isolated from the south basin by the "Great Barrier," and by the end of 1974, the lake was reduced to a few isolated small ponds in the north while the south basin was filled up to the level of 1972. These two periods saw the massive development of macrophytes in the areas which had dried up and were turned into marshy, species-poor zones. These zones then covered 50% of the lake basin (Iltis and Lemoalle 1983): in 1974, the total water covered lake area was reduced to 1,500 km^2 and in 1976 after a slight flooding, the total inundated area reached about 9,000 km^2, with vegetation cover totalling 6,000 to 7,000 km^2 (Lemoalle 1983).

With respect to phytoplankton, Compère and Iltis (1983) concluded that Lake Chad is relatively rich in phytoplankton compared to other tropical lakes. This is further intensified during dry periods and particularly marked in the northern basin, which then more or less develops into a eutrophic pond. Compère and Iltis (1983) reported biomass estimates of 40,800 t over an area of about 18,000 km^2 in 1971 while for 1975, the biomass was 240,000 t over 11,000 km^2.

Zooplankton and Benthic Fauna

The zooplankton of Lake Chad was analyzed by Saint-Jean (1983) who found no radical changes in the biomasses between the "normal" Chad phase and the period of drought. Thus, it will have to be assumed that zooplankton biomass remained constant at 0.67 t·km^{-2} dw (or 3.4 t·km^{-2} ww at a 1:5 dry to wet ratio) over the seven-year period of study.

The benthic fauna of the lake can be assumed to have a high biomass because of the high sedimentation rates generally occurring in large tropical lakes. Furthermore, the high densities of emergent and semisubmerged plants in the deltaic region and the archipelago add periphyton biomass to the already considerable benthic biomass. However, Lévêque et al. (1983) reported biomass estimates of molluscs (3.3 t·dw·km^{-2} or 16.5 t·ww·km^{-2}), worms (0.29 t·dw·km^{-2}, 1.4 t·ww·km^{-2}) and insects (0.12 t·dw· km^{-2}, 0.61 t·ww·km^{-2}) which included only those invertebrates inhabiting the sediments. The box for benthic invertebrates, with a total biomass of 18.6 t·ww·km^{-2} considered in this present modelling attempt refers only to the "normal" Chad period.

No biomass estimates were available for the periphyton associated with the macrophyte vegetation in the lake. Dejoux (1983) mentions that since the area covered by water during the "normal" Chad phase is considerable, it follows that the area of vegetational cover is large and so is the biomass of the periphyton. In general this consisted of insects (chironomids, hemipterids, odonatids, ephemerotids, lepidoptids, entomostracids), ostracods and pulmonate molluscs. An estimation of the insect biomass was attempted in the present work assuming that the references made by Lauzanne (1983) to "terrestrial insects" in the diet of fishes found in the lake (discussed later) refer to insects associated with the vegetation cover. A separate box was also attributed to shrimps (*Caridina* sp. and *Macrobrachium* sp.), for which no estimates of biomass are available. Shrimps are, however, included in the fish diet matrices reported by Lauzanne (1983).

Fishery

The complexity of the Lake Chad system is well reflected by its complex fish community. Bénech et al. (1983) summarize the changes in the lake which occurred between the "normal" phase in 1969-1972 and the dry phase in 1973-1977 as having three basic effects on the fish populations. The decrease in water level caused an obvious concentration of the fish biomass and thus resulted in an increase in inter- and intraspecific competition. This enabled the fishers to increase their efficiency, and thus to increase fishing mortality. Wave action on the shallow water resulted in resuspension of sediments which caused massive fish mortalities due to suffocation. (The high solubility of nutrients, however, caused a characteristic phytoplankton bloom leading to huge variations in daily dissolved oxygen and CO_2 levels which may have to a certain extent counteracted the impact of increased turbidity.) Anoxic conditions were then created as the lake dried up, further increasing natural mortality. These changes favored hardy species, with a capacity to modify their diet. Thus, the heterogenous fish community existing in 1971, and composed mainly of migratory species, was replaced by a more homogenous community of "marsh" species during the drought period of 1973-1977.

Materials and Methods

The different states that can be taken by a complex variable system like the Lake Chad system cannot be summarized by one single ecosystem model. However, the important biological parameters needed in the construction of a box type ecosystem model for Lake Chad are not available for all the periods of change experienced by the lake. This limits modelling attempts that would eventually enable comparisons between critical periods, such as described above.

The Lake Chad model presented here was based on the "normal" period 1970-1972 and constructed using the ECOPATH II model described by Christensen and Pauly (1992), itself based on a preliminary model (ECOPATH) described by Polovina and Ow (1983). These models describe systems at equilibrium. They assume for each trophic group in a model that

$$\text{consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \qquad \ldots 1)$$

where production is expressed as the sum of all exports resulting from biomass consumed by predation and all flows to detritus. In ECOPATH II, this is expressed as

$$B_i \cdot \left(\frac{P_i}{B_i}\right) \cdot EE_i - \left(\sum_{j=1}^{n} B_j \cdot \left(\frac{Q_j}{B_j}\right) \cdot DC_{ji}\right) - EX_i = 0 \qquad \ldots 2)$$

where B_i is the biomass of species i; P_i/B_i its production/biomass ratio, equivalent to total mortality (Z); EE_i the ecotrophic efficiency; where B_j is the biomass of predator j; Q_j/B_j the predator's relative food consumption and DC_{ji} the fraction of species i in the diet of predator j. EX_i represents the exports (including catches) of group i.

The bulk of the information used here on the production and biomass estimates for fish, invertebrate and plant populations in the lake refers to the "normal" Chad in 1970-1972 (Carmouze et al. 1983). Studies conducted by Lauzanne (1983) provide quantitative estimates of the food chain flows from detritus to the top predator, *Lates niloticus*.

Estimates of relative consumption rates (Q/B) of all but three fish populations considered here were obtained from the multiple linear regression model proposed by Palomares (1991) in the form

$$\log Q/B = -0.261 \log W_\infty + 0.759 \log T + 0.405 \log A + 0.530h + 0.466d - 0.294p \qquad \ldots 3)$$

where Q/B is the food consumption (% day^{-1}) per unit of biomass of the fish population in question, W_∞ their asymptotic weight in g, T the mean annual water temperature in °C, A the aspect ratio of the caudal fin (see also Palomares and Pauly 1989; Pauly 1989), and where h, d and p are dummy variables representing herbivores, detritivores and pellet-fed fish. Equation (3) explains 58% of the variation of the data set of Palomares (1991), which comprised 96 different fish populations.

Tables 1 and 2 summarize the data used as inputs for ECOPATH II. The fisheries catches and the Q/B estimates, as obtained using equation (3) for the fish species represented in Table 1, were assembled together with biomass and P/B estimates for invertebrates, insects and primary producers obtained from the various contributions in Carmouze et al. (1983). The top predator considered here, *Lates niloticus*, is separated from the medium-sized predators (*Bagrus* sp. and *Hydrocynus* sp.) and the smaller predators (*Eutropius* spp. and *Schilbe* sp.). The box, represented by *Alestes macrolepidotus*, includes fish species more or less strongly associated with macrophytes and which thus ingest periphyton. Benthivores include *Synodontis* spp., *Heterotis* spp. and *Hyperopisus* sp. The zooplanktivores include *Alestes baremoze, Brachysynodontis* spp. and *Hemisynodontis* sp. The box represented by *Sarotherodon galileus* refers to exclusive phytoplanktivores. Detritivores are *Citharinus* sp., *Oistichodus* sp. and *Labeo* spp.

Results and Discussion

Table 1 and Fig. 2 present results from ECOPATH II. The overall fish biomass estimates of 26 t·km^{-2} obtained by this model are reasonable given the overall catch value of 6.4 t·km^{-2}. These results reflect the observations made by Durand (1983) on the relative dominance of *A. macrolepidotus* and of zooplanktivores, which amount to 8.8 t·km^{-2}. A relatively high biomass of 5.2 t·km^{-2} for *S. galilaeus* was obtained. No reference to the abundance of this group was made for the period of "normal" Chad. However, Durand (1983) states that *S. galilaeus* successfully survived the drought period, and even experienced an important increase in its biomass by the end of 1974. Reasonable biomass estimates of 2.9 and 9.3 t·km^{-2} were obtained for the groups representing shrimps and macrophyte-associated insects, respectively.

The rich, relatively stable sediment bottom of the lake during the "normal" Chad period is favorable for the maintenance of a large biomass of benthic invertebrates. This, coupled with its high P/B ratio and the relatively low predation pressure exerted by benthivores (which have a biomass of only 2 t·km^{-2}), seems compatible with the low EE value of 0.15 obtained by the model. High predation pressure by the important *Alestes* group on zooplankton reflects the high EE value of 0.93 of the later group whereas the moderate grazing of *S. galilaeus* on phytoplankton is reflected by an EE of 0.77. The bulk of the macrophyte biomass, which is underutilized by consumers, joins the detritus, as reflected by the rather low EE value of 0.10.

The Lake Chad model in Fig. 2 thus appears to present reasonable results. It is important to note, however, that this model represents only one phase

Table 1. Input data used with ECOPATH II for the Lake Chad "normal" period model, along with parameters estimated by ECOPATH II (in brackets). All flows are in t·km^{-2}·year^{-1}; all biomasses in t·km^{-2}, all rates in year^{-1}.

Group	Catch[a]	Biomass	P/B	Q/B[b]	EE[c]	GE[d]
Lates niloticus	0.73	(2.43)	(0.43)	[illegible].3[e]	0.80	0.10
Medium predators	1.38	(3.00)	(1.58)	10.5	0.80	0.15
Small predators	0.90	(2.52)	(2.48)	16.5	0.80	0.15
Alestes macrolepidotus	0.06	(3.63)	(3.20)	16.0	0.90	0.20
Benthivores	0.35	(1.98)	(4.00)	20.0	0.90	0.20
Zooplanktivores	1.66	(5.16)	(4.00)	16.0	0.90	0.25
Sarotherodon galilaeus	0.38	(5.25)	(2.40)	16.0[e]	0.90	0.15
Detritivores	0.52	(2.12)	(4.00)	40.0	0.90	0.10
Shrimps	-	(2.89)	5.00	30.0	0.90	
Benthic invertebrates	-	18.60[f]	36.4[g]	120.0[h]	(0.15)	0.30
Insects	-	(9.30)	15.0[h]	45.0[h]	0.80	0.33
Zooplankton	-	3.40[i]	63.7[j]	(182.0)	(0.93)	0.35
Phytoplankton	-	2.25[k]	365.0[l]	-	(0.77)	-
Macrophytes	-	2,000.00[m]	1.0[n]	-	(0.10)	-

[a] Total catch = 6.4 t·km^{-2} (Durand 1983) in 1971; species composition from Lauzanne (1983).
[b] Q/B from equation (26) (Palomares 1991).
[c] Assumed values from Moreau et al. (this vol.).
[d] Assumed values.
[e] Q/B obtained from experiments (Palomares 1991).
[f] From Lévêque et al. (1983).
[g] P = 600 t·km^{-2}·year^{-1} (Lévêque and Saint-Jean 1983).
[h] Assumed from GE value.
[i] From Saint-Jean (1983).
[j] P = 217 t·km^{-2}·year^{-1}(Lévêque and Saint-Jean 1983).
[k] From Compère and Iltis (1983).
[l] Assumed value similar to that of Lake Victoria (Moreau et al., this vol.).
[m] From Iltis and Lemoalle (1983).
[n] From Carmouze et al. (1983).

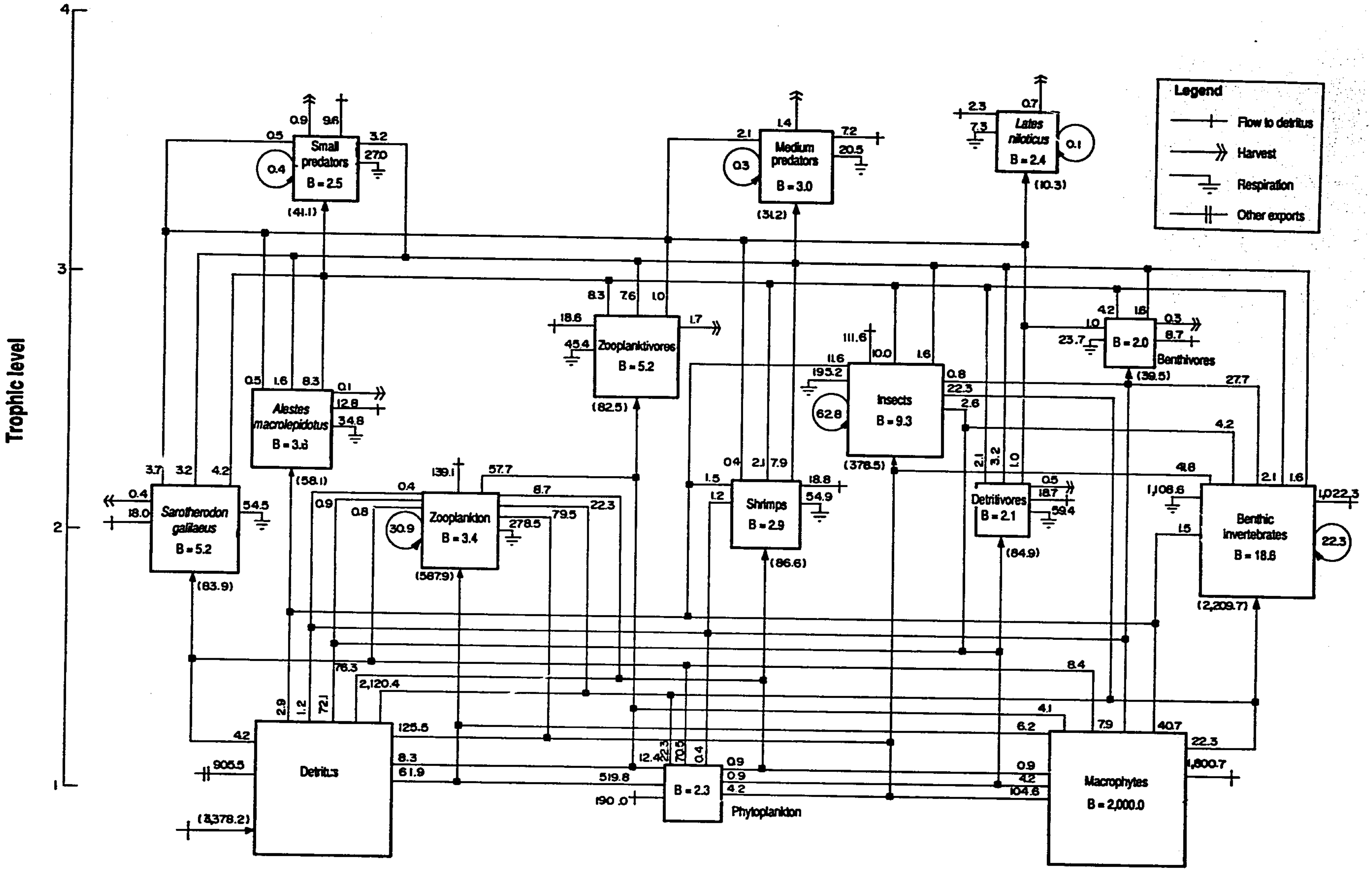

Fig. 2. ECOPATH II model of Lake Chad during the "normal" period.

Table 2. Feeding matrix of species groups in Lake Chad from Lauzanne (1983) in % (weight).

		Predator											
	Prey	1	2	3	4	5	6	7	8	9	10	11	12
1.	*Lates niloticus*	1	-	-	-	-	-	-	-	-	-	-	-
2.	Medium predators	20	1	-	-	-	-	-	-	-	-	-	-
3.	Small predators	5	10	1	-	-	-	-	-	-	-	-	-
4.	*Alestes macrolepidotus*	5	5	20	-	-	-	-	-	-	-	-	-
5.	Benthivores	10	5	10	-	-	-	-	-	-	-	-	-
6.	Detritivores	10	10	5	-	-	-	-	-	-	-	-	-
7.	Zooplanktivores	10	24	20	-	-	-	-	-	-	-	-	-
8.	*Sarotherodon galilaeus*	35	10	10	-	-	-	-	-	-	-	-	-
9.	Shrimps	4	25	5	2.5	3	-	-	-	-	-	-	-
10.	Benthic invertebrates	-	5	5	2.5	70	5	-	-	-	1	10	
11.	Insects	-	5	24	20	2	3	-	-	-	1	15	-
12.	Zooplankton	-	-	-	-	1	1	70	1	10	1	19	5
13.	Phytoplankton	-	-	-	-	1	1	15	84	1	1	1	84
14.	Macrophytes	-	-	-	70	20	5	5	10	1	1	25	1
15.	Detritus	-	-	-	5	3	85	10	5	88	95	30	10

in the evolution of Lake Chad; it would be interesting to compare this intermediate phase with the previous, more stable phase in the 1960s and the irregular dry phases from 1973 to 1985.

Also the model applies to a single ecosystem, whereas Lake Chad may be considered as element of "an ecological region" with its own functioning, which uses part of the production derived from the "adjacent river and floodplain" complex.

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RIVERS

The bulk of the world's freshwater fish catch is taken from rivers and their floodplains and deltas.

The catch rates from rivers vary more than for lakes. Low catches occur in headwaters, in areas with highly weathered soils, where primary productivity is low, while high catches often occur downstream, where nutrients and organic material from watershed areas, including sewage from cities, lead to high primary production. Further, a good part of the fish catches from rivers comes from fish passing through on feeding or breeding migrations, leading to catches in excess of what can be supported by localized primary production.

The world's total catch from all rivers, floodplains and swamps is not known. A first and rather crude estimate of total production from rivers in the tropics is 3.5 million tonnes annually, with a rather limited potential for increases (Christensen et al. 1992).

Total fish production of tropical rivers and floodplains amounts to some 4% of global production, i.e., 8% of fisheries catches in the tropics. As such it may seem to be of minor importance, but as the rivers and floodplains are harvested almost exclusively by small-scale fishers for local consumption, these 8% constitute an important food source in otherwise impoverished areas. In Africa, it may well be the most important fisheries resource system for the general population. It should also be noted that statistics of this sort seldom receive much attention, and the actual catches may be considerably underestimated.

Tropical rivers suffer from overfishing, as do most other aquatic resource systems (Fig. 1). The trends are the same when examining Fig. 2, which summarizes a time series of catch/effort data from the Nile downstream of Aswan. Here, the development from an under- to an overexploited fishery is clearly demonstrated. Over a ten-year period, the area yielded a constant 8,000 t·year^{-1}, despite a threefold increase in effort.

In order to change such negative trends, realistic management models must be developed and implemented. In order to do so, we need, first of all, to be able to describe the system we are working with. Acquiring good data is essential, and it has to be the right data - i.e., data which can be analyzed in the context of one or several models. For rivers - as for lakes - lots of experience has been gained from environmental modelling; far less is known, however, on trophic interactions and thus on how predation impacts on the yields of riverine systems.

Trophic models of rivers may be more difficult to conceptualize than environmental models. Usually we define an ecosystem as a "site" within which the trophic interactions exceed, in quantitative terms, the interactions between the site and its surrounding.

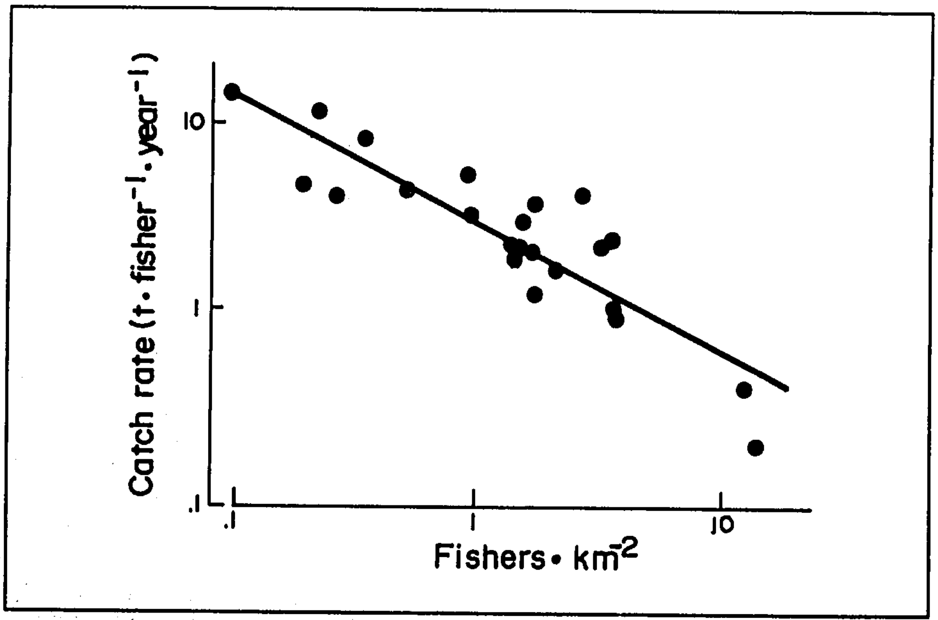

Fig. 1. Catch/effort as a function of effort for 17 rivers; C/f = 2.92* (fishers·km^{2})$^{-0.5}$. (Source: Welcomme 1985).

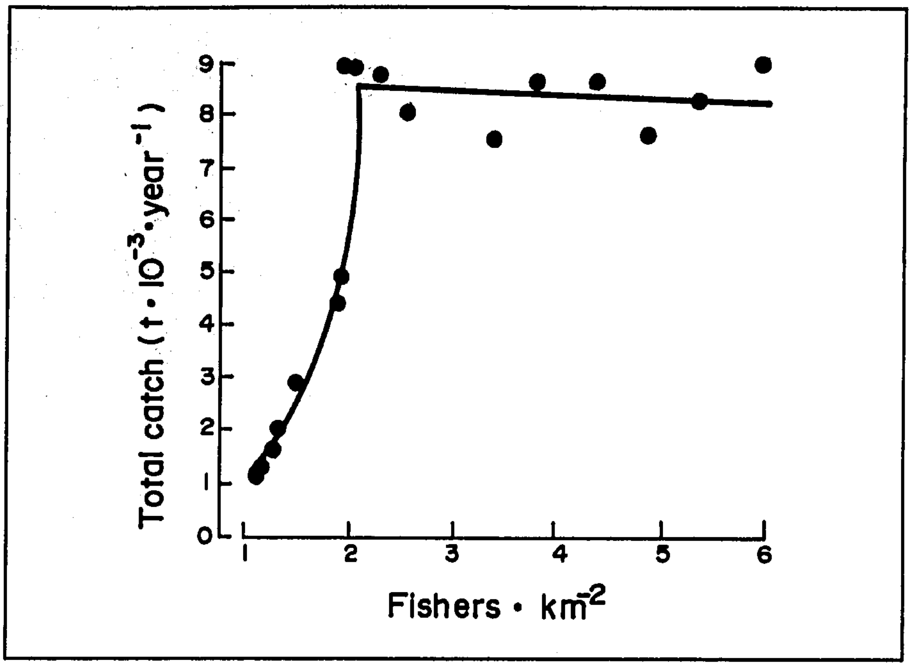

Fig. 2. Plot of total catch against the numbers of fishers for the Nile south of the Aswan Dam. (Source: Welcomme 1985).

Does this apply to rivers? How can one model a portion of a river? Can one assume, as done here, that water and phytoplankton are supplied and removed continuously, and that the transport therefore is not of major importance to the overall accounting?

Even if the water changes often in a given section of a river, the fauna (particularly the nekton) and flora (particularly the macrophyte) need not change as well. It appears that ecological successions occur mainly in the headwaters and streams, while little changes take place in larger rivers (Vannote et al. 1980).

To explain this, one should have in mind that natural rivers are not straight drainage channels, but complex systems resembling lakes in many aspects of their interactions with their surroundings. Thus, succession seems to be limited to the tributaries of the largest rivers.

Unfortunately, the present sections only include two trophic models of riverine systems - both from Europe and this is not sufficient to even begin to answer the above questions. We hope, however, that this may help to break the ice, and inspire others to follow up, and to construct models of rivers from the tropics, where they are so much more needed.

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Productivity and Energy Flows at All Trophic Levels in the River Thames, England: Mark 2

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Abstract

The trophic model for the River Thames, England, developed by the International Biological Programme (IBP) is probably the most complete ever constructed for a riverine ecosystem. A Mark 2 model is presented here, constructed using ECOPATH II. The model reinforces many of the conclusions of the earlier study and exposes certain weaknesses. In particular, the trophic role of the main fish populations and of detritus is revised.

Certain improvements that could be made to the Mark 2 model are identified, relating to the inclusion of incoming solar energy and to the efficiency of the community in converting solar energy to animal and plant tissue.

Introduction

From 1966 to 1972, the International Biological Programme (IBP) funded a noteworthy study of the Dreadnought reach of the River Thames. This was the first attempt to study and quantify the energy flow through a whole riverine ecosystem.

The work carried out attempted to quantify: energy entering the ecosystem (as light) over the whole year; primary production by phytoplankton; primary production by periphyton; production by one year and older fish (1+ group); production by 0 group fish (including egg production and production by larval/fry stages); production by invertebrate predators; production by invertebrate browsers; production by invertebrate filter feeders; production by rooted macrophytes; input of material from terrestrial leaf litter; input of allochthonous matter into the ecosystem; and predation by 0 and 1+ group fish.

Mann et al. (1972) summarized all resulting estimates of production and provided descriptions of the methods used in obtaining them. Mathews (1971) summarized all estimates made during the IBP study of fish production and fish biomass, including his own work on 0 group fish and the observation of other workers (Williams 1963, 1965, 1967) and Mann (1964, 1965) on 1+ group fish.

Certain items were not addressed in these studies:

- primary production estimates of periphyton were never completed and the resulting data were not published;
- methodology and data on fish predation were not published;
- similarly, the only record of the estimates of invertebrate production is that published by Mann et al. (1972); and
- no attempt was made to study suspended organic matter.

In spite of these omissions, this work provided the first quantified picture of the energy flow through a riverine ecosystem. Since then, the methodology available for tackling complex ecosystem studies has become more sophisticated.

The object of this paper is to reanalyze the results of the Thames IBP study, using the ECOPATH II approach and to use the new technique to:

- reassess the results of the earlier analysis of Mann et al. (1972) and then place these

results on a firmer basis, making the output comparable with more recent studies of other ecosystems;
- identify areas which were tackled incompletely or not at all; and
- use ECOPATH as a heuristic tool and discuss how the IBP approach could be updated and strengthened if such a study were to be repeated.

There is an important methodological difference in the way that the two models account for flows. The IBP model counts each unit of energy or biomass once only (i.e., it may be harvested only once). The ECOPATH model for the calculation of energy or biomass throughput, as a measure of the "size" of an ecosystem *sums all flows* so that a unit of energy or biomass may be included several times. Therefore ECOPATH will usually produce a much larger estimate of the total flow through a system than the corresponding IBP model. Furthermore, matter may also be recycled several times through feces so that the role of detritus is described more realistically by the ECOPATH model. Total energy flows from the two models are therefore different and not strictly comparable.

Materials and Methods

The methods used to obtain and analyze data obtained during IBP are provided by Mann et al. (1972), Mathews (1971) and Mathews and Kowalczewsky (1969). Methods for the study of older fish are also given in Williams (1965, 1967) and in Mann (1965).

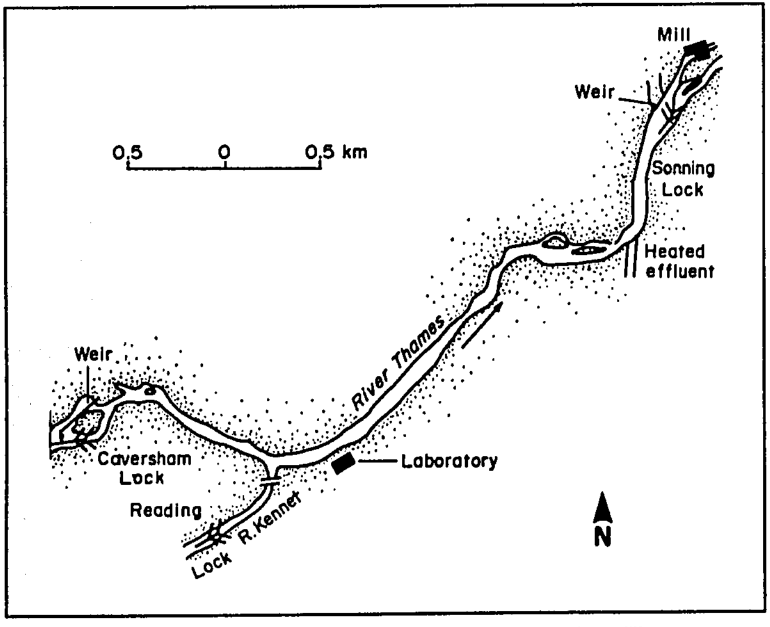

Fig. 1. Sketch map of the Dreadnought reach of the River Thames, near Reading, England. The locks at Caversham, Sonning, and on the River Kennet mark the limits of the study area.

The ECOPATH II model is the version of Christensen and Pauly (1992a, 1992b, this vol.), a modification of the original ECOPATH model applied by Polovina (1984) to a coral reef ecosystem. The model is based on a single budget equation for each group in the system:

$$P_i - M2_i - M0_i - C_i = 0$$

where P_i is the production of species (i), $M2_i$ is the predation mortality, $M0_i$ is the nonpredation mortality and C_i is the fisheries catch of species (i).

Information on biomass (B), production (P), and consumption (Q) is thus needed; if some data are lacking, the program may provide estimates, based on an assumption of steady state for all groups. Even when information is lacking, ECOPATH II frequently allows the identification of a complete model of the ecosystem. The model in this case may not provide a unique solution. Nevertheless, the model does provide a clear working hypothesis, which may be compared with other models and so may be verified and be used as a guide for future research.

Mann et al. (1972) are the source of data unless otherwise indicated; Mathews (1971) is the source for all estimates of fish production and biomass used here. Jϕrgensen (1979) is used to provide estimates of variables where they were not available from the Thames study. Fig. 3 of Mann et al. (1972) is the source for data on diet composition. All estimates of production were converted to $kcal \cdot m^{-2} \cdot year^{-1}$, whereas biomasses are in $kcal\ m^{-2}$.

Fig. 1 shows the Dreadnought reach of the River Thames, on which this study concentrated. The Thames attains a maximum depth of 4.5 m in this reach and has very steep banks being maintained and dredged regularly to keep it open for navigation by pleasure boats. A mean depth of 4.0 m was assumed for the purpose of converting phytoplankton and trypton (suspended organic matter) from volume to area basis.

The mean biomass of suspended organic matter for the River Thames below Kennet Mouth was 6.0 $g \cdot m^{-3}$, of which 1.0 $g \cdot m^{-3}$ was phytoplankton, the remainder being trypton (Mann et al. 1972, Fig. 3).

Jϕrgensen's (1979) value of 5 $kcal \cdot g^{-1}$ fresh weight for suspended organic matter and the mean depth of the Thames of 4.0 m were used to estimate a phytoplankton biomass of 20.0 kcal·m^{-2}.

Planktonic primary production was estimated by means of the oxygen light/dark bottle method, adjusted by a factor of x1.38 to reflect the difference between primary production in stationary experimental bottles and in the river, where currents ensure a well-mixed water column. The derived estimate of primary production by phytoplankton was 1,907 kcal·m^{-2}·year^{-1}.

Mann et al. (1972) noted the presence of substantial amounts of periphyton and their results indicate substantial periphyton production in depths up to 1 m, beyond which light is severely limiting. Since only 15% of the river surface lies at less than 1 m, it is likely that periphyton production is considerably less than phytoplankton production. A minimal estimate of periphyton production was obtained from analysis of stomach contents and the estimates of consumption rates by roach (*Rutilus rutilus* (L.)) and bleak (*Alburnus alburnus* (L.)) and was included by Mann et al. (1972) in their analysis of the ecosystem (their Fig. 3). For this study their estimate was increased to allow for consumption by all the species of fish and was regarded as a minimal estimate of production: it is unlikely that 95% of periphyton production is consumed by other organisms as assumed here.

Periphyton in the Thames was composed largely of filamentous algae and diatoms and was arbitrarily assumed to have a P/B ratio of half that of the much smaller phytoplankton.

Two species of macrophytes occur in the Dreadnought reach of the Thames, *Acorus calamus* and *Nuphar lutea*. Production of these was estimated to be 16.4 and 27.6 kcal·m^{-2}·year^{-1}, respectively, giving a total macrophyte primary production of 44 kcal·m^{-2}·year^{-1}.

Mathews and Kowalczewsky (1969) estimated the input of leaf litter from overhanging trees. A total of 79 kcal·m^{-2}·year^{-1} was estimated to fall into the Thames.

Mathews (1971) provided estimates of fish production, including the contribution of eggs and fry to production during the first year of life. Fry production was estimated from surveys aimed at age-group 0 and older. "Prefry", i.e., fish between the egg and the fingerling stages were fully vulnerable to fisheries, and their production was estimated using the algebraic method of Ricker (1946). Estimates of 1+ group fish production obtained from Allen (1951) curves were also provided. Detailed production estimates were carried out in this way for bleak (*A. alburnus* (L.)), roach (*R. rutilus* (L.)), dace (*Leuciscus leuciscus* (L.)) and gudgeon (*Gobio gobio* (L.)). Table 1 (from Table XX, Mathews 1971) shows the resulting estimates of production.

For this study it was decided to combine all fish production into 0 group and 1+ group boxes. Therefore the data in Table 1 were regrouped as in Table 2 and a conversion factor of 1 g live weight = 1.154 kcal (R. Britton, pers. comm.) was applied.

Mathews (1971) provided estimates of annual total instantaneous mortality rates (Z) from the egg stage to the end of the first year of life, for each of the four major species, for 1967 and 1968. The mean value was Z = 7.21 year^{-1}. This value was assumed to be an estimate of the P/B ratio (Allen 1971) for all 0 group fish. Applying

Table 1. Production (P, g·m^{-2}·year^{-1}), biomass (B, g·m^{-2}) and production/biomass ratios (P/B, year^{-1}) for four abundant fish species in the River Thames.

		Age group										
Species		0	1	2	3	4	5	6	7	8	9	Total
Bleak	P	24.2	5.3	10.8	9.0	2.6	0.7	-	-	-	-	52.8
	B	6.85	8.98	10.80	12.32	7.43	1.23	-	-	-	-	47.7
	P/B	3.56	0.59	1.00	0.73	0.35	0.53	-	-	-	-	1.11
Roach	P	8.2	1.6	1.9	2.2	1.8	0.6	0.7	0.4	0.3	0.1	17.8
	B	2.77	1.20	2.32	4.15	4.39	3.33	3.33	2.22	1.03	0.39	25.13
	P/B	2.96	1.33	0.82	0.53	0.41	0.18	0.21	0.18	0.29	0.26	0.71
Dace	P	1.16	0.35	0.29	0.27	0.23	0.17	0.09	0.04	-	-	2.60
	B	0.43	0.22	0.33	0.48	0.53	0.52	0.47	0.28	-	-	3.26
	P/B	2.70	1.59	0.88	0.56	0.43	0.33	0.19	0.14	-	-	0.80
Gudgeon	P	3.7	2.1	3.2	2,3	0.4	-	-	-	-	-	11.7
	B	1.40	2.44	3.37	4.60	3.08	-	-	-	-	-	14.9
	P/B	2.64	0.86	0.95	0.50	0.13	-	-	-	-	-	0.79

Table 2. Production (kcal·m^{-2}·year^{-1}) of fish in the River Thames and the ratio of roach and bleak production to total production (Mathews 1971; Mann et al. 1972).

	0-	1+
(a) Roach and bleak	94.0	43.0
Other major species	28.7	11.7
Minor species	13.6	6.0
(b) Total fish	136.3	60.7
(b):(a)	1.4	1.4

the P/B ratio of 7.21 to the annual production of 0 group fish (Table 2) the biomass of 0 group fish was estimated as 136.3/7.21 = 18.9 kcal·m^{-2}.

Mann et al. (1972) estimated consumption by fish of 0 group and 1+ group bleak and roach, using R. Britton's (unpublished) data on diet, digestion times and the calorific value of different components of the stomach contents.

Mann et al.'s (1972) predation estimates were adjusted to provide estimates of the predation by all species of fish (Table 3). The assumption that the mean diet composition of Thames fish is similar to the mean composition for bleak and roach seems acceptable: dace and bleak tend to be surface feeders, while roach and gudgeon tend to be bottom feeders. Amongst the minor species, perch (*Perca fluviatilis* (L.)) is zooplanktivorous when young and piscivorous when older, while bream (*Abramis brama* (L.)) is a bottom and detritivorous feeder. Other species provide only a very small component of predation.

Jϕrgensen (1979) provided estimates of the P/B ratios for various invertebrate predators, which were weighted by the production estimates provided by Mann et al. (1972). This provided a weighted mean P/B ratio for the invertebrate predators of the Thames of 3.5 year^{-1}.

A similar procedure was used to provide weighted mean P/B ratios for invertebrate browsers and invertebrate filter feeders, of 1.6 and 1.2 year^{-1}, respectively.

A value of P/B = 5.0 year^{-1} was provided by Mann et al. (1972) for young chironomids, similar to values for Chironomidae provided by Jϕrgensen (1979). An "export" of 180.5 kcal·m^{-2}·year^{-1} of young chironomids was used to produce the adult chironomids in the model.

A P/B ratio of 37.4 year^{-1} was obtained by combining appropriate values from Jϕrgensen (1979) for Thames zooplankton.

The production of macrophytes and trees was 44 and 79 kcal·m^{-2}·year^{-1} (Mann et al. 1972), respectively, all of which enters the detritus box.

A value of Q/B = 0 was assigned to adult Chironomidae, as they do not feed. After reproducing they fall into the water where they are subject to heavy predation by fish.

Values of 0.95 were assigned to the ecotrophic efficiencies of invertebrate predators, browsers and filter feeders, young and adult chironomids, and zooplankton. Such values imply that 95% of the production of these taxa is consumed by predators and 5% is reduced to detritus by decomposers.

The following values were assigned to the gross efficiencies (production/consumption ratios) for invertebrate browsers (20%), invertebrate predators (20%), filter feeders (15%), zooplankton (15%) and young chironomids (10%). These values complete the data requirements of the model and are consistent with general knowledge of the gross efficiencies for these groups observed in other areas (V. Christensen, pers. comm.). Values of Q/B in Table 5 were derived from these gross efficiencies.

Table 4 shows the diet composition for the consumers. The diet is based on the contributions of different types of organisms to 0 group and 1+

Table 3. Predation by Thames fish: quantities consumed by bleak and roach only (Mann et al. 1972) and by all species (data adjusted x1.40, Table 2).

Food item	Roach and bleak only		All Thames fish		
	0	1+	0	1+	Total
Fish 1+ group	0	0	0	0	0
Fish 0- group	0	4	0	5.6	5.6
Invertebrate predators	0	1	0	1.4	1.4
Invertebrate browsers	0	15	0	21.0	21.0
Filter feeders	0	11	0	15.4	15.4
Young chironomids	28	20	39.2	28.0	68.6
Adult chironomids	26	126	36.4	176.4	214.1
Zooplankton	97	23	135.8	32.2	172.8
Periphyton	3	155	4.2	217.0	221.4
Detritus	32	307	44.8	429.8	476.2
Total			260.4	926.8	1,187.2
Allochthonous	0	215	0	301.0	301.0
Grand total			260.4	1,227.8	1,488.2

Table 4. Input data on diet composition for the Thames Mark 2 model. Predator 1 is the fish 1+ group.

Prey	Predator 1	2	3	4	5	6	8
2. Fish 0 group	.004	-	-	-	-	-	-
3. Invertebrate predator	.002	-	-	-	-	-	-
4. Invertebrate browser	.017	-	.33	-	-	-	-
5. Filter feeders	.013	-	.33	-	-	-	-
6. Young chironomids	.023	.151	.34	-	-	-	-
7. Adult chironomids	.144	.140	-	-	-	-	-
8. Zooplankton	.026	.522	-	-	-	-	-
11. Phytoplankton	-	-	-	-	.5	-	.5
12. Periphyton	.177	.016	-	.33	-	-	-
13. Detritus	.350	.171	-	.67	.5	1.0	.5
- Import	.244	-	-	-	-	-	-

group roach and dace (Fig. 3 in Mann et al. 1972) and a general knowledge of the diet composition for other constituents of the ecosystem.

An assimilation rate of 80% was assumed for all food types except detritus. For detritus the assimilation rate (Mann et al. 1972) for roach (6.92%) was accepted as a general value. The egestion rate for 0 group and 1+ group fish was then obtained by weighing these two values by the composition of the food ingested.

Results and Discussion

Table 5 presents input to the Mark 2 model of the Thames ecosystem, together with selected output for the model.

The Dreadnought reach of the Thames is characterized by high energy circulation through the detritus. This, as Mann et al. (1972) discussed, is probably associated mainly with high nutrient levels due to sewage effluents and mineralization of sewage solids, stimulating production and causing the exceptionally high levels of fish production that were observed in the Thames (197 kcal·m^{-2}·year^{-1} being more comparable to production levels in aquaculture systems than to natural populations).

Primary Production and Energy Throughput

Primary production is dominated by the phytoplankton (1,907 kcal·m^{-2}·year^{-1}) and the periphyton production of at least 246 kcal·m^{-2}·year^{-1}, with a small contribution from macrophytes (46 kcal·m^{-2}·year^{-1}). Total primary production of the ecosystem is at least 2,172 kcal·m^{-2}·year^{-1} but could be larger, because the estimate for periphyton was obtained by back calculation from stomach content analysis.

The total energy content of the incident light was 729,000 kcal·m^{-2}·year^{-1}, thus 0.3% of the incident light is fixed during photosynthesis by the Thames ecosystem.

Table 5. Data input (without brackets) for the Mark 2 Thames model. For macrophytes and trees only total production is known, and this is split arbitrarily between P/B and B as only the total production is used in the actual calculations. Estimates given in brackets are estimated by ECOPATH II.

Group	Biomass (kcal/m^2)	P/B (year^{-1})	Q/B (year^{-1})	EE	Unassimilated food	Trophic level
1. Fish 1+ group	101.7	0.597	9.158	(0.00)	0.47	(2.12)
2. Fish 0 group	18.9	7.210	14.269	(0.00)	0.33	(2.67)
3. Invertebrate predator	(0.4)	3.500	17.500	0.95	0.20	(3.00)
4. Invertebrate browser	(12.3)	1.600	(16.000)	0.95	0.50	(2.00)
5. Filter feeders	90.9	1.280	8.533	(0.12)	0.50	(2.00)
6. Young chironomids	(51.6)	5.000	(33.333)	0.95	0.50	(2.00)
7. Adult chironomids	(36.1)	5.000	0.000	0.95	-	(1.00)
8. Zooplankton	(4.7)	37.400	(187.000)	0.95	0.50	(2.00)
9. Macrophytes	10.0	4.400	0.000	(0.00)	-	(1.00)
10. Trees	10.0	7.900	0.000	(0.00)	-	(1.00)
11. Phytoplankton	20.0	95.350	0.000	(0.43)	-	(1.00)
12. Periphyton	(5.2)	47.700	0.000	0.95	-	(1.00)
13. Detritus	10.0			(0.70)	-	

Detritus: Its Role in the Thames

Detritus provides the single most important secondary energy flow with 61% of all possible energy flow pathways with ecosystem originating from circulating through or returning to the detritus. The "ecotrophic efficiency" of detritus is estimated to be 55%, indicating that more than half of the energy entering the detritus is reused in the system.

Mathews and Kowalczewsky (1969) studied the disappearance rate of leaf litter originating from trees (mainly willows) along the River Thames bank. The disappearance of leaf litter was not caused by benthos, but was caused principally by microorganisms. The litter disappearance was accompanied by an increase in total nitrogen content of the leaf litter, presumably due to nitrogen uptake from the environment by microorganisms. The total input of leaf litter was reduced to fine particles available to filter feeders and microorganisms, before the next year's leaf crop was added to the ecosystem. Benthic browsers found on litter were thought to feed on the microorganisms, which themselves fed on and digested litter. In this respect, the invertebrate litter browsers of the Thames carry out a function analogous to that of earthworms in soils on land.

No similar experiments were conducted in the Thames on other types of detritus. The main sources for flow to the detritus are 1+ fish, filter feeders, zooplankton, young chironomids and 0 group fish, with a total of 1,878 kcal·m^{-2}·year^{-1}, i.e., 59% of the total flow through detritus. This input will be mainly in the form of feces and should therefore be more easy to break down than the leaf litter experimented on by Mathews and Kowalczkewsky. In conclusion, it seems reasonable to assume that all detritus in the Thames ecosystem can be converted into more accessible energy within a year.

Unfortunately, no estimate of the biomass of microorganisms (bacteria and fungi: Mathews and Kowalczewsky 1969) is available with which to compare the estimated amount of detritus converted to more accessible energy nor is any estimate of microorganism production yet available.

Assuming that invertebrate browsers feed on the microorganisms as these consume litter, there is an extra trophic level involved in the reduction of litter to animal tissue. The trophic position of invertebrate browsers and fish is therefore open to discussion.

This may also explain the low assimilation ratio estimated by Mann et al. (1972) of 6.92% for detritus eaten by roach (which is close to the value of 8.35% reported by Jϕrgensen (1979, Table A256); this low value for roach occurs because the food consumed itself is produced by microorganisms, with an unknown assimilation ratio, from the digestion of detritus.

Because of the potential implications of the work of Mathews (unpubl. data) and Mathews and Kowalczewsky (1969) for the role of detritus in the Thames ecosystem and elsewhere, it is suggested here that the fungi and microorganisms are the true detritivores and that the roach and dace, considered detritivores by Mann et al. (1972) because of the large amounts of detritus in their guts, are actually "detritivore browsers".

Table 6 shows that the total energy flow through detritus is greater than the net primary production. The Thames ecosystem is therefore dominated by the energy flow through the detritus. Detritus, however, does not appear in Fig. 2 except as input from trees and macrophytes into the periphyton and detritus box (and therefrom to 1+ fish), and as a small contribution to 0 group fish. The important detritus contributions from all other components were underestimated and the dominant position of energy flows through detritus was not realized. Insofar as I can recollect the team's discussions accurately, this was because:

- it was difficult then as it is now to address the question of detritus using trophic level analysis: the empirical observations needed to address the question are almost entirely lacking; and
- more detailed data, e.g., on P/B ratios, gross efficiencies and the various other efficiencies of energy transfer (Jϕrgensen 1979) used here to carry out estimates of the whole trophic structure and especially of the role of detritus in the ecosystem were not then available (indeed, it was the objective of IBP to produce such data).

Berrie (1972) discussed the role of detritus in the Thames and suggested that there is a dynamic interaction between the trypton flowing

Table 6. Summary statistics for the Thames Mark 2 model (kcal·m^{-2}·year^{-1}); see Christensen and Pauly (1992a) for further explanation and references.

Sum of all consumption	=	4,769.0
Sum of all exports	=	989.8
Sum of all respiratory flows	=	1,694.2
Sum of all flows into detritus	=	3,854.2
Total system throughput	=	11,307.2
Sum of all production	=	3,222.8
Calculated total net primary production	=	2,197.0

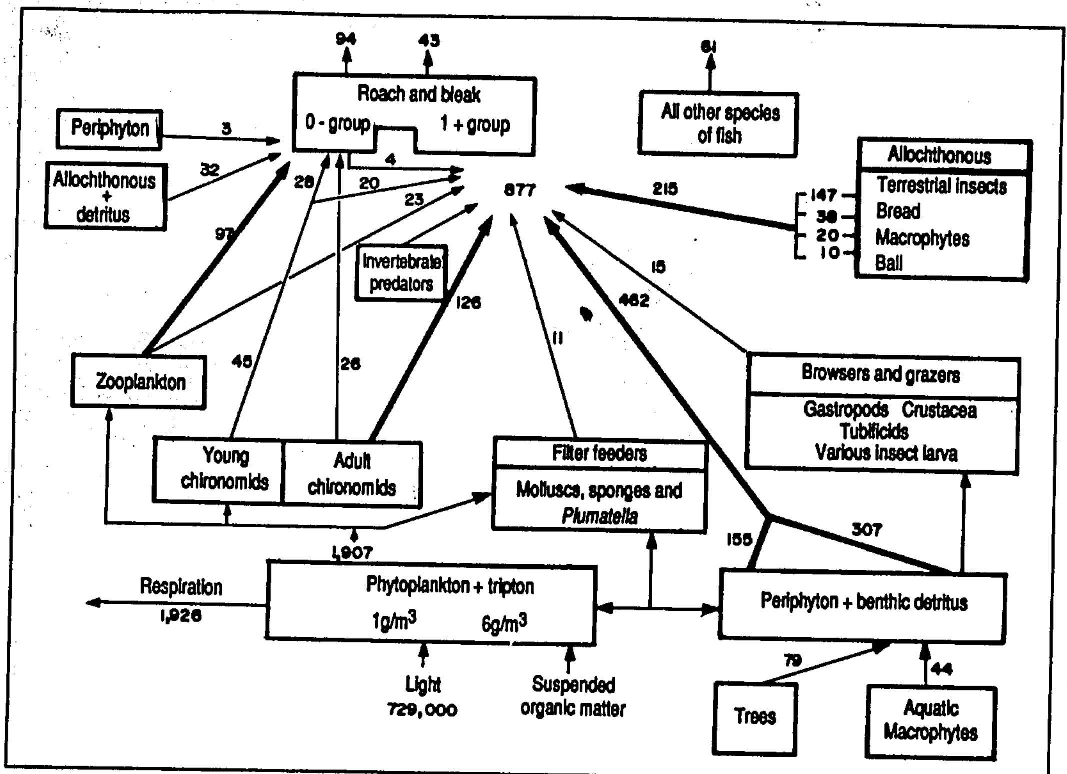

Fig. 2. Energy flow chart for the River Thames below Kennet mouth ("Mark 1"). In general, primary producers are shown at the bottom, invertebrate animals in the center and fish at the top, but to avoid complex networks of arrows, sources of periphyton, detritus and allochthonous materials are shown in two places. Heavy arrows indicate the largest of energy flows (from Fig. 3 in Mann et al. 1972).

through the ecosystem and the detritus being generated *in* the ecosystem by various populations. He also suggested that there was a dynamic relation between the trypton, benthic detritus, epiphytic detritus, and benthic and periphytic detritivores. The "ecotrophic efficiency" of detritus generated by the Thames model (Table 5) implies that 79% of the flow to detritus is recycled and that the rest is deposited as sediment within the system or else how exported, e.g., by being carried by the current downstream. This confirms Berrie's (1972) suggestion and identifies an important energy removal from the ecosystem not identified by the Mark 1 model.

It is clear that the precise role of the detritivores and the browsers needs to be studied in much more detail than was done in the Thames study. Scrutiny of the contents of this volume also suggests that the lack of critical work on detritus in aquatic ecosystems may be the single biggest omission of the IBP study and perhaps of most subsequent ecosystem analyses. Future ecosystem analysis should examine the relation between detritus, detritivores and detritivore browsers.

The difficulties identified here and the contrasts between Figs. 2 and 3 show some of the differences between models used during the IBP and more recent models. The evolution of new models came as a direct response to the creation of models such as the Thames Mark 1 model.

Energy Flow and Trophic Levels

The older model used discrete trophic "layers": Layer 1 (Fig. 2) included phytoplankton, trypton, periphyton, benthos, detritus. Layer 2 included zooplankton, chironomids, filter feeders and browsers with Layer 3, fish above. Such models deliberately refused to identify trophic levels because of the complex food webs.

The Mark 2 model shows the utility of the weighted mean trophic level generated by ECOPATH II, a concept easy to handle and understand. While the Mark 2 model also failed to tackle the trophic positions of detritus satisfactorily, this was because of a lack of data on the true detritivore (i.e., the microorganisms that digest detritus), not because of conceptual or analytical difficulties.

Fig. 3 shows the Mark 2 model's energy flows. The flows to the fish populations are essentially similar to the corresponding parts in Fig. 2. Table 6 shows a total production of 3,223 kcal·m^{-2}·year^{-1} for the Mark 2 model, of which 2,197 kcal·m^{-2}·year^{-1} is net primary production, showing that the primary production is, as expected, large compared to other production.

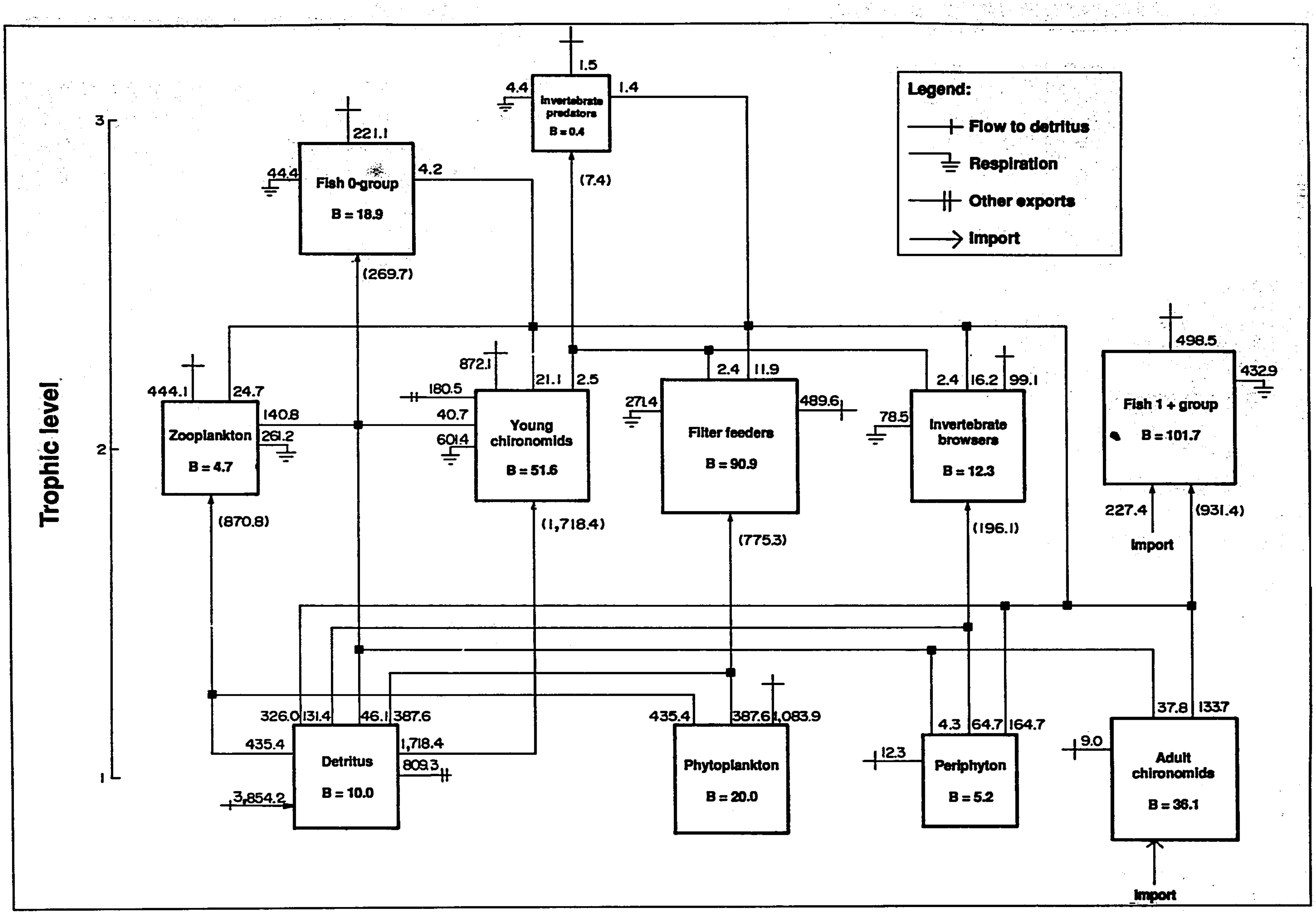

Fig. 3. Trophic flows in the River Thames below Kennet mouth ("Mark 2") constructed using the ECOPATH II model. Flows are in kcal·m^{-2}·year^{-1}. Flows from macrophytes (44.0 kcal·m^{-2}·year^{-1}) and trees (79.0 kcal·m^{-2}·year^{-1}) to the detritus are not shown. The "other export" of young chironomids is production of adult chironomids.

Table 6 also shows that the total energy throughput of the Thames ecosystem is 11,307 kcal·m^{-2}·year^{-1} compared to a total value of 2,907 kcal·m^{-2}·year^{-1} obtained by summing all production flows in Fig. 2 (Mark 1 model). The difference is mainly due to the inclusion of additional energy flows generated by the model for new knowledge about energy transfer efficiencies, as shown in Fig. 3. The Mark 1 model (Fig. 2), being the predecessor, anticipates problems addressed more completely by the Mark 2 model. The Mark 1 and 2 models also differ in the way they address energy flows and sum them (see below).

Zooplankton

Zooplankton are identified by both models as one of the most important groups in the Thames ecosystem. They have one of the largest food intakes and their respiration is exceeded only by that of 1+ group fish and filter feeders; their assimilation is second only to that of 1+ group fish.

The trophic position of Thames zooplankton is unclear: it has been included as a trophic level 2 organism in the ECOPATH II model (Fig. 3). But various zooplankton species may exist at different trophic levels. The great importance of the zooplankton arises from the unexpectedly high production and consumption rates of the prefingerling and fingerling fish: Mann et al. (1972) noted that this was perhaps the most unexpected result of the Thames ecosystem study.

Other Invertebrates

Other invertebrates channel large energy flows and include young chironomids, filter feeders, invertebrate browsers and invertebrate predators in decreasing order of importance. Mann et al. (1972) noted that filter feeders contributed little of their production to other living groups, and that most of the production was transferred to detritus. The Mark 2 model confirms this. They also noted that the large biomass (1 t per 100 m of river) was a major contribution to removal of excess organic matter from the river, and may have been a natural response to the increased organic level provided by municipal discharges into the Thames.

Production estimates of chironomids (Mann et al. 1972) for the Thames were very low (15.2 kcal·m^{-2}·year^{-1}) compared with the estimated amount of adults consumed (147 kcal·m^{-2}·year^{-1}, recorded as "allochthonous" by Mann et al. [1972, Fig. 3]). This was probably because of difficulty in obtaining good samples of young chironomids by any of the methods used: actual "allochthonous" input of adult chironomids may also have been higher.

Fish Groups

Compared to 0 group fish, the food intake, respiration and assimilation of 1+ group fish are high. This is remarkable because 0 group fish provide an average of 69% of total fish production, with an estimated trophic efficiency of 0.5. This high efficiency is reasonable because 0 group production includes that of larvae and prefingerlings.

Interestingly, 1+ group fish have a trophic level of only 2.12, considerably lower than that of 0 group fish (Table 5). This is so because of the very large contribution of detritus to the diet of 1+ group fish.

Mixed Trophic Impacts

Fig. 4 shows the direct and indirect impacts any of the groups have on all other groups in the system (Christensen and Pauly 1992a, 1992b). Some examples of how to interpret the results: 1+ group fish have a negative trophic impact on nearly all other groups in the system due to either predation or competition. Invertebrate browsers have a strong positive influence on invertebrate predators and phytoplankton has a strong positive effect on zooplankton, both of which are reasonable. The negative effect of detritus on adult chironomids is unexpected. Fig. 4, as a whole, shows that detritus is one of the most dynamic components, confirming the important role assigned by Berrie (1972) to detritus in the Thames.

It is difficult to compare the role played by detritus in the Thames with that in most other systems. The role of detritus is in the present applications based on general knowledge of ecological relationship only. Nevertheless it appears that detritus is more important in the Thames than in most other study areas where detritus is either very much less important relative to primary production (e.g., Lakes George [Moreau et al., this vol.]; Kariba [Machena et al., this vol.]; and Tanganyika [Moreau et al., this vol.]) or, while important relative to primary production still of lesser importance than in the Thames (Lakes Turkana [Kolding, this vol.]; Malaŵi [Degnbol, this vol.]; Kinneret [Walline et al., this vol.]). Possibly the relatively unimportant role of detritus in many other models reflects the lack of research on detritus rather than the underlying ecosystem structure.

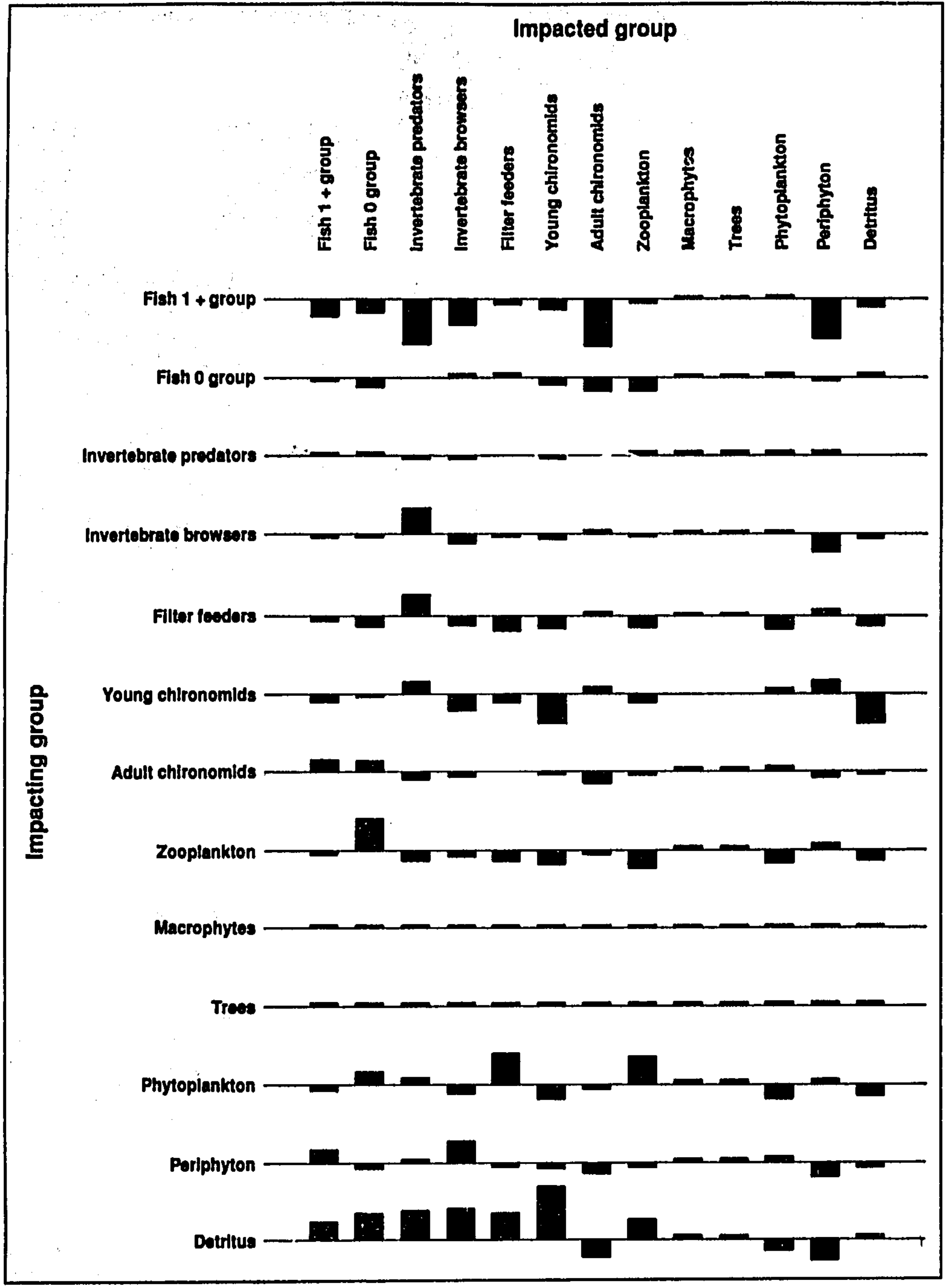

Fig. 4. Mixed trophic impacts in the River Thames below Kennet mouth ("Mark 2") constructed using the ECOPATH II model. The bars show the direct and indirect impact any of the groups have on all other groups in the system.

Conclusion

Mark 1 Model

Apart from the omission of the detritus from the Mark 1 model, the Mark 2 model of the Thames also exposes a major weakness in the original study: the only published biomass estimates were those summarized by Mathews (1971) for fish and that for the phytoplankton (Mann et al. 1972). Yet all of the Thames IBP studies provided biomass estimates.

Loss of the Thames data shows the difficulties of data conservation, a matter that should be considered a natural part of any project involving data collection (Mathews 1993).

Mark 2 Model

The Mark 2 model provides a similar picture of the Thames ecosystem to that provided by the Mark 1 model, but is more complete; it handles trophic levels and the foodweb easily and in more detail, and provides a much more complete picture of the ecosystem.

The Mark 2 model is weaker in one respect: it makes no reference to incident light and does not estimate the gross efficiency of primary production. This could, however, have been addressed in the present model by allocating a "consumption" to the primary producers. The transfer efficiency of sunlight deserves further attention: it is likely that some ecosystems will process light energy more efficiently than others and that those with large energy inputs from detritus may be different from those without.

Uniqueness

The Mark 2 model of the Thames is not necessarily a unique solution to the available data: many estimates of P/B ratios and various trophic efficiencies had to be introduced, either from Jϕrgensen (1979) or on the basis of general knowledge of such values in other ecosystems. Still it is unlikely that other possible models will vary greatly from the one provided here.

Future Work

The Mark 1 model was an excellent stimulus to further analysis; likewise the Mark 2 model may be used as a heuristic device to stimulate further research into the Thames and other riverine systems, especially into:

- the role of detritus, detritivores and "detritivorous browsers" as defined above and in Figs. 3 and 4;
- the role of zooplankton;
- the roles of prefingerling production and consumption none of which has been investigated sufficiently in the Thames.

The lack of followthrough on the Thames work, in spite of the useful output produced, was characteristic of the whole IBP.

One reason for this has been the perceived difficulty in handling the large amount of data, and the complex analyses that extensions of the trophic approach required. It seems that ECOPATH II, with its analytical routines, may provide a tool that can encourage ecologists to attempt again to make holistic ecosystem models.

There is no doubt in this context that any trophic modelling, including ECOPATH II, is insufficient to describe an ecosystem completely. A fully predictive ecological model needs to take more into account than trophic interactions. Nevertheless it is equally certain that a clear understanding of the transfer of energy (and information) through an ecosystem is a *sine qua non* for comparing its structure with other ecosystems.

The ECOPATH II approach is the most complete as yet available; its application leads to a rich variety of hypotheses for future research and it is perhaps the best hope for identifying a research program leading towards a combined ecosystem engineering/management approach. The ability to manage our ecosystems in the future will certainly be an important factor in successful conservation of the environment. ECOPATH II offers a useful approach for tackling this question.

Acknowledgements

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A Preliminary Model of the Garonne River (Toulouse, France) Ecosystem in Spring

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Abstract

The ecology of the Garonne River near Toulouse, France, and of one of its semi-isolated meanders or *bras mort* is described briefly, based mainly on samples collected in April 1990 and 1991 and with emphasis on five species of fishes (*Rutilus rutilus, Cyprinus carpio, Carassius carassius, Ictalurus melas* and *Micropterus salmoides*), and on their prey organisms. This information is used to construct a preliminary springtime trophic model of a segment of the Garonne River, which is then discussed.

Introduction

The Garonne River originates in the Pyrennées Mountains, in the valley of Aran, and stretches about 50 km within Spanish territory before reaching France where it runs 575 km before reaching the Atlantic Ocean. The course of the Garonne can be subdivided into three regions:

1. the Pyrennées region, characterized by rocky substrate, often with rapids and wider areas with even bottom, but with a slope always greater than 3‰;
2. the region from Neste to Tarn at the foot of the Pyrennées, where the slope declines from over 3‰ in the area between Neste and Salat, to 1‰ in the area between Salat and Toulouse and to less than 1‰ in the flood-prone area between Toulouse and Tarn; and
3. the coastal region, regularly influenced by the tidal cycles, where the slope remains less than 1‰.

The model presented here refers to region (b), about 12 km downstream from Toulouse, an area characterized by a number of meanders, parts of the old riverbed (known in French as *bras morts* or "dead arms"). Although filled with semistagnant waters during other periods, in spring when the snow in the Pyrennées melts, these *bras morts* form an active part of the Garonne as a whole.

The *bras mort* of Port-Vieux (PV), selected for this particular study, is situated near the town of

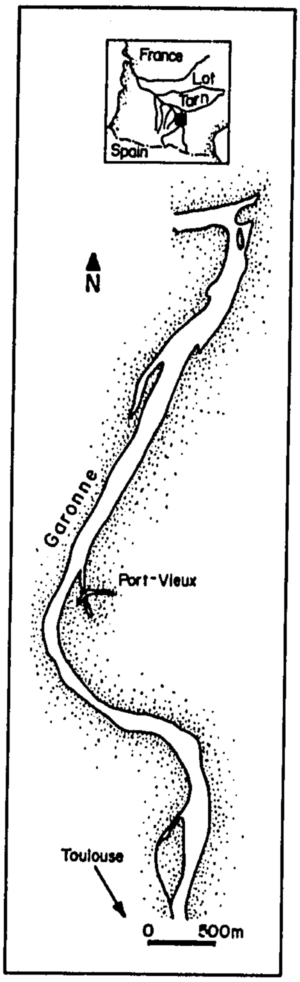

Fig. 1. The *bras mort* of Port-Vieux (PV), and the adjacent segment of the Garonne River; inset: map of southwestern France, showing the course of the Garonne.

St. Caprais (Fig. 1). It is 364 m long, has a mean width of 15 m, a mean depth of 1.7 m and an area of 5,000 m^2. It communicates with the river downstream and did not dry up during the bad droughts in 1989 and 1990. The river, which in this area slopes only moderately, has gravel as substrate and is flanked by muddy banks.

Note that this study does not only refer to the *bras mort* of Port-Vieux but also to the segment of the Garonne where this *bras mort* is found (see Fig. 1). The water of the *bras mort* differs from the waters of the Garonne River in the following (Bengen et al. 1992b):

1. water temperatures are, in summer, about 4°C higher in the inner portion of the *bras mort* than in the Garonne proper;
2. the organic content of the water is about three times greater in the inner portion than at the mouth of the *bras mort*, or in the Garonne proper;
3. the nitrogen and phosphorus content of the water decreases progressively from the Garonne into the *bras mort*; and
4. chlorophyll *a* is highest at the inner portion of *bras mort* at 140 µg·l^{-1} in spring and summer, while it is only 35.2 and 26.4 µg·l^{-1} in its outer portion and in the Garonne proper, respectively.

However, in spring, the exchange of water between the Garonne and *bras mort* waters tends to make these two communicating water bodies rather similar (Bengen et al. 1992b). Furthermore, cyclic changes in the structure of the fish populations identified in the area imply strong migratory fluxes between the main river body and the *bras mort* (Bengen et al. 1992c). Thus, it seems appropriate to use data gathered predominantly from the Port-Vieux *bras mort*, in spring, to construct an ecosystem model meant to also describe the adjacent segment of the Garonne River.

Materials and Methods

Plankton

Plankton samples were obtained in April 1990 and 1991 from both the Garonne proper and the Port-Vieux *bras mort* by filtering 100 l of water using a plankton net with a mesh size of 70 µm and an opening of 0.40 cm. Counting of the formalin-preserved fixed samples was done in the laboratory mainly by the second author with the use of a Sedgewick Rafter grid and an Olympus B01 inverse microscope. Results were expressed first as a function of individuals counted per 100 l of water, then converted to relative biomass using mean weights per species based on the study of Arias-Gonzalez and Richeux (1990).

The phytoplankton population (Table 1) in the *bras mort* consisted of 54.5% red algae, 38.6%

Table 1. Phytoplankton populations identified from samples obtained from the Port-Vieux *bras mort* in April 1990/1991 with dry-wet weight conversions adapted from Arias-Gonzalez and Richeux (1990).

Species group	Dry weight per individual (10^{-3}µg)	Wet weight (µg)	Fresh biomass (µg·l^{-1})
Chlorophytes			
Ulothrix	3.72	0.272	41.3
Pediastrum boryanum	0.440	0.163	6.51
P. simplex	0.260	0.157	30.1
Scenedesmus	0.210	0.155	22.3
Closterium	1.94	0.213	3.40
Hyalotheca	0.610	0.168	12.8
Echinosphaerella	0.212	0.155	4.26
Cladophora	3.90	0.278	23.9
Bulbochaeta	2.10	0.218	8.39
Cyanophytes			
Lingbya	0.675	0.170	25.3
Diatoms			
Melosira	0.24	0.156	29.3
Meridion	0.031	0.149	1.64
Fragilaria	0.270	0.157	3.76
Synedra	0.216	0.155	24.2
Diatoma vulgare	0.410	0.162	11.6
D. elongatus	0.350	0.160	39.6
Navicula	0.700	0.171	13.0
Cymbela	0.240	0.156	1.87
Gomphonema	0.715	0.172	1.80
Gyrosigma	0.730	0.172	1.69
Nitzschia	0.216	0.155	31.8
Surirella	23.0	0.915	21.0
Cymatopleura	7.00	0.381	6.29
Asterionella	0.270	0.157	18.2
Total			396

green algae and 6.9% brown algae. Total phytoplankton biomass was estimated at 2.54 $\mu g \cdot l^{-1}$ (dry weight) per m^2.

The zooplankton population (Table 2) was composed of 79.9% rotifers, 10.5% cladocerans and 9.8% copepods; the estimated biomass was 5.65 $mg \cdot l^{-1}$ dry weight.

Macroinvertebrates

Data obtained from the work of Gaber (1988) were used to estimate macroinvertebrate biomass (Table 3); these samples were taken along perpendicular transect lines over three longitudinal profiles with four replicates.

The macroinvertebrate population in this area was found to consist of 76.9% oligochaetes, 16.9% dipterids, 3.7% crustaceans and 2.5% others (molluscs and insects other than Dipteridae). Total macroinvertebrate biomass was estimated at 70 mg·(dry weight) m^{-2}.

Benthic Producers

Quantitative information on the macrophyte population was not available at the time of study, with the exception that 40% of the area studied is covered by aquatic vegetation (Yulianto 1991).

Table 2. Zooplankton populations identified from the plankton samples obtained from the Port-Vieux *bras mort* in April 1990/1991 with dry-wet weight conversions adapted from Arias-Gonzalez and Richeux (1990).

Species group	Dry weight per individual (µg)	Wet weight (µg)	Fresh biomass ($\mu g \cdot l^{-1}$)
Cladocerans			
Alona	4.05	105	30,156
Bosmina	3.04	78.6	12,892
Copepods			
Cyclops	7.30	189	74,721
Canthocanyrus	7.30	189	4,529
Rotifers			
Brachionus calyciflorus	0.30	7.81	8,310
B. plicatilis	0.42	10.9	829
B. bidentata	0.20	5.22	501
B. pala	0.40	10.4	707
Keratella cochlearis	0.11	2.90	2,529
K. quadrata	0.35	9.10	692
K. serulata	0.31	8.07	5,358
K. hiemales	0.40	10.4	712
K. stipitati	0.26	6.78	325
Filinia	0.42	10.9	3,104
Cephalodella	0.22	5.74	71.8
Encentrum	0.23	6.00	192
Trichocerca	0.36	9.36	548
Total	-	-	146,176[a]

[a] Note that this total appeared far too high when incorporated into an ECOPATH II model of the Garonne/Port Vieux *bras mort* (see text).

Table 3. Invertebrate groups identified in the bottom samples obtained from the Port-Vieux *bras mort* adapted from Gaber (1988) and using dry/wet weight conversions from Arias-Gonzalez and Richeux (1990).

Species group	Dry weight per individual (mg)	Wet weight (mg)	Fresh biomass ($mg \cdot m^{-2}$)
Molluscs			
Gastropods			
Physidae	0.022	0.57	9.12
Lymnalidae	0.024	0.64	1.92
Ferrissidae	0.017	0.43	2.58
Acroloxidae	0.026	0.71	2.84
Lamellibranchs			
Sphaeridae	0.023	0.62	1.86
Annelids			
Oligochaetes	0.005	0.02	123
Hirudinids			
Glossiphoniidae	0.067	2.1	206
Piscicolidae	0.073	2.3	64.4
Arthropods			
Crustaceans			
Asellidae	0.028	0.8	238
Gammaridae	0.037	1.1	1.10
Insects			
Ephemeropterids			
Caenidae	0.025	0.7	13.3
Potamanthidae	0.058	1.8	3.60
Odonatids			
Calopterygidae	0.226	7.4	7.4
Coleopterids			
Elmidae	0.0059	0.05	45.0
Tricopterids			
Ecnomidae	0.235	7.70	23.1
Polycentropodidae	0.247	8.10	8.10
Dipterids			
Athericidae	0.016	0.40	0.40
Ceratopogonidae	0.14	0.31	2.79
Chironmidae	0.14	0.33	441
Psychodidae			
Clogmia	0.014	0.32	3.52
Psychoda	0.15	0.35	0.350
Megalopterids			
Sialidae	0.064	2.00	10.0
Total	-	-	1,165

Fish Populations

Belaud et al. (1990) studied the structure of the fish populations in six *bras morts* along the Garonne River. This study shows that in the Port-Vieux *bras mort*, the most abundant group is the cyprinids (80.9%), especially *Rutilus rutilus* (25.0%) and *Scardinius erythrophthalmus* (14.5%); catfish (*Ictalurus melas*) made up of further 8.9% of the samples, whereas two percids, *Perca fluviatilis* (4.3%) and *Stizostedion lucioperca* (0.6%) and two centrarchids, *Micropterus salmoides* (1.9%) and *Lepomis gibbosus* (1.8%) made up the rest of the samples.

The food consumption per unit biomass for the species groups representing carnivores (*M. salmoides)*, omnivores (*R. rutilus* and *I. melas*) and planktivores (*C. carpio* and *C. carassius*) were obtained from analysis of stomach contents, extracted mainly by the first author. The samples were spaced at two-hour intervals, and ranged from 2000 to 0600 hours for night samples and from 0800 to 1800 hours for day samples. Fish were sampled in April 1990 and 1991 with the use of an electrogen EPMC at 420 volts (intensity of 3-4 amperes) in the inner waters of the *bras mort*. In the outer portion of the *bras mort*, near the Garonne proper, samples were obtained with a 10-m long, 2-m deep monofilament net of 40-mm mesh size, left submerged for 30 minutes and the fish caught therein were immediately killed and brought onshore where they were measured and weighed, then gutted and the stomachs conserved in 5% formalin. Weights of stomach contents were subsequently obtained by difference (full - empty gut). Diet compositions (see Table 4) were reconstructed by the second author from counts and weight conversions, as outlined above for plankton samples; the macroinvertebrates were counted and weighed separately. Daily rations (Table 5) were estimated by the first author using the MAXIMS program of Jarre et al. (1990); these estimates were then used, along with growth parameter estimates from Bengen (1992, see Table 6) to estimate the relative food consumption (Q/B) of the fish populations in question.

Table 4. Diet compositions (in % volume) of five fish species from the Garonne River obtained from stomach contents analysis of samples taken in April 1990 and April 1991.

	M. salmoides	*I. melas*	*R. rutilus*	*C. carpio*	*C. carassius*
Phytoplankton					
day	0	20.8	25.4	59.4	20.6
night	3.35	21.1	15.4	-	16.3
mean	-	20.9	20.4	-	18.4
Zooplankton					
day	0	14.1	39.5	21.6	77.8
night	5.55	19.3	40.3	-	79.1
mean	-	16.6	39.9	-	78.4
Macroinvertebrates					
day	0	50.2	8.13	14.3	-
night	31.0	32.4	5.29	-	-
mean	-	41.6	6.71	-	-
Fish					
day	0	6.65	19.7	-	-
night	60.1	9.16	18.8	-	-
mean	-	7.86	19.2	-	-
Macrophytes					
day	0	8.22	7.20	4.12	1.58
night	0	16.0	20.0	-	4.59
mean	-	12.0	13.6	-	3.08
Others					
day	-	0.03	0.07	0.58	0.02
night	-	2.09	0.21	-	0.01
mean	-	1.04	0.19	-	0.12

Table 5. Parameters related to the dynamics of stomach contents in four fish species from the Garonne River, as estimated using the MAXIMS method of Jarre et al. (1990).

	I. melas	*R. rutilus*	*C. carpio*	*C. carassius*
Ingestion rate (g·hour^{-1})	0.374	0.860	0.208	1.18
Evacuation rate (hour^{-1})	0.132	0.220	0.118	0.0973
Maximum stomach contents (g)	1.32	2.18	3.24	-
1st feeding period (hour^{-1})	2:00	7:00	9:00	16:00
1st stop	4:00	9:00	12:00	22:00
2nd feeding period	18:00	16:00	20:00	-
2nd stop	20:00	2:00	23:00	-
Daily ration (g)	1.44	8.45	3.54	7.06
Sum of squared residuals	0.782	1.13	1.02	8.50

Table 6. Growth and mortality parameters of five fish species from three *bras morts* of the Garonne River, used for the estimation of Q/B.[a]

	M. salmoides	*I. melas*	*R. rutilus*	*C. carpio*	*C. carassius*
L_∞ (cm), TL	48.8	35.0	52.0	62.6	43.6
W_∞ (g)	1,395	579	1,715	2,797	1,077
K ($year^{-1}$)	0.30	0.52	0.23	0.28	0.35
t_0 (year)[b]	-0.48	-0.30	-0.63	-0.49	-0.43
ϕ'	2.85	2.80	2.79	3.04	2.82
c.f.	1.20	1.35	1.22	1.14	1.30
M ($year^{-1}$)[c]	0.49	0.76	0.40	0.43	0.56

[a] Adapted from Bengen (1992a).

[b] Estimated using an empirical equation in Pauly (1979).

[c] Estimated using an empirical equation in Pauly (1980) and a mean annual temperature of 12.2°C for the Port-Vieux *bras mort.*

Table 7. Species composition of fish samples in Port-Vieux *bras mort* (adapted from Bengen 1992a).

Family	Species	No.	Biomass ($g{\cdot}m^{-2}$) by age group I	Biomass ($g{\cdot}m^{-2}$) by age group II	Mean ($g{\cdot}m^{-2}$)
Cyprinidae	*Rutilus rutilus*	76	0.86	2.6	1.8
	Blicca bjoerkna	25	0.28	0.87	0.57
	Abramis brama	23	0.26	0.81	0.53
	Alburnus alburnus	12	0.13	0.41	0.27
	Scardinius erythrophthalmus	44	0.50	1.5	1.0
	Leuciscus leuciscus	25	0.28	0.87	0.57
	Leuciscus cephalus	8	0.09	0.28	0.18
	Rhodeus sericeus amarus	22	0.26	0.81	0.53
	Carassius carassius	4	0.04	0.14	0.09
	Cyprinus carpio	3	0.03	0.11	0.07
	Tinca tinca	3	0.03	0.11	0.07
Poeciliidae	*Gambusia affinis*	4	0.04	0.14	0.09
Ictaluriidae	*Ictalurus melas*	27	0.31	0.94	0.62
Anguillidae	*Anguilla anguilla*	1	0.01	0.03	0.02
Percidae	*Perca fluviatilis*	13	0.15	0.46	0.30
	Stizostedion lucioperca	2	0.02	0.06	0.04
Centrarchidae	*Micropterus salmoides*	6	0.06	0.20	0.13
	Lepomis gibbosus	5	0.06	0.19	0.13
Total	all	303	3.44	10.6	7.00

No direct estimates of fish biomass were available; however, the numbers of individuals sampled in the Port-Vieux *bras mort* from 1989 to 1991 are available (Table 7). This information was used, together with the growth parameters in Table 6, to estimate the mean weight of individuals. In spring, there is a predominance of young fish in the *bras mort* as the spawning stock, which usually migrate upstream, has not yet reached peak levels. Thus, our biomass estimates were based on the assumption that the population consisted entirely of fish aged 1 and 2 years. For the species for which growth parameters were not available, the mean lengths were taken over from species with similar shapes. Thus, *Blicca bjoerkna* was related to *Abramis brama*, while *Alburnus alburnus, Scardinius erythrophthalmus, Leuciscus leuciscus, L. cephalus* and *Rhodeus sericeus amarus* were related to *R. rutilus*. However, the group "other cyprinids" include all cyprinids other than *R. rutilus* and *C. carpio*, both of which form their own group. The biomass value for top predators consists mainly of the biomass of *M. salmoides*, plus *Anguilla anguilla, P. fluviatilis, S. lucioperca* and *L. gibbosus*.

Based on the information given above a model of trophic interactions in the system was constructed with the help of ECOPATH II system (Christensen and Pauly 1992).

Results and Discussion

The results obtained through ECOPATH II indicate a zooplankton biomass of 24 $g{\cdot}m^{-2}$, much lower than that in Table 2, which is 10 times as high as zooplankton estimates for other freshwater systems. Several factors can be conceived as having led to this obvious overestimate; one likely explanation would be that the samples were taken over a zooplankton patch since counts were based on only two samples for the whole study site.

The biomass estimated for benthic producers is 12.9 $g \cdot m^{-2}$. Given that 40% of the area is covered with vegetation (mostly aquatic plants) and that not much of this population is consumed by the other groups, this value is acceptable.

The ecotrophic efficiencies estimated by ECOPATH II for this ecosystem are generally low with the exception of the macroinvertebrates and zooplankton. The fish populations in this system are largely unexploited, thus a relatively large fraction of the fish are left to grow big and old. An analytical study of the seasonal fluctuations in population structure of the fishes in this part of the Garonne River performed by Bengen et al. (1992a) clearly shows the old age effect implied by the low values of EE found here (Table 8).

The high consumption of macroinvertebrates together with their relatively low biomass result in a high value of EE (=0.95). Predation pressure on the zooplankton is also high because of the high biomass of planktivorous cyprinids. On the other hand, feeding pressure on phytoplankton by the fish populations is relatively low (only *C. carpio* is a true herbivore among the species studied).

In spring, when the snow melts, the river experiences a rush of water from the mountains.

Table 8. Inputs to ECOPATH II model of the Port-Vieux *bras mort* and adjacent segment of the Garonne River in spring, with corresponding outputs (in brackets). Biomass values for all fish groups were based on estimated values in Table 7.

Group	B ($g \cdot m^{-2}$)	P/B[a] ($year^{-1}$)	Q/B[b] ($year^{-1}$)	EE
Micropterus salmoides	0.10	0.5	6.0	(0.12)
Ictalurus melas	0.50	0.8	12.7	(0.04)
Rutilus rutilus	1.25	0.5	14.5	(0.03)
Cyprinus carpio	0.05	0.4	6.0	(0.15)
Other cyprinids	3.07	0.6	12.0	(0.25)
Macroinvertebrates	1.16	3.96	11.0[c]	(0.95)
Zooplankton	(23.95)	5.0[d]	20.0[e]	(0.95)
Phytoplankton	6.73	307.0[f]	0	(0.15)
Benthic producers	(9.91)	5.0[g]	0	0.10[h]
Detritus	-	-	0	(0.07)

[a] P/B values for fish groups are obtained from natural mortality estimates given in Table 6.

[b] Q/B estimates for fish group are obtained from the MAXIMS method of Jarre et al. (1990), see Table 5.

[c] Adapted from Reyes-Marchant et al. (this vol.).

[d] Assumed at GE = 0.25 (production/consumption).

[e] Mean freshwater zooplankton Q/B adapted from Jφrgensen (1979).

[f] From this study.

[g] Assumed.

[h] Low value assumed given that benthic producers are usually not consumed while alive.

Table 9. Diet composition of the consumers in the trophic model of the Port-Vieux *bras mort* and adjacent segment of the Garonne River.

Prey	Predator						
	1	2	3	4	5	6	7
1. *Micropterus salmoides*	0.01	-	-	-	-	-	-
2. *Ictalurus melas*	0.025	-	-	-	-	-	-
3. *Rutilus rutilus*	0.03	-	-	-	-	-	-
4. *Cyprinus carpio*	0.005	-	-	-	-	-	-
5. Other cyprinids	0.35	0.04	-	-	-	-	-
6. Macroinvertebrates	0.50	0.25	0.10	0.10	-	0.05	-
7. Zooplankton	0.05	0.10	0.50	0.20	0.70	0.50	0.15
8. Phytoplankton	0.03	0.10	0.20	0.40	0.20	0.10	0.60
9. Benthic producers	-	0.10	0.10	0.10	0.05	0.05	-
10. Detritus	-	0.41	0.10	0.20	0.05	0.30	0.25

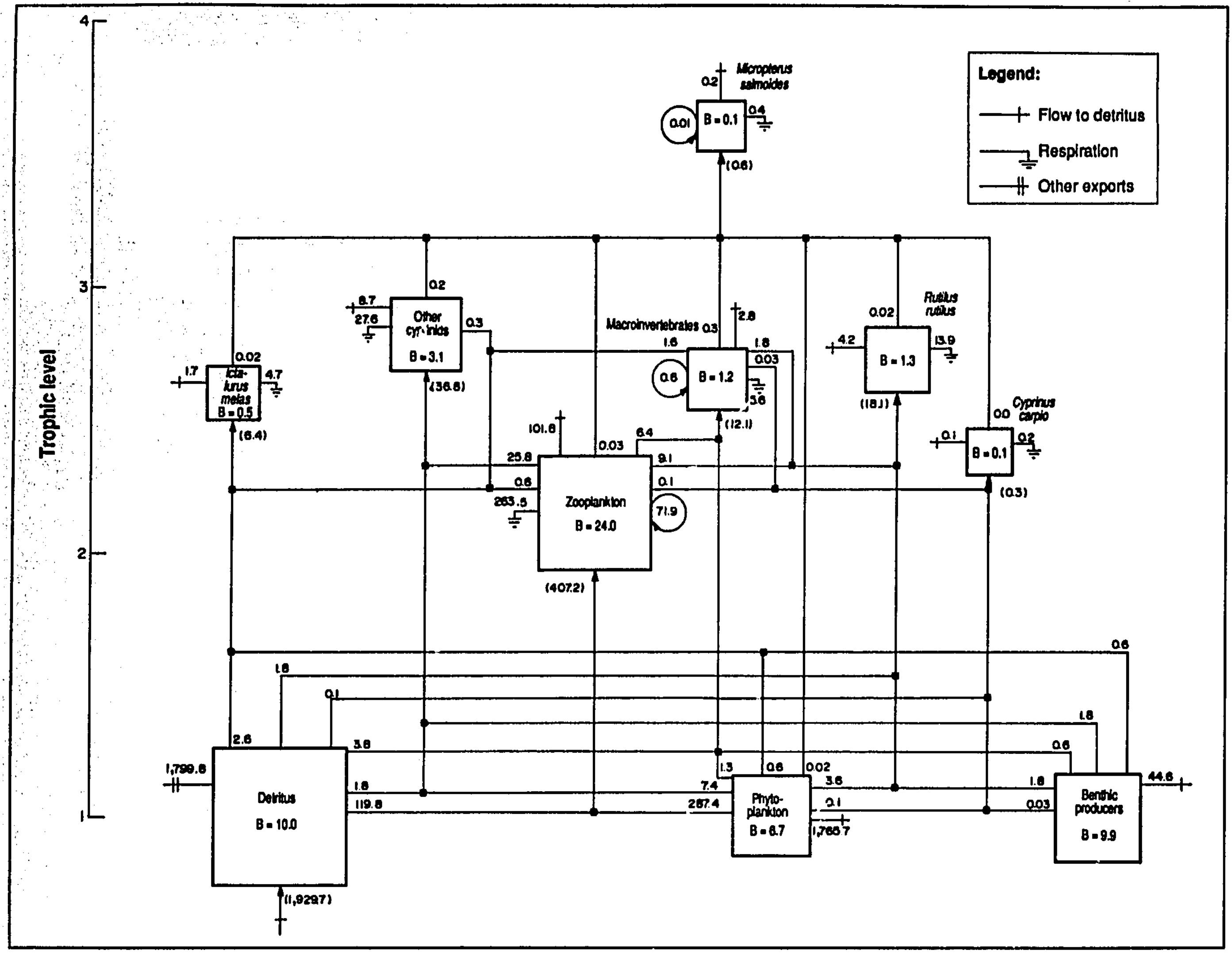

Fig. 2. Trophic springtime model of the *bras mort* of Port-Vieux and the adjacent segment of the Garonne River, as constructed with the ECOPATH II program, based on the input data in Tables 8 and 9. All flows are in g·m^{-2}·year^{-1}; biomasses (B) in g·m^{-2}.

This flooding brings along dissolved nutrients which enhance the growth of phytoplankton. On the other hand, during the flooding period, the Port-Vieux *bras mort* has a wide connection with the main river body thus increasing the volume and surface area of this segment of the Garonne. Thus, the fish are "diluted" and their biomass appears low; this is enhanced by the absence, during this period, of seasonally migrating species of *Alosa*, which reach this area of the Garonne only in May-June.

It must be reiterated here that these results are indeed very preliminary. The Garonne River, though interesting to the sports fishers, has not been well studied by the fishery biologists of the region. Various masteral and doctorate theses on the different components of this ecosystem are now either being proposed or under way to provide more information to enable the modelization of this part of the river. Thus, a future more comprehensive model is expected.

Further studies on this and similar systems will indicate whether the approach used, and the results presented therein are appropriate to describe systems such as investigated here.

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COASTAL AREAS

This section includes contributions from nonreef coastal areas, such as lagoons, estuaries, mangroves and shallow bays. These are generally highly productive areas; very tentatively the total catch from tropical coastal areas has been estimated to be some 5.7 million tonnes annually (Christensen et al. 1992).

Coastal areas are heterogeneous, encompassing freshwater, estuarine as well as marine habitats. They can be characterized: (1) by high productivity, attributable to mangrove litterfall and substantial import of nutrients from river runoff, and (2) by virtue of being an important nursery area for fish, penaeid shrimps and other organisms. These factors also influence the deeper, more offshore areas as discussed in several contributions in the subsequent section, on shelf systems.

Coastal systems are exploited mainly by small-scale fishers. In recent years, this use has in many areas, led to conflicts with expanding coastal aquaculture operations, especially where governments support export-oriented capital-intensive shrimp culture, often at the expense of small-scale fishing opportunities.

The fisheries in most tropical coastal areas are characterized by growth overfishing. High fishing pressure forces fishers to use mesh sizes far below the optimal in some areas along with destructive fishing methods. The fisheries, therefore, become highly opportunistic and dependent on seasonal pulses of new recruits; such pattern indicates that appropriate management regimes would offer substantial potential for increasing the catches.

The section presents five trophic models from Mexico, one from Mozambique, one from the southeast coast of India and one from the Mediterranean; most of these models are of a rather tentative character.

An important conclusion from the present contributions is perhaps that the nearshore areas have been neglected in connection with fisheries management approaches. Exceptions exist fortunately, Mexico being one good example.

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Toward a Trophic Model of Tamiahua, a Coastal Lagoon in Mexico

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Abstract

Tamiahua Lagoon, located on the east coast of Mexico, has an area of 800 km². The lagoon receives a flow of fish recruits from the Gulf of Mexico, of which several are important from a fisheries and ecological point of view. The trophic relations and their importance in the structure of the lagoon community were quantified by means of an ECOPATH II model. The results show that the lagoon imports detritus from adjacent systems, and uses it to sustain the benthos community which is the food base for almost all the fish. Therefore, the trophic chains in the lagoon tend to be short, and there are no third-order predators.

Introduction

The search for a simple mathematical model for quantifying interactions of natural resources, notably of fish stocks, led to the development of the ECOPATH model by Polovina and Ow (1983) and Polovina (1984). Pauly et al. (this vol.) and Christensen and Pauly (1992, this vol.) proposed a modified version of this, ECOPATH II, with enhanced characteristics and less restrictions, notably on the ability to estimate missing population parameters. Moreover, ECOPATH II can estimate relations between ecosystem components and their impacts on each other.

Tamiahua Lagoon is a typical coastal lagoon of the Gulf of Mexico (Fig. 1) and receives water from the sea and from several rivers. Located on the east coast of Mexico, it has a length of 85 km, a maximum width of 32 km and a total area of 800 km². Benthic producers are only present in 10% of the area due to the impact of oil exploration activities, which resulted in high mortality of the benthic communities. Various studies have been carried out on different aspects of the communities that inhabit this lagoon (Contreras 1985; Chávez et al. 1987; Miranda 1988; Abarca-Arenas 1990). Most of the species occurring in the lagoon do so only temporarily, i.e., they use the lagoon as a nursery and feeding area. There are few species which spend their entire life within Tamiahua Lagoon.

The purpose of this work was to apply the ECOPATH II model to the data available on this system, mainly to improve understanding of its fish community.

Methods

The ECOPATH II model determines the structure of the trophic community using the following linear model for all group (i) in a system:

$$B_i \cdot \left(\frac{P_i}{B_i}\right) \cdot EE_i - \left(\sum_{j=1}^{n} B_j \cdot \left(\frac{Q_j}{B_j}\right) \cdot DC_{ji}\right) - EX_i = 0$$

which assumes a steady-state condition of the system and where B_i = biomass of group (i); P_i/B_i = production/biomass ratio of group (i); EE_i = ecotrophic efficiency of group (i); Q_j/B_j = consumption/biomass ratio of predator (j); DC_{ji} = fraction of prey (i) in the predator (j) diet; EX_i = export from the system of group (i); (i) prey and (j) predator(s).

Primary productivity data used for the model were based on Contreras (1985) and Miranda (1988), here adopting a value of 105 $g \cdot m^{-2} \cdot year^{-1}$.

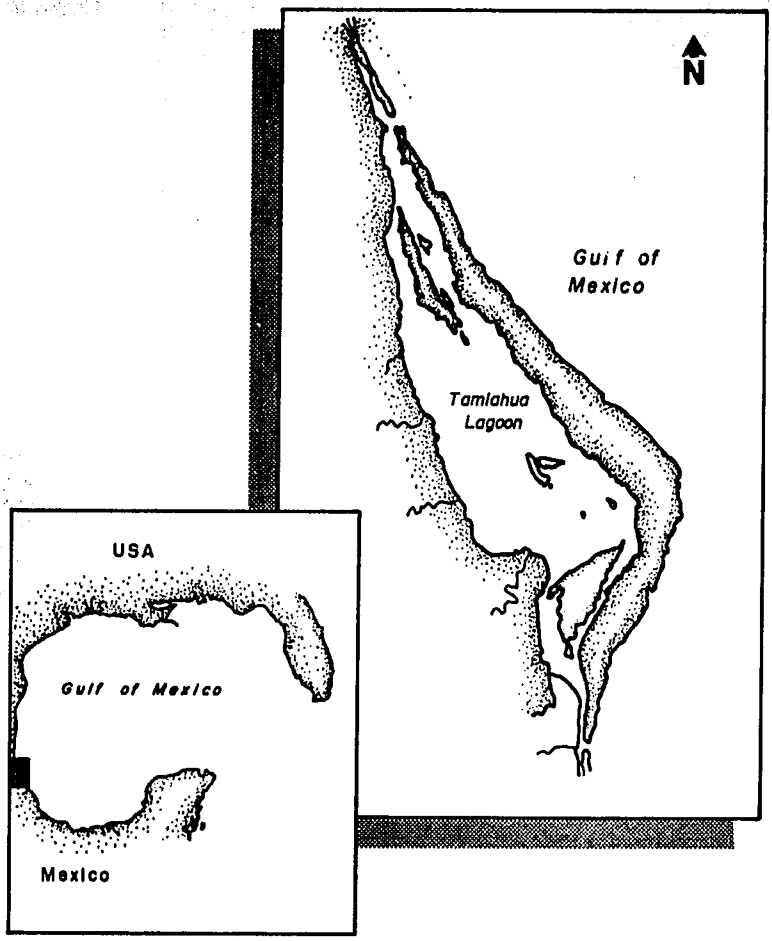

Fig. 1. Location of Tamiahua Lagoon in relation to the Gulf of Mexico.

Sampling in the lagoon was conducted over a two-year period, during which almost 80 fish species were collected. Since most of these use the system as a nursery area for a small period of time of their life only, only the species that were present over longer periods of the years were considered for this work. In doing this, it is assumed that these species form a steady-state system; thus we ignored their occasional or seasonal migrations into the sea or adjacent rivers. The fish diet compositions were obtained from the stomach contents using a volumetric method, and comparing these data with those of other works (Darnell 1961; Yañez-Arancibia and Nugent 1977; Yañez-Arancibia and Day 1980; de la Cruz and Franco 1981; Abarca-Arenas et al. 1982; Yañez-Arancibia and Lara 1983; de la Cruz et al. 1985; Abarca-Arenas 1987; Chávez et al. 1987).

Two anchovy species (*Anchoa hepsetus* and *A. mitchilli*) were lumped into one box because they use the resources almost in the same way (Abarca-Arenas 1990). A number of other important species were treated separately. The biomasses of the fish species were calculated using the swept-area and related methods, as described by Yañez Arancibia et al. (1985). For the shrimp box, which consists primarily of *Penaeus duorarum*, the food composition was taken from Gracía (1989), while the diet of the benthos, consisting mainly of amphipods, annelids and molluscs, was taken from Batllori et al. (1987). The "other decapods" group consists mainly of crabs of the genus *Callinectes;* parameter estimates for this were taken from E.A. Chávez and M.S. Fernandez (unpubl. data). In the last box, "other fish", the data were pooled from the most abundant species remaining from the fish samples.

Production/biomass (P/B) ratio estimates were taken from several sources: *Mugil curema* and *Diapterus auratus* from Abarca-Arenas et al. (1982), for *Bairdiella chrysoura* from a similar species from Palomares and Pauly (1989), anchovies from Nuñez (1987), shrimps from Arreguín-Sánchez and Chávez (1986), Guzman (1987) and Valero-Pacheco (1989); other decapods and benthos from Batllori et al. (1987), Arreguín-Sánchez (1976) and Stevenson (1981).

Consumption/biomass ratio (Q/B) as defined by Pauly (1986) were estimated using the method proposed by Palomares and Pauly (1989). Data used for the estimation are presented in Table 1. Parameters for those species not included in the table were taken from similar species given in Pauly (1986) and Palomares and Pauly (1989). The estimate for *Mugil curema* is from Palomares (1991).

The existing fisheries statistics are very incomplete and, to some extent, of a contradictory character, therefore fishery catches are not included in the present preliminary description. For this reason the transfer efficiencies and other fishery-related parameters arising from this preliminary model should not be used for comparison with other systems.

Table 1. Parameters used to estimate consumption/biomass ratio using the empirical model of Palomares and Pauly (1989) for carnivorous fishes of Tamiahua Lagoon, Mexico, with T = 26°C constant in all groups; A = aspect ratio of caudal fin; W_∞ = asymptotic weight (g). Values for *M. curema* and *S. notata* are approximated from maximum observed weights.

Groups	W_∞	A
B. chrysoura	178	1.90
Anchovies	20	2.50
D. auratus	99	2.74
M. curema	(2,400)	1.84
O. saurus	287	3.41
S. notata	(100)	1.37

Table 2. Predator-prey matrix for the Tamiahua Lagoon, Mexico. Legend: ZP: zooplankton; OD: other decapods; BC: *Bairdiella chrysoura*; OF: other fishes; ANC: anchovies; BEN: benthos; DA: *Diapterus auratus*; SN: *Strongylura notata*; MC: *Mugil curema*; PHP: phytoplankton; OS: *Oligoplitus saurus*; DET: detritus; SHR: shrimps.

	Predator										
Prey	ZP	BC	ANC	DA	MC	OS	SHR	OD	OF	BEN	SN
ZP	-	0.04	0.35	0.04	-	0.23	0.10	-	0.20	-	0.19
BC	-	-	-	-	-	0.09	-	-	-	-	-
ANC	-	0.02	-	-	-	0.18	-	-	-	-	0.10
DA	-	-	-	-	-	0.09	-	-	-	-	-
SHR	-	0.22	0.14	0.02	-	0.04	-	-	0.10	-	0.21
OD	-	0.12	0.10	0.02	-	0.17	-	-	0.10	-	0.06
OF	-	-	0.01	-	0.00	0.09	-	-	-	-	-
BEN	-	0.55	0.29	0.76	0.06	0.09	0.50	-	0.30	0.10	0.40
SN	-	-	-	-	-	-	-	-	-	-	-
PHP	1.0	0.04	0.04	0.13	0.10	0.02	0.30	0.30	-	0.30	0.04
DET	-	0.03	0.06	0.03	0.84	0.01	0.10	0.70	0.30	0.60	0.00

Results and Discussions

The trophic interactions between the components of the ecosystem are shown in Table 2. These data and the biomasses, P/B and Q/B ratios, as presented in Table 3, constitute the basic input for the ECOPATH II model. For top predators, the ecotrophic efficiency (EE) was computed by the program, while EE for anchovies was assumed to be 0.20 to reflect that this group is only lightly exploited and predated upon. For the other decapods and benthos, EE was assumed to be 0.95. Table 3 also shows the results obtained from the ECOPATH II program for the unknown parameters values (in brackets).

Table 4 gives some system summary statistics for the Tamiahua Lagoon.

The flows obtained from the model are shown in Fig. 2. It can be seen that the benthos has the highest food intake, followed by the zooplankton. This is important since these groups and the other decapods are the main food for the other parts of the ecosystem, in accordance with Darnell (1961). The trophic level of the top predators (2.8-3.4) are low compared with those in other systems (e.g., Arreguín-Sánchez et al., this vol.), where top predators such as sharks have values greater than 3.6.

Table 3. Initial input data and other characteristics of the ecosystem model of Tamiahua Lagoon. Estimates in brackets were calculated by the ECOPATH II program.

Group	Biomass ($g{\cdot}m^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE
Zooplankton	(1.1)	5.0	60.0	0.95
Bairdiella chrysoura	0.5	0.4	5.9	(0.01)
Anchovies	(0.6)	0.6	8.8	0.20
Diapterus auratus	0.0	1.4	6.1	(0.09)
Mugil curema	0.9	1.0	4.5	(0.00)
Oligoplitus saurus	0.0	0.3	3.0	(0.00)
Shrimp	0.8	7.6	19.2	(0.39)
Other decapods	(0.8)	2.5	8.5	0.95
Other fishes	3.0	0.4	3.0	(0.07)
Benthos	(10.8)	4.0	25.0	0.95
S. notata	0.0	0.3	2.0	(0.00)
Phytoplankton	2.5	102.6	0.0	(0.06)
Detritus	10.0	-	-	(0.94)

Table 4. Summary statistics for the Tamiahua Lagoon system. Flows are in $g{\cdot}m^{-2}{\cdot}year^{-1}$.

Sum of all consumption	380.4
Sum of all exports	11.4
Sum of all respiratory flows	244.9
Sum of all flows to detritus	185.6
Total system throughput	822.4
Sum of all production	315.8

Conclusion

The ECOPATH II model displays a great capacity for integrating important ecosystem aspects in an easy way. Unfortunately, reliable fisheries data were not available for incorporation into the model; still important aspects of the Tamiahua Lagoon ecosystem were revealed. Notably, the trophic chain is shorter than usually found in marine systems, because the top predators do not feed only on fishes but on benthic organisms as well.

It is clear that the benthic community has great importance as a food supply to the fishes in the Tamiahua Lagoon, and that it has strong relations with phytoplankton and detritus provided by adjacent systems.

The primary productivity of the Tamiahua Lagoon seems very low compared to other tropical estuarine systems.

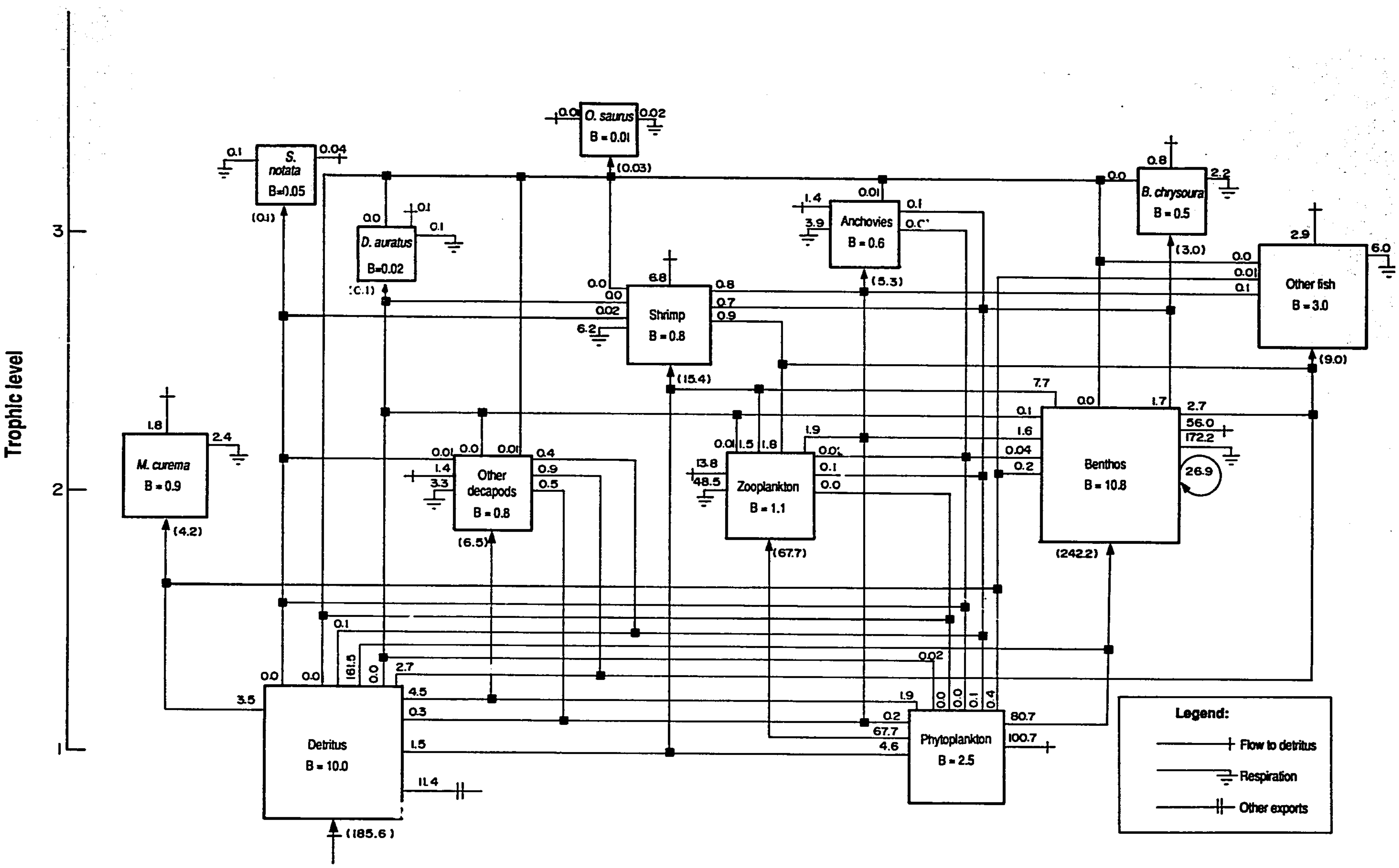

Fig. 2. Flow diagram of the fish community of Tamiahua Lagoon, Mexico, presenting results from ECOPATH II. All biomasses are in g·m^{-2} and rates in g·m^{-2}·year^{-1}.

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Trophic Dynamic Structure of Celestun Lagoon, Southern Gulf of Mexico

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Abstract

This paper is an extension of previous work on Celestun Lagoon, Yucatan Peninsula, Mexico, a tropical brackishwater body of 28.1 km^2 and 14.13 million m^3. The lagoon system relies upon three main sources of primary productivity, i.e., phytobenthos imports from outside, benthic producers in the system and phytoplankton. The fisheries take 0.061 g·m^{-2}·year^{-1} from six species of fish and one penaeid shrimp. Based primarily on information from the lagoon, a balanced model of the flows in the ecosystem is constructed using the ECOPATH II software system. As a number of important parameters had to be estimated based on assumed mass balance, the derived model should be considered preliminary. Fish biomass from swept area analyses were found to be too low to meet demands in the system, indicating sampling problems. The value of a balanced trophic model for closer examination of data quality is apparent.

Introduction

It is generally assumed that up to 90% of exploited fish stocks in the Gulf of Mexico are linked to estuarine environments; 15-25% of fish catches are obtained within these ecosystems. High nutrient concentration is one of the reasons for the high productivity of coastal lagoons. However, most of the production does not originate from the phytoplankton, but from mangrove and phytobenthos whose embodied energy is available for consumers only after decaying into detritus (Newell 1982). Mangroves are known to export nearly 30% of their net production to neighboring bays and thereby to contribute to the productivity of fisheries (Pannier and Pannier 1974). Moreover, the many fisheries operating in coastal lagoons may serve as indicators of their relative importance for the trophic dynamics of these water bodies (Nixon 1982).

The purpose of the present paper is to estimate the biomass budget and the energy flows among the different compartments of the trophic web of Celestun, a brackishwater lagoon of the southern Gulf of Mexico (Fig. 1), to find quantitative indicators of its structure and function.

Celestun Lagoon is very shallow (average depth less than 0.5 m) and very elongated (22.5 km), with the long axis parallel to the shoreline. Most of its bottom is covered by seaweeds. It does not receive any river flows, but freshwater from the karst

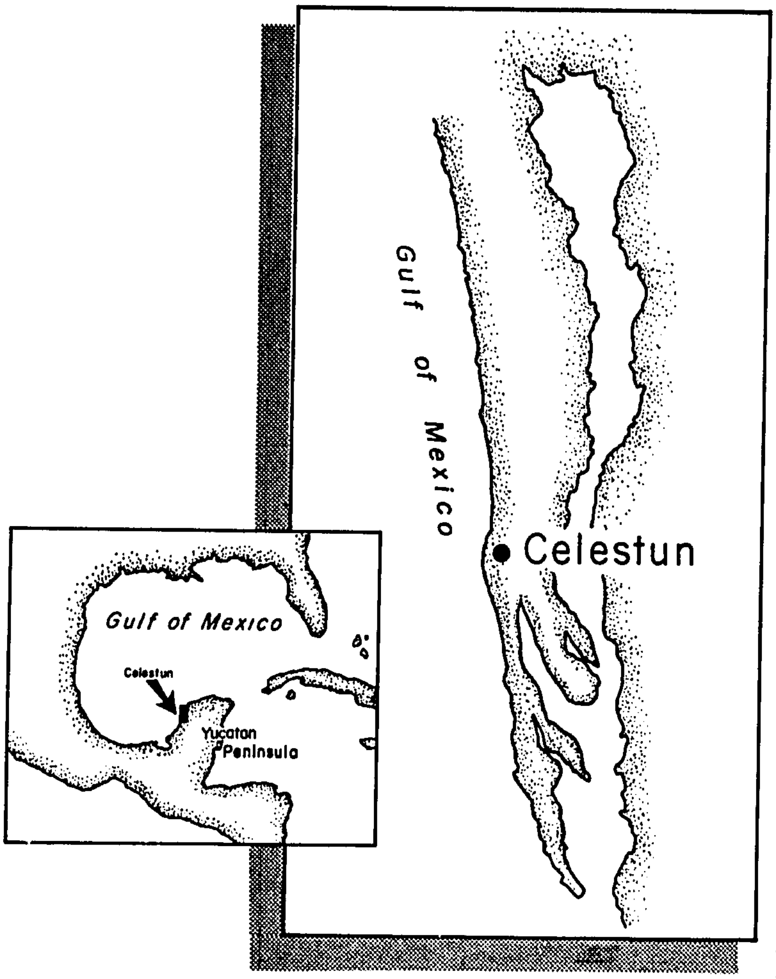

Fig. 1. Map of Celestun Lagoon, southern Gulf of Mexico.

underground maintains a permanent salinity gradient, the lagoon being mesohaline near its head, and euhaline at its mouth. The shorelines are covered by a dense mangrove swamp, especially on the east side. This area is an important feeding and nesting ground for migratory birds, mainly during the winter months. The climate is tropical and semi-dry, with a rainy season in the summer and a yearly rainfall of 777 mm.

Methods

Primary productivity of phytoplankton was measured using the clear and dark bottles method (Strickland and Parsons 1972) for two months in autumn and two months in spring. Phytoplankton biomass was determined using the chlorophyll method described by SCOR-UNESCO (1966). The standing crop of phytobenthos was measured using 0.1 m quadrants in a network of stations. Its productivity was estimated using a regression on production *versus* biomass (Zieman 1950; Howarth and Teal 1980; Day et al. 1982). Mangrove productivity was measured by a method involving the collection of foliage (Trejo 1986).

Zooplankton standing crop was measured for each of the main taxa and productivity of this compartment was based on *Acartia tonsa*, whose biomass represents more than 90% of the zooplankton and whose growth rate was followed throughout the year.

Zoobenthos was collected using 0.1 m quadrants and was sieved through a 500-μm mesh. Productivity was estimated using Robertson's empirical formula (after Rainer 1982),

$$P = (B/42)\exp(5.25 - 0.726 \ln t_{max}) \quad ...1)$$

where B is the biomass at the time of sampling, t_{max} is the estimated life span of a species in years and P is annual productivity. P and B must be given using the same density units.

This formula was applied to the most abundant groups, i.e., the polychaetes, meiobenthos (including amphipods), penaeid shrimps, and gastropods and bivalves. Rough estimates of longevity used were 1, 1, 3, 1, 3 and 3 years respectively. For polychaetes the model could not be balanced using the sampled biomass of 0.4 $g \cdot m^{-2}$. Instead a biomass (of 1.1 $g \cdot m^{-2}$) was estimated based on an ecotrophic efficiency of 0.95. For all invertebrates the Q/B's were estimated based on an assumed gross food conversion efficiency (P/Q) of 0.2.

Fish were sampled by means of a try trawl net in the rainy as well as in the dry season. Samples were sorted by species and size; food content was analyzed by size groups of main components and daily ration was estimated for each species following Pauly (1986). Biomass estimates based on the swept area method were deemed too unreliable to be of use. Instead, biomasses were estimated from an assumed ecotrophic efficiency of 0.95 for the fish species. Population parameters were estimated for the seven most abundant species using modal progression analysis and the ELEFAN I and II programs (Ricker 1975; Pauly 1982; Brey and Pauly 1986). A first estimation of fish production was done by means of the Allen (1971) method, and more accurate analyses (cohort and yield per recruit analysis) were carried out for the seven most important fish species (Chávez et al. 1992).

The basic equation of the ECOPATH II approach (Christensen and Pauly 1992), used here for model construction is,

$$B_i * (P_i/B_i) * EE_i = \Sigma_j[B_j * (Q_j/B_j) * DC_{ji}] + EX_i \qquad ...2)$$

where B_i = biomass of group (i); P_i/B_i = production/biomass ratio for group (i); EE_i = ecotrophic efficiency of group (i); B_j = biomass of predator (j); Q_j/B_j = consumption/biomass ratio for predator (j); DC_{ji} = fraction of group (i) in the diet of predator (j). EX_i is the exponent of (i).

Values of the consumption/biomass (Q/B) ratios for fish were obtained using the empirical equation of Palomares and Pauly (1989) as follows:

$$\mathrm{Ln}Q/B = -0.1775 - 0.2018 \ln W_\infty + 0.6121 \ln T + 0.5156 \ln A + 1.26F \qquad ...3)$$

where W_∞ = maximum asymptotic weight in g; T = mean habitat temperature in degrees centigrade; A = aspect ratio of the caudal fin, calculated from drawings in Guitart (1977) and Fischer (1978); and F = food type (0 for carnivores; 1 for herbivores). The derived Q/B values (% day^{-1}) were subsequently converted to an annual basis. The estimate for *Mugil* spp. is from Palomares (1991). The relative abundances of fish species were determined from samplings in the lagoon and from fish landings recorded locally. Through analysis of gut contents, a prey-predator matrix was constructed as shown in Table 1. Other parameters, such as catches, biomasses, P/B ratio and ecotrophic efficiencies, are shown in Table 2.

All inputs used in ECOPATH II were standardized to g·(wet weight)·$km^{-2}year^{-1}$.

For nonassimilated food, the default value supplied in ECOPATH II of 20%, was used for all consumers.

Table 1. Diet composition of consumers of Celestun Lagoon, Mexico. Group 1 is *Lutjanus* and group 2, *Arius*.

	Predator												
Prey	1	2	3	4	5	6	7	8	9	10	11	12	13
3. *Callinectes*	-	-	0.10	-	-	-	-	-	-	-	-	-	-
4. *Orthopristis*	0.11	0.05	-	0.05	-	-	-	-	-	-	-	-	-
5. *Lagodon*	0.10	-	0.05	-	-	0.00	-	-	-	-	-	-	-
6. *Bairdiella*	0.10	0.10	0.05	-	-	-	0.01	-	-	-	-	-	-
7. *Eucinostomus*	-	0.05	0.05	0.06	0.05	0.01	-	-	-	-	-	-	-
8. *Mugil*	-	0.02	-	0.01	0.02	0.11	0.01	-	-	-	-	-	-
9. *Penaeus*	-	-	0.10	-	-	0.05	-	-	0.05	-	-	-	-
10. Molluscs	-	0.03	0.65	0.12	0.09	0.00	0.03	-	-	-	-	-	-
11. *Polychaeta*	0.30	0.39	-	0.06	0.00	-	0.04	-	-	-	-	-	-
12. Meiobenthos	0.39	0.21	-	0.57	0.40	0.70	0.71	-	0.20	0.10	0.15	0.10	-
13. Zooplankton	0.01	0.15	-	0.10	0.10	0.12	0.21	-	-	-	-	0.05	0.05
14. Phytoplankton	-	-	-	-	-	-	-	-	-	0.05	-	-	0.35
15. Benthic producers	-	-	-	-	0.13	0.01	-	0.30	0.30	0.15	0.10	0.20	0.30
16. Detritus	-	-	-	0.03	0.20	-	-	0.70	0.45	0.70	0.75	0.65	0.30

Table 2. Input data (without brackets) for the analysis of the trophic structure of the Celestun Lagoon ecosystem, Mexico, with ECOPATH II program (in g·m^{-2}·$year^{-1}$). Export includes catches. The biomasses are expressed in g·m^{-2}, P/B is the production/biomass ratio ($year^{-1}$) and Q/B the consumption/biomass ratio ($year^{-1}$). EE is the ecotrophic efficiency. Parameters estimated by the program are given in brackets.

Group	Export	Biomasses (estimated)	P/B	Q/B	EE
1. *Lutjanus*	0.492	(0.74)	0.70	5.6	0.95
2. *Arius*	0.164	(0.60)	0.29	9.9	0.95
3. *Callinectes*	0.0	(0.36)	1.10	9.1	(0.83)
4. *Orthopristis*	0.082	(1.12)	1.30	10.0	0.95
5. *Lagodon*	0.082	(0.83)	0.89	10.5	0.95
6. *Bairdiella*	0.016	(1.21)	1.10	8.8	0.95
7. *Eucinostomus*	0.082	(1.86)	1.00	7.3	0.95
8. *Mugil*	0.0	(1.46)	1.20	12.3	0.95
9. *Penaeus*	0.082	0.3	4.50	22.5	0.95
10. Molluscs	0.0	24.9	2.00	10.0	(0.10)
11. *Polychaeta*	0.0	(1.1)	4.50	22.5	0.95
12. Meiobenthos	0.0	32.7	10.00	50.0	(0.68)
13. Zooplankton	0.0	9.0	18.00	90.0	(0.80)
14. Phytoplankton	0.0	3.5	90.00	0.0	(0.94)
15. Benthic producers	0.0	350.0	4.50	0.0	(0.39)
16. Detritus	(1,481.6)	2,400.0	-	-	(0.51)

Results and Discussion

Primary Productivity

The phytoplankton gross primary productivity (GPP) show wide seasonal variation, being highest in September, when the amount of photosynthetically useful energy (Ep) was 787.8 g·m^{-2}·day^{-1} and the GPP = 8.7 g·m^{-2}·day^{-1}. In May, the Ep value was 825.6 g·m^{-2}·day^{-1}, but GPP dropped to only 1.3 g·m^{-2}·day^{-1}.

The phytobenthos is represented mainly by *Chara* sp., an algae; seagrasses represent only 4% and other algae only 1.1%. Macrophytobenthos standing crop was 3,412 g·m^{-2}. Mangrove defoliation has been estimated to 2.58 g·m^{-2}·day^{-1} (Trejo 1986), while the turnover rate is 1.42 year^{-1} (Day et al. 1982). Using an average of the estimates by Heald (1969) and Twilley (1985), who stated that 42% and 75% respectively of organic matter is exported, the amount of net production imported to the lagoon can then be estimated to 7.9 g·m^{-2}·day^{-1}.

ZOOPLANKTON

Clear seasonal changes occur, in synchrony with pulses of nutrients and primary productivity. In the dry season community structure is diverse and herbivore biomass is low, caused by a high predatory pressure. During the rainy season, grazing by herbivore plankton is low. This plankton displays a high turnover rate, and its production is low (P/B = 0.25 month^{-1}). In the cold season the herbivore biomass and production are the highest (B= 0.99 g·m^{-2}; P/B = 2.08 month^{-1}) and at the beginning of this season they may consume up to 70% of NPP.

ZOOBENTHOS

The biomass and production values used in this study are higher than those reported by Sanders (1956), Warwick et al. (1978), and Wolf and Wolf (1978) for temperate areas. The differences may, however, be explained by the different climates, in addition to the intense energy flux into the lagoon ecosystem from the adjacent mangrove and the open sea in Celestun.

Fish Fauna and Fishery

The model was balanced based on assumed ecotrophic efficiencies of 0.95 for the fish groups. EE is the part of the production that is used for catches or for predation (Table 2). This indicates high exploitation and predation rates, and can be seen as the signature of a productive system with a high turnover rate. The estimated fish production is similar to that estimated by Bahr et al. (1972) in Louisiana.

The role of the fisheries within the system is equivalent to a predator with a mean trophic level of 4.2, showing the fisheries dependence on the apex predators, lutjanid fishes (trophic level 3.4). An overview of the trophic flows in the system is given in Fig. 2.

Of the total system throughput, 19% was used for respiratory processes, 17% was exported and 33% went to the detritus (Table 3).

Table 3. Summary statistics for the Celestun Lagoon ecosystem, Mexico (in g·m^{-2}·year^{-1}).

Input total net primary production	1,890
Sum of all consumption	2,801
Sum of all exports	1,483
Sum of all respiratory flows	1,687
Sum of all flows into detritus	2,998
Total system throughput	8,969
Sum of all production	2,443

Some limitations of the model were observed, mainly associated with the steady-state assumption: high seasonal variations occur, and these produce major changes in trophic structure and production. This is not reflected in the present model which reports average conditions, but it could have been done by constructing seasonal models. Moreover, uncertainty and time delays in processes associated with ecosystem dynamics are not considered, which will constrain its direct use for management purposes; however ECOPATH II provides a useful scheme for organizing the community trophic structure. As an example, it is possible to assess the impacts of a specific group on the others by using the mixed trophic impact routine of ECOPATH II. In Fig. 3 a schematic representation of such impacts of some of the commercially important species is shown. Of interest is that the two top predators, *Lutjanus* and *Arius*, have a positive impact on *Penaeus* because of the predation on *Callinectes* and *Bairdiella* which both feed on shrimps.

A main result of the present study is that it has been possible to derive a balanced trophic model of the Celestun Lagoon using primary data from the area. This indicates that the data were largely compatible with each other. Indeed, no dubious input value was identified, apart from the fact that the fish biomasses estimated from the swept area method were far too low to be realistic.

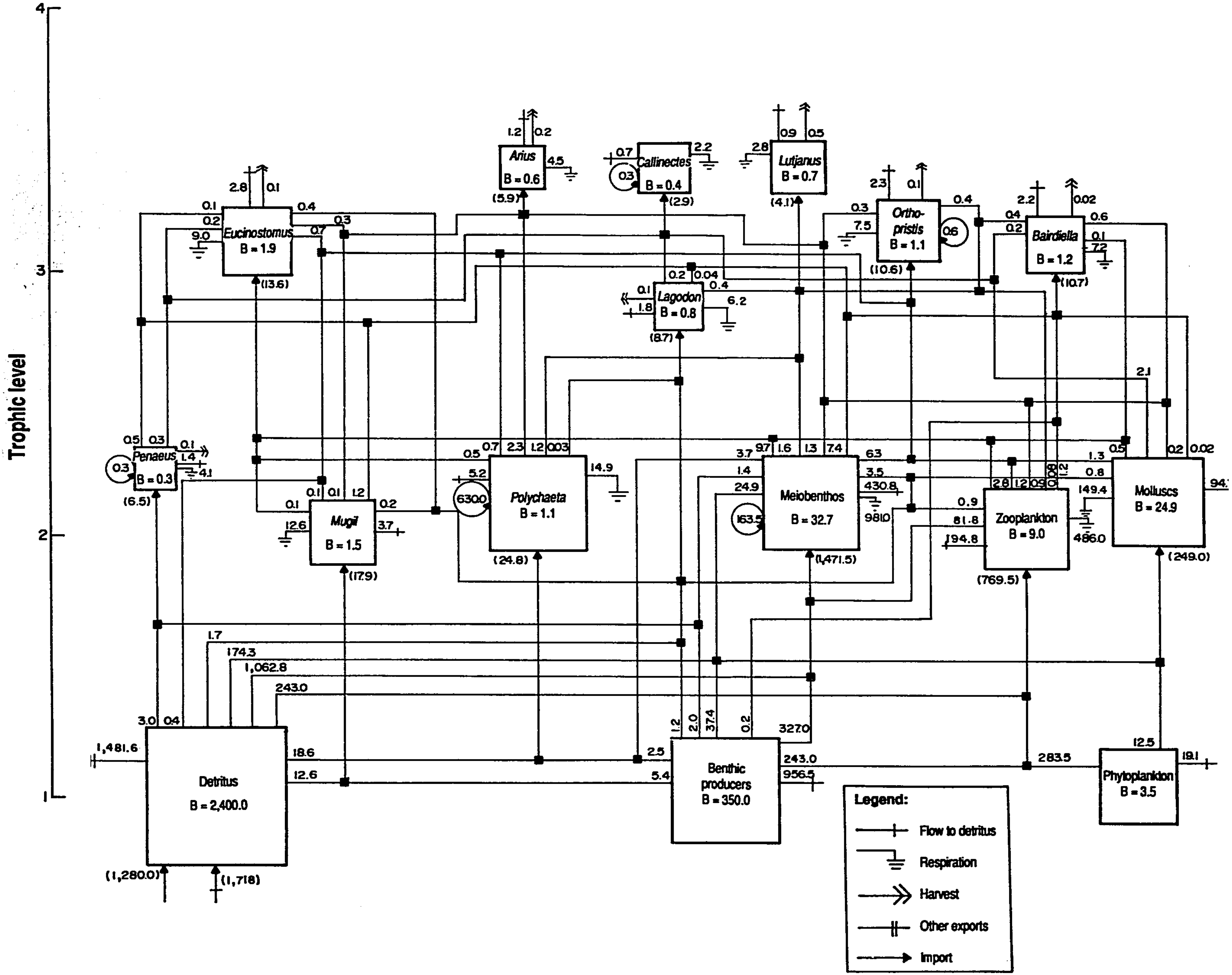

Fig. 2. Trophic interactions in Celestun Lagoon, southern Gulf of Mexico. All flows are in g·ww·m^{-2}·year^{-1} while biomasses (B) are in g·m^{-2}.

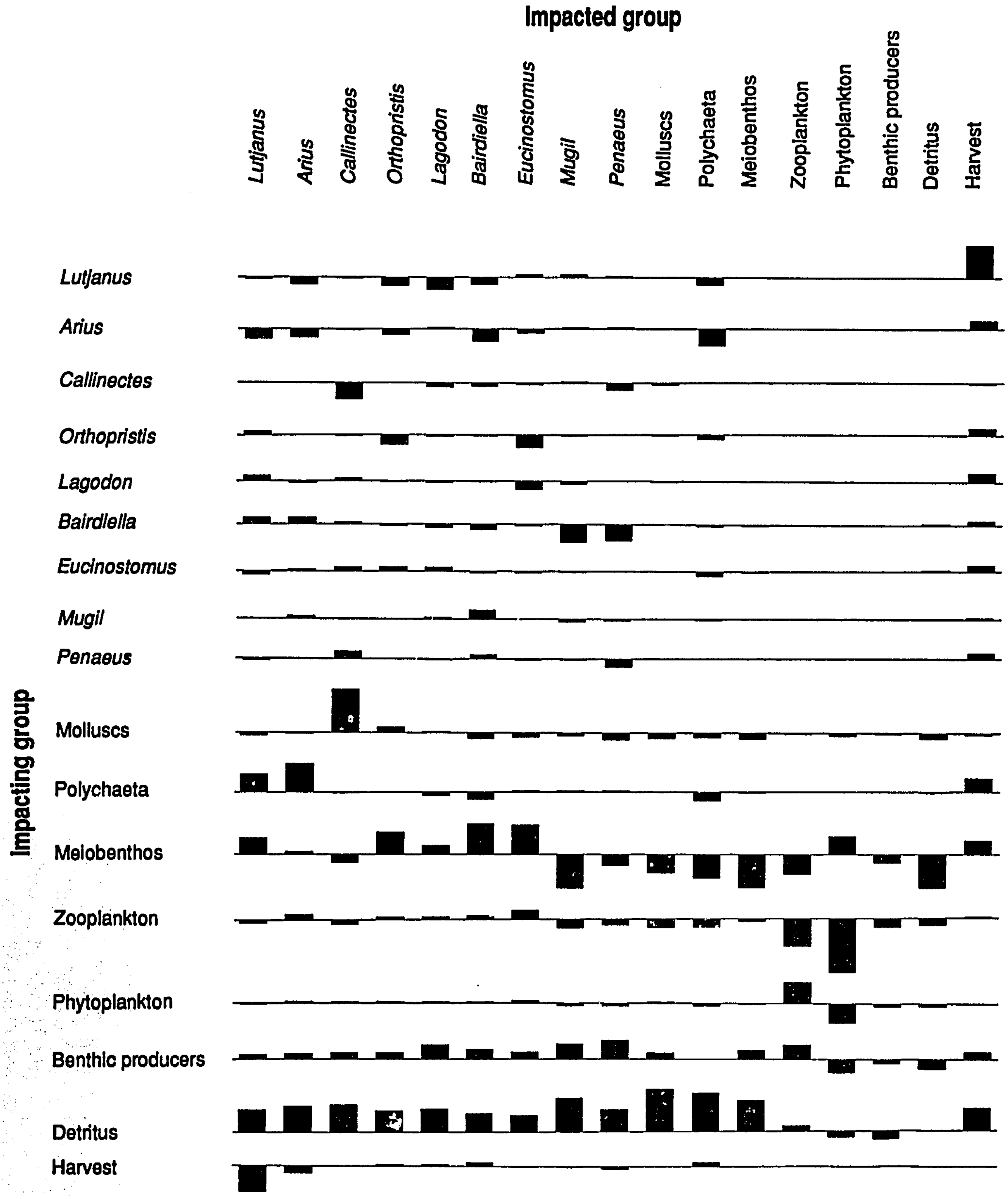

Fig. 3. Mixed impacts of the compartments of the Celestun Lagoon ecosystem, southern Gulf of Mexico.

Acknowledgements

The authors appreciate very much the detailed revision of our draft and the valuable comments and suggestions made by Dr. Villy Christensen.

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A Preliminary Model of Mandinga Lagoon, Veracruz, Mexico

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DE LA CRUZ-AGUERO, G. 1993. A preliminary model of Mandinga Lagoon, Veracruz, Mexico, p. 193-196. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Abstract

Based on one-year sampling of the communities in the Mandinga Lagoon, Mexico, a model of trophic interactions was constructed. In addition to original data, some parameters were based on information from other Mexican coastal areas. The model is very preliminary, and no catch data are included. The available phytoplankton production estimate was very low and therefore not used; instead a production rate was estimated that could balance consumption by copepods. A balanced ecosystem model could be derived with only minor modifications of the input parameter which shows that the available data are largely internally consistent.

Introduction

Tropical coastal lagoons (and estuaries) serve as nursery and feeding grounds for the juveniles of many commercially exploited fish species. Land drainage and organic matter inputs from mangrove are the main energy sources supporting detritus food webs. Among the rich lagoon fauna, fishes are the more conspicuous group. Besides their economic importance, the fishes play a major role in transferring biomass between lagoons and the sea. The advent of new approaches for ecosystem structure and function analysis, like the ECOPATH II (Christensen and Pauly 1992) model, allowed to obtain new insight on the subject from old data from the Mandinga Lagoon fish community.

Mandinga Lagoon, Veracruz, is a typical coastal lagoon of the Western-Central Gulf of Mexico (Fig. 1). It is a shallow (1-3 m depth) tropical lagoon with two main waterbodies connected to each other by a short, narrow (50-100 m wide) channel and always connected to the sea by a long and narrow (50-200 m wide), deeper channel through the Jamapa River mouth. The system is almost surrounded by mangrove forest and receives supplementary freshwater from the Arroyo Hondo River.

Methods

From September 1982 to August 1983 a general ecological survey was performed in Mandinga Lagoon, Veracruz, Mexico. Samples of sediments, zooplankton, benthos and fish communities, as well as hydrological factors, were taken on a monthly basis for 14 stations. In addition to stomach contents, biomass and sedimentary organic matter data, critical values for P/B and Q/B were taken from the literature, mostly from the other models from Mexico in this volume. There is no information on catches from the lagoon.

Units for the model were in g·wet weight·m^{-2}·$year^{-1}$. Input data are shown in Tables 1 and 2.

Results and Discussion

A biomass for crabs of 0.169 g·m^{-2} was estimated. The analysis showed that the resulting production of crabs was not large enough to balance consumption. Thus, the biomass was calculated from an assumed ecotrophic efficiency of 0.95, leading to a biomass of 0.2 g·m^{-2}, not far from the original value.

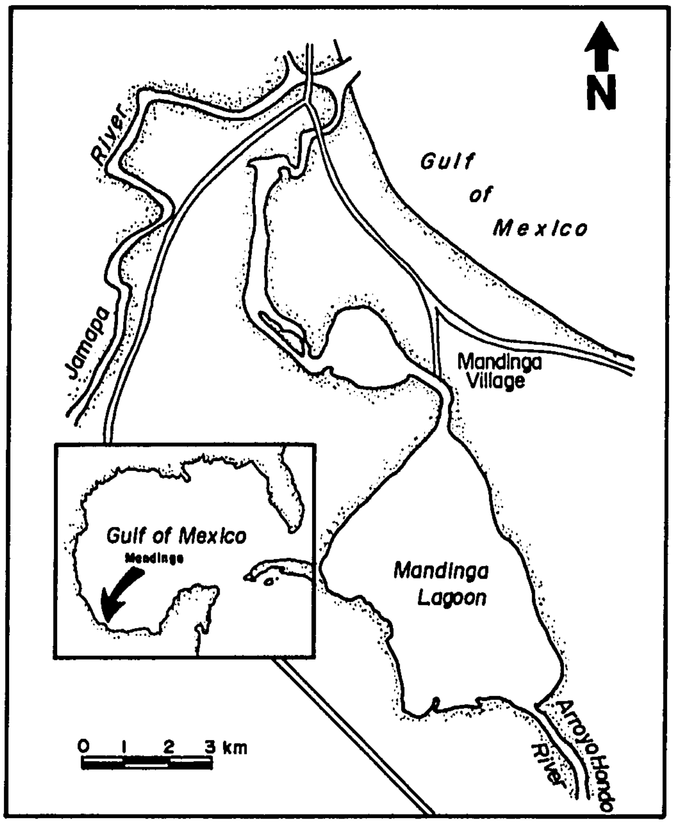

Fig. 1. Map of Mandinga Lagoon, Mexico.

Table 1. Input data (without brackets) and estimated parameters (in brackets) for the Mandinga Lagoon, Mexico. The biomasses are in g m^{-2}, the flows in g·m^{-2}·year^{-1}.

	Group	Biomass	P/B	Q/B	EE	Trophic level
1.	Zooplankton	(9.07)	17.00	120.0	(0.95)	(2.0)
2.	Ichthyoplankton	(1.47)	15.00	110.0	(0.95)	(2.9)
3.	Microbenthos	(2.57)	7.00	25.0	(0.95)	(2.1)
4.	Crabs	(0.20)	2.50	8.5	(0.95)	(2.6)
5.	Shrimps	(0.29)	3.50	19.0	0.90	(2.6)
6.	Mullets	0.11	0.70	12.3	0.86	(2.1)
7.	Jacks	0.03	0.70	10.0	0.14	(3.7)
8.	Sea catfishes	0.15	0.45	10.0	0.08	(2.9)
9.	Mojarras	0.16	1.38	15.3	0.05	(2.9)
10.	Snooks	0.04	0.50	5.4	0.00	(3.7)
11.	Flatfishes	0.01	0.30	9.1	0.00	(3.0)
12.	Rays	0.01	0.20	10.8	0.00	(3.2)
13.	Drums and croakers	0.03	0.35	10.0	0.00	(3.5)
14.	Herrings	(0.77)	0.80	11.7	(0.95)	(3.5)
15.	Needlefishes	0.03	0.30	7.2	0.00	(3.7)
16.	Gobies	(4.14)	0.30	12.3	(0.95)	(2.8)
17.	Snappers	0.01	0.30	4.7	0.00	(3.9)
18.	Other fishes	0.47	0.30	5.4	0.08	(3.3)
19.	Phytoplankton	(3.76)	157.00	0.0	0.95	(1.0)
20.	Detritus	315.00	-	-	(1.00)	(1.0)

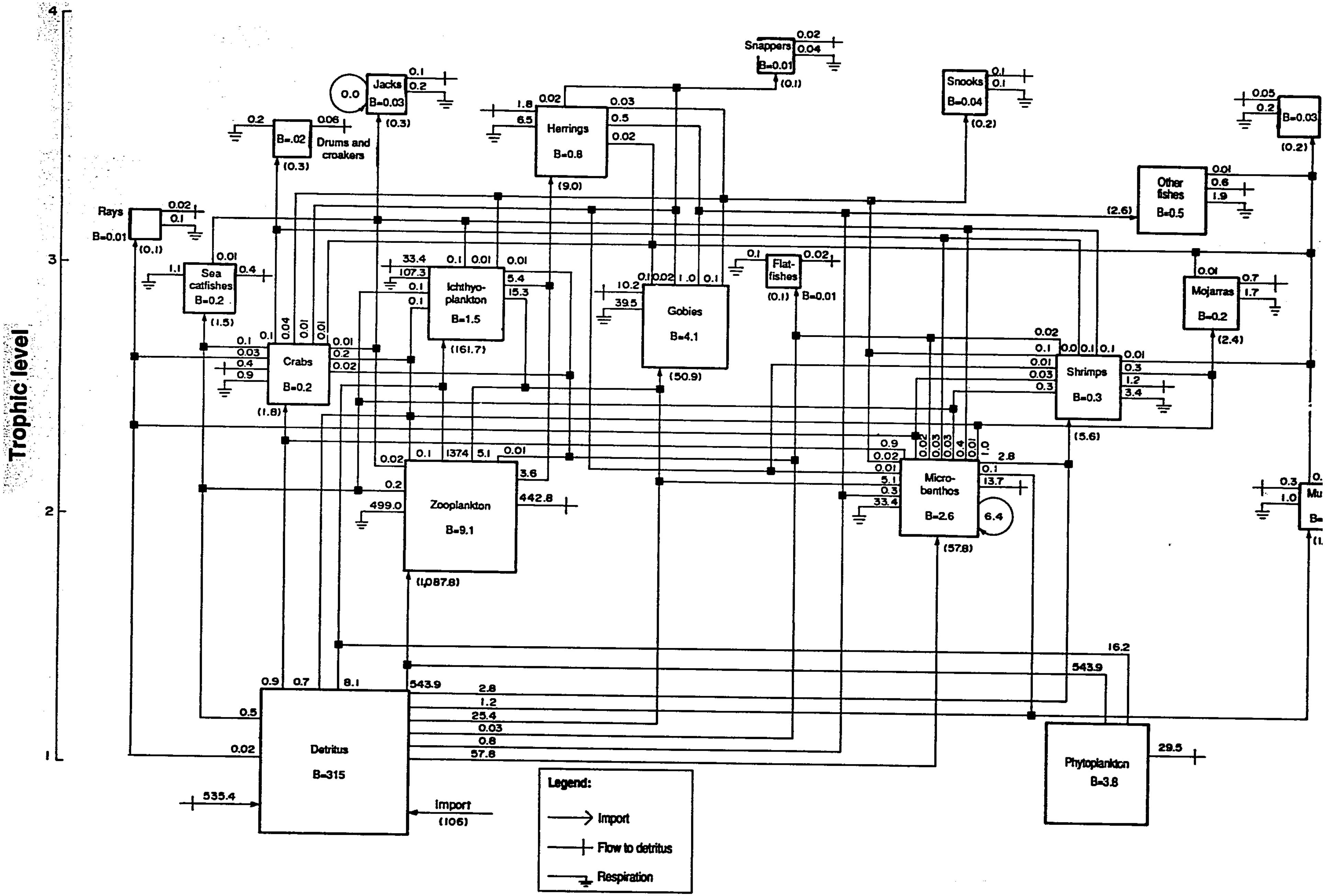

Fig. 2. A quantitative representation of the annual flows (g·m^{-2}) in the Mandinga Lagoon, Mexico.

Table 2. Predator-prey matrix from Mandinga Lagoon, Mexico.

	Predator								
Prey	ZOO	ICH	MIC	CRA	SHR	MUL	JAC	CAT	MOJ
ZOO	-	0.85	-	-	-	-	0.07	0.13	0.04
ICH	-	-	-	-	-	-	0.52	0.05	0.03
MIC	-	-	0.10	0.50	0.50	0.10	0.03	0.25	0.43
CRA	-	-	-	-	-	-	0.02	0.07	0.08
SHR	-	-	-	-	-	-	0.33	0.19	0.12
MUL	-	-	-	-	-	-	-	-	-
JAC	-	-	-	-	-	-	0.01	-	-
CAT	-	-	-	-	-	-	0.02	-	-
MOJ	-	-	-	-	-	-	-	-	-
HER	-	-	-	-	-	-	-	-	-
NEE	-	-	-	-	-	-	-	-	-
GOB	-	-	-	-	-	-	-	-	-
SNA	-	-	-	-	-	-	-	-	-
OTH	-	-	-	-	-	-	-	-	-
PHY	0.50	0.10	-	-	-	-	-	-	-
DET	0.50	0.05	0.90	0.50	0.50	0.90	-	0.31	0.30

	Predator								
Prey	SNO	FLA	RAY	DRU	HER	NEE	GOB	SNA	OTH
ZOO	-	0.05	-	-	0.40	-	0.10	-	-
ICH	0.05	0.10	-	-	0.60	-	0.30	-	-
MIC	0.10	0.30	0.20	0.10	-	-	0.10	0.10	0.10
CRA	0.18	0.15	0.30	0.35	-	0.05	-	0.10	-
SHR	0.27	0.15	0.30	0.55	-	0.05	-	0.20	-
MUL	-	-	-	-	-	0.30	-	-	-
JAC	-	-	-	-	-	-	-	-	-
CAT	-	-	-	-	-	-	-	-	-
MOJ	-	-	-	-	-	0.05	-	-	-
HER	0.15	-	-	-	-	0.10	-	0.30	0.20
NEE	-	-	-	-	-	-	-	-	-
GOB	0.25	-	-	-	-	0.40	-	0.30	0.40
SNA	-	-	-	-	-	-	-	-	-
OTH	-	-	-	-	-	0.05	-	-	-
PHY	-	-	-	-	-	-	-	-	-
DET	-	0.25	0.20	-	-	-	0.50	-	0.30

Legend:	ZOO	Zooplankton	MOJ	Mojarras
	ICH	Ichthyoplankton	HER	Herrings
	MIC	Microbenthos	NEE	Needlefishes
	CRA	Crabs	GOB	Gobies
	SHR	Shrimps	SNA	Snappers
	MUL	Mullets (*Mugil* sp.)	OTH	Other fishes
	JAC	Jacks	PHY	Phytoplankton
	CAT	Catfishes	DET	Detritus

Some detritus is imported from neighboring mangroves and rivers. Assuming this to be 106 $g{\cdot}m^{-2}{\cdot}year^{-1}$ (a rather low estimate), makes it possible to balance the detritus box so that input equals output ("EE"=1.00; Fig. 2).

The primary production in the lagoon was originally estimated to be only 100 $g{\cdot}m^{-2}{\cdot}year^{-1}$. This seems to be very low; the reason why this should be so low is not clear. Instead of using this low primary production estimate, a new one was obtained, based on the assumption that half of the diet of zooplankton is phytoplankton and the rest detritus. This leads to a primary production of around 590 $g{\cdot}m^{-2}{\cdot}year^{-1}$, a more realistic estimate.

The trophic interactions in the lagoon are summarized in Fig. 2.

It is known that there are interactions between the fish population in the lagoon and the neighboring coastal areas but these have not been quantified, rendering the interpretation of our results somewhat ambiguous. It is recommended that this aspect should be studied further.

From the present preliminary study, it is clear that ECOPATH II is a useful tool for understanding the fundamental processes involved in trophic interactions in lagoons.

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A Trophic Box Model of the Coastal Fish Communities of the Southwestern Gulf of Mexico

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Abstract

The trophic structure of the nearshore fish communities of the southwestern Gulf of Mexico was analyzed through application of the ECOPATH II model. Emphasis was on commercially exploited species of which sharks, mackerels, shrimps and crabs are the most important. The area considered corresponds to the region of the western gulf in which fishing activity is mostly developed. Most of the fish data used for the predator-prey matrix were taken from the literature, while invertebrate information was from specific studies conducted previously.

Introduction

A variety of human activities are carried out in the coastal environment of the southwestern Gulf of Mexico. These are mainly associated with transport and commerce, industrial developments such as oil and electricity, and fishing (Fig. 1). Environmental impact studies of these activities have been made at some specific localities; however, none of these deals with the role of fisheries resources within the structure and organization of the ecosystems in the region.

A variety of species are exploited and the total annual yield is around 30,000 t, of which 10% comes from mackerels, mainly *Scomberomorus maculatus* and *S. cavalla*. Chávez et al. (1976) describe the main fisheries from this region; Chávez (1981) and Arreguín-Sánchez et al. (1992) studied the main pelagic fisheries with a multispecies approach, while shrimps were studied by Arreguín-Sánchez and Chávez (1985), Castro et al. (1986), and Castro and Arreguín-Sánchez (1991). Further, most of the studies existing from this region have been conducted on the adjacent coastal lagoons, such as those by de la Cruz and Franco (1981), Abarca-Arenas et al. (1982), Bozada et al. (1982), Abarca-Arenas (1987), Chávez et al. (1987), Torruco and Chávez (in press), Abarca-Arenas and Valero-Pacheco (this vol.) and de la Cruz-Aguero (this vol.).

The human activities in the southwestern central Gulf of Mexico must be maintained and evaluated as part of larger coastal systems (Capurro 1989). With regard to the fishery, the question of how ecosystems respond to perturbation produced by fishing needs to be addressed. Likewise, the relative role of target resources in the food web needs attention (Laevastu and Larkins 1981; Beddington 1984; Steele 1984). Therefore the aim of this contribution is to obtain a preliminary knowledge of the trophic structure of the ecosystems of the southwestern coastal area of the Gulf of Mexico and of the functional role of its major fisheries resources.

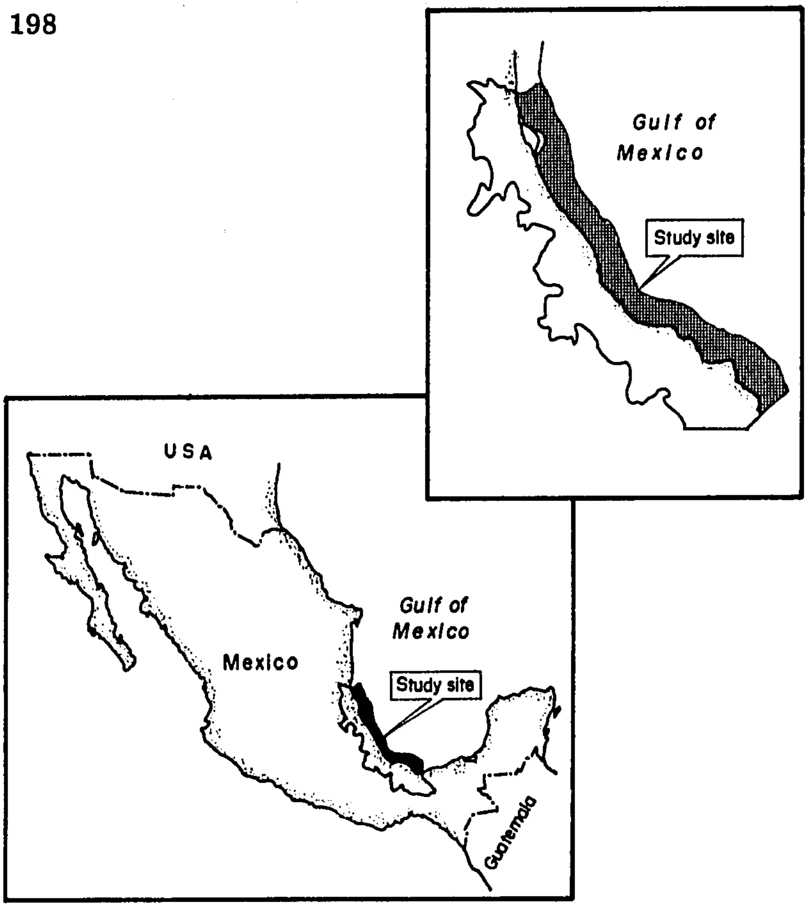

Fig. 1. Coastal area of southwestern Gulf of Mexico as covered in this study.

Methods

Trophic community structure is analyzed with the ECOPATH II model, which assumes that the ecosystem is in steady state. Populations and their interdependencies are described by deterministic linear equations. Characteristics of the ECOPATH II model are discussed in detail elsewhere (Polovina 1984; Christensen and Pauly 1992a, 1992b). The basic ECOPATH equation describes a steady-state ecosystem where the utilized production of each compartment corresponds to the consumption by all predators plus all exports as follows:

$$B_i \cdot \left(\frac{P_i}{B_i}\right) \cdot EE_i - \left(\sum_{j=1}^{n} B_j \cdot \left(\frac{Q_j}{B_j}\right) \cdot DC_{ji}\right) - EX_i = 0 \quad ...1)$$

where B_i = biomass of groups (i); P_i/B_i = production/biomass ratio of group (i); EE_i = ecotrophic efficiency of group (i); B_j = biomass of predator (j); Q_j/B_j = consumption/biomass ratio for predator (j); DC_{ji} = fraction of group (i) in the diet of predator (j); and EX_i is export of group (i).

As stated by Christensen and Pauly (1992a, 1992b), at least three out of the four parameters of equation (1) must be known previously for each compartment. One of the most important features of the model is that it is based upon a series of simultaneous equations linked through the data provided by the predator-prey matrix.

Data used for the analyses were obtained as follows:

Conversion from wet to dry weight was done using conversion factors of 30% for microcrustaceans, 20% for molluscs and fishes and 13% for benthic producers.

Primary production, microcrustacean and annelid biomass data were taken from estimates reported in Chávez et al. (1976) and El-Sayed and Turner (1980). The biomass of shark was estimated from the assumption that the catches of sharks lead to an ecotrophic efficiency of 0.95 (B = C/(EE·P/B).

Stomach contents studies of the consumers in this region are scarce, and most of the data for food habits of fishes were taken from García (1976) who put emphasis on invertebrate consumption. Fish diets data were complemented using studies in adjacent coastal lagoons such as those conducted by de la Cruz and Franco (1981), Abarca-Arenas et al. (1982), Bozada et al. (1982), Abarca-Arenas (1987), Barba-Torres and Gaspar-Dillones (1987), and Torruco et al. (1989). Where required, additional information about diet composition was assembled from the literature: Chávez and Fernández (1976), Berrien and Finan (1977), DeVane (1978), Naughton and Saloman (1981), Sierra and Popova (1982), Castro (1983), Saloman and Naughton (1984), Finucane and Vaught (1986) and Polovina and Ralston (1987). Based on this, the predator-prey matrix shown in Table 1 was constructed.

The values of the production/biomass (P/B) ratio were obtained from estimates of the instantaneous total mortality rates cited in the literature as: mackerels from Chávez (1981); mojarras from Abarca-Arenas (1987) and Batllori et al. (1987); grunts from Manooch (1976); sharks from Alvarez (1988), Alvarez and Arreguín-Sánchez (1990); groupers and snappers from Polovina and Ralston (1987); Contreras et al. (1990) and González et al. (1990); shrimps from Arreguín-Sánchez and Chávez (1985) and Castro and Arreguín-Sánchez (1991); crabs from Chávez and Fernández (1976), Bozada et al. (1982). For other species, P/B values were estimated through the application of standard methods (Ricker 1975; Brey and Pauly 1986) using information collected by Chávez et al. (1976). The

Table 1. Predator-prey matrix from a coastal ecosystem in the southwestern Gulf of Mexico.

	Predator										
Prey	HER	ANC	LF	SM	KM	JAC	MOJ	ST	GR	SHA	RG
HER	-	-	0.13	0.25	0.46	0.28	-	-	-	-	-
ANC	-	-	0.47	0.18	0.30	0.04	-	0.02	-	-	-
LF	-	-	-	-	-	0.00	-	-	-	-	-
SM	-	-	-	-	-	-	-	-	-	0.47	0.03
KM	-	-	-	-	-	0.00	-	-	-	0.14	0.02
JAC	-	-	-	-	-	0.00	-	-	-	-	0.18
MOJ	-	-	-	0.02	-	-	-	-	-	0.07	0.22
ST	-	-	-	-	-	-	-	-	-	0.00	0.01
GR	-	-	-	-	-	0.05	-	-	-	0.10	-
SHA	-	-	-	-	-	-	-	-	-	-	-
RG	-	-	-	-	-	-	-	-	-	0.03	-
RS	-	-	-	-	-	-	-	-	-	0.14	0.20
CF	-	-	-	-	-	0.02	-	-	-	-	-
FLO	-	-	-	-	-	0.01	-	-	-	-	-
SHR	0.04	0.15	0.03	0.19	0.25	0.33	0.06	0.02	0.11	0.02	0.18
CRA	-	-	-	0.04	-	0.07	0.01	0.02	0.06	0.01	0.16
MOL	-	-	0.23	0.08	-	0.19	0.18	0.15	0.16	-	-
MIC	0.35	0.35	0.14	-	-	-	0.30	0.36	0.18	-	-
OF	0.03	0.05	-	0.23	-	-	0.01	-	-	0.01	-
ANN	0.08	0.03	-	-	-	-	-	0.04	0.25	-	-
ZP	0.36	0.43	-	0.01	-	0.01	0.32	0.35	0.24	-	-
PHP	-	-	-	-	-	-	-	-	-	-	-
BP	0.09	-	-	-	-	0.00	0.13	0.03	0.01	-	-
DET	0.05	-	-	-	-	-	-	-	-	-	-

	Predator									
Prey	RS	CF	FLO	SHR	CRA	MOL	MIC	OF	ANN	ZP
HER	-	0.03	-	-	-	-	-	-	-	-
ANC	-	0.02	-	-	-	-	-	-	-	-
LF	-	-	-	-	-	-	-	-	-	-
SM	-	-	-	-	-	-	-	-	-	-
KM	-	-	-	-	-	-	-	-	-	-
JAC	-	-	-	-	-	-	-	-	-	-
MOJ	0.43	-	-	-	-	-	-	-	-	-
ST	0.01	-	-	-	-	-	-	-	-	-
GR	0.16	-	-	-	-	-	-	-	-	-
SHA	-	-	-	-	-	-	-	-	-	-
RG	-	-	-	-	-	-	-	-	-	-
RS	-	-	-	-	-	-	-	-	-	-
CF	-	-	-	-	-	-	-	-	-	-
FLO	-	-	-	-	-	-	-	-	-	-
SHR	-	0.00	0.09	-	0.10	-	-	0.20	-	-
CRA	-	0.02	0.09	-	-	-	-	-	-	-
MOL	-	0.04	-	-	-	-	-	-	-	-
MIC	-	0.12	0.60	0.20	0.10	-	-	0.30	-	0.05
OF	0.37	0.14	-	-	-	-	-	-	-	-
ANN	-	0.23	0.09	0.55	0.15	-	0.20	0.10	-	-
ZP	0.01	0.36	-	-	0.05	0.20	-	0.20	-	-
PHP	-	-	-	-	-	0.30	0.30	-	-	0.70
BP	0.03	0.04	-	0.10	-	0.15	-	-	0.05	-
DET	-	0.02	0.12	0.15	0.60	0.35	0.50	0.20	0.95	0.25

Legend:

HER = herrings
ANC = anchovies
LF = lizardfish
SM = Spanish mackerel
KM = king mackerel

JAC = jacks
MOJ = mojarra
ST = seatrout
GR = grunts
SHA = sharks

RG = red grouper
RS = red snapper
CF = catfish
FLO = flounder
SHR = shrimps

CRA = crabs
MOL = molluscs
MIC = microcrustaceans
OF = other fishes
ANN = annelids

ZP = zooplankton
PHP = phytoplankton
BP = benthic producers
DET = detritus

P/B estimates for herring (1.0) and anchovies (0.7) reported by Nuñez (1987) seem to be too low, instead it was assumed that the gross food conversion efficiency (GE = production/consumption) was 0.2 for these groups. A similar efficiency was used to estimate P/B for the "other fish" while P/B for microcrustacean were estimated based on a gross efficiency of 0.30.

Values of the consumption/biomass (Q/B) ratios, as defined in Pauly (1986, 1989) and were obtained using the equation proposed by Palomares and Pauly (1989) as follows:

$$\ln(Q/B) = -0.01775 - 0.2018\ln W_\infty + 0.6121\ln T + 0.51561\ln A + 1.26F \qquad \ldots 2)$$

where W_∞ = maximum asymptotic weight in g; T = mean habitat temperature in °C; A = aspect ratio of the caudal fin, here calculated from drawings in Guitart (1977) and Fischer (1978); F = food type (= 0 in carnivores; 1 in herbivores and 0.5 for omnivores). The resulting Q/B estimates (% day^{-1}) were then converted to annual rates.

For shrimps, the Q/B was estimated from an assumed gross food conversion efficiency of 0.20 while a lower value of 0.15 was assumed for the detritivore annelids.

As this study aims at understanding the role o the main fisheries resources within the ecosystem the area was selected to cover the location of th major fishing grounds. There is no information o the amount of energy exchanged between the are considered and adjacent regions. Therefore th ecosystem was assumed to be closed apart from a annual import of 522 $g{\cdot}m^{-2}$ detritus from coasta lagoons, and catches were the only source of exports The import of detritus was estimated so that inpu and output from the detritus box would balance Catch data were taken from the records of th Ministry of Fisheries (SEPESCA 1987).

Values for unassimilated food were taken fron defaults given by the ECOPATH II, 20%, apart fron zooplankton where 40% was used to obtain a mor reasonable respiration/biomass ratio.

All inputs used in ECOPATH II wer standardized to $g{\cdot}m^{-2}year^{-1}$ dw for flows, $g{\cdot}m^{-2}$ fo biomass and $year^{-1}$ for P/B and Q/B. For group where biomass, consumption or productio parameters were not available, assumed values o 0.95 for ecotrophic efficiency were used as input fo the model. Table 2 presents some of the inpu parameters. Estimates of consumption/biomass ratio were estimated from equation (2) from data show in Table 3.

Table 2. Input data (without brackets) and calculated estimates (in brackets) for the model of the southwestern Gulf of Mexico. Exports include catches and are in g dw·m^{-2}·$year^{-1}$, biomasses in g dw·m^{-2}, P/B is the production/biomass ratio and Q/B the consumption/biomass ratio, both on an annual basis. The ecotrophic efficiency gives the proportion of the production that is harvested or predated upon, while the gross efficiency is the ratio between production and consumption.

Group	Export	Biomass	P/B	Q/B	Ecotrophic efficiency	Gross efficiency
Herrings	0.003	(2.01)	(2.34)	11.7	0.95	0.20
Anchovies	-	(0.75)	(3.94)	19.7	0.95	0.20
Lizardfish	-	(0.01)	0.30	8.3	0.95	(0.04)
Spanish mackerel	0.068	(0.67)	1.10	10.2	0.95	(0.11)
King mackerel	0.064	(0.55)	0.50	8.9	0.95	(0.06)
Jacks	0.034	(0.17)	0.70	10.0	0.95	(0.07)
Mojarra	0.095	(1.63)	1.38	15.3	0.95	(0.09)
Seatrout	0.001	(0.06)	0.48	6.8	0.95	(0.07)
Grunts	0.042	(2.70)	0.36	8.6	0.95	(0.04)
Sharks	0.097	0.17	0.60	7.8	0.95	(0.08)
Red grouper	0.002	(0.09)	0.45	4.6	0.95	(0.10)
Red snapper	0.033	(0.91)	0.36	4.4	0.95	(0.08)
Catfish	0.013	(0.10)	0.45	10.0	0.95	(0.05)
Flounder	-	(0.03)	0.30	9.1	0.95	(0.03)
Shrimps	0.078	(2.29)	7.57	(37.9)	0.95	0.20
Crabs	0.070	(1.10)	2.12	8.5	0.95	(0.25)
Molluscs	0.040	(5.32)	1.80	8.3	0.95	(0.22)
Microcrustaceans	-	(9.13)	7.38	(24.6)	0.95	0.30
Other fishes	0.024	(2.05)	(2.52)	12.6	0.95	0.20
Annelids	-	22.09	4.85	(32.3)	(0.98)	0.15
Zooplankton	-	(2.11)	21.76	119.7	0.95	(0.18)
Phytoplankton	-	2.65	(102.56)	0.0	0.95	-
Benthic producers	-	4.13	(14.63)	0.0	0.95	-
Detritus	-	1.90	-	-	(1.00)	-

Table 3. Parameters used to estimate Q/B (consumption/biomass ratio) for fishes of the ecosystem of the southwestern Gulf of Mexico. T = 26.3°C constant in all groups; F = 0 for all groups; W_∞ = maximum asymptotic weight, (g wet weight); A = aspect ratio of the caudal fin.

Group	W_∞	A
Herrings	193.2	2.22
Anchovies	20.2	2.50
Lizardfish	902.7	2.06
Spanish mackerel	2,070.0	4.32
King mackerel	10,629.0	6.19
Jacks	3,503.8	5.10
Mojarra	170.1	3.54
Seatrout	1,070.0	1.52
Grunts	1,235.0	2.50
Sharks	1,508.0	2.24
Red grouper	14,406.0	1.96
Red snapper	9,631.0	1.50
Catfish	298.3	1.94
Flounder	72.3	0.92

Results

A diagram showing the trophic flows was constructed and is shown in Fig. 2, while the estimated parameters are given on Table 2. The estimated biomass seems very reasonable, but it should be emphasized that further studies are needed to improve the model.

Of the primary production, 82% is supported by phytoplankton while the remaining 18% comes from benthic primary producers. From the balance of the flows of energy in the whole system, 64% of total combined primary and detritus production is estimated to be imported from other systems; we assume this is contribution from the coastal lagoons along the shoreline of this region (Torruco and Chávez, in press; Abarca-Arenas and Valero-Pacheco, this vol.; de la Cruz-Aguero, this vol.). The input is tentatively quantified to 522 $g \cdot m^{-2} \cdot year^{-1}$ in order to balance input to and output from the detritus box.

The role of the fishery within the system is equivalent to a predator with a mean trophic level of 4.4. This trophic level is within the range of the trophic levels estimated for the top predators.

Of the total system throughput of 3,213 g $dw \cdot m^{-2} \cdot year^{-1}$, 27% was due to respiratory processes and 28% went to the detritus.

The system was aggregated in discrete trophic levels using the method suggested by Ulanowicz (in press), and implemented by Christensen and Pauly (1992a, 1992b). In this analysis, the flows through each group in the system are distributed on discrete trophic levels depending on their origin. The results are shown on Table 4 along with trophic transfer efficiencies by trophic levels.

It can be concluded from the table that the quantitatively most important herbivores/detritivores are the annelids, zooplankton, microcrustaceans and molluscs, while shrimps and microcrustaceans dominate the first predatory level along with five fish species. The higher predatory levels include an array of fish species. On the top, sharks, groupers and jacks reach trophic level VIII but with only minute flows.

The trophic transfer efficiencies (Table 4) are, with 18-20%, quite high for the herbivory and first predatory levels, respectively. The higher predatory levels show efficiencies from 10 down to 7.5%. This levelling off of transfer efficiencies is something often assumed to be the case, but rarely demonstrated quantitatively.

The direct and indirect trophic impacts of each group on the others were assessed using the Leontief matrix routine in the ECOPATH II software (Christensen and Pauly 1992a, 1992b). It makes obvious that the primary producers have an important impact on the ecosystem; on the other hand, the impacts of the commercially important species are not so clear (Fig. 3). The most important groups are the two mackerels which interact with many other groups in the ecosystem as impacted and impacting groups. It is interesting to note that mackerels are the most important fishing resources in this area and that, therefore, substantial changes in ecosystem structure could potentially be induced by fishing.

Discussion

A scheme describing the trophic structure of the nearshore area of the western Gulf of Mexico was obtained. The role of fishing suggests a high level of exploitation which is conducted over several trophic levels, ranging from 2.9 for shrimps to 5.0 for sharks. From this point of view, fishing makes a better usage of the ecosystem here than in other parts of the Gulf of Mexico, such as the continental shelf of Yucatan (Arreguín-Sánchez et al., this vol.).

Although most of the inputs used to construct the model were taken from data collected in the study area, some refer to different time periods which is problematic for a steady-state model, if changes have occurred over time. In addition, the system was assumed to be closed, apart from import of detritus and export of catches. Under these conditions, most of the estimates of the rates of flows of biomasses must be taken with a grain of salt, as the above assumptions do not necessarily reflect actual conditions.

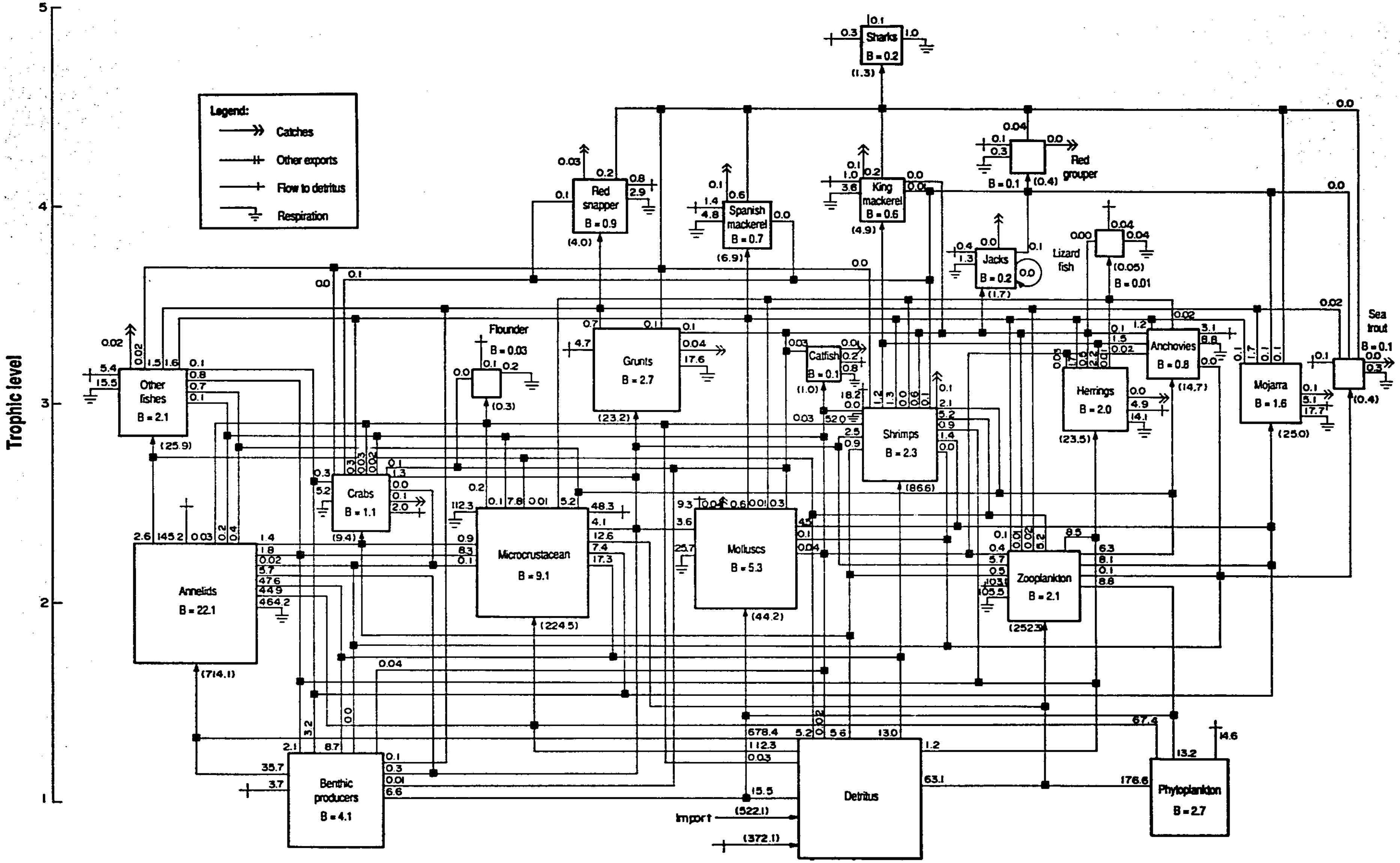

Fig. 2. The southwestern Gulf of Mexico ecosystem showing all flows (>15%) in the system. Flows are in g·dw·m^{-2}·year^{-1}. Biomasses are g·dw·m^{-2}.

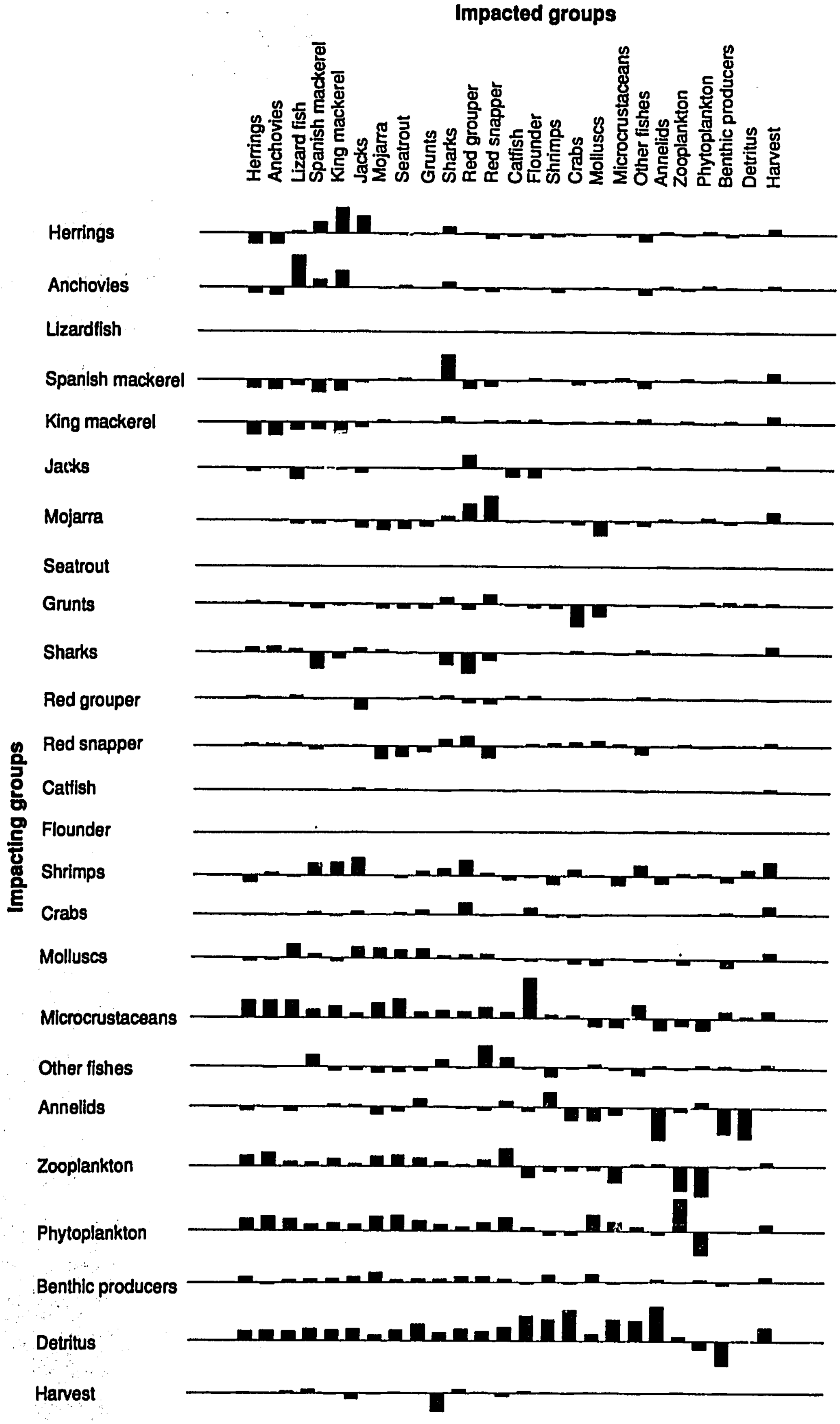

Fig. 3. Mixed trophic impacts for the commercially most important groups of the southwestern Gulf of Mexico nearshore ecosystem.

Table 4. Trophic aggregation of the groups in the western Gulf of Mexico model. The groups are arranged by average trophic level. For each group, the breakdown of flows (g·dw·m^{-2}·$year^{-1}$) by discrete trophic levels are presented. The bottom row gives the transfer efficiencies for each trophic level.

Average trophic level	Group	Trophic level I	II	III	IV	V	VI	VII	VIII
4.8	Sharks	-	-	0.04	0.41	0.71	0.16	0.01	0.00
4.3	Red grouper	-	-	0.08	0.19	0.14	0.03	0.00	0.00
4.0	King mackerel	-	-	0.61	3.58	0.67	0.06	0.00	-
4.0	Red snapper	-	0.10	0.55	2.64	0.69	0.04	0.00	-
3.9	Spanish mackerel	-	-	1.58	4.32	0.94	0.07	0.00	-
3.8	Lizardfish	-	-	0.02	0.03	0.01	0.00	0.00	-
3.8	Jacks	-	0.01	0.56	1.02	0.14	0.01	0.00	0.00
3.3	Anchovies	-	-	11.2	3.25	0.30	0.01	-	-
3.2	Catfish	-	0.06	0.77	0.17	0.04	0.00	0.00	-
3.2	Grunts	-	0.31	18.7	3.93	0.31	0.01	-	-
3.2	Seatrout	-	0.01	0.32	0.06	0.00	0.00	0.00	-
3.1	Flounder	-	0.03	0.18	0.06	0.00	0.00	-	-
3.0	Mojarra	-	3.23	17.8	3.83	0.23	0.01	-	-
3.0	Other fishes	-	5.20	15.1	5.46	0.26	-	-	-
3.0	Herrings	-	3.25	16.9	3.15	0.29	0.01	-	-
2.8	Shrimps	-	21.8	61.8	3.48	-	-	-	-
2.5	Crabs	-	5.66	2.85	0.88	0.04	-	-	-
2.2	Molluscs	-	35.5	8.43	0.35	0.09	-	-	-
2.2	Microcrustaceans		180	45.1	-	-	-	-	-
2.1	Zooplankton	-	241	10.1	2.54	-	-	-	-
2.0	Annelids	-	714	-	-	-	-	-	-
1.0	Phytoplankton	272	-	-	-	-	-	-	-
1.0	Benthic producers	60.5	-	-	-	-	-	-	-
1.0	Detritus	921	-	-	-	-	-	-	-
	Total	1,253	1,211	213	39.3	4.88	0.40	0.02	0.00
	Total transfer efficiencies (%)	-	17.6	18.6	12.9	09.9	8.0	7.5	7.5

With regard to the steady-state assumption of the model, we must point out to the problems that will result because time delays in processes associated with ecosystem dynamics are not considered. According to some authors (Beddington 1984; Sissenwine 1984; Steele 1984), fishing can act as a perturbation producing changes in the ecosystem structure. In this case, energy is dissipated through the food web, and the effect on different trophic levels will not be simultaneous in time; i.e., the effect will emerge in quite different places and times. It is important to keep this in mind when using tools such as ECOPATH II for management purposes.

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Trophic Fluxes on the Campeche Bank, Mexico

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Abstract

The principal trophic interactions that occur between various species from a 250 km² beach seine fishery area of the Campeche Bank, Mexico, were quantified with the ECOPATH II system using catch data, stomach contents data, consumption rates and biomass estimates. This information was collected from 1985 to 1990 on twelve fish species which represent 93% of the total catch.

Total production of the system was 2,047 g·m^{-2}·year^{-1} dry weight, from which 30% is used for respiratory process and 19% goes to the detritus. Some 70% of the primary production is used by the next trophic level. Detritus is considered the principal source of energy. An additional contribution of 150 g·dw·m^{-2}·year^{-1} to the detritus was estimated as imported from other systems, i.e., from the adjacent Celestun Lagoon.

Of the different trophic groups, microbenthic organisms, which mostly use detritus as a source of energy, were considered the principal link to the top carnivores. Of the fisheries resources, *Opisthonema oglinum* is the most productive. It was concluded that this kind of trophic model is a useful generalized approach for the study of community structure and a potential tool for the management of marine ecosystems.

Introduction

Several small artisanal fisheries are operating along the coast of the Peninsula of Yucatan in Mexico. Of these, the beach seine fishery has been the main economic activity in the 250 km² modelled area off the Celestun port (Fig. 1). The beach seine fishery operates from February to August, when fishers divert their effort to other seasonal species such as octopus, mackerels and some demersal fishes (Arreguín-Sánchez 1989). Catches of the beach seine fishery are composed of around 54 species (fishes and crustaceans) with 12 representing 93% of the total catch (Arreguín-Sánchez et al. 1987). Annual yield is around 6,000 t and the potential yield some 10,000 t·year^{-1}.

The structure of aquatic communities in areas where fish resources are exploited had been recognized as important, and several attempts have been made to describe the amount and direction of energy transfers occurring within a community (Walter 1979; Platt et al. 1981; Pimm 1982; Ulanowicz 1986; Pauly 1989a). Beddington (1984) and Sissenwine (1984) among others have referred to the variability of natural ecosystems and populations, stressing the need to understand the ecosystem's organization and how the community responds to exploitation of one or more of its components. From this, it can be derived that one of the first steps for the ecosystem studies is to know the system structure and organization in quantitative terms.

In tropical and subtropical ecosystems, the complexity and intensity of interactions between species are the most important processes in the ecosystem dynamics (Beddington 1984; Steele 1984). Interactions affect the diversity, abundance, distribution and persistence of the different components (Yañez-Arancibia and Sánchez-Gil 1988).

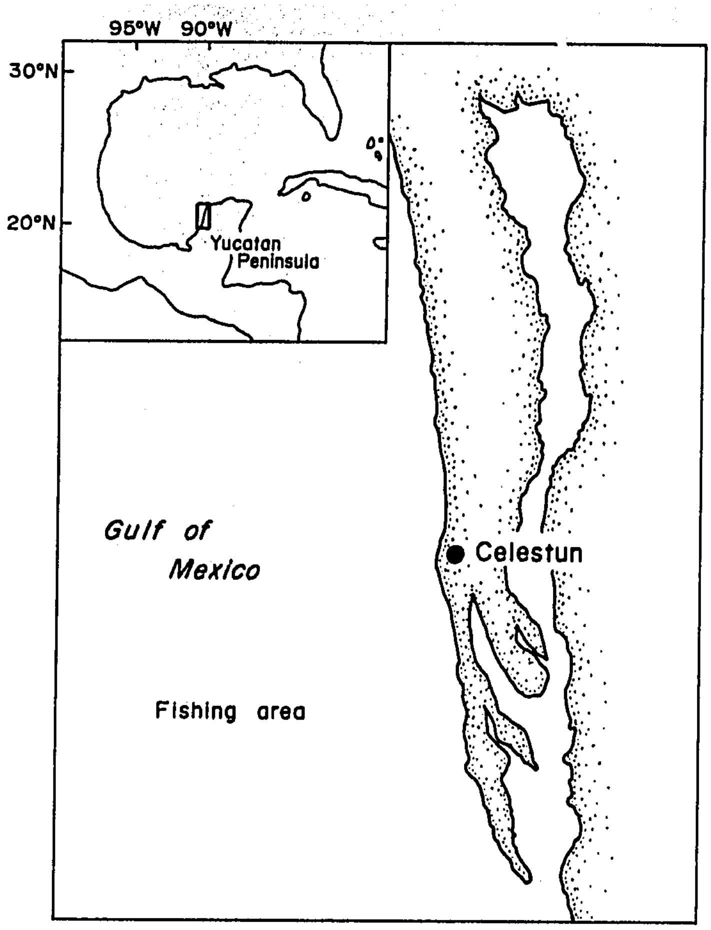

Fig. 1. Map showing the beach seine fishery area of the Campeche Bank, Mexico.

This paper attempts to describe and to improve the understanding of the trophic relationships and the structure of coastal community exploited by the beach seine fishery near Celestun, with emphasis on the commercially important species.

Methodology

Trophic structure is described through the application of the ECOPATH II model, under the assumption that the ecosystem is in steady state, and with population interactions described by deterministic, linear equations (Polovina and Ow 1983; Polovina 1984; Christensen and Pauly 1992a, 1992b).

The basic equation in the system is as follows:

$$B_i\cdot\left(\frac{P_i}{B_i}\right)\cdot EE_i-\left(\sum_{j=1}^{n}B_j\cdot\left(\frac{Q_j}{B_j}\right)\cdot DC_{ji}\right)-EX_i=0 \qquad ...1)$$

where B_i = biomass; P_i/B_i = production/biomass ratio; EE_i = ecotrophic efficiency; Q_j/B_j = consumption/biomass ratio; DC_{ji} = fraction of prey (i) in the average diet of predator (j); EX_i = export out of the system (including fishing) of group (i); (i) and (j) represent interacting species (or boxes), where (i) = prey and (j) = predator(s). The summation term denotes the total biomass consumed by predators (j) of the species (i).

Conversion from wet to dry weight was done using conversion factors of 30% for microcrustaceans, 20% for molluscs and fishes, and 13% for benthic producers.

Input data were obtained as follows: primary production from estimations by Herrera (1985, 1988) for phytoplankton. As there were no specific data for benthic primary producers, indices reported in Yañez-Arancibia and Day (1988) from adjacent regions were initially introduced in the model. Batllori et al. (1987) presented data on abundance of zooplankton, annelids, microcrustaceans and molluscs from an adjacent area. It seems however that these abundances were too high to be used in this area. Stomach contents of fishes were analyzed for the main fish species within the fishery during four years (1985-1989) by Vega and Hernandez (1987) and Vega (1990), and included the following species: pigfish, *Orthopristis chrysoptera*; pinfish, *Lagodon rhomboides*; herring, *Opisthonema oglinum* and *Harengula jaguana*; seabream, *Archosargus rhomboidalis*; catfish, *Arius felis* and *Arius melanopus*; mojarra, *Eucinostomus gula* and *Eucinostomus argenteus*; grunt, *Haemulon plumieri*; croaker, *Bairdiella chrysoura*; and cowfish, *Acanthostraceon quadricornis*. The catch data for exports (EX_i) were obtained from the Ministry of Fisheries (SEPESCA 1986); however, as mentioned by Arreguín-Sánchez et al. (1987), Arreguín-Sánchez (1989) and Chávez et al. (1992), catch composition of the beach seine fishery shows strong seasonal and annual changes (see Fig. 2). Because of this and the equilibrium assumption, it was necessary to average

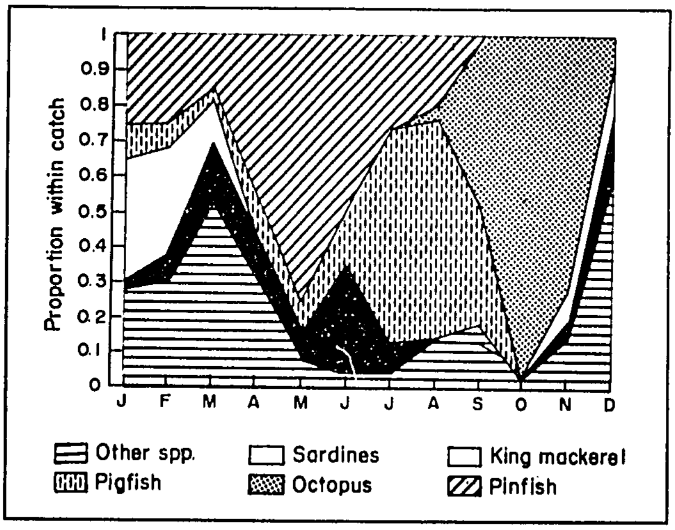

Fig. 2. Seasonal changes in catch composition in Celestun, Yucatán, Mexico.

the catch records taken during the period of 1982 and 1985. The values of P/B ratios (as instantaneous rate of total mortality) were taken from Chávez et al. (1992) for the same period.

The consumption/biomass (Q/B) ratios, as defined in Pauly (1986, 1989b), were obtained using the equation proposed by Palomares and Pauly (1989) as follows:

$$\ln Q/B = -0.178 - 0.202 \ln W_\infty + 0.612 \ln T + 0.516 \ln A + 1.26F \qquad ...2)$$

where: W_∞ = asymptotic or maximum weight; T = mean habitat temperature in °C; A = aspect ratio of the caudal fin calculated from drawings in Guitart (1977) and Fischer (1978); F = food type (0 in carnivores; 1 in herbivores and 0.5 in omnivores). The estimated Q/B values (% day^{-1}) were then converted to an annual basis.

With the above data, a predator-prey matrix was built and other inputs used in ECOPATH II were standardized to dry weight $g \cdot m^{-2} \cdot year^{-1}$. The ecotrophic efficiency was assumed to be 0.95 for all groups where data were missing. The gross efficiencies of four of the groups (6-9) where P/B and Q/B were known were around 0.12. This 0.12 was used as gross efficiency to estimate P/B for groups 11-15. For the smaller "other fish", the gross efficiency was assumed to be higher, 0.20. For unassimilated food, the default of 0.2 was used throughout.

Beach seine fishing takes place all along the coast of the Campeche Bank. As information for the whole area was lacking, it was necessary to design a sampling scheme representative of the area. This scheme, developed by Solana and Arreguín-Sánchez (1991), uses statistical methods which consider the population dynamics of the main species within the fishery.

Table 1. List of keys used as abbreviations for group names in the flow diagram and on other tables. Where estimates do not add up to 100%, other taxa are also included.

		%
1	Copepoda	
	Harpacticoid	2.50
	Calanoid	97.50
2	Worms	
	Polichaeta: Nereidae	95.60
	Oligochaeta	0.11
	Nematodes	4.26
3	Molluscs	
	Bivalvia	4.87
	Gastropoda	45.13
4	Microcrustaceans	
	Euphausiacea	0.08
	Sergestida	0.03
	Amphipoda	46.35
	Isopoda	9.42
	Tanaidacea	11.77
	Mysidacea	11.66
	Ostracoda	9.32
	Stomatopoda	0.03
	Cumacea	11.34
5	Decapoda	
	Penaeidae	40.38
	Brachyura	52.90
6	*Orthopristis chrysoptera*	
7	*Lagodon rhomboides*	
8	*Opisthonema oglinum*	
9	*Harengula jaguana*	
10	*Archosargus rhomboidalis*	
11	Catfish: *Arius felis, A. melanopus*	
12	Mojarra: *Eucinostomus gula, E. argenteus*	
13	*Haemulon plumieri*	
14	*Bairdiella chrysoura*	
15	Other fishes	
	Syngnathidae	0.95
	Engraulidae	18.95
	Anguillidae	6.14
	Synodontidae	2.93
	Sparidae	23.41
	Carangidae	0.22
16	Phytoplankton	
	Rhabdonema	50.00
	Striatella	50.00
17	Benthic producers	
	Seagrasses	25.59
	Benthic macrophytes	74.41
18	Detritus	

Results and Discussion

The main groups used in the trophic box model are summarized in Table 1. On the basis of the relative proportions within stomachs, the prey-predator matrix was constructed (Table 2). Input values for catch, biomass, P/B and Q/B ratios, and ecotrophic efficiency are shown in Table 3, along with estimated values. Specific inputs associated with estimations of Q/B ratios are given in Table 4.

When running the ECOPATH II, the balance of flows showed values of primary production that were too low; this was compensated with the importation of 150 $g \cdot dw \cdot m^{-2} \cdot year^{-1}$ of detritus, to make input match output. Although there is no specific information available, this value seems reasonable because the area under study is adjacent to a coastal lagoon known to export detritus (Celestun Lagoon, whose trophic structure is analyzed by Chávez et al., this vol.). The ecosystem associated with the beach seine fishery thus receives additional energy from the coastal lagoon, which thereby supports part of the ecosystem's production. Other groups contributing to the main sources of energy are those connected with the benthic environment, such as the microcrustaceans and annelids. A diagram with balanced flows and biomass is shown in Fig. 3.

Table 2. Predatory-prey matrix from the beach seine fishery. Group numbers are given in Table 1.

	Predator															
Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	-	-	0.20	-	-	-	-	0.04	-	-	-	0.07	-	-	-	0.15
2	-	-	-	0.20	0.10	0.11	0.06	-	0.17	0.01	0.39	0.09	0.32	0.05	0.13	0.04
3	-	-	-	-	0.35	0.11	0.28	0.01	0.01	0.24	0.03	0.02	0.06	0.08	0.31	0.30
4	-	0.05	-	-	0.10	0.57	0.29	0.52	0.37	0.21	0.12	0.61	0.31	0.25	0.04	0.15
5	-	-	-	-	-	0.01	0.06	0.00	0.06	0.01	0.09	0.16	0.20	0.14	0.01	0.15
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05	0.01
7	-	-	-	-	-	-	-	-	-	-	-	-	-	0.11	-	0.01
8	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	0.02
9	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	0.02
10	-	-	-	-	-	-	-	-	0.00	-	0.01	-	-	0.01	-	-
11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	0.07	0.10	0.11	0.36	-	0.12	0.04	0.08	0.35	0.06	-
13	0.95	-	0.35	0.30	-	-	0.02	-	-	-	-	-	-	-	-	-
14	0.05	0.15	0.25	-	-	0.01	0.15	0.22	0.02	0.52	0.01	0.01	0.02	-	0.33	-
15		0.80	0.20	0.50	0.45	0.13	0.04	0.10	0.01	0.01	0.20	-	-	0.02	0.12	0.15

Table 3. Input values (without brackets) and estimated parameters (in brackets) for the trophic model of an area of Campeche Bank close to Celestun, Mexico.

Group	Catches	Biomass	P/B	Q/B	EE	GE
Copepoda	0.00	(2.51)	18.62	93.10	0.95	0.20
Worms	0.00	(19.36)	2.75	13.75	0.95	0.20
Molluscs	0.00	(21.18)	1.72	8.60	0.95	0.20
Microcrustaceans	0.00	(10.31)	5.62	18.73	0.95	0.30
Decapoda	0.00	(3.71)	2.70	11.00	0.95	(0.25)
O. chrysoptera	1.70	(1.91)	1.20	9.80	0.95	(0.12)
L. rhomboides	0.41	(0.65)	1.60	12.70	0.95	(0.13)
O. oglinum	1.35	(1.52)	1.60	13.70	0.95	(0.12)
H. jaguana	0.17	(0.75)	1.57	13.30	0.95	(0.12)
A. rhomboidalis	0.14	(0.31)	0.48	11.70	0.95	(0.04)
Catfish	0.11	(0.10)	(1.16)	9.70	0.95	0.12
Mojarra	0.14	(0.07)	(2.62)	21.80	0.95	0.12
H. plumieri	0.40	(0.36)	(1.16)	9.70	0.95	0.12
B. chrysoura	0.10	(0.08)	(1.32)	11.00	0.95	0.12
A. quadricornis	0.10	(0.10)	(1.06)	3.80	0.95	0.12
Other fishes	0.20	(6.56)	(1.44)	7.20	0.95	0.20
Phytoplankton	-	(7.81)	46.42	0.00	0.95	-
Benthic producers	-	(8.90)	12.50	0.00	0.95	-
Detritus	-	12.40	-	-	(0.96)	-

Table 4. Summary of inputs associated with estimations of consumption/biomass (Q/B) ratio in predators. W_∞ is the asymptotic weight in g, while A is the aspect ratio of the caudal fin. The temperature is 26°C.

Species	W_∞	A	Q/B (year^{-1})
A. rhomboidalis	366	2.82	11.7
E. argenteus (mojarra)	29	3.46	221.6
E. gula (mojarra)	14	2.81	22.5
L. rhomboides	167	2.45	12.7
O. chrysoptera	249	1.75	9.8
A. felis (catfish)	343	1.92	9.7
C. spixii	434	1.92	9.2
H. jaguana	135	2.47	13.3
O. oglinum	158	2.77	13.7
B. chrysoura	178	1.90	11.0
A. quadricornis	296	1.50	8.8
H. plumieri	616	2.41	9.7

The system was aggregated into discrete trophic levels, *sensu* Lindeman using the appropriate ECOPATH II routine. It was observed that the throughput of the system consists of 50% of detritus/primary production, 41% of herbivores, 7% first-order carnivores, 1.1% of second-order carnivores and 0.1% of third-order carnivores (top predators).

The transfer efficiencies between trophic levels range from 18 to 12% (geometric mean 13.7%) with a tendency towards lower efficiency at the higher trophic levels (Table 5).

Interactions between components of the system can be evaluated using the mixed trophic impact routine of ECOPATH II (see Christensen and Pauly 1992a, 1992b; Ulanowicz 1990). Here, this routine, which is based on the Leontief matrix, is used to

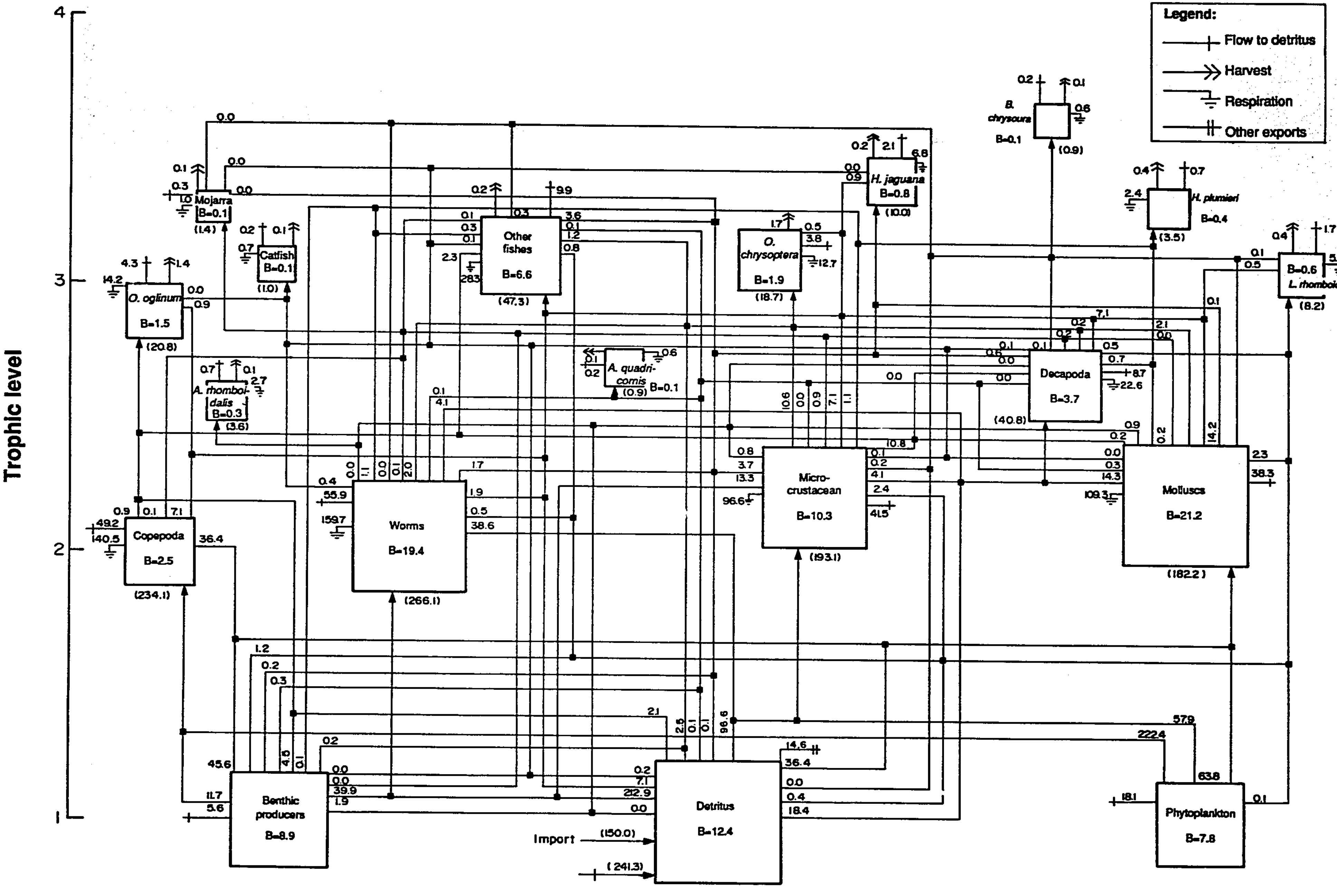

Fig. 3. Trophic interactions in an area of the Campeche Bank off Celestun. B gives biomass (g·dw·m^{-2}) and P, production (g·dw·m^{-2}·year^{-1}). For legend see Table 2.

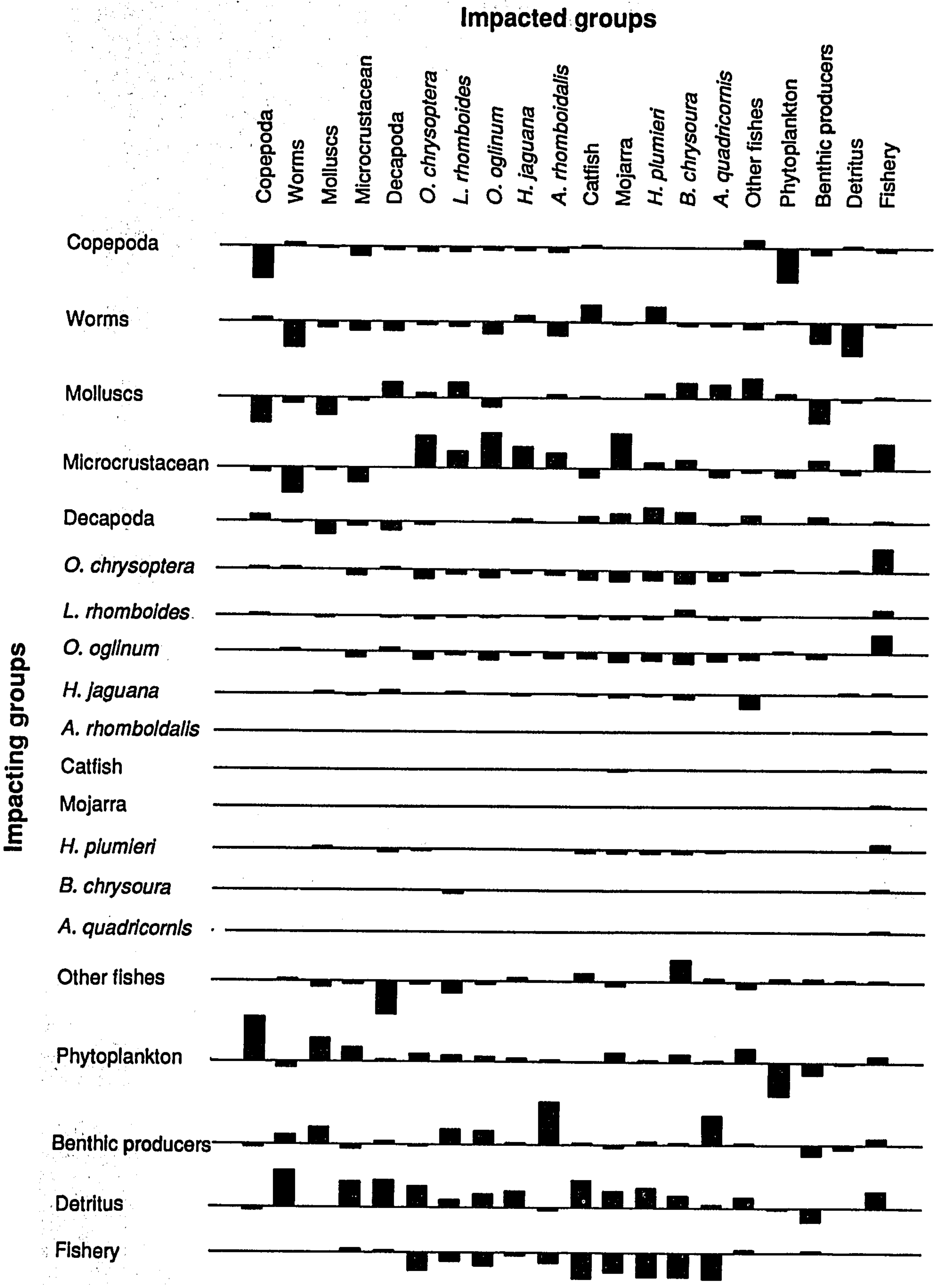

Fig. 4. Mixed trophic impacts in the system analyzed by the Leontief matrix. The figure shows positive (above line) and negative (below line) impacts.

Table 5. Trophic aggregation for all flows combined into discrete trophic levels *sensu* Lindeman (g·dw·m^{-2}·year^{-1}) and transfer efficiencies (%).

Trophic level	Import	Consumed by predators	Export	Flow to detritus	Respiration	Throughput	Transfer efficiency (%)
I	150	826.554	14.566	23.676	0.000	1,014.796	-
II	0	150.711	0.980	179.742	495.121	826.555	18.4
III	0	22.364	3.011	32.550	92.799	150.724	16.8
IV	0	2.287	0.743	4.777	14.549	22.356	13.6
V	0	0.200	0.078	0.487	1.521	2.286	12.2
VI	0	0.016	0.007	0.042	0.134	0.200	11.7
VII	0	0.001	0.001	0.003	0.011	0.016	12.3
VIII	0	0.000	0.000	0.000	0.001	0.001	12.0
Sum						2,016.935	
Amount extracted to break cycles						30.420	
Total throughput						2,047.355	

evaluate positive and negative impacts. Fig. 4 shows the impacts in the system. The groups that have a strong impact on the other components include detritus, benthic producers, phytoplankton, microcrustaceans, annelida and zooplankton. It can be seen that primary producers and detritus have a positive and very important impact on most other groups, for instance, on *Opisthonema oglinum.*

Conclusion

The fishery in this system acts as a predator occupying the highest trophic level of 4.06, with *Bairdiella chrysoura* (trophic level 3.65) as the next highest predator. Total throughput has a similar or higher level as for other marine ecosystems in the Gulf of Mexico such as the north continental shelf of Yucatan (Arreguín-Sánchez et al., this vol. [a]) and the nearshore community of the western Gulf of Mexico (Arreguín-Sánchez et al., this vol. [b]).

Although ecosystem statistics and flows of biomass could be considered as reasonable average values, some problems concerned with the input data must be taken into account. For example, the area considered was that covered by the beach seine fishery, not a system with natural boundaries. Some of the commercially important fish species undertake seasonal migrations associated with reproduction, and their aggregation close to the shore benefits the fishers. These features result in seasonal changes of the trophic structure of the ecosystem shown and the catch composition (Fig. 2). It is obvious that under these conditions, there are exchanges of energy within the whole ecosystem that the populations inhabit, which ought to be considered as imports and exports of the beach seine subsystem. Therefore it is necessary to obtain a clear understanding of the seasonal fluctuations. An additional point is that the P/B ratios used here may be biased because the methods used to estimate the instantaneous rates of mortality (Chávez et al. 1992) do not account for migrations.

Finally it is important to note that the results obtained so far only give a first crude approximation of the ecosystem structure. It is important to obtain better input data to improve the model.

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The Maputo Bay Ecosystem (Mozambique)

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Abstract

A preliminary trophic model is presented of the Maputo Bay ecosystem (Mozambique), based on information on the main fisheries in the area. The model was built using the ECOPATH II software system (ver. 2.1) so that input and output for all groups in the system are balanced.

The model estimates the sum of all production generated in Maputo Bay to 2,650 t·km^{-2}·year^{-1} for a total area of about 1,100 km^2; the annual yield of the fisheries sum to more than 7,000 t, accounting for about 1% of the total biological production of the system.

Introduction

Maputo Bay is located just outside the capital city of Mozambique. The bay's resources support a number of artisanal fisheries, as well as semi-industrial shrimp fishing. More than 5,000 t of fish and around 700 t of valuable penaeid shrimps are taken from Maputo Bay each year.

Several studies have been made on the biology and dynamics of the two main species of shrimp, *Penaeus indicus* and *Metapenaeus monoceros*, and of *Hilsa kelee*, the small pelagic fish that supports a traditional gillnet fishery. The ecology of the habitats around the island of Inhaca has also been object of several studies.

The present study is an attempt to combine much dispersed information into a description of this complex and important ecosystem.

The Study Area

Maputo Bay is situated between 25°51'S and 26°18'S (Fig. 1).

The total area of the bay (within the coastline, but excluding the estuaries) was measured to 1,100

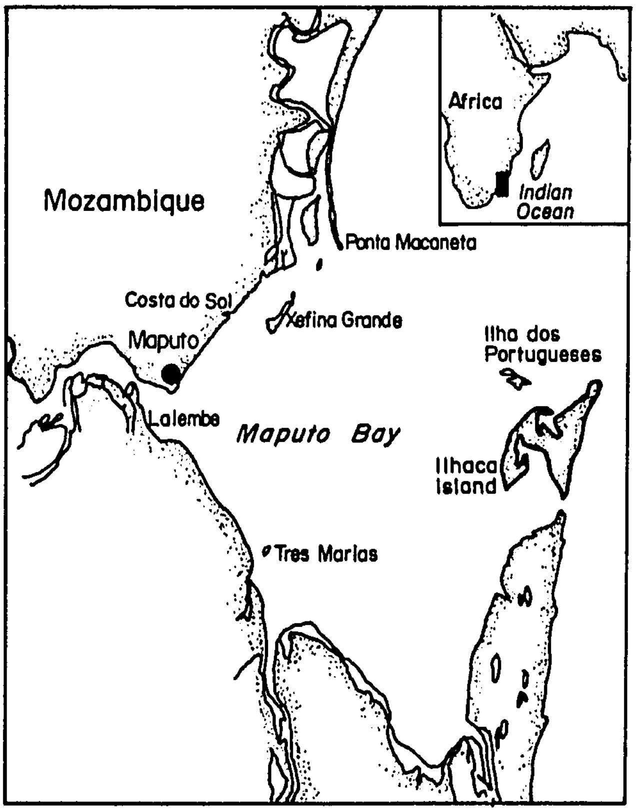

Fig. 1. Localization and main features of Maputo Bay, Mozambique.

km^2 using a digital planimeter on a hydrographic map with a scale of 1:250,000. The bay is shallow and the bottom is generally sandy though muddy at the mouths of rivers. The area covered by sandbanks is 285 km^2. The grounds deeper than 5 m total 381 km^2, and those deeper than 10 m, 171 km^2 (Ulltang 1980).

There are three main rivers opening into the bay: Nkomati on the north, Maputo on the southern bank, and Umbeluzi flowing through the Espírito Santo estuary, together with some smaller rivers or long mangrove channels (Tembe, Matola and Coque). The runoff of these rivers amounts to some 6 km^3·year^{-1} (Saetre and Jorge da Silva 1982).

The climate in Maputo is subtropical, with an average yearly temperature of 24.5°C, but with great amplitude (absolute extremes of 47.1°C and 0.2°C). Average humidity is 72-74% and rainfall is always below 900 mm·year^{-1} (Coelho 1972). Rainfall in Maputo in 1987 and 1988 was, respectively, 557 and 617 mm, while evaporation in the same years amounted to 1,076 and 1,181 according to data released by the Meteorological Institute.

The wind system is directly under the influence of the Indian Ocean southeast trade winds, with easterlies dominant throughout the year, but with significant variation (Saetre and Jorge da Silva 1982).

Inside the bay, between May 1969 and July 1970, the mean monthly sea surface temperatures at the Espírito Santo estuary and in the bay varied between 19.2°C and 28.0°C, with a maximum difference of 2°C (Coelho 1972). Temperature range on the shallow sand flats and inside the mangrove channels, however, is much wider. At the bottom near Costa do Sol it has been found to vary between 16.0°C and 32.4°C, with a mean of 23.3°C (de Freitas 1986).

Outside the bay, the surface salinity varies between 34.4 and 35.5 ppt (Saetre and Jorge da Silva 1982). Again, in the mangrove swamps, this parameter varies with rainfall and exposure, with values between 8 and 42 ppt (Macnae and Kalk 1969).

Water circulation inside the bay is not well known and seems to be a complex influenced by the tidal amplitude (more than 3.5 m in spring tides), the wind system and the bottom topography.

Ecological Characterization of Maputo Bay

Macnae and Kalk (1969) describe the different communities that can be found on the shores around the island of Inhaca. Dionísio et al. (1976) studied the pelagic food chain at the entrance of the Espírito Santo estuary. De Freitas (1986) produced a paper on the ecology of juvenile shrimps at Costa do Sol flats. A checklist of animals and plants living in the shores of the region is given by Day (1969). Concerning the commercial species of both vertebrates and invertebrates, one can refer to the guide by Fischer et al. (1990).

The Maputo Bay area includes numerous habitat types. Of these, the sheltered rocks, the loose stone and coral debris zone, the coral reefs, the sandy beaches and the tubiculous polychaete zone will not be dealt with here specifically due to their limited impact on the dynamics of the ecosystem. Instead the mangrove forest, the sand shoals, the shallow seagrass beds, the deep fine sand bars, the deeper muddy-sand grounds and the pelagic zone will be given a summarily treatment.

The mangrove forests of Inhaca can possibly be considered typical for the whole area. The whole bay has about 11,150 ha of mangrove swamps of which 270 ha are on Inhaca (de Freitas 1986). The total area of mangroves measured on the hydrographic map reaches 143 km^2.

The mangrove channels are known to be a major nursery area for the main commercial species of penaeid shrimps, *Penaeus indicus, P. monodon* and *Metapenaeus monoceros* (MacNae and Kalk 1969; de Freitas and Diniz 1972; de Freitas 1986).

Several species of fish inhabit the mangrove channels. Some are important food species caught in beach seines, belonging to the families Teraponidae and Ambassidae. Others are small fish characteristic of muddy areas, like Gobiidae or Periophthalmidae.

Molluscs are abundant on upper sand shoals in the area and are the basis of an important collection fishery on the west side of the bay.

Bandeira (1991) states that on the western shores of Inhaca and between this and Ilha dos Portugueses 52% of the intertidal region is covered by seagrasses. If we assume that all intertidal banks in Maputo Bay feature identical coverage, we estimate a total area covered with seagrasses of some 140 km^2.

On the productivity of the system, Bandeira (1991) cites various authors who reported values between 2.5 and 54.8 kg·m^{-2}·year^{-1}. Raising these values to the total area indicates a contribution to the primary production from the seagrass beds of 320 to 7,000 t·km^{-2}·year^{-1}.

The lowest section of the intertidal seagrass beds, where the water table is never below the surface, is richest in species (almost entirely tropical) and probably also in biomass. It is rich in echinoderms, some of which with commercial interest.

It is well known that many fish breed, seek shelter or forage in seagrass beds. This is therefore a most important area for fishing. At Inhaca, the fishers (see Wynter 1990) use these grounds extensively to harvest, besides the invertebrates mentioned above, many fish species characteristic of the neighboring reefs. These include labrids, lethrinids, mullids, muraenids, scarids, serranids and teraponids, but also fish typical from open coastal waters, including sparids, clupeids, scads, and even some of more oceanic character, like the Indian mackerel, *Rastrelliger kanagurta* and the kingfish, *Caranx* spp.

In some areas, the tidal channel is separated from the intertidal flats by a shallower stretch of clean fine sand, lacking the reduced layer. The commonest animal on Inhaca's sand bars is the sea star *Astropecten granulatus*. Sand dollars, *Echinodiscus auritus* and *E. biperforatus*, are also abundant.

The area of the bay deeper than 5 m (381 km^2) features muddy sand and represents the main fishing ground for the shrimp trawlers.

Monteiro (1975) studied the food composition of five species of carnivorous fish of importance in the shrimp fishery. Dionísio et al. (1976) analyzed the stomach contents of other species and found that the pelagic species, *Thryssa vitrirostris, T. setirostris* and *Megalaspis cordyla*, as well as the demersal *Terapon jarbua* also eat shrimp. They did not provide figures allowing quantification, however.

The pelagic fishery (with gillnets) is responsible for the higher proportion of the total catches. The main species is *Hilsa kelee*, an Indo-Pacific estuarine clupeoid. Many studies have been made of this fishery (Monteiro 1974; Sousa 1982; Gjφsaeter and Sousa 1983, 1986). Other studies on the ecology of the pelagic zone are also available.

Silva (1956, 1960) authored the first known studies of plankton from Mozambique. More recently three quantitative studies were done by biology students (Antunes et al. 1975; Dionísio et al. 1976; Gove and Cuamba 1989).

Gove and Cuamba (1989) give mean figures of net plankton abundance of 4.8 and 2.7 ml·m^{-3} for two stations near Inhaca; also from this area, Antunes et al. (1975) give numbers for Inhaca of more than 60,000 diatoms, around 2,000 dinoflagellates, 192 crustaceans and 209 other zooplankton forms per liter of seawater. Dionísio et al. (1976) record counts between 37,000 and 127,000 diatoms, 30-3,090 dinoflagellates, 20-190 crustaceans and 113-1,003 planktonic eggs per liter of seawater from the estuary, between September 1975 and February 1976.

The main known consumers of the plankton in Maputo Bay are *Hilsa kelee* and *Liza macrolepis* (also taken with gillnets inside the estuaries, but for which no further studies appear to have been conducted). *Pellona ditchela*, a pelagic component of shrimp by-catch is also feeding on plankton (Dionísio et al. 1976).

Fisheries

The main fisheries in Maputo Bay are gillnet fishery for Kelee shad, *Hilsa kelee*, and shrimp trawling. These fisheries have been described and studied over the years (de Freitas and Araújo 1974; Monteiro 1974; Ulltang 1980; Gjφsaeter and Sousa 1983, 1986; Sousa 1982, 1985, 1987).

Although there have been some changes in the distribution of fishing effort during the last ten years, the catches have been relatively stable; the Kelee shad yielding about 3,000 t and the shrimp fisheries responsible for an average of 700 t of penaeid shrimps and some 2,000 t of fish (Gjφsaeter and Sousa 1986).

Other commercial fishing activities in Maputo Bay include the reef fisheries around Inhaca Island, that yield some 200 t·year^{-1}; clam collection from the muddy sandbanks (a maximum of 250 t recorded for 1965 by Araújo 1973); and crab fishing in the mangroves. Gjφsaeter and Sousa (1986) give a figure of 500 t for artisanal line fishing inside Maputo Bay.

Artisanal Gillnet Fishery

The Kelee shad, *Hilsa kelee*, is a small pelagic fish inhabiting coastal and estuarine waters at depths less than 20 m. It contributes to an important gillnet fishery at Maputo Bay and also in other bays and estuaries along the Mozambican coast (Gislason and Sousa 1985).

The fishery in Maputo Bay is conducted throughout the year but the best fishing season lasts from April to August.

The catch and effort of the semi-industrial fleet for the period 1972-1985 is given by Gjφsaeter and Sousa. The catches were at a stable level around 1,000 t·year^{-1} until 1982, after which they decreased sharply. Effort was fairly stable until 1984 and then declined drastically.

Catch and effort statistics for 1985 and 1986 of the artisanal fishery and of the semi-industrial fishery for 1986 are given by Sanders et al. (1988). The artisanal catches were then found to be 3,700-3,000 t, whereas the semi-industrial catches declined to 43 t.

The reproduction, age and growth of *Hilsa kelee* are described in Gjφsaeter and Sousa (1983).

Spawning takes place in the wet season, from October to January, with a peak in December. A small increase in percentage of spawning females is also evident in June. The size at first maturity is around 14-15 cm.

The age was determined by counting daily growth rings in otoliths. Further studies on age were presented by Sousa and Gjφsaeter (1987).

The growth of *Hilsa kelee* was estimated by Sousa and Gjϕsaeter (1987).

No data on natural mortality are available and a tentative value was thus provided using the empirical formula of Pauly (1980). Gjϕsaeter and Sousa (1986) applied the Schaefer model to data from the semi-industrial fishery (Schaefer 1954) and estimated maximum sustainable yield for the semi-industrial fishery of about 1,000 t·year^{-1}.

Based on the assumption that there is the same ratio between the increase in effort of the semi-industrial gillnetters and the artisanals for each year and similarly for the catches, the total maximum sustainable yield for *Hilsa kelee* in Maputo Bay will be around 3,400 t.

This indicates that the present fishing effort is too high and should be reduced. A preliminary assessment of yield per recruit was done. The results suggested that the introduction of a new mesh size could increase the yield by increasing the recruitment.

As a result of the recommendations new gillnets began to be produced in a national netmaking factory and an increase in mesh size from 2 to 2-1/4 inches was observed (Sousa 1988). At the same time no new fishing licenses were allowed for the gillnet fishery in Maputo Bay.

Shrimp Fisheries

In Maputo Bay, shrimps are exploited by artisanal beach seines and by a semi-industrial fleet of about twenty small stern trawlers (de Freitas and Araújo 1974; Ulltang 1980; Gjϕsaeter and Sousa 1986).

The estimates of shrimp catches by the semi-industrial fishery are based on logbooks. The catches by the artisanal fisheries from 1984 onwards (as well as those for the semi-industrial, for 1989) were estimated on the bases of actual sampling of catch per boat and by counting the number of boats (Sousa 1985, 1987).

The main species of shrimp caught are *Penaeus indicus* (55-65% of the total shrimp catch), *Metapenaeus monoceros* (25-45%) and *Penaeus semisulcatus* (8-10%), while *Penaeus japonicus, P. monodon* and *Metapenaeus stebbingi* are caught in small proportions (de Freitas and Diniz 1972; Ulltang 1980). Population studies of the two main species of shrimp in Maputo Bay showed total mortalities in the range of 3.0 to 7.2 year^{-1} with an average of 5.3 year^{-1}.

It is difficult to assess the abundance of shrimp in Maputo Bay, due to their extended distribution and the existence of different fisheries. Ulltang (1980) calculated biomass for a mean year, 1977-1978, using the swept area method and the catch rates of the semi-industrial trawlers; two values are given, considering all the area below 5 m, and those below 10 m of water, respectively, 141 and 63 t.

The catches of fish in the artisanal and semi-industrial fisheries can be derived from data in Sousa (1987).

The species composition of the by-catch of the semi-industrial shrimp trawlers is summarized by Gjϕsaeter and Sousa (1986) and Sousa (1990).

Population parameters of some pelagic species were taken from Gislason and Sousa (1985), Gjϕsaeter and Sousa (1986) and (Sousa 1990) and supplemented by estimates of M calculated using the empirical formula of Pauly (1980) or applying the mean length model (Beverton and Holt 1956) to data in Sousa (1990), to obtain estimates of total mortality, Z (Table 1). The table shows discrepancies as total mortalities are lower than natural mortalities for two species. This shows that there are problems using generalized formulas to obtain point estimates. There is bound to be a high variance on all estimates derived this way.

Concerning demersal species, Gislason (1985) published growth parameter estimates of two sciaenids from Maputo Bay. Using his estimates and the methods referred to in the previous paragraph, estimates of mortality can be presented (Table 1). As for the pelagics, there are inconsistencies (Z < M). It can be assumed that this is due to the same problem as discussed above.

Other Artisanal Fisheries

Unfortunately there are no studies of the biology of the species caught by the smaller artisanal fisheries in Maputo Bay, which include setnet and fish weirs, beach seining off Inhaca, line fishing and collection of crabs, echinoderms and molluscs along the shore.

As mentioned, the fish species caught at Inhaca include typical estuarine, muddy bottom fishes, coral

Table 1. Growth and mortality parameters of the main species of small pelagic and demersal fish species in Maputo Bay. Note inconsistencies where M>Z.

Species	L_∞ (TL; cm)	K (year^{-1})	M (year^{-1})	Z (year^{-1})
Hilsa kelee[a]	21.5	1.10	1.98	2.04
Pellona ditchela[a]	22.8	0.96	1.78	1.98
Thryssa vitrirostris[a]	25.6	0.6	1.27	0.64
Leiognathus equulus[a]	23.0	0.8	1.58	0.75
Otolithes ruber[b]	42.9	0.14	0.42	0.74
Johnius dussumieri[b]	29.8	0.16	0.51	0.37

[a] Pelagic
[b] Demersal

reef species and even oceanic species (Smith 1969). A recent record of fish trade indicates an annual yield of the order of some 250 t, taken with beach seines, setnets and handlines (IDPPE 1989).

Fish catches with beach seine at Inhaca were studied by Macnae and Kalk (1969) and Caixeiro (1972). From one observation from 1969, they include some 20% of teraponids; 17% of the goldlined seabream, *Rhabdosargus sarba*; 16% of Indian mackerel, *Rastrelliger kanagurta*; 16% of shrimp scad, *Alepes djedaba*; and 7% of bonefish, *Albula vulpes*. Setnets, also at Inhaca, get many reef species (lethrinids, scarids, muraenids) as well as the species species caught with beach seines.

Gathering of crabs, echinoderms and molluscs is an activity performed mainly by women (Wynter 1990) and includes the subsistence activity that provides the main protein income to the families living near the shore. According to Oliveira (1972) and Wynter (1990), there is a number of molluscs that are caught mainly for household consumption, like the snails, *Polynices mamilla* and *Murex ramosus*, the ark shells, or the sea urchins at Inhaca.

Other species are normally marketed, like the mangrove crab, *Scylla serrata*; the clams, *Meretrix* and *Eumarcia paupercula*; the sand mussel, *Modiolus philippinarum*. Concerning the crab, there are no records of catches or sales. Piatek (1981) presents an estimate of catches for the whole country of 1,000 t and a potential of 5,700 t, based on a figure of 3.4 kg·km^{-2}·year^{-1}, calculated for South Africa. If we consider that this potential is presently tapped in the mangroves around Maputo and Inhaca (about 100 km^{2}), we end up with a figure of 340 t, of the same order of magnitude as known for clams, therefore considered acceptable.

For the molluscs, Araújo (1973) mentions a maximum of 250 t produced at Maputo in 1965; recent sales records (IDPPE 1989) show that 86 producers delivered 69 t of clams only in the area of Ponta Macaneta. Considering that this area corresponds roughly to one-third of the nearshore muddy sandbanks of Maputo Bay, and considering the household consumption of these products, an estimate of 250 t·year^{-1} is probably the minimum catch from these resources.

The sea cucumbers, *Holothuria scabra* and *H. atra*, are an important export product; Montecino (1988) reports a total of 4,666 kg of dried product sold by two Inhaca cooperatives to a state company between 1985 and 1988. This may roughly correspond to one-half of the local production; considering a processing coefficient of 1:15 (Costa and Montecino 1990), an estimate of 141 t of live sea cucumbers collected at Inhaca per year can be proposed.

Gjøsaeter and Sousa (1986) give an estimate of 500 t for the annual catch by handlines in Maputo Bay. Although there are no studies of this fishery, it is known that the catch primarily consists of demersal fish, of the same species that are caught by the shrimp fisheries (*Otolithes ruber*, *Pomadasys kaakan* and other haemulids, serranids, ariids, etc.).

Modelling the Maputo Bay Ecosystem

Even though the Maputo Bay area has been studied intensively only rather limited information exists of energy flows and productivity within the system. Our model is therefore rather coarse and is not intended to give an authoritative description of the system; it should be seen more as a first attempt, to inspire future work. It is certainly found important to get an overview of the resources in the bay and of their internal trophic relations in order to improve the management of the fisheries and to direct fisheries research.

The software system ECOPATH II, version. 2.1 (Christensen and Pauly 1992) was used as the main tool for this attempt of estimating the biological flows in Maputo Bay. The rationale of the method and the main studies that led to the modelling tool are described by Christensen and Pauly (this vol).

The groups of species selected for this study (Table 2) reflect the existing knowledge of the ecology of the area. The model includes ten groups of which four are fish groups, three invertebrates, two primary producers, and the remaining detritus. The composition of the fish groups is presented in Table 3.

The groups differ much in abundance; the "sharks and rays" groups being quite small but considered of importance as the apex predators. It should be added that another group of predators has been omitted, the birds. Large flocks of flamingos, *Phoenicopterus ruber*, can be seen in protected areas south of Inhaca and inside the estuary, and sea gulls, terns and pelicans are also present. It is not possible at present to include these groups in the model due to lack of knowledge of their consumption and food preferences. It is judged however that the

Table 2. Data used as input to calculate the trophic relationships in Maputo Bay fisheries (catches, in t·km^{-2}·year^{-1}; P/B and Q/B in year^{-1} units).

Group	Catches	P/B	Q/B	EE
Sharks and rays	0.01	0.2	3.1	0.65
Jacks and scombrids	0.15	1.5	12.0	0.75
Small pelagic fish	4.10	2.0	40.7	0.85
Demersal fishes	1.45	0.7	7.1	0.80
Crabs, clams, shrimps	1.34	5.5	20.0	0.80
Heterotrophic benthos	-	6.0	30.0	0.85
Zooplankton	-	40.0	280.0	0.85
Benthic producers	-	12.5	-	0.50
Phytoplankton	-	70.0	-	0.90

Table 3. Species composition of the main fish groups defined for the ECOPATH II box model of the Maputo Bay ecosystem.

Demersal fish	Weight (%)	Small pelagic fish	Weight (%)
Ariidae	0.35	Ariommidae	0.03
Bothidae	1.03	Clupeidae	91.18*
Cynoglossidae	6.71	Engraulididae	2.45
Chirocentridae	0.97	Leiognathidae	6.10
Drepanidae	0.39	Sphyraenidae	0.24
Ephippidae	0.86		
Gerreidae	4.00	Scombridae	
Haemulidae	11.48*	Carangidae	73.0*
Lutjanidae	0.21	Scombridae	27.0*
Mugilidae	0.92		
Mullidae	3.93	Sharks and rays	
Muraenesocidae	0.37	Carcharhinidae	-
Platycephalidae	2.17	Dasyatidae	-
Polynemidae	0.17	Galeorhinidae	-
Psettodidae	1.34	Rajidae	-
Sciaenidae	39.67*	Rhinobatidae	-
Serranidae	0.16	Torpedinidae	-
Sillaginidae	6.54		
Soleidae	0.04		
Sparidae	0.07		
Synodontidae	0.90		
Teraponidae	7.65		
Trichiuridae	3.34		
Others (commercial)	0.09		
Noncommercial	5.23		

*Main species

Carangidae - *Alepes djedaba*
Clupeidae - *Hilsa kelee*
Scombridae - *Rastrelliger kanagurta*
Haemulidae - *Pomadasys maculatus*
Sciaenidae - *Otolithes ruber*
Johnius dussumieri
Johniops sina

impact of the birds is likely to be quite limited compared to the fish predators and the fishery, and that it is therefore acceptable to exclude them from this first modelling attempt.

The group including jacks and scombrids represents the oceanic fish that periodically enter the bay, but whose main source of food is likely to be outside the bay. The group takes part of its food as "import" to reflect that it also feeds outside the bay.

Apart from the fish groups, the exploited benthic animals are all assumed to use the same energy sources - benthic producers, mainly seagrass, the small infauna and detritus. The available knowledge of these groups is rather incomplete, and it has therefore been necessary to make a number of assumptions to construct the model. These are described below.

Estimated production/biomass ratios (P/B) corresponding to the mean values of the instantaneous rates of total mortality, Z, were used for the group representing species for which mortality estimates were available from the area (Table 1). For plankton and benthos, estimates of P/B ratios were adopted from Polovina (1984) and Silvestre et al. (this vol).

Consumption/biomass ratios (Q/B) have not been estimated from experiments in the area. Instead approximated values were derived for a number of the important fish species using the empirical relationship given by Palomares and Pauly (1989). Based on information on asymptotic size, aspect ratio of the tail (indicator of activity) and food type, estimates of Q/B can be derived, which in Palomares and Pauly's study were able to explain nearly 75% of the variance of the data set they used. The Q/B ratios for a number of Maputo Bay fish species are given in Table 4. For groups where estimates for more than one species were available, the group Q/B was taken as an arithmetic mean of the individual estimates. It might have been better to average based on weighted consumption by groups; however, the individual values were in all cases, very similar, and information on relative consumption was lacking.

The information on primary productivity is very incomplete. As mentioned, productivity estimates exist for the important seagrass component ranging from 320 to 7,000 $t \cdot km^{-2} \cdot year^{-1}$, while the estimates for phytoplankton are too sparse and perhaps too unreliable to be of use. Instead the primary productivity is estimated from what is necessary to balance the herbivore consumption in the system. This is done assuming that the ecotrophic efficiency (EE), i.e., the part of the production that is used for catches and for predation, is 0.50 for the benthic producers, so that half of the production is used directly, while the rest is used only after it has

Table 4. Calculation of Q/B for selected species from Maputo Bay.

Species	Group	L_∞ (cm)	W_∞ (g)	A (h^2s^{-1})	F	Q/B[a]
Carcharhinus melanopterus	Sharks and rays	180[c]	50,000[e]	1.641	0	3.1
Euthynnus affinis	Scombridae	75[c]	9,000[c]	9.506	0	11.0
Rastrelliger kanagurta	Scombridae	30[b]	300[b]	3.925	0	13.9
Hilsa kelee	Small pelagics	25[b]	160[b]	2.090	1	40.1
Pellona ditchela	Small pelagics	23[b]	85[b]	1.719	1	41.2
Otolithes ruber	Demersal fish	43[d]	800[c]	1.229	0	6.2
Pomadasys kaakan	Demersal fish	80[c]	5,000[c]	4.089	0	8.0

Parameters: A - Caudal aspect ratio; F - Food type (carnivorous = 0; herbivorous/detritivorous = 1)

Sources and formulae:

[a] $\log Q/B = -0.1775 - 0.2018\log W_\infty + 0.6121\log T + 0.5156\log A + 1.26F$ (Palomares and Pauly 1989)

[b] L_∞ and W/L relationship from Gislason and Sousa (1985)

[c] W/L relationship (in graph) from van der Elst (1981)

[d] L_∞ from Gislason (1985)

[e] W_∞ adapted from other species in van der Elst (1981)

passed through detrital breakdown processes. For the phytoplankton, the EE is assumed to be 0.90 to reflect that this group is heavily fed upon.

Using these values of EE results in a total primary production estimate of 2,359 t·km^{-2}·year^{-1}, i.e., within the range for the seagrass production. This is probably the best that can be derived with the present sparse dataset; assuming a lower EE for the benthic producers would lead to a higher primary production estimate, while a higher EE would lead to a lower primary production estimate. There is, however, no way of knowing the better way to move before measurements are available.

The food composition of the main consumer groups from Maputo Bay was estimated from the available local studies, as introduced earlier. The estimates are not very accurate, and the derived diet composition (Table 5) should therefore be considered very preliminary. It is however in line with the specific knowledge from the system and the general knowledge from elsewhere.

Biomass data from the area are very sparse. Therefore all biomasses are calculated from catches and assumed ecotrophic efficiencies. An input value of 0.85 was originally adopted for all consumer groups, assuming that 85% of the production of these groups would either be caught or predated upon. The EEs were however subsequently changed in a series of ECOPATH II runs in order to obtain values of natural and fishing mortality that resemble those estimated in Table 1.

The derived biomasses seem rather high when compared with biomass and catch levels in other Mozambican stocks but it is not clear if this reflects actual conditions or the way the model was balanced. Again, use of higher EE values would have led to different biomass estimates. If EE was assumed to be 0.95 for all fish stocks, the total biomass of these stocks would be estimated as 12.7 t·km^{-2} as compared to 19.7 t·km^{-2} with the present EEs.

Some of the results from the model of Maputo Bay are summarized in Table 6. In addition, Fig. 2 gives a representation of the trophic interactions in the area. It appears that the main flows among the consumers are among the heterotrophic benthos, the zooplankton and the small pelagics, while the

Table 5. Assumed diet composition of the groups selected for modelling the Maputo Bay. Group 8 is benthic producers, 9 is phytoplankton, 10 is detritus, and 11 is import from outside the bay.

Consumer	Prey										
	1	2	3	4	5	6	7	8	9	10	11
1. Sharks and rays	0.01	0.20	0.600	0.10	-	-	0.010	-	-	-	0.08
2. Jacks and scombrids	-	0.01	0.650	0.02	-	-	0.150	-	0.020	-	0.15
3. Small pelagic fish	-	-	0.013	-	-	-	0.123	-	0.864	-	-
4. Demersal fishes	-	-	0.150	0.05	0.48	0.150	0.010	0.15	-	0.010	-
5. Crabs, clams, shrimps	-	-	-	-	0.02	0.750	0.020	0.15	0.010	0.050	-
6. Heterotrophic benthos	-	-	-	-	-	0.015	-	0.85	-	0.135	-
7. Zooplankton	-	-	-	-	-	-	0.015	-	0.985	-	-

Table 6. Summary of selected outputs obtained with ECOPATH II for the Maputo Bay ecosystem.

Group	Biomass (t·km^{-2})	F (year^{-1})	M (year^{-1})	Trophic level
Sharks and rays	0.1	0.10	0.10	3.5
Jacks and scombrids	0.2	0.71	0.80	3.1
Small pelagic fish	11.9	0.35	1.65	2.1
Demersal fishes	7.5	0.19	0.51	3.3
Crabs, clams, shrimps	6.7	0.20	5.30	2.8
Heterotrophic benthos	23.3	-	-	2.0
Zooplankton	2.1	-	-	2.0
Benthic producers	99.7	-	-	1.0
Phytoplankton	15.9	-	-	1.0

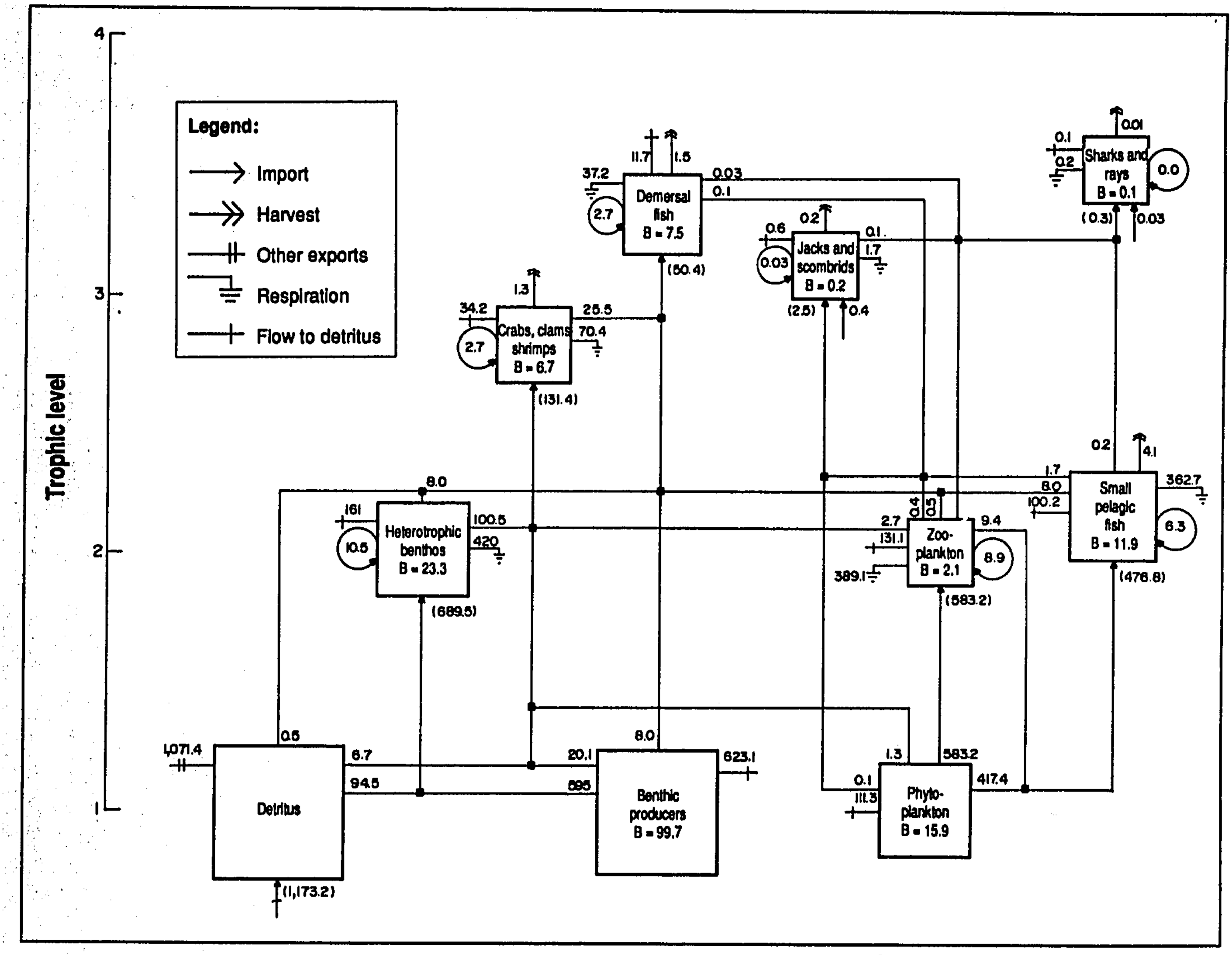

Fig. 2. Box model of the Maputo Bay ecosystem [annual production (P) and mean biomass (B) in t·km^{-2}]; production flows in t·km^{-2}·year^{-1} (wet weight).

other fish groups only play a minor role trophically. For instance, the food intake of the shark and ray group is less than 1 thousandth of what is taken by the small pelagics. The fishery is found to operate on a trophic level of 3.5, which is very similar to that occupied by the top predators. This is a good part of the explanation for the high catch levels from the area; were the fishery concentrated on higher trophic levels, its catches would be much lower.

It is estimated from the model that there is a net export of 1,071 t detritus km^{-2}·year^{-1}. This estimate is however not very certain. It is estimated as the difference between all flows into and out of the detritus box and is strongly influenced by the assumed parameters for assimilation rate. We have here adopted the ECOPATH default of 20% of the food not being assimilated for all consumer groups. This estimate is generally considered quite appropriate for fish groups but it may be an underestimate for certain other groups, especially for zooplankton. This may be seen from the estimated respiration/biomass ratio of 184 for zooplankton which is quite high. Had 40% been used for unassimilated food for zooplankton, this would have resulted in a respiration/biomass ratio of 128, a more reasonable though still high value. At the same time this would have increased the estimate of export of detritus to 1,190 $t{\cdot}km^{-2}{\cdot}year^{-1}$.

The estimate of net export of detritus is also strongly influenced by the exclusion of bacterial processes from the model. Had bacterial processes been included, it would have reduced the estimate for export of detritus due to bacterial respiration. Still there would have been a net export of detritus which is in line with what is assumed to occur from the area.

Due to the sparsity of data, the present model of the Maputo Bay ecosystem should be considered as tentative. We do, however, find it important that it has been possible to derive a balanced model of the trophic flows in the system from the sparse information we have available. A major result from this exercise is that we now have an overall view of the system which will enable us to focus future research activities on areas of importance for improving our understanding of how the system functions.

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A Trophic Model of a Mediterranean Lagoon, Etang de Thau, France

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Abstract

An attempt was made to model a littoral lagoon in the French Mediterranean, the Etang de Thau. The model was structured around commercially important fish groups with a top predator (i.e., *Anguilla anguilla*) biomass evaluated at 11.0 t·km^{-2}. Reasonable estimates of biomasses for the other fish species/groups were obtained. The flows in the system are dominated by the zooplankton and benthic producers.

Introduction

The Etang de Thau (Fig. 1) is a relatively deep (mean = 5 m, maximum = 10 m) littoral lagoon situated in the Mediterranean and bordered by the towns of Sète, Mèze and Marseillan, France. It covers an area of 88 km^2 and measures 19.5 km·4.5 km (Audouin 1962). Seawater exchange occurs in a diurnal cycle at $7\cdot10^5$ to $35\cdot10^6$ m^3·day^{-1}. Mean annual water temperature is 15.3°C and mean salinity is 37.6 ppt (Bach 1985).

Thau is a relatively well investigated area. Recent ecological studies initiated in the lagoon were centered around the idea of a statistical modelling scheme using path analysis that would

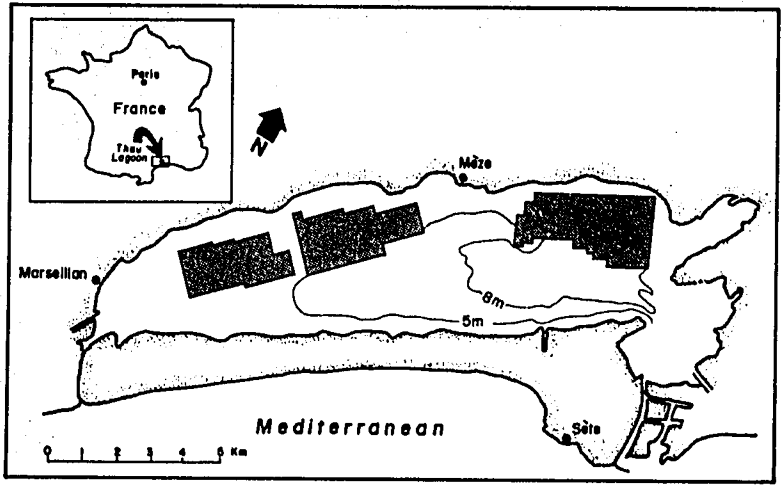

Fig. 1. Map showing the Thau Lagoon region. Areas in boxes indicate zones of oyster culture. Inset shows the lagoon area in France (adapted from Outin et al. 1988).

lead to a knowledge of how the lagoon functions (Amanieu et al. 1989). These studies, however, have just begun and their results are still unavailable.

It was possible, though, to extract enough information from the published literature and use it in the context of ECOPATH II to obtain a preliminary trophic model of the lagoon. Following is a brief description of how this information was standardized and assembled for use in the model.

Materials and Methods

ECOPATH II uses a balanced equation of the form:

$$B_i \cdot \frac{P_i}{B_i} \cdot EE_i = \sum_{j=1}^{n} B_j \cdot \frac{Q_j}{B_j} \cdot DC_{ji} + EX_i$$

where B_i is the average biomass of group i, P_i/B_i its production/biomass ratio, EE_i its ecotrophic efficiency (see Christensen and Pauly 1992). The summation gives the total predation mortality, here Q_j/B_j is the consumption/biomass ratio for predator j while DC_{ji} gives the proportion prey i contributes to the diet of predator j, EX_i is the total export (catches) of group i. This model is discussed in more detail by Christensen and Pauly (1992 and this vol.) to which we refer for details.

Table 1 lists the input parameters used for the model of the lagoon for the 1980s. Note that the parameter values (e.g., P/B, EE and Q/B) were averaged to represent annual means for each species group. Missing values indicate either that no information was available in the literature or that literature data could not be used because they could not be standardized. The missing parameters were later estimated by ECOPATH II. Values of P/B for fish groups were

Table 1. Inputs used in ECOPATH II for the Thau Lagoon system for the 1980s. Estimated parameters are given in brackets.

Species considered	Groups	Catch ($t \cdot km^{-2}$)	Biomass ($t \cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	GE (P/Q)
Anguilla anguilla	Eels	7.80	(11.0)	0.8	4.0[a]	0.94	0.20
Dicentrarchus labrax	Adult predators						
Sparus aurata		1.20	(6.1)	1.0	4.9	0.90	0.21
Solea vulgaris							
Mugilidae	Adult mugilids	0.18	(9.2)	1.0	5.0	0.90	0.20
Dicentrarchus labrax	Young predators	0.32	(11.5)	3.0	8.0	0.90	0.38
Sparus aurata							
Solea vulgaris							
Atherinidae	Silversides	0.20	(9.1)	1.6	11.6	0.90	0.14
	Molluscs	267	(477.0)	0.7[a]	5.0[a]	(0.80)	0.14
	Benthos	1.00	(13.1)	4.0[b]	36.0[b]	0.90	0.11
	Zooplankton	-	267.0	20.0[c]	60.0[a]	(0.98)	0.33
	Phytoplankton	-	15.0	40.0[c]	-	(0.88)	-
	Benthic producers	-	1,071.0	8.4[d]	-	(0.01)	-
	Detritus	-	5,000.0	-	-	(0.82)	-

[a] Q/B estimated from (P/B)/GE.
[b] P/B and Q/B general values from J. Moreau (pers. comm.).
[c] Polovina (1984).
[d] Aliño et al. (this vol.).

estimated, in the absence of other data, from longevity (t_{max}, in years), using Hoenig's (1983) empirical equation

$$\ln Z = 1.44 - 0.984 \ln t_{max}$$

since P/B is assumed to be equivalent to Z. Pauly's (1989) empirical formula for food consumption was used, for fish groups, to obtain estimates of Q/B. Most ecotrophic efficiency (EE) values were assumed, whereas gross efficiency (GE) values were either assumed as for zooplankton (0.3) or obtained from (P/B)/(Q/B). Note also that Q/B estimates for the "adult" and "young" categories were obtained by setting body weight to W_∞ and W_1 (at age 1 year), respectively.

Top Predator Group

Eels, *Anguilla anguilla*, were considered as top predators in the Thau Lagoon model. Recent reports by Quignard (1984) indicated eel catch in the lagoon at 60% of the total catch. In 1971, total catch amounted to 26 $t{\cdot}km^{-2}$ (Anon. 1984). Assuming that the steady decrease in total catch continued on to the late 1980s, and that eel catch remained at a constant 60% of the total catch, an eel catch equivalent to 7.8 $t{\cdot}km^{-2}year^{-1}$ can be estimated. These assumptions were based on the knowledge that eels normally stay in the lagoon anywhere between four and ten years.

Adult Predators

Three important commercially exploited species, *Dicentrarchus labrax*, *Sparus aurata* and *Solea vulgaris*, make up this group of adult predators. To separate catches of adult from juvenile fish, it was assumed that juveniles included fish aged 0-1 year and adults aged 2 years or more. No catch estimates in terms of weight were available; however, numbers of individuals caught were reported by Farrugio and Le Corre (1986) who also provided growth parameter estimates for the three fish populations considered here. Thus, catch in weight was reconstructed as presented in Table 2.

Mugilids

Mugilids were included as two separate groups to account for the diet shift from juvenile carnivores to adult herbivores/omnivores. For the species considered here, Bach (1985) reported a catch of 0.2 $t{\cdot}km^{-2}year^{-1}$. The five species, *Mugil cephalus*, *Cheilon labrosus*, *Liza saliens*, *Liza ramada* and *Liza aurata*, were caught as "trash fish" by four commercial gears used in the lagoon. Assuming that juveniles stay carnivorous up to a maximum length of 10 cm and that these comprise 10% of the catch (Cambrony 1983), then adult mugilids contribute 0.18 $t{\cdot}km^{-2}$ to the annual catch.

Young Predators

Juveniles of most of the species considered here were zooplanktivores and thus treated as a separate group. For *D. labrax*, *S. aurata* and *S. vulgaris*, catch figures were obtained from Table 2; whereas the assumptions made for the mugilid population above indicated a catch estimate of 0.32 $t{\cdot}km^{-2}year^{-1}$.

Table 2. Reconstructed mean weights from mean lengths obtained from growth parameters and length-weight relationships (L is TL in cm and W in g) for three commercially exploited species in the Thau Lagoon adapted from Farrugio and Le Corre (1986). ML is mean length (cm), MW is mean weight (g) and N is the number in the catch.

	Age	ML	MW	N[a]
Dicentrarchus labrax	0	3.4	4	138,718
$Lt = 85.5\ (1\text{-}e^{-0.18(t+0.22)})$	1	17.1	50	160,697
$W = 0.1065\ L^{2.985}$	2	28.4	235	76,990
	3	37.9	563	58,545
	4	45.9	1,003	21,111
	5	52.5	1,505	4,817
	6	58.0	2,034	3,854
Sparus aurata	0	9.2	10	506,168
$Lt = 53.9\ (1\text{-}e^{-0.26(t+0.74)})$	1	19.3	114	117,337
$W = 44.8 \times 10^{-3}\ L^{2.65}$	2	27.1	281	42,210
Solea vulgaris	0	11.5	10	82,610
$Lt = 50.5\ (1\text{-}e^{-0.24(t+1.1)})$	1	19.9	70	31,835
$W = 0.039\ L^{3.22}$	2	26.5	172	1,963
	3	31.7	288	590

[a] Adapted from Table 5 of Farrugio and Le Corre (1986).

Silversides

Members of this group remain zooplanktivorous throughout their lifetime. It was thus difficult to access them as two separate groups of juveniles and adults and they were here considered as one group. They probably have a strong impact on the zooplankton population as they stay in the lagoon practically all their lifetime. The estimate of annual catch, mainly for *Atherina boyeri*, was 0.2 t·km^{-2} (Bach 1985). This was the only group of fish species for which Q/B estimates pertained to the whole population.

Molluscs

Most of the mollusc biomass in the lagoon come from culture grounds. This and a general lack of benthos studies make it difficult to estimate production and biomass for natural and cultured populations combined. A simple assumption was thus made: that overall mollusc biomass ≈ cultured mollusc biomass. Anon. (1984) reported a mean annual production of cultured molluscs in the order of 30,000 t (341 t·km^{-2}) while a mean biomass estimate of 42,000 t (477 t·km^{-2}) was reported by Grentz (1990). These figures indicated a P/B ratio of 0.70 year^{-1}. Based on an assumed EE of 0.8 (i.e., 80% of the production is utilized for predation or catches), the harvest was estimated to be 267 t·km^{-2}year^{-1}.

Benthos

The apparent lack of available information on this group posed a problem for modelling. Though Amanieu et al. (1989) mentioned several ongoing studies on this group, little information was available on production, biomass and catch estimates of the natural populations. The lagoon is a source of bivalve, gastropod and other edible macroinvertebrates as can be deduced from the numerous seafood restaurants lining the main road to the Sète fish market. Thus, there exists a certain amount of exploitation of benthos, assumed to be 1.0 t·km^{-2}·year^{-1}.

Zooplankton

Jouffre (1989) reported a recent estimate of mean annual zooplankton biomass of 3,000 t dry weight. A mean wet to dry weight conversion factor of 15% was obtained from several estimates for marine zooplankton listed in Jϕrgensen (1979). Thus, zooplankton wet biomass was estimated to 20,000 t wet weight (267 t·km^{-2}), quite a high abundance.

Phytoplankton

Mean phytoplankton production of 204 gC·m^{-2}·year^{-1} was reported by Henard (1978). Using a C to dry weight conversion factor of 50% and a wet to dry weight factor of 70% (J. Moreau, pers. comm.), a value of 583 t·km^{-2}·year^{-1} was obtained. With a P/B ratio of 40 this corresponded to a biomass of 15 t·km^{-2}.

Benthic Producers

Biomass (in dry weight) of the macrophytobenthos present in the lagoon was estimated at 150 t·km^{-2} (Gerbal 1990). A wet to dry weight conversion factor of 14% adopted from Jϕrgensen (1979) for *Potamogeton* sp. resulted in an estimate of wet biomass of 1,071 t·km^{-2}.

Results and Discussion

The biomass estimates obtained from ECOPATH II are included in Table 1, while other estimates are in Table 3. Table 4 lists the model's summary statistics. The biomass estimate for eels is 11.0 t·km^{-2} based on an assumed EE of 0.95. The biomasses for adult and young predators might well be underestimates given that Farrugio and Le Corre (1986) estimated a cumulative biomass of 56 t·km^{-2} for European bar, sea bream and sole. Furthermore, Quignard (1984) mentioned a total fish catch of 26 t·km^{-2} for 1971. This is three times the total fish catch (9 t·km^{-2}) used in this model of the 1980s. There was an increase in fishing effort in the lagoon (Bach 1985), and thus lower biomass estimates

Table 3. Estimated parameters (t·km^{-2}year^{-1}) of species groups of the Thau Lagoon system obtained from ECOPATH II for the 1980s.

Group	Flow to detritus	Food intake	Respiration	Assimilation
Eels	9.4	44.0	26.4	35.2
Adult predators	6.5	29.4	17.5	23.5
Adult mugilids	10.1	45.8	27.5	36.7
Young predators	21.8	91.9	39.1	73.5
Silversides	22.5	105.1	69.6	84.1
Molluscs	542.7	2,385.0	1,574.1	1,908.0
Benthos	99.7	472.2	325.3	377.7
Zooplankton	6,510.0	16,020.0	4,272.0	9,612.0
Phytoplankton	75.1			
Benthic producers	8,888.0			

Table 4. Summary statistics (in t·km^{-2}·year^{-1}) for the ECOPATH II model obtained for the Etang de Thau in the 1980s.

Sum of all consumption	19,193.4
Sum of all exports	3,245.0
Sum of all respiratory flows	6,351.4
Sum of all flows into detritus	16,185.7
Total system throughput	44,975.5

should be expected in recent years. Moreover, the groups emphasized by Farrugio and Le Corre (1986) consisted of migratory species which stay in the lagoon for only a part of the year. This further complicated the estimation of mean annual fish biomass in the lagoon.

The EE's estimated by ECOPATH seem reasonable. The high zooplankton EE of 0.98 was acceptable given that the lagoon serves as a nursery ground for fry and juveniles of both migratory and sedentary species (Cambrony 1983; Rosecchi 1985). Thus, there was considerable predation pressure on zooplankton.

Overall, the ECOPATH II model presented in Fig. 2 seems reasonably balanced. However, the seasonal shifts in the ecosystems were not considered. It is recommended, therefore, that the next modelling attempts focus on producing separate models for different seasons where seasonal shifts and migratory patterns could be accounted for.

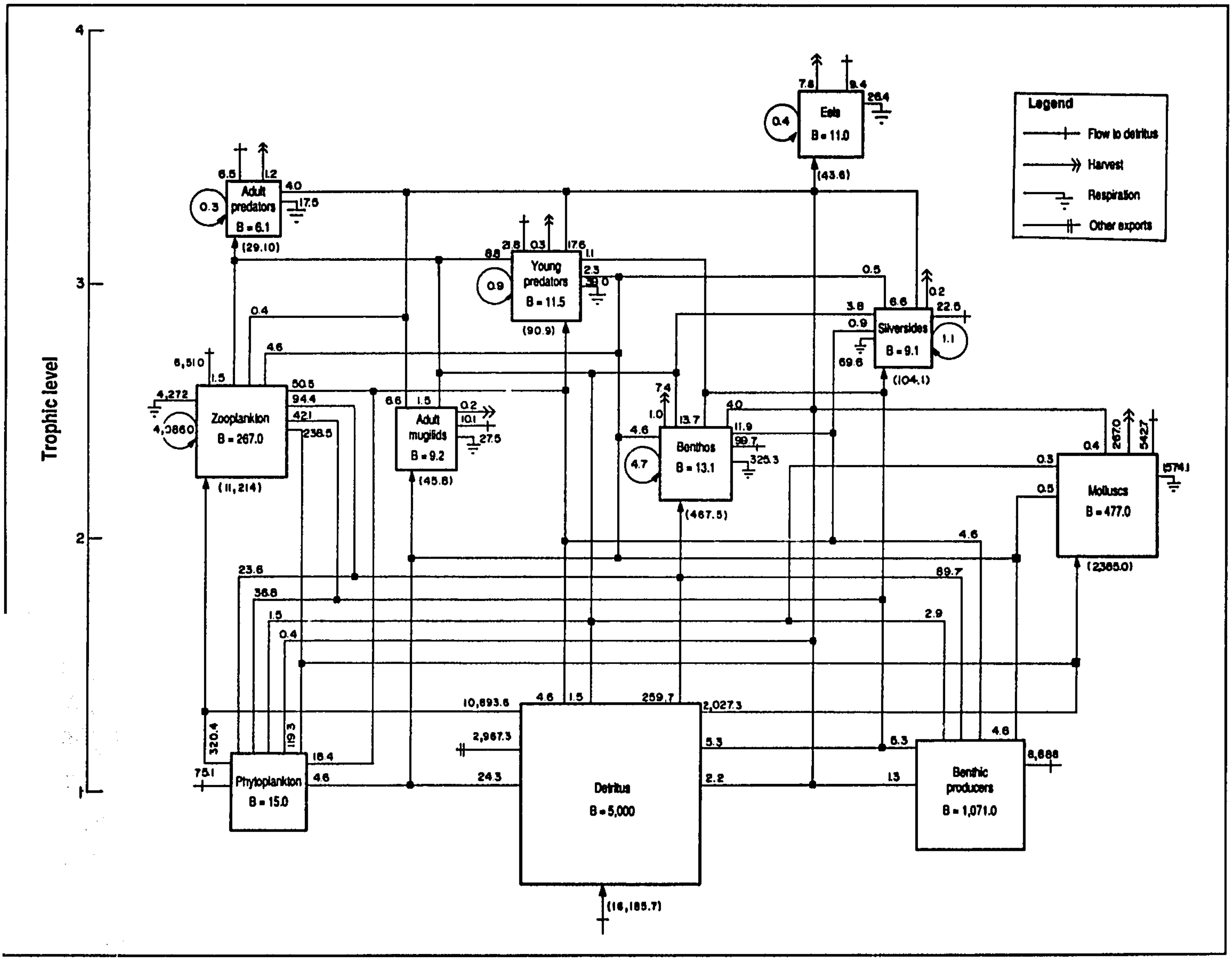

Fig. 2. A quantitative representation of the trophic interactions in Lagoon Etang de Thau, France. All flows are expressed in t·km^{-2}·year^{-1}, while biomasses (B) are in t·km^{-2}.

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Trophic Model of an Estuarine Ecosystem at the Southeast Coast of India

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SANTHANAM, R., A. SRINIVASAN and M. DEVARAJ. 1993. Trophic model of an estuarine ecosystem at the southeast coast of India, p. 230-233. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Abstract

The present investigation details the trophic connections existing among the planktonic, pelagic and benthic components of the Pullavali brackishwater, a tropical estuarine ecosystem at the southeast coast of India where such studies have not been made hitherto. The production and loss of energy (gC·m^{-2}year^{-1}) at successive trophic levels were estimated for a habitat area of 1.5 km^2 adopting random sampling, standard methods of R.B. William and assumptions of D.J. Crisp. A box trophic model postulated, using observed and assumed data of this estuarine ecosystem, showed a net primary production of 410 gC·m^{-2}year^{-1}, secondary production of 92.25 gC·m^{-2}year^{-1}, benthic production of 37.75 gC·m^{-2}year^{-1}, pelagic fish yield of 2 gC·m^{-2}year^{-1} and demersal fish yield of 0.25 gC·m^{-2}year^{-1}.

A comparison made with a shallow temperate estuary (Bogue Sound, North Carolina) showed that the net primary production in the tropical estuarine ecosystem was higher than that of the other ecosystem. However, the Pullavali brackishwater and Bogue Sound showed more or less similar efficiency in the different trophic levels as evidenced by the total fish yields, 0.55% and 0.50% of net primary production, respectively.

Introduction

Trophic relationships of coastal ecosystems in different latitudes can be studied through the measurement of energy flows. Although the planktonic, pelagic and benthic zones have been studied separately, their trophic connections are very little understood. Therefore an integrated investigation was undertaken in the Pullavali brackishwater (Lat. 8°40' N; Long. 78°06'E) (Fig. 1), a tropical estuary in the southeast coast of India. Its trophic status is compared to that of Bogue Sound (Lat. 34°45'N; Long. 76°30'W), a shallow temperate estuary in North Carolina, USA.

Materials and Methods

The estimation of hydrobiological parameters, such as depth, temperature, light extinction coefficient, salinity, dissolved oxygen, primary production, benthic production and fish yield, was made based on a monthly random sampling scheme during 1985 and standard methods of Williams (1986) and Anon. (1989). The production and loss of energy (gC·m^{-2}·year^{-1}) at successive trophic levels were estimated and presented in a box model based mainly on the assumptions of Crisp (1975).

Results and Discussion

The data recorded of the hydrobiological characteristics and fishery potential of the Pullavali brackishwater are shown in Table 1. The values of average net primary production, secondary production, benthos production, pelagic fish yield and demersal fish yield observed during the present study, were 410, 92.25, 37.75, 2 and

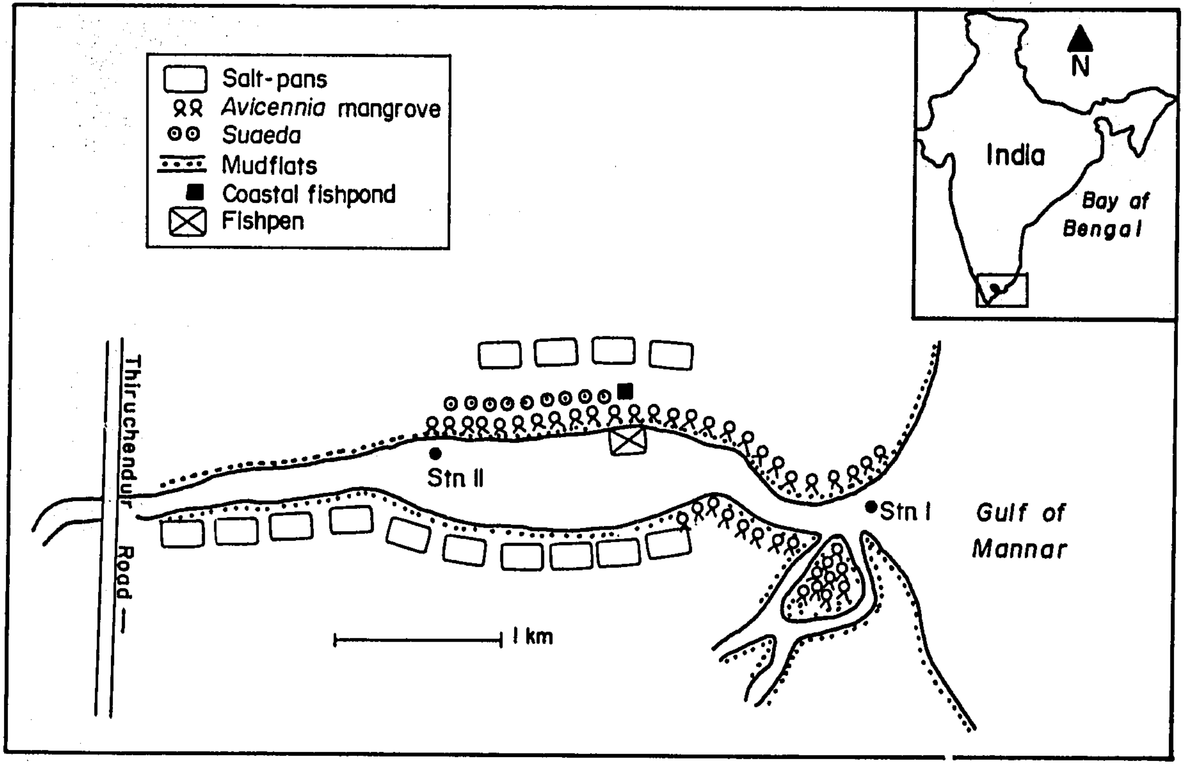

Fig. 1. Map showing the Pullavali brackishwater, India.

0.25, gC·m^{-2}·year^{-1}, respectively. The efficiency of transformation of energy between pelagic organisms was found to be higher (0.5%) than that between benthic organisms (0.01%). Benthos production was found to be 16% of total available organic carbon (236 gC·m^{-2}·year^{-1}) which was contributed by bacteria (30.75 gC·m^{-2}·year^{-1}), detrital algae (102.5 gC·m^{-2}·year^{-1}), herbivore feces (92.5 gC·m^{-2}·year^{-1}) and land debris (10.5 gC·m^{-2}·year^{-1}). A summary of the energy pathways involved here is shown in Fig. 2.

As far as the tropical and temperate estuarine ecosystems are concerned, the efficiency of different trophic levels was more or less the same, as evidenced by the total fish yield, which amounted to 0.55% and 0.50%, respectively, of the net primary production. Yet the absolute fish yields are very different (2.25 and 0.22 gC·m^{-2}·year^{-1}). The higher value was due to the higher net primary production (410 gC·m^{-2}·year^{-1}) in the tropical Pullavali brackishwater compared to the temperate estuary (42.5 gC·m^{-2}·year^{-1}). The sustained high primary production observed in the eutrophic Pullavali brackishwater could be due to the input of nutrients from mangrove litter falls coupled with the influence of sewage.

Table 1. Hydrobiological characteristics and fisheries potential in tropical and temperate estuaries.[a]

Parameter (units)	Pullavali estuary SE coast of India	Bogue Sound North Carolina
Habitat area (km^2)	1.5	400
Mean tidal amplitude (m)	0.7	0.8
Mean depth (m)	1.7	1.2
Light extinction coefficient	1.5-2.2	1.0-2.0
Temperature (°C)	24.8-30.0	7.9-27.6
Salinity (‰)	26.4-34.2	20-30
Dissolved oxygen (mg l^{-1})	6.2-8.4	not reported
Net primary production (gC·m^{-2}·year^{-1})	410	42.5
Secondary production (gC·m^{-2}·year^{-1})	92.5[b]	9.6
Total fish yield (gC·m^{-2}·year^{-1})	2.25	0.22

[a] Williams (1986).
[b] Assumed/calculated values after Crisp (1975).

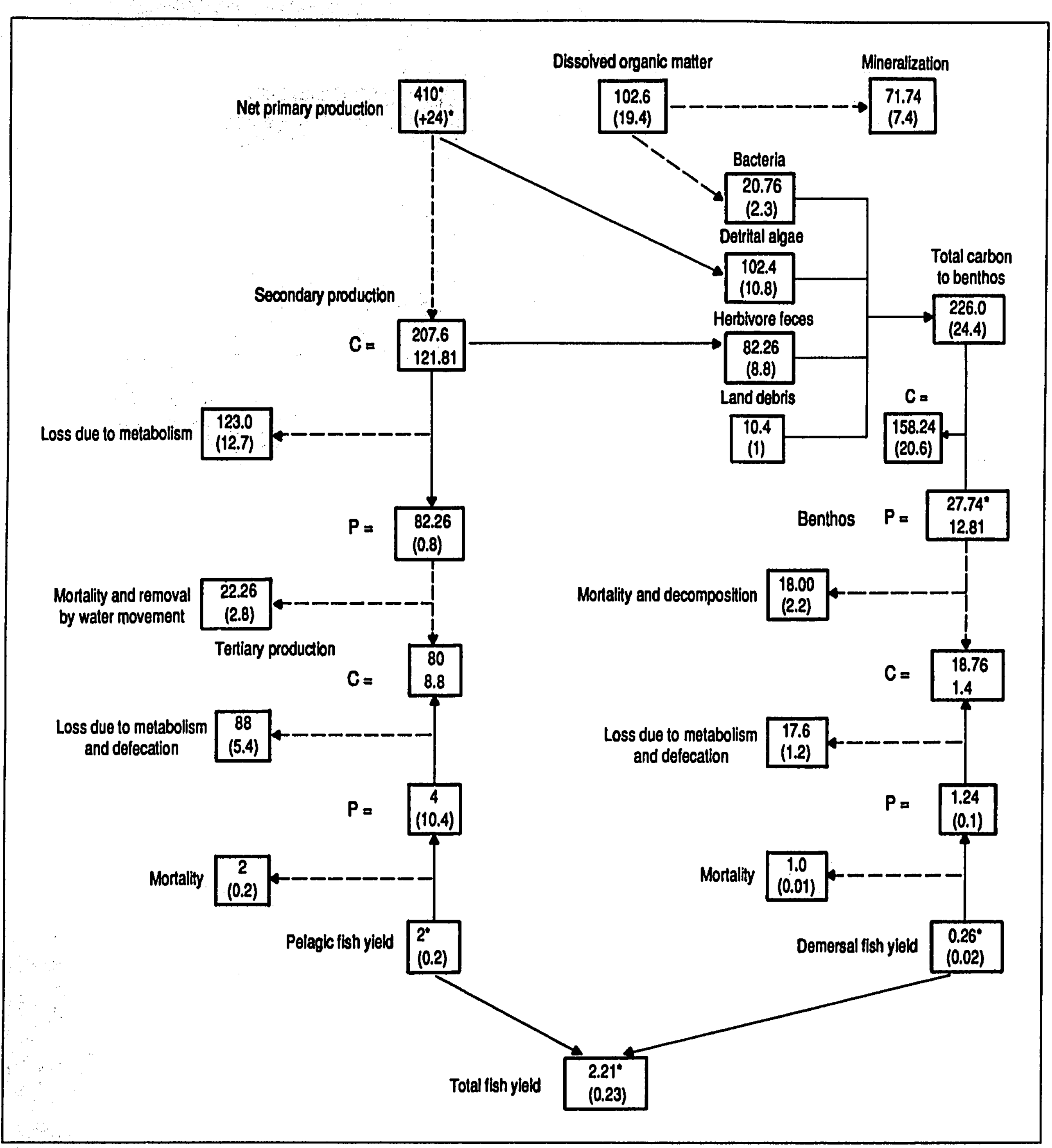

Fig. 2. Trophic model of the Pullavali estuary. Values in gC·m^{-2}·year^{-1}. C = consumption; P = production; * = observed values. Other values are after Crisp (1975). Figures in parentheses relate to the temperate estuary.

Explanations to numbers in trophic box model:

1. Net primary production.
2. Assumption that 20% of primary production is released as dissolved organic matter.
3. Assumption that 30% of dissolved organic matter is incorporated in benthic bacteria.
4. Assumption that 75% of the microalgae are eaten by herbivores.
5. P/C or growth efficiency assumed at 30%.
6. Assumed value (following Crisp 1975).
7. Pelagic fishing mortality, assumed 50% of total.
8. Demersal fishing mortality, assumed 80% of total.
9. Growth efficiency of fish population (P/C) taken as 1/15.

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CORAL REEFS

Smith (1978) attempted to estimate the proportion of the ocean surface area that can be attributed to coral reefs. He estimated a total of 617,000 km^2 of coral reefs for the entire world.

Based on Munro (1977), Smith (1978) assumed a fisheries yield of 8 t·km^{-2}·year^{-1} for coral reefs *and adjacent reef areas*; this led him to an estimated annual yield (potential or realized) of 6 million tonnes for the entire coral reef regions of the world.

However, yield per coral reef surface area appears to be extremely variable, both for natural reasons and due to different levels of exploitation or reef degradation (Munro 1984), and the above figure, which may be a reasonable estimate of the "mean yield", could well be increased given improved management or decreased if overfishing and coral reef destruction continue unabated.

The potential fish yield from coralline areas is high, perhaps much higher than hitherto assumed. For example, Fig. 1 shows the relationship between yield from coral reefs and fishing effort. The figure does not indicate any levelling of catches due to increased effort, i.e., reefs seem to be able to sustain a considerable fishing pressure (compared to other resource systems) if it is applied wisely. Noteworthy also are some community-based management initiatives from several intensively fished Philippine reefs. Here, increases in catches by a factor of 2 to 3 have been experienced mainly through abolishing destructive fishing methods and introducing community-based enforcement of fish sanctuaries (Fig. 2). Overall, yields of the order of 30 t·km^{-2}·year^{-1}, far higher than for other systems, have been observed in several studies (e.g., White and Savina 1987).

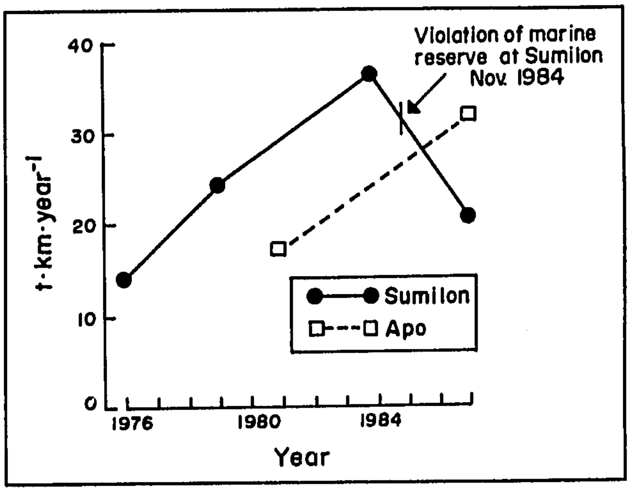

Fig. 2. Change in fish yield reported for Sumilon and Apo Islands, reflecting the effects of different management schemes. (Source: White and Savina 1987)

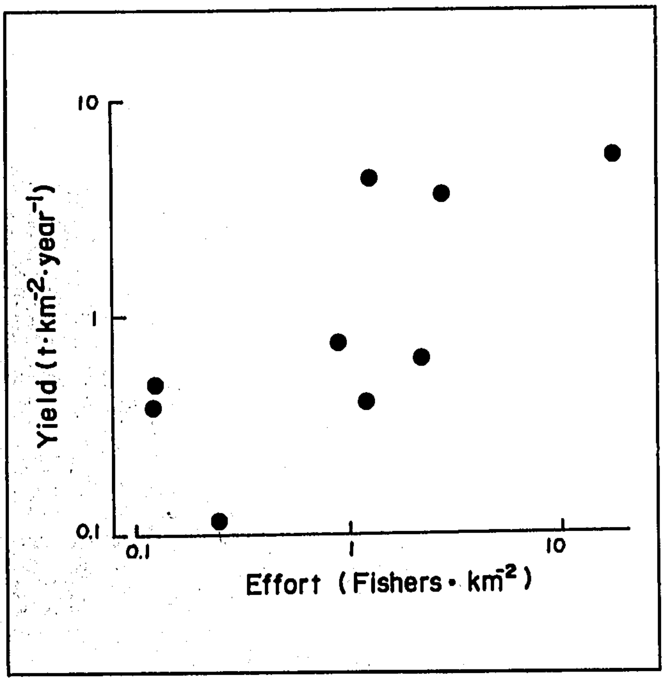

Fig. 1. Fish yields *vs.* fishing effort in coral reefs. (Source: Marten and Polovina 1982).

Noting both this, and the food requirements of steadily increasing coastal populations in developing countries, we see a need for development of fisheries management models, especially for coralline areas. The purpose of such models should be to identify how to increase production in a sustainable fashion.

The biological understanding of reefs is increasing. The focus is, however, rarely on quantifying interactions, even if the two Odum brothers' work at Eniwetok Atoll showed the way decades ago (Odum and Odum 1955). Later, better quantified models include J.J. Polovina's (1984) model of the French Frigate Shoals, Hawaii, discussed in his foreword to this volume, along with the two models presented in this section. The first of these, referring to the Bolinao reef flat area, is preceded by a paper which provides details on methods to compute and standardize parameter estimates for various groups to be included in a model of a reef, and, by extension, to other ecosystems.

In addition to modelling resource interactions, the need for understanding how coastal fisher populations exploit the reef resources is becoming clearer. Several studies have addressed this, and it has also been done in practice in the aforementioned Philippine experiments with community-based fisheries management (see McManus et al. 1993).

Combining biological and sociological understanding in the form of appropriate management models is still an outstanding task, however.

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Estimates of Relative Food Consumption by Fish and Invertebrate Populations, Required for Modelling the Bolinao Reef Ecosystem, Philippines*

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Abstract

Estimates of food consumption per unit biomass in five important invertebrate groups and eight species of fish are presented for taxa which either occur or can be used to represent major elements of the coral reef ecosystem of Bolinao, Pangasinan, Philippines. A brief discussion is presented on how these estimates can be used to construct a steady-state trophic model of the Bolinao reef ecosystem, and of the application of the methods used therein to other taxa and/or ecosystems.

Introduction

When studying the trophic structure, i.e., energy flow and predator-prey relationships of coral reef ecosystems, it is of vital importance to relate the food consumption (Q), biomass (B) and production (P) of each reef organism to the production of its food resource (Winberg and Duncan 1971; Mann 1978; Polovina 1984; Olson and Mullen 1986). Furthermore, the evaluation of the magnitude and nature of these interactions are relevant aspects of ecosystem and multispecies fisheries management (Palomares and Pauly 1989 and see contributions in this volume).

This paper (of which Sambilay et al. 1992 is a summary version) provides estimates of the food consumption of some fish and invertebrate groups occurring in Bolinao Reef in Lingayen Gulf, Pangasinan, Philippines. The results can be used as initial estimates of input parameters to an ecosystem model as constructed using the ECOPATH or ECOPATH II models and software. Details of the procedures on how these estimates were obtained are also provided to serve as example for approaches such as used here for taxa and/or areas not considered here.

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Materials and Methods

Materials

The estimates of the food consumption per unit biomass (Q/B) of five invertebrate groups and eight species of fish presented here were derived using growth and feeding data obtained from the literature, except for two species of coral reef fishes (*Zebrasoma scopas* and *Myripristis murdjan*) which are based on experiments conducted (by S. Opitz) at the Institut für Meereskunde, Kiel University, Germany.

Except for recent estimates of food consumption of *Siganus fuscescens* by Hernandez et al. (1990) and Espinosa (1991), food consumption studies based on samples obtained in the Bolinao area are currently unavailable. However, the estimates presented here refer to tropical or subtropical species of the Indo-Pacific faunal zone (except for two datasets, pertaining to an Atlantic sea urchin and an octopus) of which most have been recorded from the Bolinao area (Aprieto and Villoso 1982; Mines 1986; M. Lopez, unpubl. data).

Methods

ESTIMATION OF CONSUMPTION FROM DATA ON FOOD CONVERSION EFFICIENCY

Gross food conversion efficiency (K_1, Ivlev 1961) is defined as

$$K_1 = (\text{growth increment/food intake}) \quad ...1)$$

for any period of time. The relationship of K_1 with the size of the organism can be expressed as a function of weight (Pauly 1986; Silvert and Pauly 1987), i.e.,

$$K_1 = 1 - (W/W_\infty)^\beta \quad ...2)$$

where W_∞ is the asymptotic weight of the organisms in the population in question, as also used in the von Bertalanffy growth function (VBGF), which has the form

$$W_t = W_\infty\left(1-e^{-K(t-t_0)}\right)^b \quad ...3)$$

where K is the rate (dimension: time^{-1}) at which W_∞ is approached; t_0 is the theoretical age the organisms would have at length zero if they had always grown according to the VBGF; and b is the exponent of a length-weight relationship of the form

$$W = a \cdot L^b \quad ...4)$$

(see below for the estimation of the VBGF parameters). Equation (2) can be written:

$$-\log_{10}(1-K_1) = \beta\log_{10}W_\infty - \beta\log_{10}W \quad ...5)$$

which has the form of a linear regression, from which W_∞ and β can be estimated. Alternatively, when W_∞ is known, β can be estimated from

$$\beta = (\overline{-\log_{10}(1-K_1)})/(\log_{10}W_\infty - \overline{\log_{10}W}) \quad ...6)$$

If several factors other than size (W) affect K_1, (5) can be extended to the multiple linear regression

$$-\log_{10}(1-K_1) = a - \sum_{i=1}^{n}\beta\log_{10}W + \sum b_i v_i \quad ...7)$$

where for i=1 to n, b_i is the partial slope associated with the factor v_i, affecting the growth of the organisms studied, such as, e.g., temperature, food type, etc. (Pauly 1986; Palomares 1987; Palomares and Pauly 1989).

From (2), one can express the rate of food consumption (dq/dt) at age t as

$$dq/dt = (dw/dt)/(K_{1(t)}) \quad ...8)$$

where $K_{1(t)}$ is the conversion efficiency expressed as a function of age, as can be obtained by combining (2) and (3), and in which the growth rate (dw/dt) is the first derivative of the VBGF, or

$$dw/dt = W_\infty bK(1-e^{-K(t-t_0)})^{b-1}\, e^{-K(t-t_0)} \quad ...9)$$

Cumulative food consumption (Q_c) from any age t_r to t_{max} can therefore be estimated from

$$Q_c = \int_{t_r}^{t_{max}} \frac{(dw/dt)dt}{K_{1(t)}} \quad ...10)$$

Food consumption per unit biomass per unit time (Q/B) in an age-structured steady-state population (Pauly 1986) can thus be computed by

$$Q/B = \int_{t_r}^{t_{max}} \frac{(dw/dt)e^{-z(t-t_r)}dt}{1-\left(1-e^{-K(t-t_0)}\right)^{\sigma\beta}} \Big/ \int_{t_r}^{t_{max}} W_t e^{-z(t-t_r)}dt \quad ...11)$$

where t_r and t_{max} are the ages at recruitment and exit from the population, respectively; Z is the instantaneous mortality between ages t_r and t_{max}; and the exponential terms ($e^{-Z(\ldots)}$) express the decay of the population through time, starting from an arbitrary number of recruits (here set equal to 1). Apart from allowing the estimation of Q/B, this model also enables the estimation of maintenance ration (R_m) and of trophic efficiency (E_T). This is because maintenance ration is defined as "Q/B at W_∞" and trophic efficiency (E_T, production per unit of food consumed) can be reexpressed as

$$E_T = Z \cdot (B/Q) \qquad \ldots 12)$$

A few of the Q/B values estimated below originally referred to habitat (or experimental) temperatures (T') of less than 27°C. The appropriate upward adjustment was performed by multiplying the original estimates of Q/B by a factor "V" obtained from

$$V = 27^{0.6121}/T' \qquad \ldots 13)$$

where 27 refers to the temperature at Bolinao in °C, and 0.6121 is the partial regression coefficient associated with temperature in the empirical model of Palomares and Pauly (1989).

Throughout this paper, Q/B values will be expressed either on an annual or daily basis; in the latter case, we shall express Q/B as % BWD, i.e., per cent of body weight per day. Unless otherwise mentioned, the consumption rates in this contribution refer to live or wet weight (ww).

ESTIMATION OF RELATIVE POPULATION CONSUMPTION FROM ESTIMATES OF INDIVIDUAL RATION

When daily ration (R_d), i.e., the daily food consumption of the fish of a certain size is known, the concepts presented above can be used, when growth parameter and mortality estimates are also available, to estimate population food consumption per unit biomass (Q/B).

Thus, substituting R_d for "food intake" and dw/dt for "growth increments" in (1) gives

$$K_1 = (dw/dt)/R_d \qquad \ldots 14)$$

and the estimation of ß and Q/B can proceed as outlined above.

There are numerous methods for estimation of ration in fishes (see Elliott and Persson 1978; Mann 1978; Windell 1978; Palomares and Pauly 1989; and references therein). A method which seems particularly applicable to Bolinao reef fishes is the analysis of diurnal cycles of stomach contents (Sainsbury 1986 as modified by Jarre et al. 1991).

ESTIMATION OF GROWTH PARAMETERS (W_∞, K and t_0)

Estimates of the parameters of the VBGF were obtained predominantly from literature data and a number of conversions. Of these, the conversion of estimates of asymptotic length (L_∞) to asymptotic weight (W_∞) was the most important. This was performed based on (4), with approximate values of L_∞ estimated from

$$L_\infty \approx L_{max}/0.95 \qquad \ldots 15)$$

where L_{max} is the maximum length reported from the population in question (Pauly 1984).

When length-weight relationships with appropriate estimates of the parameters "a" and "b" were not available, values of "a" were obtained from length-weight data pairs and setting $a = W/L^3$, assuming isometric growth, i.e., b = 3. Through this contribution, we use cm for lengths and g for (wet) weight.

Estimates of K were obtained by either fitting the VBGF to length-at-age data, using the program of Gaschütz et al. (1980), which also yielded estimates of L_∞ and of t_0, or from the equation

$$\log_{10}K = \bar{\phi}' - 2 \log_{10}L_\infty \qquad \ldots 16)$$

In this, $\bar{\phi}'$ is the mean of several values of

$$\phi' = \log_{10}K + 2 \log_{10} L_\infty \qquad \ldots 17)$$

where K and L_∞ are growth parameter estimates for taxa (preferably species or genera) related to the one for which an estimate of K is to be obtained (Pauly 1979; Pauly and Munro 1984).

Rough estimates of t_0 were obtained, finally, from an empirical equation derived by Pauly (1979), i.e.,

$$\log_{10}(-t_0) = -0.40 - 0.28 \log_{10}L_\infty + 1.04 \log_{10}K \qquad \ldots 18)$$

where K is expressed in $year^{-1}$, L_∞ in cm (total length) and t_0 is a very preliminary estimate of "age" at length zero. Pauly (1986) performed a sensitivity analysis of (11) which showed that t_0, t_r and t_{max} have very little influence on the estimation of Q/B; hence, the use of (18) appears acceptable.

Some estimates of food consumption for echinoderms (sea urchins, holothurids) taken from the literature referred to specimens of "average" size. We have assumed this to correspond to half the asymptotic length.

ESTIMATION OF TOTAL MORTALITY OF EXPLOITED ORGANISMS OF BOLINAO REEF

The edible organisms of Bolinao reefs (holothurids, sea urchins, molluscs, shrimps, fishes, etc.) are all strongly exploited, and we shall assume here that their level of fishing mortality (F) is about equal to that of their natural mortality M (see Pauly 1984 for a discussion of this assumption). Hence, since Z = F + M, we have Z = 2M.

In fishes and invertebrates with high metabolic rate (octopus, squid and shrimp), M (year^{-1}) was estimated from

$$\log_{10}M = -0.211 - 0.0824 \log_{10}W_\infty + 0.6757 \log_{10}K + 0.4687 \log_{10}T \quad \text{...19)}$$

where W_∞ refers to asymptotic wet weight in g, K refers to year^{-1} and T is expressed in °C (Pauly 1980): T is set here at 27°C.

In the case of the low-metabolism echinoderms (sea urchins and holothurids), M was assumed to be lower than implied by (19), i.e., about equal to K (as is demonstrably the case in tropical sea urchins, see Longhurst and Pauly 1987, Fig. 10.2).

Note that the values of "Z" obtained as described above should not be used for fisheries assessment, although they might assist in obtaining reasonable estimates of Q/B when used in conjunction with equation (11).

Results

Sea Cucumbers

Sea cucumbers (holothurids) are ecologically important components of coral reef ecosystems; marketed as "trepang" or "bêche-de-mer," they are also of great economic importance (Conand 1989).

We present here estimates of growth, mortality and food consumption for two groups of sea cucumbers: (1) "*Holothuria* spp." and (2) "other holothurids".

Table 1 presents available growth parameter estimates for two *Holothuria* species. From these, we estimated for *H. pulla* the values L_∞ = 30.7 cm and K = 0.238 year^{-1} which imply, if one relies on a relationship established from data on fishes, that t_0 = -0.7 year^{-1}. The assumption that M = K and Z ≈ 2M leads to Z = 0.6 year^{-1}.

Table 1. Growth parameter estimates of three species of the genus *Holothuria*.

Species	L_∞(cm)	K(year^{-1})	ϕ'	Source
H. atra	32.4	0.110	2.06	Conand (1989)
H. scabra	29.0	0.524	2.64	This study[a]
H. pulla	30.7	0.238	2.35	Means

[a] Based on the analysis of the length-frequency data in Fig. 6 of Shelley (1985), using the Compleat ELEFAN software of Gayanilo et al. (1989).

Pinto (1982) performed feeding experiments with *H. pulla* sampled in Talin Bay, Batangas, Philippines. He estimated that "average"-sized specimens consumed 1.35 g of seagrass per day.

Assuming "average" to correspond to $L_\infty/2$ (i.e., 15.4 cm), one can use the length-weight relationship established by Conand (1989) for *H. atra* (which resembles *H. pulla*), i.e.,

$$W = 0.486\ L^{2.13} \quad \text{...20)}$$

to estimate as 164 g the weight of Pinto's "average" specimens. From the above data, one can estimate Q/B = 0.88% of body weight·day^{-1} (BWD) and R_m = 0.59% BWD.

Table 2 presents growth parameter estimates for "other holothurids". They lead to rough estimates of L_∞ and K for *Opheodesoma spectabilis* of 32.6 cm and 0.178 year^{-1}, respectively, with the estimate of asymptotic length matching the reported maximum size of 30 cm for *Opheodesoma* spp. (Reyes-Leonardo 1984) and the rule of thumb $L_\infty \approx L_{max}/0.95$.

This leads to t_0 = -0.8 year and M = 0.2 year^{-1} given the assumption that M/K = 1 (see above).

A length-weight relationship for *O. spectabilis* is not available. We assume it is the same as from *H. atra* (which has a similar body shape); thus L_∞ = 32.6 cm corresponds to W_∞ = 812 g.

Pinto (1982) estimated from his seagrass-feeding experiments a ration of 2.2 g·day^{-1} for "average"-sized *O. spectabilis*. Making the same assumption as above with regard to their length leads to a mean weight of 186 g for the

Table 2. Growth parameter estimates of miscellaneous holothurids, as used to infer L_∞ and K in *Opheodesoma spectabilis*.

Species	L_∞(cm)	K(year^{-1})	ϕ'	Source
Actinopyga echinites	29.5	0.090	1.894	Conand (1989)
Actinopyga mauritana	34.0	0.120	2.142	Conand (1989)
Holothuria spp.	-	-	2.350	See Table 1
Stichopus chloronotus	34.2	0.450	2.721	Conand (1989)
Opheodesoma spectabilis	32.6	0.178	2.277	Means

experimental animals, which would thus have a ration of 1.18% BWD. These parameters, combined with the growth parameters above, and $Z \approx 2M = 0.4$ year^{-1}, lead to Q/B = 1.22% BWD and R_m = 0.88% BWD.

Finally, combining our estimates for *Holothuria* spp. and "other holothurids" gives Q/B = 1.05% BWD and R_m = 0.73% BWD as mean value for sea cucumbers as an ecological group.

Sea Urchins

Sea urchins (echinoids) are ecologically important grazers in coral reef ecosystems, besides representing, in many areas, a valuable export commodity (Kato and Schroeter 1985). The account below, which presents the basis for our estimates of the relative grazing rate of a generic sea urchin population, is based on data from four groups: (1) *Echinometra mathaei*, (2) *Diadema* spp., (3) *Tripneustes* spp., and (4) *Echinometra picta*.

1. *Echinometra mathaei*. Ebert (1982) published the following growth parameter estimates for *Echinometra mathaei*: L_∞ = 4.1 cm (S_∞ in Ebert's notation, referring to ambitus length or largest diameter), K = 0.29 year^{-1}; the corresponding values of asymptotic weight, t_0 and Z ($\approx$ 2M $\approx$ 2K, see above) are 31.3 g (assuming b = 3 and a = 0.456), -0.01 year and 0.58 year^{-1}, respectively.

2. *Diadema* spp. Downing and El-Zahr (1987) presented data (in their Table 1) on the gut content of *E. mathei* specimen of 3.71 cm on the average (23 g), which allowed estimate of a mean gut content (over one daily cycle) of 1.53 g, of which 93% is $CaCO_3$, or 0.09 g organic matter.

They also performed experiments to assess the time needed for their specimens of *E. mathei* to empty their guts. From their data (Fig. 1), we estimated an instantaneous gut evacuation rate of 1.91 day^{-1}.

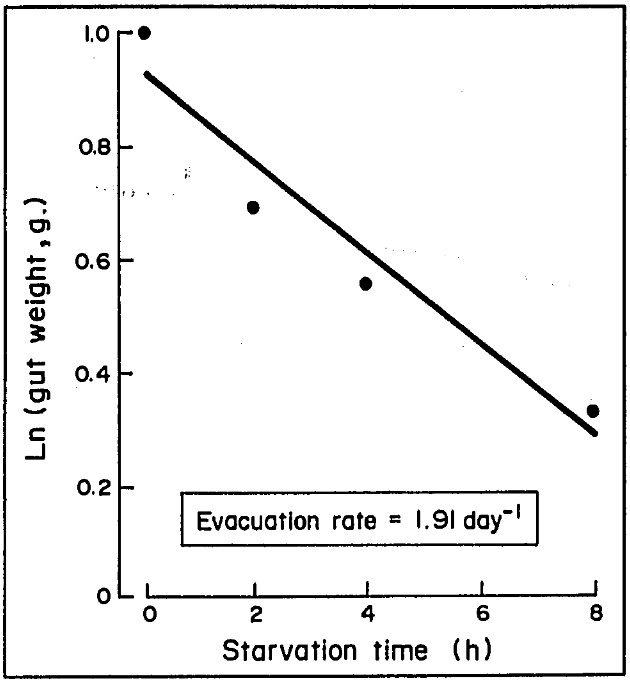

Fig. 1. Evacuation of gut contents in the sea urchin *Echinometra mathaei* as used to estimate the instantaneous evacuation rate (based on data point in Fig. 4 of Downing and El-Zahr 1987).

3. *Tripneustes* spp. Elliott and Persson (1978) showed that

$$R_d = \text{mean gut content} * \text{evacuation rate} \quad ...21)$$

Both *T. gratilla* and *T. ventricosus* (for which ration estimates are available, see below) reach sizes of up to 15 cm (George and George 1979); hence, L_∞ = 15.8 cm ($\approx$ 15 cm/0.95) will be used here together with K = 0.841 year^{-1}, as derived from ϕ' above. We also have t_0 = -0.22 year and Z $\approx$ 2K = 1.7 year^{-1}.

Ebert (1975) gave for *T. gratilla* a complex length-weight relationship, which reexpressed to the format used here, reads

$$W = 0.959\ L^{2.62} \quad ...22)$$

Combining the available growth and mortality estimates with the ration estimate in Table 3 gives ß = 0.276, and hence, Q/B = 1.34% BWD and R_m = 0.83% BWD.

Table 3. Estimates of daily feeding rates in *Tripneustes ventricosus*.

S (cm)	WW (g)	Feeding rate (g·day^{-1})	R_d (% BWD)	Source
7.5	177	4.40 (ww)	2.49	Ebert (1975)
12.1	742	1.44 (dw)	0.61[a]	Tertsching (1989)

[a] Computed from dry weight equivalent of 742 g, i.e., sea urchins are assumed to contain 68% water (see Appendix 1).

4. *Echinometra picta*. Pinto (1982) presented an estimate of seagrass consumption by "average"-sized *E. picta* which, if combined with appropriate growth parameters and Z estimates, leads to Q/B > 90% BWD. This is unrealistically high and will not be considered in further analyses.

Hence, combining (1), (2) and (3), values of Q/B = 0.98% BWD and R_m = 0.64% BWD can be suggested for sea urchins as an ecological group.

Penaeid Shrimps

Various crustaceans occur in or about coral reefs. The account below aims at providing an estimate of the relative food consumption of a population of penaeid shrimps, as represented by (1) *Penaeus monodon* and (2) *Metapenaeus monoceros*.

1. *Penaeus monodon.* This species is reported to reach 33.6 cm total length (Holthuis 1980), and hence we shall use, for $L_{max}/0.95 \approx L_{\infty}$, an asymptotic length of 35 cm. Direct estimates of the value of the parameter K were not available, and hence, we estimated it via ϕ' and the data for *Penaeus* spp. in Table 4, as 0.35 year^{-1}.

Table 4. Growth parameters of miscellaneous penaeid shrimps as used to estimate ϕ' and K values for *Penaeus monodon*. M = male, F = female (adapted from Pauly et al. 1984).

Species		TL_{∞} (cm)	K (year^{-1})	ϕ'
Penaeus duorarum	(M)	17.6	1.45	2.652
		17.6	1.20	2.570
P. kerathurus	(F)	21.0	0.80	2.548
	(M)	18.0	0.90	2.465
P. setiferus	(F)	22.5	1.25	2.801
	(M)	19.2	1.55	2.757
P. monodon	(-)	35.0	0.35[a]	2.632[b]

[a] See text.

[b] Mean of other values.

For the length-to-weight conversion, we used the generalized relationship for penaeid shrimps of Pauly et al. (1984)

$$W = 0.008(TL)^3 \qquad ...23)$$

which provides W_{∞} = 343 g. The other estimates used here are t_0 = -0.46 year, Z ≈ 2M = 1.8 year^{-1}.

Vijayaraghavan et al. (1988) fed juvenile *P. monodon* of 0.15 g mean weight with *Artemia* cysts and nauplii. The mean observed weight increment and amount of feed ingested were 0.197 g and 0.790 g, respectively, and hence K_1 = 0.25.

From (6), β = 0.0371; the Q/B value derived from (11) is 4.48% BWD; maintenance ration is 2.58% BWD.

2. *Metapenaeus monoceros.* This is reported to reach 17.25 cm total length, from which, according to (15), $L_{\infty} \approx$ 18 cm. No direct estimate of K is available, and hence we have estimated this parameter indirectly, using growth parameter estimates for other species of the genus *Metapenaeus* and the corresponding estimates of ϕ' (Table 5).

This resulted in K = 0.67 year^{-1} and the related estimates of t_0 = -0.27, and Z ≈ 2M = 3.2 year^{-1}. Asymptotic weight was derived via (23) and equaled 47 g.

Table 5. Some estimates of growth parameters in *Metapenaeus* spp. (from Pauly et al. 1984).

Species	TL_{∞} (cm)	K (year^{-1})	ϕ'
Metapenaeus brevicornis	13.3	0.93	2.216
	14.2	0.90	2.262
M. affinis	17.5	1.20	2.565
M. kutchensis	14.0	1.15	2.353
	14.0	1.20	2.371
	13.5	1.05	2.282
	13.8	1.10	2.321
M. monoceros	18.0	0.67	2.338

Table 6 summarizes the results of feeding experiments with *M. monoceros* used here. As might be seen, the wide variety of feeds and experiment conditions led to widely varying values of K_1, even after adjusting for the effect of body weight on K_1. Here, we have ignored this variability and derived a single value of β = 0.0249, applicable to intermediate food and experimental conditions.

This value of β, combined with the growth parameters above, leads to Q/B = 11.38% BWD and R_m = 7.37% BWD.

Based on the estimates for the two species above, "shrimp" as an ecological group, have a Q/B = 7.93% BWD and R_m = 4.98% BWD.

Octopus

Various species of octopus occur on tropical reefs, inclusive of Philippine coral reefs (Roper et al. 1984). It is not certain whether *Octopus vulgaris*, the "common octopus," which is reported for the South and East China Seas, actually occurs on Philippine coral reefs but it is possible, given that "this species, or species-complex is widely distributed around the world (with) taxonomic and geographic parameters (that) still are not precisely defined" (Roper et al. 1984).

Growth parameters for *O. vulgaris* have been published by Guerra (1979) based on samples collected off Northwest Africa and in the Mediterranean (near Barcelona). We used the latter sets of parameters because these refer to warmer waters and hence, more akin to the condition prevailing in the Philippines.

Table 6. Food intake of *M. monoceros* on different diets.

No.[a]	Diet	dw (g) initial	dw (g) final	Food (g dw)	K_1	ww[b] mean
1.	mangrove leaves	0.091	0.124	0.321	0.103	0.44
2.	mangrove leaves	0.089	0.114	0.251	0.100	0.42
3.	mangrove leaves	0.085	0.117	0.225	0.142	0.41
4.[c]	dry pellets	12.746	13.697	2.512	0.379[d]	13.22
5.[c]	dry pellets	3.653	4.292	2.051	0.311[d]	3.97
6.[c]	dry pellets	5.303	8.953	3.443	1.060[d]	7.13
7.[c]	dry pellets	5.546	8.992	6.805	0.506[d]	7.27
8.[c]	dry pellets	4.787	8.029	5.547	0.584[d]	6.41
9.[c]	dry pellets	2.741	5.130	4.237	0.564[d]	3.94
10.	trash fish	0.507	0.562	0.418	0.132	2.19
11.	low protein pellets	0.096	0.111	0.228	0.066	0.42
12.	Artemia	0.103	0.189	0.287	0.300	0.60
13.	Formula 5	0.167	0.271	0.851	0.122	0.90
14.	Formula 7	0.099	0.175	0.462	0.164	0.56
15.	Formula 8	0.072	0.136	0.471	0.136	0.42
16.	fish meal	0.200	0.201	0.465	0.002	0.82
17.	fish meal	0.239	0.299	1.010	0.060	1.10
18.	fish meal	0.394	0.505	2.104	0.053	1.84
19.	Cooper 6	0.185	0.192	0.521	0.014	0.77
20.	Cooper 6	0.253	0.337	1.175	0.071	1.21
21.	Cooper 6	0.407	0.500	2.750	0.034	0.64
22.	Formula 10	0.259	0.365	0.985	0.108	1.28
23.	Formula 10	0.443	0.630	2.970	0.063	2.20
24.	Tamil Nadu	0.156	0.148	0.505	-0.017[d]	0.30
25.	pellet 7	0.262	0.299	1.532	0.024	1.15
26.	pellet 7	0.392	0.466	4.515	0.016	1.76

[a] Nos. 1-3, Ramadhas and Vijayaraghavan (1979); 4-15, Royan et al. (1977); 16-26, Vijayaraghavan et al. (1978).

[b] Weight conversion based on body water composition of *M. monoceros* = 75.6% (see Appendix 1).

[c] Originally presented as ww.

[d] Not used, unrealistically high (or negative).

The growth parameter estimates are L_∞ = 30 cm (mantle length, ML), K = 0.72 year^{-1} and t_0 = -0.25. Guerra (1979) also presented a length-weight relationship for western Mediterranean specimens of *O. vulgaris*, i.e.,

$$W = 0.42\ (ML)^{2.987} \qquad ...24)$$

Hence, W_∞ = 10,850 g. From this, M = 0.82 year^{-1} and Z ≈ 1.64 year^{-1}.

Some estimates of K_1 for *O. vulgaris* are given in Table 7.

Combined with the growth parameter estimates presented above, this leads to β = 0.2312, which, when used in conjunction with the estimate of Z above, leads to Q/B = 1.39% BWD and R_m = 0.856% BWD, both of which pertain to a mean temperature of 15°C. Conversion to the temperature prevailing at Bolinao leads to Q/B ≈ 2.0% BWD and R_m ≈ 1.23% BWD for octopus as an ecological group.

Table 7. Estimated conversion efficiencies of *O. vulgaris* (from O'Dor and Wells 1987, based on experiments by Mangold and Boletzky 1973).

Weight range (g)	$\bar{W}$ (g)	Temperature (°C)	K_1
112-1,267	690	20	0.48
82-450	266	15	0.55
80-461	271	10	0.56

Squids

Squids occur in the pelagic areas of and around coral reefs, including Bolinao reef (Balgos 1990) and can be expected to consume a sizeable proportion of the secondary production of such areas, as is also the case in other ecosystems they inhabit (see contributions in Boyle 1987).

Estimates of food consumption of squids presented here are based on parameter estimates adapted from Longhurst and Pauly (1987), who combined population data pertaining to tropical with experimental data pertaining to temperate squids (Table 8).

These estimates, however, refer to low temperatures and thus need to be adjusted such that increased metabolism at higher temperatures, i.e., tropical reef areas, is accounted for. The adjusted estimates of Q/B and R_m are 6.53% BWD and 4.23% BWD for *L.*

Table 8. Parameters used in the estimation of Q/B and R_m of squids (adapted from Longhurst and Pauly 1987).

Parameter units	*Loligo duvaucelli* / *L. opalescens*	*Sepioteuthis lessoniana* / *Illex illecebrosus*
ML_∞ (cm)	29.00	27.00
W_∞ (g)	150.00	650.00
K ($year^{-1}$)	1.00	0.73
t_0 (year)	set = 0	set = 0
Z (=2M, $year^{-1}$)	3.16	1.70
ß	0.083	0.230
Q/B (% BWD)	5.094	1.414
R_m (% BWD)	3.300	0.869
Temp. (°C)	18.0	10.0

duvaucelli and 2.60% BWD and 1.60% BWD for *S. lessoniana*.

Combining these results in Q/B = 4.56% BWD and R_m = 2.92% BWD for squids as an ecological group.

Saurida undosquamis

The brushtooth lizardfish *Saurida undosquamis* (Synodontidae) is reported to reach "about 40 cm (and) to feed on bottom-feeding invertebrates and fishes" (Abe and Pathansali 1974).

The growth parameters of *S. undosquamis* population in the Visayan Sea, Philippines, were estimated by Ingles and Pauly (1984) as FL_∞ = 30.5 cm (TL = 33.7 cm) and K = 0.8 $year^{-1}$. The corresponding estimate of t_0 = -0.2 year.

Data in SEAFDEC (1979) allowed estimates of the length-weight relationship

$$W = 0.043\ (TL)^3 \qquad ...25)$$

which, combined with the estimate of asymptotic length, yields W_∞ = 1,646 g. From this, M = 1.35 $year^{-1}$, and hence, Z ≈ 2.7 $year^{-1}$.

Data on the diel feeding pattern of *S. undosquamis* off Oman coast were presented by Budnichenko (1977). These data, reproduced here as Table 9, suggest that *S. undosquamis*, like numerous other piscivores, feeds mainly at dusk and dawn (Hobson 1972).

Jarre et al. (1991) presented a method to analyze such data. The presentation of their model would require too much space for inclusion here, and we refer therefore to their paper and the accompanying software. Some of the results obtained from the analysis of Table 9 and pertaining to fishes with a mean standard length of 15 cm (=17.6 cm TL; 234 g) are:

• Start of first feeding period	: 03h48'
• End of first feeding period	: 07h30'
• Start of second feeding period	: 12h24'
• End of second feeding period	: 23h42'
• Food ingestion rate	: 0.16 $g \cdot h^{-1}$
• Stomach evacuation rate	: 0.35 h^{-1}
• Asymptotic weight of stomach contents	: 0.42 g
• Daily ration	: 2.43 g (=1.04% BWD)

A graph showing the fit of the model to the data is given as Fig. 2. As might be seen, the fit is "good," but there are few data points, and the results are thus tentative.

The ration estimates, combined with the growth and mortality parameters given above, lead to Q/B = 1.17% BWD and R_m = 0.49% BWD.

Table 9. Data on the diel cycle of stomach content of *Saurida undosquamis* sampled off Oman (adapted from Budnichenko 1977, Fig. 2).

Time	Mean stomach contents (g)[a]
01h30'	0.441
05h30'	0.317
09h30'	1.199
13h30'	0.264
17h30'	0.090
21h30'	0.362

[a] Converted from relative weights (in %); the value for 13h30' is a mean of two observed stomach content weights taken during this period.

Myripristis murdjan

The big-eye soldierfish *Myripristis murdjan* (Holocentridae) feeds at night on large zooplankton and small fishes; it reaches a length of about 30 cm (De Graaf 1977) which shall be used here as estimate of asymptotic (total) length.

Growth data for this species are not available, but growth parameter estimates for the related *M. amaena* are given in Dee and Radtke (1989). However, they suggest a much slower growth than in other holocentrids, which may be an artifact of the method they used for ageing (otolith microstructures presumed to be daily). For this reason, we have used, for the estimation of K from L_∞, a value of ϕ' estimated as the mean of the single value for *M. amaena* and that for *Holocentrus* spp. (see Table 10). This yielded, for TL_∞ = 30 cm, the estimate of K = 0.239 $year^{-1}$.

These estimates allow computation of t_0 = -0.69 year. The length-weight relationship of *M. amaena* derived by Dee and Radtke (1989), of the form

$$W = 0.031\ (SL)^{3.042} \qquad ...26)$$

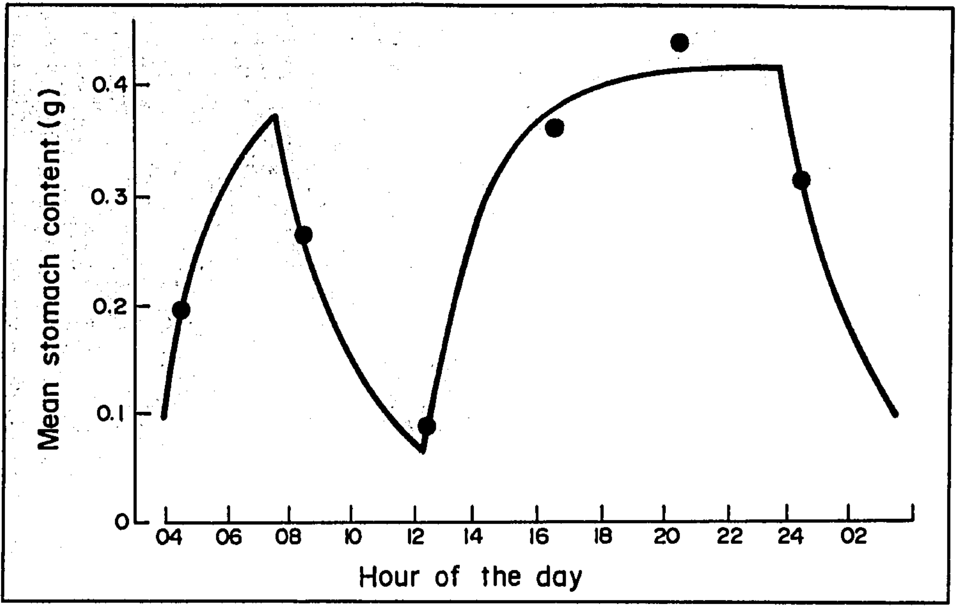

Fig. 2. Diurnal changes of stomach contents in lizardfish *Saurida undosquamis* off Aden; the data points (from Budnichenko 1977), fitted with the model of Jarre et al. (1991), suggest that this fish feeds mainly at dusk and dawn. The estimate of daily ration is 2.43 g or 1.04% BWD (see text).

Table 10. Published growth parameters of some soldierfish, as used to infer an approximate value of K in *Myripristis murdjan*.

No.	Species	FL_∞ (cm)	K ($year^{-1}$)	ϕ'	Source
1.	*Holocentrus sciurus*	40	0.26	2.62	Nicholson and Hartsuijker (1983)
2.	*H. ascensionis*	30	0.26	2.37	Nicholson and Hartsuijker (1983)
3.	*H. diadema*	14.7[a]	1.13	2.39	Pauly (1978), based on Gundermann and Popper (1975)
4.	*H. rufus*	23	0.29	2.19	Nicholson and Hartsuijker (1983)
5.	*Holocentrus* spp.	-	-	2.393	ϕ' mean of Nos. 1-4
6.	*Myripristis amaena*	21.5[b]	0.239	2.043	Dee and Radtke (1989)
7.	*M. murdjan*	26.3	0.239	2.218	ϕ' mean of Nos. 5 and 6

[a] Referred to as *Sargocentron diadema* in Dee and Radtke (1989).
[b] Converted from total to fork length via a ratio of 1.14:1.

was used for the conversion of our estimate of TL = 30 cm (= 22.5 cm SL) because these two species have very similar shapes (Tinker 1978). This led to an estimate of W_∞ = 402 g, which allowed estimation of M = 0.67 $year^{-1}$.

Growth and food conversion experiments were conducted at the IfM using six specimens of *M. murdjan*. These fishes yielded six positive values of K_1, of which the upper three, pertaining to the less stressed fish, are presented in Table 11, along with the weights of the fish from which they were derived. Combined with the estimate of W_∞ given above, these data led to an estimate of ß = 0.0216.

Table 11. Partial results of aquarium growth experiments on *Myripristis murdjan* fed *Neomysis integer*.

Mean W (g)	Increment	Food intake (g)	K_1[a] (g)
5.560	0.36	3.094	0.116
5.835	0.35	3.982	0.088
6.245	0.47	8.079	0.058

[a] Only highest three of six K_1 values obtained.

Combining this with an estimate of Z ≈ 2M = 1.34 $year^{-1}$ leads to Q/B = 5.29% BWD and R_m = 3.02% BWD.

Epinephelus fuscoguttatus

The brown-marbled grouper *Epinephelus fuscoguttatus* (Serranidae) is reported to reach 120 cm and to feed on "bottom-living crustaceans and fishes" (Chan et al. 1974). The growth parameters for a Philippine population were estimated, using a combination of original and comparative data, as TL_∞ = 91.7 cm, W_∞ = 12,338 g, K = 0.19 $year^{-1}$, t_0 = -0.66 year (Palomares and Pagdilao 1988).

Cage experiments conducted in Guiuan, Eastern Samar, Philippines, with *E. fuscoguttatus* fed chopped trash fish led to a multiple regression for predicting food conversion efficiency from weight and food ingested, and corresponding to equation (7), of the form

$$C = 0.2838 - 0.05188 \log_{10}W - 0.00933 R_1 \qquad ...27)$$

where $C = -\log_{10}(1-K_1)$; W is the mean weight of the fish during each of the 14 growth increments used to derive the model; and R_1 is the food ingested. Palomares and Pagdilao (1988) showed how this model led, after some manipulations, to Q/B = 1.1% BWD, for $Z \approx M$ = 0.44 $year^{-1}$, as well as to R_m = 0.8% BWD. Palomares and Pagdilao (1988) also performed some simulations showing the dependence of Q/B on Z. From their Fig. 3, one can estimate, for $Z \approx 2M$, an approximate value of Q/B = 5 $year^{-1}$, or 1.37% BWD.

Epinephelus tauvina

The greasy grouper *Epinephelus tauvina* (Serranidae), which mainly feeds on "bottom-living crustaceans and fishes," is reported to reach up to 150 cm (Chan et al. 1974). Available estimates of asymptotic length are much lower, however, and their mean is 69 cm (Table 12).

The other growth parameter estimates used here are W_∞ = 4,135, estimated from $W = 0.0151 L^{2.96}$ (C. Pagdilao, unpubl. data), K = 0.145 $year^{-1}$ (see Table 12) and t_0 = -0.94.

Table 12. Growth parameters for *Epinephelus tauvina*.

L_∞ (TL, cm)	K ($year^{-1}$)	ϕ'	Source
36.0[a]	0.292	2.578	Loubens (1980)
102.0	0.121	3.100	Mathews and Samuel (1985)
69.0[b]	0.145	2.839[b]	(Means)

[a] From TL = 1.16 SL (Chan et al. 1974), SL_∞ = 30.7 cm.
[b] Mean values.

Table 13 presents the results of three cage growth experiments with greasy groupers, for which we derived ten pairs of W, K_1 data.

These data, together with the estimate of W_∞ above, lead to an estimate of ß = 0.154 (see Fig. 3). Combining this with $Z \approx 2M$ = 0.78 $year^{-1}$ yields an estimate of Q/B = 0.56% BWD and R_m = 0.26% BWD.

Table 13. Weight and gross food conversion efficiency (K_1) of *Epinephelus tauvina* in three separate feeding experiments: 1-4, from Tanomkiat and Pimoljinda (1986); 5 and 6, from Sugama et al. (1986b); and 7-10, from Danakusumah et al. (unpubl. data).

No.	Food type	Body weight (g)[a] W_i	W_f	$\bar{W}$	K_1
1.	"Formula 1"	0.940	16.0	8.5	0.3531
2.	"Formula 2"	0.887	16.6	8.8	0.3611
3.	"Formula 3"	0.854	15.1	8.0	0.6969
4.	Minced fish	0.953	11.0	6.0	0.2529
5.	*Sardinella*	110.000	1,619.0	865.0	0.1316
6.	*Sardinella*	730.00	2,349.0	1,540.0	0.1960
7.	trash fish	129.00	248.0	188.5	0.2016
8.	trash fish	195.00	395.0	295.0	0.1299
9.	trash fish	266.00	411.0	338.5	0.1212
10.	trash fish	789.00	1,080.0	934.5	0.2616

[a] W_i = initial; W_f = final; $\bar{W}$ = mean.

Lutjanus johnii

John's snapper *Lutjanus johnii* (Lutjanidae) is reported to reach a maximum of 70 cm in Southeast Asia and to feed on "bottom-living invertebrates and fishes" (Talbot and Chan 1974). Estimates of L_∞ and K were derived here from length-at-(relative)age data in Druzhinin (1970) for females and males separately, along with indirect estimates of t_0; means over both sexes were computed directly to L_∞ and t_0, and indirectly (via ϕ') for K (Table 14). The mean value of L_∞ = 84.35 cm was converted to an estimate of W_∞ = 8,844 g using

$$W = 0.007678L^{3.147} \qquad ...28)$$

derived from data in Druzhinin (1970).

Table 14. Growth parameter estimates for *Lutjanus johnii*, as obtained from length-at-age data in Druzhinin (1970).

Sex	L_∞ (cm)	K ($year^{-1}$)	t_0 (year)	ϕ'
Males	94.00	0.122	-1.440	3.033
Females	74.70	0.195	-0.678	3.037
Means	84.35	0.152	-0.845	3.035

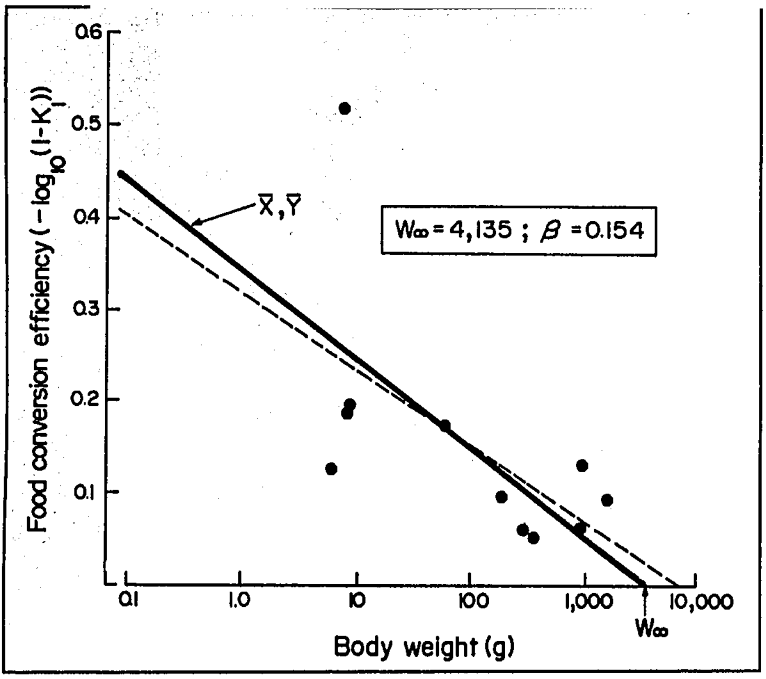

Fig. 3. Relationship between food conversion efficiency (K_1) and body weight (g·ww) in greasy grouper *Epinephelus tauvina*, as used to estimate the parameter $\beta = 0.154$. Dotted lines represents a Type I linear regression; solid line is forced through mean of x, y values and external estimate of asymptotic weight (based on data in Table 13; see text).

The results of the floating cage growth and feeding experiments used here to obtain W, K_1 data are summarized in Table 15.

They lead to an estimate of $\beta = 0.0535$ which, combined with $Z \approx 0.76$ year^{-1}, yields Q/B = 1.34% BWD, and R_m = 0.74% BWD.

Table 15. Summary of growth and feeding data on *Lutjanus johnii*, as obtained by Sugama et al. (1986a).

Body weight (g)[a]			Ingested	
W_i	W_f	$\overline{W}$	food (g)[b]	K_1
145.0	206.2	175.6	442	0.1385
206.2	306.0	256.1	584	0.1709
306.0	472.0	389.0	814	0.2039
472.0	601.3	536.6	1,102	0.1173
601.3	752.8	677.0	1,200	0.1262
752.8	915.0	833.9	1,286	0.1261
915.0	1,128.0	1,021.5	1,661	0.1282

[a] W_i = initial; W_f = final; $\overline{W}$ = mean.
[b] *Sardinella* spp. fed twice daily to satiation.

Zebrasoma scopas

The blue-line sailfin-tang *Zebrasoma scopas* (Acanthuridae), of which *Z. flavescens* is a commonly used synonym, is reported to feed, near Okinawa, on filamentous microalgae (Sano et al. 1984). Direct estimates of growth parameters for this fish, which reaches about 20 cm, do not appear to have been published.

Following an initial attempt by Dalzell (1989), we estimated a value of K for *Z. scopas* from (1) average growth parameters in acanthurids, and (2) growth parameter estimates reported from the related *Z. veliferum* and a set value of L_∞ (Table 16).

Table 16. Preliminary growth parameter estimates in two species of *Zebrasoma*.

Species	FL_∞ (cm)	K (year^{-1})	ϕ'	Source/remarks
Z. veliferum	25	0.330	2.31	From R. Withrow, Waikiki Aquarium, Hawaii, pers. comm. to Dalzell (1989)
Z. scopas	19	0.876	2.50	Dalzell (1989) setting $L_{max} = L_\infty$, and using the mean ϕ' of all acanthurids for which he had growth estimates
Z. scopas	20	0.628	2.40	Intermediate values used in this study

The estimate of TL_∞ = 20 cm, combined with the estimate of K, allows the estimation of t_0 = -0.285 year.

Dalzell (1989) derived for *Z. scopas* the length-weight relationship

$$W = 0.123 \cdot FL^{2.41} \quad ...29)$$

from which W_∞ was estimated as 168 g; this leads to M = 1.38 year^{-1}.

The food conversion experiments conducted with two specimens of *Z. scopas* (at the IfM) yielded very variable results, including negative growth and conversion efficiencies. Table 17 presents the few positive growth increments that were obtained.

Table 17. Food conversion efficiency of an aquarium-held specimen of *Zebrasoma scopas*. The food was almost exclusively mysids; some algae were provided to balance the food, but their energetic contribution can be neglected.

Mean fish weight during increment (g)	Growth increments (g)	Food ingested (g) (g)	K_1
21.2	1.55	11.4	0.136
22.0	1.71	43.3	0.039

The value of ß derived from these data is 0.0453.

From this, the growth parameters derived above and $Z \approx 2M = 2.76$ year^{-1}, we obtain Q/B = 7.75% BWD and R_m = 4.73% BWD.

Siganus spinus

The little spinefoot *Siganus spinus* (Siganidae) which reaches a length of 20 cm is reported to "browse on a wide range of bottom algae" (Woodland 1984).

Pauly (1978), based on Horstmann (1975), estimated for this fish TL_∞ = 24.4 cm, K = 2.32 year^{-1} and t_0 = -0.21 year. The length-weight relationship

$$W = 0.012\ TL^{3.077} \qquad ...30)$$

presented by von Westernhagen and Rosenthal (1976) allows estimation of W_∞ = 234 g. The estimate of $Z \approx 2M$ used here is 6.5 year^{-1}.

Daily ration estimates for *S. spinus* in Guam (in % body carbon day^{-1}) are available (Table 18).

From these data, an estimate of ß = 0.07 is obtained which, when combined with the above parameters, yielded Q/B = 13.13% BWD and R_m = 8.85% BWD.

Scomber japonicus

The Japanese mackerel, which occurs in the Philippines (see Herre 1953), where it is listed under the synonym *Pneumatophorus japonicus*, is a zooplanktivore and piscivore, of which growth parameters are given in Table 19.

Table 18. Daily ration for *Siganus spinus*, adapted from Bryan (1975).

Fork[a] length (cm)	Weight (g)	Assimilation (% of body carbon day^{-1})
5.1	1.91	47
5.2	2.03	60
5.4	2.28	27
5.9	2.99	9
10.7	18.59	20
11.4	22.58	11
11.9	25.76	7
12.3	28.52	39
13.1	34.60	6
13.2	35.42	8
14.0	42.44	24

[a] The ratio FL:TL is 1:1.06.

Table 19. Selected sets of growth parameters of *Scomber japonicus*.[a]

FL_∞ (cm)	K (year^{-1})	ϕ'	Location
46.4	0.400	2.935	Japanese waters
45.5	0.340	2.848	Northwest Pacific
44.0	0.441	2.931	Northwest Pacific, Russian waters
45.3[a]	0.391	2.905	Means

[a] From Pauly (1978).

Data in Frey (1936) allow computation of the length-weight relationship

$$W = 0.00979\ FL^3 \qquad ...31)$$

and hence, given FL_∞ = 45.3 cm, W_∞ = 910 g. The empirical equations in the Methods section allowed, further, the estimation of t_0 = -0.36 year and $Z \approx 2M$ = 1.74 year^{-1}.

The food conversion data used here for estimating the food consumption of *S. japonicus* stem from Hatanaka and Takahashi (1956) and Hatanaka et al. (1957) who maintained their fish on a diet of either anchovies or euphausids.

The food conversion efficiencies were computed for each weight group; the temperature, food type and feeding status were tabulated; and a multiple regression was derived which had the form

$$\begin{aligned} C = {} & 0.0145 - 0.0843 \log_{10} W \\ & + 0.1111 \log_{10} T + 0.0754P \\ & + 0.0344U \qquad ...32) \end{aligned}$$

where $C = -\log_{10}(1-K_1)$, W the mean weight of the fish (in g) within a growth interval, T the water temperature (in °C), p the food type and U the feeding status. The variables P and U were assigned values of 0 or 1, as follows:

$P = 0$: the fish were fed euphausids;
$P = 1$: the fish were fed anchovies;
$U = 0$: the fish were fed regularly; and
$U = 1$: the fish were starved before the experiment.

The multiple correlation coefficient of equation (32) was $R = 0.492$ (d.f. = 138) and all four partial regression coefficients were significant ($P < 0.01$).

The equation was solved, following the method of Pauly (1986) for $W_\infty = 910$ g, $P = 0.5$, $U = 0$, and $T = 16°C$, the mean temperature in the experimental tanks (the equation could have been solved for 27°C, as occurs in the Bolinao area, but this would have involved an extrapolation to outside of the temperature range covered by the experiments). This resulted in $\beta = 0.0629$ which, combined with the estimates presented above, yielded Q/B = 2.95% BWD and R_m = 1.70% BWD. These values, adjusted for a temperature of 27°C, are 4.06% BWD and 2.34% BWD, respectively.

Discussion

The food consumption estimates derived above for five groups of invertebrate and eight species of fishes are summarized in Table 20. The relative (population-weighted) estimates of food consumption range from 3.58 year^{-1} (in echinoids) to 47.9 year^{-1} (in herbivorous siganids). Our results indicate that pelagic fishes and invertebrates have higher food consumption (Q/B) and lower ecological efficiencies (E_t) than demersals, with the same rule also applying to herbivores/detritivores in relation to carnivores.

Similar rules are embodied in the empirical equation of Palomares and Pauly (1989), derived from 33 fish populations

$$\ln Q/B = -0.1775 - 0.2018 \ln W_\infty + 0.6121 \ln T + 0.5156 \ln A + 1.26\,P \qquad \ldots 33)$$

where Q/B is as defined above, on a daily basis, W_∞ is the asymptotic weight of the fishes in question, T the environmental temperature in °C (see also equation 13), A the aspect ratio of the caudal fin (as defined in Fig. 2 of Palomares and Pauly 1989) and P the food type, with $P = 0$ for carnivores, and $P = 1$ for herbivores.

Fig. 4, based on the data in Table 20, shows the relationship between the estimates of Q/B as presented for fishes in the Results section and estimates of Q/B obtained through the empirical model of Palomares and Pauly (1989). There is a good match between these two sets of estimates, the only clear outlier being No. 6 (*Zebrasoma scopas*).

Thus, as far as estimates of Q/B are concerned which pertain to using their caudal fin as (main) organ of propulsion, we conclude that the empirical model of Palomares and Pauly (1989) can be used to obtain reasonable estimate of Q/B. Indeed this model, being based on a large amount of data, may be more reliable than the results of simple feeding experiments, especially

Table 20. Summary of statistics related to the food consumption of the 13 taxa investigated in this contribution.[a]

No.	Species group	Aspect ratio	E_t	R_m (% BWD)	Q/B (% BWD)	Q/B (year^{-1})
	Invertebrates					
	- Sea cucumbers	-	0.1305	0.73	1.05	3.83
	- Sea urchins	-	0.2718	0.64	0.98	3.58
	- Shrimps	-	0.0864	4.98	7.93	28.94
	- Octopus	-	0.2942	1.23	2.00	7.30
	- Squids	-	0.1971	2.92	4.56	16.64
	Fishes					
1.	*Saurida undosquamis*	1.96	0.6323	0.49	1.17	4.27
2.	*Myripristis murdjan*	3.53	0.0694	3.02	5.29	19.31
3.	*Epinephelus fuscoguttatus*	2.08	0.1760	1.00	1.37	5.00
4.	*E. tauvina*	1.54	0.3824	0.26	0.56	2.04
5.	*Lutjanus johnii*	1.91	0.1554	0.74	1.34	4.89
6.	*Zebrasoma scopas*	2.25	0.0976	4.73	7.75	28.29
7.	*Siganus spinus*	3.17	0.1356	8.85	13.13	47.92
8.	*Scomber japonicus*	5.85	0.1174	2.34	4.06	14.82

[a] This refers to food types mentioned in the text; note that herbivores/detritivores eat more than carnivores.

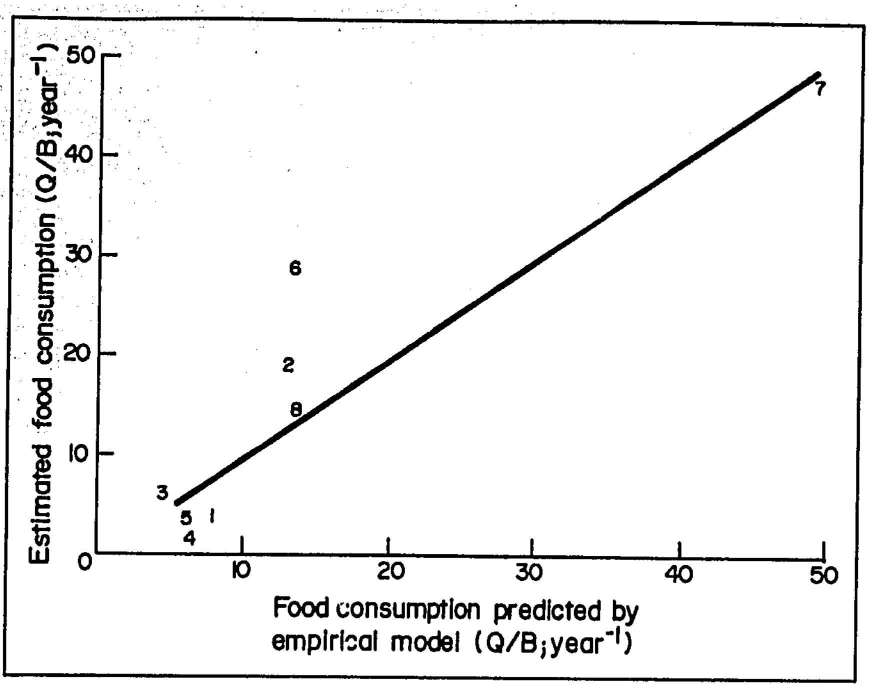

Fig. 4. Plot of the estimated food consumption (Q/B) of the fishes in Table 20 vs. Q/B values obtained through the empirical model of Palomares and Pauly (1989).

for active, easily stressed fishes such as *Z. scopas*, *Dascyllus trimaculatus* (Palomares 1987) or *Holacanthus bermudensis* (Menzel 1958).

The invertebrate groups in Table 20 do not represent all groups, or even the major groups - in terms of energy throughput - of coral reef ecosystems such as those near Bolinao. Thus, it will be necessary, when constructing a model of such reef, to consider the metabolic requirements of several taxa not considered here. An example of such group, to which the methodology presented above would be particularly applicable, are the sea hare (Family Aplysiidae), whose growth and mortality were reported upon by Pauly and Calumpong (1984), and whose feeding and general biology were studied by Carefoot (1967), Calumpong (1979), Kandel (1979) and others.

On the long run, however, empirical relationships linking Q/B and other rates, and/or with their shape will be required for major marine invertebrate groups, if coral reef modelling is to advance more rapidly than has hitherto been the case.

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Initial Parameter Estimations of a Coral Reef Flat Ecosystem in Bolinao, Pangasinan, Northwestern Philippines

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Abstract

Initial parameter estimates for the reef flat around Santiago Island, Bolinao, Pangasinan, in the Philippines, were obtained for 24 subcomponents of the ecosystem. Four primary producer groups (benthic seaweed, seagrass, corals and phytoplankton), five invertebrate benthos (sea cucumbers, sea urchins, coral polyps, crustaceans and molluscs), 12 commercially important fish groups, zooplankton, squids and a detritus box were quantified utilizing ECOPATH II. Reasonable estimations of ecotrophic efficiencies were obtained for most of the components. The model helped to indicate areas for further investigation of the system, especially biomass estimations of cryptic species and the food consumption for key top predators such as the moray eel (*Gymnothorax pictus*).

Introduction

Tropical reefs are diverse and complex ecosystems. Understanding their structure and function relationships is a formidable challenge. Ecosystem models, such as ECOPATH II (Christensen and Pauly 1992 and this vol.), provide a useful tool in gaining insights about such systems. These initial estimations of the Bolinao reef flats in the Philippines indicate leads for further refining the quantification of the components of the system. Verifying the inputs and outputs can also be used in various fisheries-related decision options and in investigating processes important in developing countries' multispecies, multigear fisheries activities.

Materials and Methods

Background

Bolinao, Pangasinan Province, is located in the southwestern corner of Lingayen Gulf in northwestern Luzon, Philippines, at 16°25'N latitude and 119°55'E longitude. The Bolinao Marine Laboratory, a field station of the University of the Philippines Marine Science Institute (UPMSI), is situated proximal to the reef flat study site referred to in this paper. Most of the information used here stems from the various research projects of UPMSI, while some estimates were obtained from secondary sources, referring to comparable areas. Presented are various data sources and our computed approximations adopted for the Bolinao reef flat. The area of the reef flat is approximately 240 km^2 with an average depth of 2 m, dominated by seagrass (del Norte and Pauly 1990). The site is situated on a fringing back reef flat; scattered coral patches, composed of *Pavona decussata* and *Porites,* cover about 10% of the ground. Detailed descriptions of the macrobenthic invertebrates are in de Guzman (1990). Campos et al. (1989) gave an overview of the fisheries yields of the area and Nañola et al. (1990) provided fish visual census estimation. Trono and Lluisima (1990) estimated standing crop seasonality of the *Sargassum* zone of these reef flats which occupies the area before the coral community crest zone. Plankton productivity was investigated by L.T. McManus and G.S. Jacinto (unpubl. data). The currency of the model is g·ww·m^{-2}year^{-1}.

Plankton Biomass and Productivity Estimates

The average annual zooplankton biomass observed by L.T. McManus was 262-312 mg·dw·m^{-2}. We estimated this to be 2.87 g·ww·m^{-2} with a P/B ratio of 40 and a gross food conversion efficiency (GE) of 0.30. Chlorophyll *a* measurements averaged 0.12 g·dw·m^{-3} (G.S. Jacinto, unpubl. data), which was converted to 0.3 g·ww. Based on Larkum's (1983) estimated range of phytoplankton productivity, a P/B ratio of 30.4 year^{-1} was estimated.

Invertebrate Productivity and Biomass

Sea cucumber mortality (Z) rates from Leonardo and Binohlan (1986) were used for P/B values. Gross efficiency (P/Q) was assumed to be 0.20. Sea urchin had the highest invertebrate herbivore biomass (35.8 g·m^{-2}year^{-1}) (M.J. Trinidad Roa and J.N.D. Pasamonte, unpubl.), and a P/B of 7.5 year^{-1}. Mollusc biomass values were based on Klump and Polunin's (1989) biomass estimates for macroinvertebrates in the Great Barrier Reef. P/B values were computed from ELEFAN II estimates of *Strombus luhuanus* (W. Licuanan, pers. comm.). P/B estimates for squids (*Sepioteuthis lessoniana*) were taken from Balgos (1990). The GE for crustaceans was assumed to be 0.30. The sessile invertebrate consumer biomass estimate of 200 g·m^{-2} was based on an estimate of 40% of 500 g·ww·m^{-2} for coral polyp biomass (Sorokin 1981) for the reef crest in the Great Barrier Reef. Sessile invertebrate producer biomass was based on Benson and Muscatine's (1974) estimate of 45% of the protein biomass of the *Pocillopora damicornis*. The P/B ratios of sessile invertebrate producers were also estimated based on Sorokin (1981) and the P/B of sessile invertebrate consumers was adjusted to 0.1 instead of 0.04 (year^{-1})

Benthic Plant Production and Biomass

Seagrass biomass of 61.7 g·organic matter·m^{-2} and productivity of 1.4 gC·m^{-2}day^{-1} were based on Fortes (1990) and were converted to a biomass estimate of 702 g·ww·m^{-2} and a P/B ratio of 8.43. Used were an average seaweed biomass of 832 g·ww·m^{-2} based on Trono and Lluisima's (1990) study, and a productivity based on growth studies estimated at 12,763 g·ww·m^{-2}year^{-1}, thus a P/B of 15.34 year^{-1}.

Fish Production and Biomass

Siganus fuscescens had the highest fish biomass of 1.82 g·ww·m^{-2}, based on del Norte and Pauly's (1990) virtual population analysis. Most of the other reef fish biomass estimates were based on fish visual census (Nañola et al. 1990). These provided good estimates for fishes in the coral associated species, such as *Siganus spinus*, pomacentrids (damselfish), scarids and chaetodontids (other omnivorous fish). The biomass of cryptic and camouflaged fish groups in the seagrass areas was complemented with nighttime trawl data, although the trawl data may also underestimate biomasses.

Consumption and Exports

Estimated exports were based on fisheries catch data. Invertebrate fish catches for sea urchins (gonads = 0.26 g·m^{-2}·year^{-1}), sea cucumber (1.57 g·m^{-2}·year^{-1}) and gastropods (2.34 g·m^{-2}·year^{-1}) were taken from de Guzman (1990). Estimates for crustaceans were from the ASEAN/US Coastal Resources Management Project in Bolinao led by L.T. McManus. Fish catch data were based on the USAID Fish Stock Assessment /Collaborative Research Support Program FSA/CRSP monitoring of Bolinao reef fisheries organized by J.W. McManus.

Food consumption estimates from Pauly et al. (this vol.) provided a good basis for many of the Q/B values in this paper: crustaceans (based on shrimp), cardinalfishes, *Siganus spinus* (soldierfish, *Myripristis murdjan*), groupers (*Epinephelus tauvina* and *E. fuscoguttatus*) and other herbivorous fish (e.g., *Dascyllus melanurus*). Q/B for *S. fuscescens* was based on

Hernandez et al. (1990). Data on *Stegastes apicales* for damselfishes, parrotfishes and other omnivorous fishes were recomputed based on Klump and Polunin's (1989) blenny and molluscs. The wrasse Q/B was estimated based on the caudal fin aspect ratio of *Choerodon ancorago* using Palomares and Pauly's (1989) equation with T = 27°C and W_∞ = 1,300 g. Other consumption estimates were calculated using gross efficiency inputs of 0.30 or 0.20 (see Table 1).

Predation Flows

Aside from the diet composition of *Siganus fuscescens,* which is based on gut content analysis of specimens from the study site, inputs for the diet composition matrix were largely based on Hiatt and Strasburg's (1960) works in the Marshall Islands. Sea urchin diet composition was based on Guieb's (1981) work in a similar reef flat of Calatagan, Batangas, southern Luzon, Philippines. Diet proportion was adjusted, using available knowledge on generally accepted feeding habits, so that the estimated ecotrophic efficiencies did not exceed unity.

Results and Discussion

Fig. 1 illustrates the major trophic flows in the Bolinao reef flat ecosystem, while Fig. 2 presents all the trophic flows in the system, including exports respiration and flows to detritus.

Although the system output in general seems comparable with commonly accepted values, some caveats must be expressed with regard to components of the system. For the predators, EE values ranged between 0.63 and 0.98, whereas values for the damselfish (EE = 0.40) and sea urchins (EE = 0.14) were rather low. This can possibly be attributed to the relatively high biomass estimates of these groups, perhaps caused by overrepresentation in visual censuses. Conversely, underestimation in visual census surveys of cryptic (moray eel) or camouflaged species may have caused too low biomasses estimates for such groups.

The high estimate of biomass for sea urchin may be appropriate for many areas of Bolinao. On the other hand, much higher estimates of exports might be present as the fisheries catch was estimated by multiplying by 5 the recorded processed gonads sold from the area. Also, it was possible that these sea urchins had a relatively high episodic mortality, perhaps due to diseases as might be observed from many empty sea urchin tests from time to time in some areas. The input values for P/B, based on the assumption that the total mortality equals two times the natural mortality may not be tenable, which could also cause bias in the Q/B values.

Table 1. Input values and estimated parameters (in brackets) for ECOPATH II model of the Bolinao reef flat, Philippines.

	Group	Export ($g \cdot m^{-2} year^{-1}$)	Biomass ($g \cdot m^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	GE (P/Q)
1.	Seagrasses	0.000	702.00	8.43	0.00	(0.14)	-
2.	Seaweeds	0.988	832.00	15.34	0.00	(0.03)	-
3.	Zooplankton	0.000	2.87	40.00	(133.33)	(0.91)	0.3
4.	Sea cucumber	1.570	0.37	4.45	(22.25)	(0.95)	0.2
5.	Sea urchins	1.300	35.77	7.51	(25.00)	(0.14)	0.3
6.	*Siganus fuscescens*	2.760	1.82	2.21	124.00	(0.73)	0.0
7.	*Siganus spinus*	0.800	0.71	6.50	47.92	(0.18)	0.1
8.	Groupers	0.176	0.24	(0.80)	4.00	(0.92)	0.2
9.	Wrasse	0.300	0.34	1.51	7.55	(1.00)	0.2
10.	Moray	0.095	0.10	(1.30)	(6.50)	0.95	0.2
11.	Damselfishes	0.100	0.73	3.30	54.70	(0.40)	0.1
12.	Gobies	0.040	0.04	14.02	70.09	(0.95)	0.2
13.	Parrotfish	0.974	1.30	(5.60)	28.00	0.95	0.2
14.	Cardinalfishes	0.325	0.41	(3.88)	19.39	(0.95)	0.2
15.	Squids	0.750	(0.65)	3.10	(16.64)	0.95	0.2
16.	Other planktivorous fish	0.006	0.08	2.73	13.65	(0.92)	0.2
17.	Other piscivorous fish	0.169	0.34	(1.00)	5.00	(0.98)	0.2
18.	Other herbivorous fish	0.004	0.01	(3.00)	15.00	(0.76)	0.2
19.	Other omnivorous fish	0.106	0.71	(6.18)	30.90	(0.91)	0.2
20.	Sessile invertebrate consumers	0.000	200.00	0.10	(0.50)	(0.12)	0.2
21.	Sessile invertebrate producers	0.000	90.00	3.20	0.00	(0.13)	-
22.	Other invertebrates	0.000	15.81	(3.00)	15.00	0.95	0.2
23.	Crustaceans	0.276	(6.24)	8.40	28.00	(0.95)	0.3
24.	Molluscs	2.340	3.11	2.80	5.60	(0.95)	(0.5)
25.	Phytoplankton	0.000	0.30	30.42	0.00	(0.92)	-

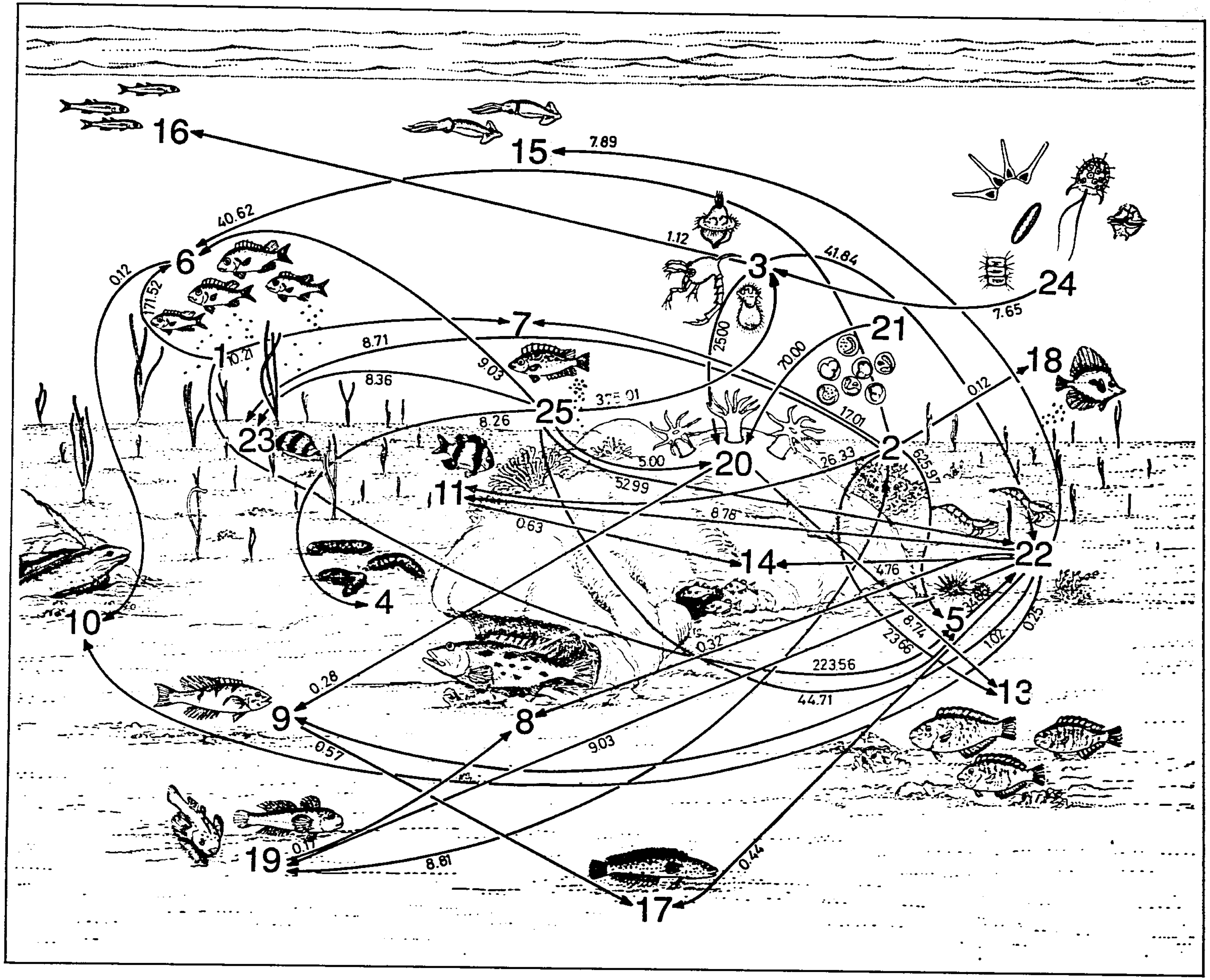

Fig. 1. Major trophic flows (g·m^{-2}year^{-1}) of the Bolinao reef flat ecosystem, Philippines. Only the quantitatively more important flows are illustrated (see also Fig. 2).

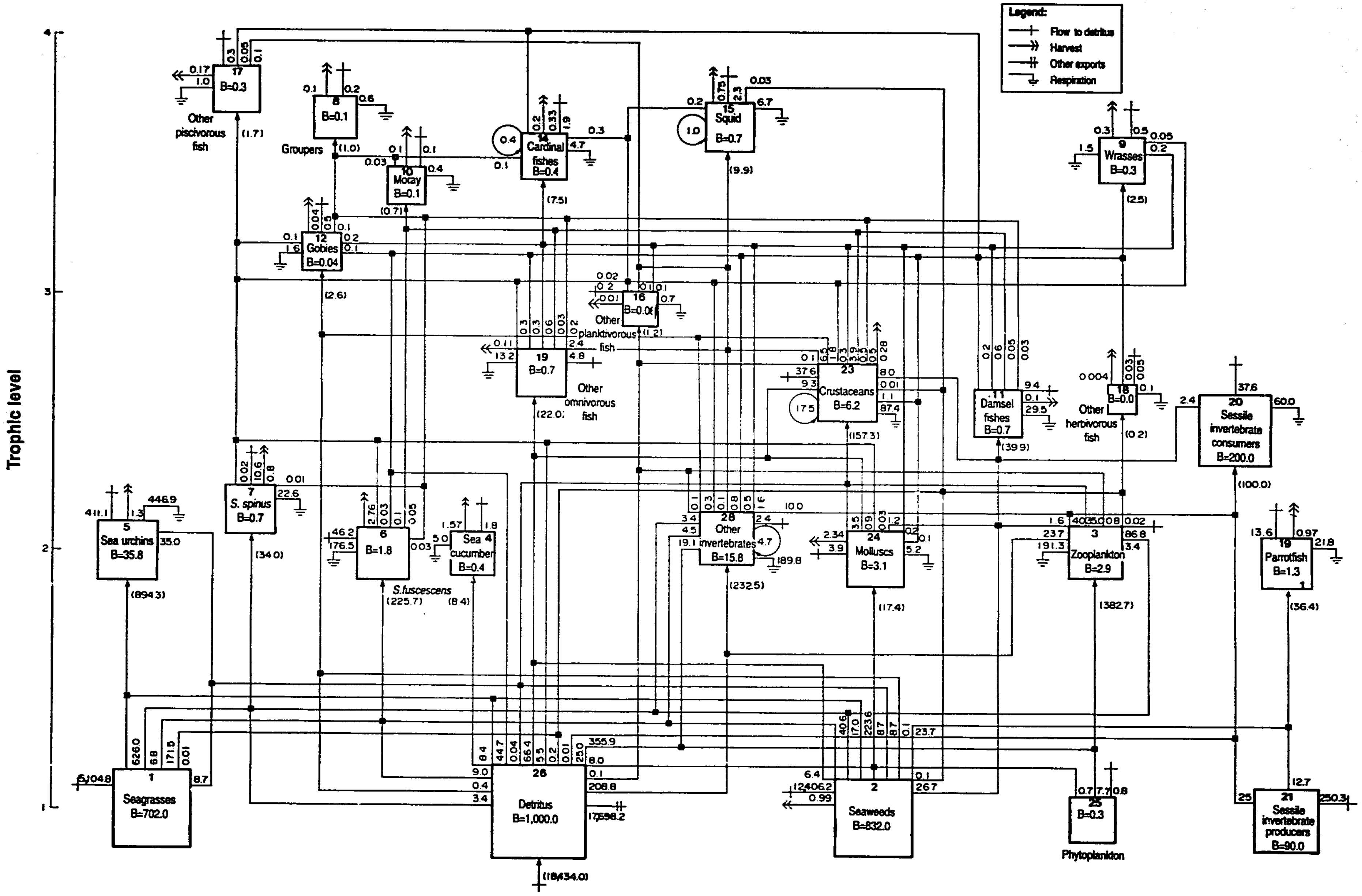

Fig. 2. Trophic flows (g·ww·m^{-2}year^{-1}) in the Bolinao reef flat ecosystem, Philippines.

Table 2. Trophic transfer matrix for the Bolinao reef flat model showing distribution of flows ($g \cdot m^{-2} year^{-1}$) by groups and trophic levels. The bottom line gives the trophic transfer efficiencies (%) by trophic level for the entire system.

Group	Average trophic level	Trophic level						
		I	II	III	IV	V	VI	Overall flow
Other piscivorous fish	3.8	-	0	0.6	0.6	0.3	0.0	1.5
Groupers	3.7	-	-	0.5	0.4	0.1	0.0	1.0
Squids	3.7	-	-	6.1	4.2	0.5	-	10.8
Cardinalfishes	3.6	-	-	5.0	2.5	0.3	0.0	7.8
Wrasse	3.6	-	-	1.7	0.8	0.1	0.0	2.6
Moray	3.4	-	0	0.4	0.2	0.0	0.0	0.6
Gobies	3.2	-	1	1.2	0.9	-	-	3.1
Other planktivorous fish	3.0	-	0	1.0	0.1	-	-	1.1
Other omnivorous fish	2.7	-	12	5.8	4.3	-	-	22.1
Other herbivorous fish	2.6	-	0	0.0	0.0	0.0	0.0	0
Crustaceans	2.6	-	93	81.6	-	-	-	174.6
Sessile invertebrate consumers	2.5	-	50	49.8	0.2	-	-	100
Damselfishes	2.5	-	27	8.2	4.9	0.0	-	40.1
Siganus spinus	2.2	-	27	6.7	0.1	-	-	33.8
Other invertebrates	2.1	-	232	5.1	-	-	-	237.1
Zooplankton	2.1	-	383	-	-	-	-	383
Siganus fuscescens	2.0	-	221	4.4	0.1	-	-	225.5
Sea cucumber	2.0	-	8	-	-	-	-	8
Sea urchins	2.0	-	894	-	-	-	-	894
Parrotfish	2.0	-	36	-	-	-	-	36
Molluscs	2.0	-	17	-	-	-	-	17
Seagrasses	1.0	5,918	-	-	-	-	-	5,918
Seaweeds	1.0	12,763	-	-	-	-	-	12,763
Sessile invertebrate producers	1.0	288	-	-	-	-	-	288
Phytoplankton	1.0	9	-	-	-	-	-	9
Detritus	1.0	18,434	-	-	-	-	-	18,434
Total	-	37,412	2,002	178	19.3	1.3	0.0	39,612.6
Trophic transfer efficiencies (%)	-	-	9.1	11.9	10.3	10.8	12.8	-

The gross efficiency for molluscs seems unrealistically high (0.5), indicating that half of the consumed food is turned into production. Although the biomass estimate of the sessile invertebrate consumers (which here may include soft corals, sponges and tunicates) are speculative, they seem to provide acceptable results. It is still not very clear how to treat the symbiotic nature of these organisms in the trophic predator-prey interaction process.

A representation of the breakdown of trophic flows by group and trophic level using the trophic aggregation routine of ECOPATH II is given in Table 2. The seaweeds contribute the majority of the flows among the producers. The contribution from the corals only amounts to a small percentage of the overall production, while the phytoplankton shows a negligible production. On the herbivore/detritivore level (II) the most important group is the sea urchins (45%) followed by zooplankton, other invertebrates and *S. fuscescens*. The first-order carnivore level (III) is dominated by crustaceans and the corals. The higher trophic levels include fishes and squid.

The trophic transfer efficiencies (Table 2) give the proportion of the flows entering a trophic level that is ultimately transferred to the next trophic level or to the fishery. The transfer efficiencies fluctuate between 9% and 13% without any trend. They are thus very much in agreement with what is considered "Good Latin" in ecology textbooks.

Overall, the ECOPATH II model has provided us with some insights into prioritizing and refining our estimations of the structural components (e.g., biomass estimates) of the Bolinao reef flat and the functional relationships, (i.e., predator-prey interactions and ecotrophic efficiencies). This may go a long way in helping us in our research thrusts and in pursuing management options for the Bolinao fisheries.

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A Quantitative Model of the Trophic Interactions in a Caribbean Coral Reef Ecosystem

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Abstract

A detailed steady-state model of the trophic interactions and organic matter transfer in a Caribbean coral reef is presented, based mainly on published data on fishes and invertebrates sampled in the Virgin Islands. System parameters and mixed trophic impacts were calculated with the ECOPATH II program. This preliminary version of the model consists of 21 boxes with 9 fish species group and 11 nonfish groups which include primary producers and detritus. The balanced model indicates that a thermodynamically feasible model of a coral reef can be constructed from published data and parameter calculations derived from multivariate statistics.

Introduction

Coral reefs are tropical marine shallow-water ecosystems, characterized by three key features: (1) high species diversity, (2) pronounced complexity of relationships within the system community and (3) high rates of production in usually nutrient-poor and plankton-impoverished oceanic waters. All three features are interconnected, and thus, they recycle and conserve organic matter effectively within the system. Features (1) and (2) challenge the skill of modellers to simplify diversity and complexity and still produce a representative image of the system under consideration.

An attempt is presented here - as part of a larger study - to construct a thermodynamically feasible model of a coral reef ecosystem from published data and various parameter calculations derived from multivariate statistics. The ECOPATH II program (Christensen and Pauly, this vol.) was selected as a suitable tool for such an approach. Its predecessor, ECOPATH (Polovina 1984), was originally developed for modelling a coral reef in Hawaii. It assumes the system to be in a steady state, i.e., that the biomass of the elements of the system does not change from one modelled time interval to the next; this in our opinion, holds true for coral reefs to a higher degree than for many other ecosystems. ECOPATH and ECOPATH II require relatively easily obtainable input information for the system components and produce a box model wherein trophic linkages are described quantitatively. ECOPATH II is a strongly modified and enhanced version of ECOPATH. In addition to quantifying trophic flows between compartments, it computes a variety of indices for comparison of systems based mainly on theoretical concepts developed by Ulanowicz (1986) and includes routines for an objective aggregation of species groups and determination of mixed trophic impacts. For an exhaustive description of features and functioning of ECOPATH II, see Christensen and Pauly (1992a, 1992b).

The coral reefs fringing the Virgin Islands, Caribbean were selected for the present model. The choice was primarily determined by the exhaustive investigations on feeding habits of West Indian reef fishes carried out by Randall (1967), combined with the then low exploitation rates by fisheries. For this modelling effort, which describes a reef in the 1960s-1990s, an unexploited system was assumed. These fringing reefs form one of several distinct ecological subsystems that are interconnected through various components and processes. Based on our own independent literature studies, we agree with Jacobsen and Browder's (1987) concept of distinctive, though interconnected subsystems (Fig. 1). This concept enabled us to define an area with minimal exchange with surrounding systems, which makes the steady-state assumption more realistic.

To our knowledge the preliminary model presented here describes for the first time quantitative trophic linkages and organic matter transfer within a Caribbean coral reef system. A strongly enhanced version of the model with an exhaustive description of its construction is presented by Opitz (1991).

Materials and Methods

The database of the model consists exclusively of published data, mainly based on investigations in the Virgin Islands and Puerto Rico. The database was completed with information from the wider Caribbean sea, mainly Jamaica (e.g., Munro 1983), Cuba (e.g., Alcolado 1990; Claro 1990), Florida and Venezuela. In some cases data from even more remote areas had to be applied.

The system components were grouped into two qualitatively distinct main groups: fish species and nonfish taxa. For each main group inputs to ECOPATH II were prepared in a group specific way. The various procedures are described below. The currency of the model is g live weight per m^2; all rates are annual.

Fish Species

From Randall (1967, 1968, 1983), the fish species occurring on reefs and related subsystems of the Virgin Islands were determined; 250 fish species were thus identified. For the majority, a diet matrix was developed based on Randall (1967). Biomass values (in g live weight·m^2) were obtained from censuses carried out by Boulon (1986) and from quantitative estimates (e.g., Randall 1968, 1983; Clavijo et al. 1980). Production/biomass (P/B) values originated from estimation of natural mortality M (no exploitation by fisheries). Most values of M were computed with an empirical equation suggested by Pauly (1980). Annual consumption (Q/B) was obtained applying an empirical relationship developed by Palomares and Pauly (1989), which requires estimates of asymptotic weight (W_∞), mean environmental temperature, aspect ratio (A, square of the height of the caudal fin over its area) and the food type. W_∞ was obtained directly from published sources or converted from L_∞ through appropriate length-weight relationships.

Mean environmental temperature was read off DHI tables (1967) to be approximately 28°C. The aspect ratio was determined with a video

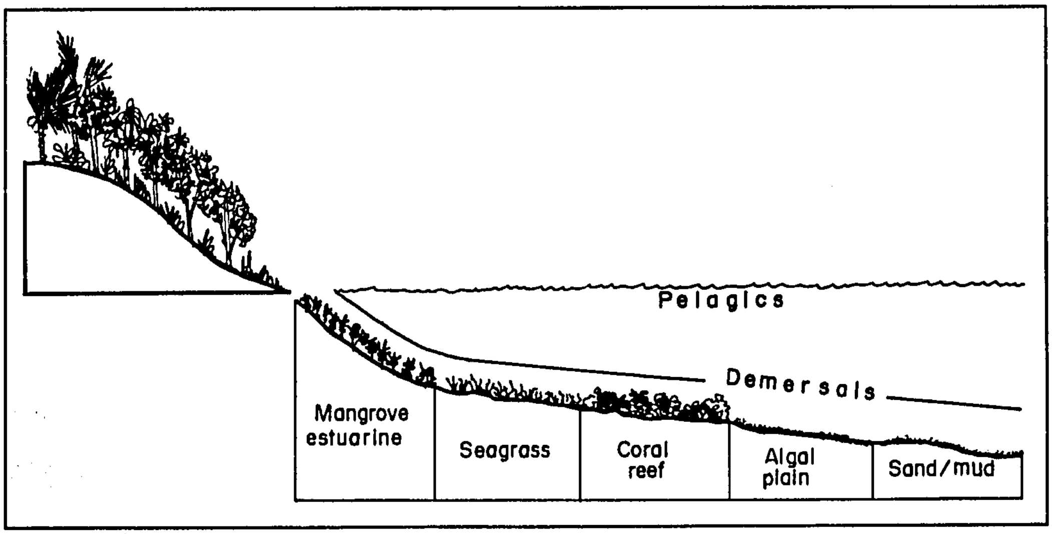

Fig. 1. Schematic representation of the subsystems included in the Caribbean reef ecosystem model (from Jacobsen and Browder [1987] modified).

image analyzing system, mainly from photographs in Randall (1968). The corresponding food type was assigned to each species from the diet composition (0 = carnivorous, 1 = omnivorous). To produce energetically consistent species groups, fish species were aggregated into compartments by cluster analysis. Aggregation parameters were asymptotic weight, aspect ratio and percentage of herbivory. To separate pelagic schooling forms from demersal species the habitat (1. pelagic-midwater, 2. demersal-off bottom) was introduced as an additional aggregation feature outside the cluster analysis. Large predators such as sharks, scombrids and others were not grouped for this last feature since information on habitat is too fragmentary or lifestyle is too variable to yield reliable results. Table 1 shows assemblage characteristics and representative species (based on biomass) of the resulting nine fish species groups. The corresponding input values obtained through the above-described methods for the ECOPATH II parameter estimation routine are listed in Table 2. Group values are the medians of species specific values.

Nonfish Groups

From the stomach analyses in Randall (1967) a list of approximately 400 species of invertebrates and sea turtles and 130 benthic algae and spermatophytes was assembled, then reduced to 36 taxonomic groups. A diet matrix was prepared from a voluminous collection of published sources on the food and feeding habits of reef invertebrates, especially those listed in Randall (1967). Various methods were used to estimate vital statistics for these invertebrates; the quality of estimated values varied strongly between taxa and parameters and not all taxa could be provided with estimates for the required input parameters. Then, the 36 taxa were further reduced to 11 nonfish groups (NFG) with taxonomic affinities and intuition providing aggregation criteria. No objective ecological criterion, e.g., food type or size, could be applied systematically, since size-specific or diet-specific information could be obtained only for very few species or even genera.

Composition of Nonfish Groups

"Cephalopods" comprise squids and octopuses mainly *Octopus vulgaris*. Four taxa form the "echinoderms" group; echinoids with the predominantly herbivorous *Diadema antillarum* having the highest biomass of sea urchins on reefs and seagrass flats in the Virgin Islands; the asteroids, holothuroids and ophiuroids. Crinoids were dealt with summarily: no component of the community was found to feed directly on crinoids

Table 1. Assemblage characteristics for nine fish species groups defined by cluster analysis. N = number of species per group; ADC = average distance between clusters (= similarity index); W_∞ = asymptotic live weight in kg; A = aspect ratio of group (median of species-specific values); H = habitat (a feature not included in cluster analysis); P = pelagic, D = demersal. Under diet, "Carn." is carnivorous, "Omni." is omnivorous and "Herb." is herbivorous.

Fish species group	N	ADC	W_∞	A	Diet	H	Representative species
Large sharks/rays	13	0.54	90-700	7.0[a]	Carn.	P/D	*Dasyatis americana* *Galeocerdo cuvieri*
Scombrids/jacks/sharks	17	0.38	2-80	5.0	Carn.	P/D	*Caranx ruber* *Scomberomorus regalis*
Large schooling fish	17	0.55	0.15-2.80	3.0	Carn.	P	*Harengula humeralis* *Opisthonema oglinum*
Small schooling fish	6	0.50	0.008-0.110	1.9	Omni.	P	*Jenkinsia lamprotaenia* *Atherinomorus stipes*
Large groupers	2	0.48	90-380	1.3	Carn.	D	*Epinephelus itajara* *Mycteroperca bonaci*
Large carnivorous reef fish	107	0.55	0.1-70	1.3	Carn.	D	*Diodon holacanthus* *Ocyurus chrysurus*
Large herbivorous reef fish	21	0.53	0.6-23	1.8	Herb.	D	*Scarus guacamaia* *Scarus vetula*
Small omnivorous reef fish	52	0.50	0.002-0.450	1.3	Omni.	D	*Thalassoma bifasciatum* *Nystactichthys halis*
Small herbivorous reef fish	10	0.59	0.004-0.330	1.3	Herb.	D	*Sparisoma radians* *Coryphopterus glaucofraenum*

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[a] Approximate value for sharks (with heterocercal tails) assumed to also reflect activity level of rays.

Table 2. Results of ECOPATH II parameter estimation for construction of box model. Inputs which had to be modified are shown in parentheses. P/B = production/biomass ratio; Q/B = consumption/unit biomass; EE = ecotrophic efficiency (part of production consumed by predators).

Species group	Trophic level	Biomass (g·m^2)		P/B (year^{-1})		Q/B (year^{-1})		EE
Large sharks/rays	3.84	1.0[a]	(96.06)	0.24[a]	-	4.90[a]	-	0.59
Scombrids/jacks/sharks	3.86	4.4[a]	(37.19)	0.48[a]	-	8.90[a]	-	0.48
Large schooling fish	3.74	20.0[a]	(32.01)	0.83[a]	-	12.70[a]	-	0.73
Small schooling fish	3.80	30.0[a]	(5.09)	1.80[a]	(1.50)	20.05[a]	-	0.93
Large groupers	4.10	4.0[a]	(18.11)	0.37[a]	-	2.30[a]	-	0.11
Large carnivorous reef fish	3.41	75.0[a]	(187.77)	0.64[a]	-	7.30[a]	-	0.95
Large herbivorous reef fish	2.01	100.0[a]	(124.64)	1.05[a]	(0.97)	22.80[a]	-	0.97
Small omnivorous reef fish	2.93	10.0[a]	(12.63)	1.60[a]	(1.57)	12.80[a]	-	0.87
Small herbivorous reef fish	2.01	10.0[a]	(5.18)	1.82[a]	-	37.45[a]	-	0.90
Sea birds	4.62	0.015[c]	-	5.40[c]	-	80.00[c]	-	0.16
Sea turtles	2.79	0.070[c]	(0.015)	0.20[c]	(0.15)	3.50[c]	-	0.30
Cephalopods	3.89	8.0[b]	(10.00)	3.10[d]	(3.06)	11.70[e]	-	0.77
Echinoderms	2.40	600.0[f]	(880.00)	1.20[g]	(1.50)	4.00[h]	(3.1)	0.52
Crustaceans	2.98	120.0[f]	(160.00)	1.60[i]	(1.10)	10.00[j]	(20.0)	0.85
Miscellaneous molluscs/worms	2.35	430.0[f]	-	2.50[k]	(2.90)	7.00[b]	(6.0)	0.94
Sessile animals	2.06	1,000.0[l]	-	0.80[m]	-	9.00[n]	(12.0)	0.94
Zooplankton	2.80	30.0[o]	(18.00)	45.00[c]	(40.00)	165.00[p]	-	0.90
Decomposers/microfauna	2.00	60.0[q]	-	100.00[r]	(150.00)	215.00[b]	(350.0)	0.79
Phytoplankton	1.00	25.0[r]	-	70.00[c]	-	-	-	0.78
Benthic autotrophs	1.00	1,375.0[s]	-	13.25[t]	-	-	-	0.30
Detritus	1.00	2,000.0[u]	-	-	-	-	-	0.99
Range of % change		-97/+489	(100)	-33/+46	(100)	-50/+29	(100)	
Mean % change		42	-	2.8	-	-2.7	-	
Median % change		-20	-	0	-	0	-	

Sources:

[a] See text for explanation.

[b] Assumed value, based on comparisons with similar group/area.

[c] Polovina (1984) for French Frigate Shoals.

[d] Mean of females and males of *Octopus vulgaris* from Buchan and Smale (1981).

[e] Mean of squids (Pauly et al., this vol.) and octopuses (food conversion values for *O. vulgaris* from Buchan and Smale [1981] and growth parameters from Guerra [1979]; Q/B computed with MAXIMS [Jarre et al. 1990]).

[f] Table IV in Lewis (1981, after Glynn 1973); conversion factor dw-ww from Pauly et al. (this vol.).

[g] Mean of Lewis (1981) and Schwinghamer et al. (1986).

[h] Mean of echinoids and holothurians from Pauly et al. (this vol.). Value for echinoids weighted by occurrence of genus in stomach analyses of reef fishes by Randall (1967).

[i] Mean of four values for amphipods, isopods (Schwinghamer et al. 1986), lobsters (Buesa Mas 1969) and crabs (Polovina 1984).

[j] Mean of four values for amphipods (Cammen 1980), shrimps (Pauly et al., this vol.), lobsters and crabs (Polovina 1984).

[k] Mean of three values for polychaetes, gastropods and bivalves (Schwinghamer et al. 1986).

[l] Sponges: 750 g·m^{-2} ww (Wilkinson 1987; value reduced for 25% inorganic sceletal material); corals: 200·gm^{-2} ww (Alcolado 1990; value reduced for 75% algal symbionts); tunicates and bryozoans roughly 50 g·m^{-2} ww (Dahl 1973).

[m] Odum and Odum (1955) and Sorokin (1987).

[n] Mean of sponges (based on Wilkinson 1987) and corals (based on Sorokin 1987).

[o] Based on Sorokin (1987); value per m^2 for assumed mean water depth of 10 m.

[p] Mean of Polovina (1984) and Sorokin (1987).

[q] Sum of: bacteria in substrate, foraminifera (Odum and Odum 1955) and bacteria in water column (Sorokin 1987).

[r] Based on Sorokin (1987).

[s] Odum and Odum (1955); 211 g C m^{-2} = 703 g·m^{-2}·dw = 2,818 g·m^{-2} ww.

[t] Gonzalez-Liboy (1979): mean daily rate (%) * 3.65.

[u] Calculated after Pauly et al. (this vol.) with PP = 4,500 g C·m^{-2}·year^{-1} and euphotic depth = 40 m.

and therefore they were not included in the database. "Crustaceans" comprise a wide variety of taxa ranging from small-sized groups like isopods, amphipods and tanaids to larger groups such as shrimps, lobsters, hermit crabs and crabs. All molluscs except the cephalopods and all groups of wormlike animals were included in the box "miscellaneous molluscs/worms". They were chitons, gastropods, bivalves, scaphopods, sipunculids, echiurids and polychaetes. The "sessile animals" group was also very heterogeneous; it comprised sponges, hydrozoans (fire corals), gorgonians (sea fans), zoantharians (sea anemones), seleractinians (stony corals), bryozoans, barnacles and tunicates. Corals were separated from their algal symbionts, which were combined with "benthic autotrophs". "Decomposers/microfauna" comprise benthic and pelagic bacteria populations and foraminiferans which form the bulk of the biomass of this group (see Odum and Odum 1955). "Benthic autotrophs" included fleshy macrophytes, filamentous endolithic algae, filamentous epilithic and sand-dwelling algae, encrusting coralline algae, symbiotic zooxanthellae and seagrasses. "Detritus" is the pool for dead organic material, including particulate organic matter (POM) and dissolved organic matter (DOM). Final group values of input parameters were obtained by identifying the median of available values for components of a group. In various cases a single value per parameter per group was accepted as representative for the whole group. The values, together with a very condensed summary on the origin of ECOPATH II input parameters for 11 NFGs, are listed in Table 2.

ECOPATH II Parameter Estimation Routine

The original values of the parameters and the diet matrix for components of a Virgin Islands reef yielded ecotrophic efficiencies (EE) that in several cases exceeded 1. The EE values were the leading check parameters for equilibration of the model. EE is the part of production consumed by predators, so EE must be < 1; for primary producers it should be < 0.7. Part of the original biomass inputs had to be considerably modified to equilibrate the model. The biomass of "large sharks/rays" needed to be lowered from 96 to 1 $g{\cdot}m^{-2}$. Biomass estimation of large predators with wide ranging movements is critical. It is mostly determined by accidental presence of individuals during census. Another focus of change was the shift in the food matrix from "crustaceans" to "miscellaneous molluscs/worms" as prey item (i.e., usually to a lower trophic level). Gross efficiencies, depending on the relation of consumption and production, were within an appropriate range for the boxes of the system, so that these parameters needed to be modified only slightly. The extent of modifications necessary to equilibrate the model is shown in Tables 2 and 3.

Results and Discussion

The box model resulting from outputs of the ECOPATH II parameter estimation routine is depicted in Fig. 2. Trophic relations are tight, the high EE values (Table 2) indicate only little surplus biomass production. The box model shows that the system's secondary production is based mainly on detritus and benthic autotrophs with short pathways. A comparison of total fish biomasses (254 g live weight$\cdot m^{-2}$) from the ECOPATH II model for a Caribbean coral reef with independent estimates (e.g., Randall 1963, 160 $g{\cdot}m^{-2}$ for a Virgin Islands fringing reef; Talbot and Goldman 1972, 209 $g{\cdot}m^{-2}$ for an offshore reef of the Great Barrier reef) reveals that the model estimate is reasonable, especially when considering that Randall (1963) did not include pelagic fish species (groups 1-4 in the present model) in his biomass estimate. Their weight here contributes 55 $g{\cdot}m^{-2}$ to the total biomass. Subtracting this value from total fish biomass yields a reef fish biomass of about 200 $g{\cdot}m^{-2}$, i.e., within the range of the two earlier estimates.

Fig. 3 shows the results of an ECOPATH II routine called "mixed trophic impacts". This routine computes direct and indirect trophic impacts that any group in the system has on the other groups in the system. The figure gives a quick overview of these trophic interactions. It is clear that the largest impacts are caused by the lower trophic levels whereas the top predator groups only influence few other groups. For instance the large sharks and rays mainly impact the sea birds and turtles, which in turn do not have any noticeable trophic impact on any other group.

In order to balance the model it was as discussed earlier necessary to use considerably lower biomass estimates for the large predator groups (sharks, scombrids, groupers, large carnivores) than those estimated from visual censuses, while the biomass estimates to be used for two major prey groups (zooplankton, small schooling fish) had to be increased. This is assumed to be mainly because the visual censuses tend to overestimate the larger species due to both attraction towards divers and high probability that the observer actually sees the larger species. Following the same line of arguments the opposite mechanisms may well lead to an underestimation of smaller prey species which may tend to hide when divers approach.

For the zooplankton the increase in biomass (from 18 to 30 $g{\cdot}m^{-2}$) needed to balance the model can perhaps be caused by the use of a production/biomass (P/B) ratio from another area (French Frigate Shoals, Hawaii). Had a higher P/B been used, it would not have been necessary to change the biomass estimate.

The discrepancies uncovered here should be seen as important results of this study. By relating parameters from different groups to each other a check of the compatibility of such is

Table 3. Diet composition matrix for components of a Caribbean coral reef system. Values in brackets refer to original inputs that were modified during the parameter estimation routine. Group 19 is phytoplankton; 20 is benthic autotrophs; and 21 refers to detritus, including POM and DOM.

		Fish species group									Nonfish groups											
No.	Predator\prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Large sharks/rays	.010 (.049)	.010 (.026)	.015 (.026)	.073 (.077)	.034 (.001)	.140 (.145)	.120 (.051)	.084	.010	.003 (.010)	.000 (.020)	.024	.021 (.008)	.160 (.183)	.269 (.259)	.011	-	-	-	-	.016
2	Scombrids/jacks/sharks	- (.005)	.001 (.086)	.070	.213	- (.118)	.125 (.174)	.190 (.103)	.080 (.202)	.222	-	-	.021 -	- (.050)	.040 (.008)	.018	-	.020	-	-	-	-
3	Large schooling fish	- (.005)	.001 (.053)	.002	.040	- (.005)	-	.021	-	-	-	-	- (.007)	- (.194)	.005	.196	-	.720	-	-	.015	-
4	Small schooling fish	-	-	-	.004	-	-	-	-	-	-	-	- (.015)	-	.012	- (.971)	.006	.974	.002	.002	-	-
5	Large groupers	.010 (.041)	-	-	-	-	.492 (.042)	.096 (-)	-	-	-	.000 (.035)	-	-	.402 (.502)	-	-	-	-	-	-	-
6	Large carn. reef fish	- (.006)	.001 (.013)	.004 (.056)	.030	- (.062)	.050 (.011)	.090 (.024)	.010	.008	-	- (.017)	.010 (.055)	.120 (.276)	.070 (.266)	.330 (.068)	.070	.120	-	- (.018)	.087	-
7	Large herb. reef fish	-	-	-	-	-	-	-	-	-	-	-	-	-	.001	-	.005	-	-	-	.906	.088
8	Small omni. reef fish	-	-	-	.002	-	.007 (.022)	-	.015	.016	-	- (.026)	- (.157)	.043 (.164)	.080 (.039)	.220 (.163)	.050	.160	-	- (.188)	.216	.191
9	Small herb. reef fish	-	-	-	-	-	-	-	-	-	-	-	-	.001	-	.001	-	.004	-	-	.988	.006
10	Sea birds	-	.100	.400	.300	-	.090	.017	.041	.002	-	-	-	-	-	-	-	.050	-	-	-	-
11	Sea turtles	-	-	-	-	-	-	-	-	-	-	-	-	.040	.125	.045	.400	-	-	-	.390	-
12	Cephalopods	- (.075)	- (.075)	.065	.065 (.003)	- (.001)	.010 (.006)	-	.005	-	- (.160)	-	.110 (.200)	- (.330)	.125	.420 (.150)	-	.200	-	-	-	-
13	Echinoderms	-	-	-	-	-	-	-	-	-	-	-	-	.059	.003	.052	.197	.003	.022	.003	.554	.107
14	Crustaceans	- (.003)	- (.020)	-	.005 (.031)	- (.002)	.005 (.014)	.032 (-)	.002	.001	- (.023)	- (.052)	.002 (.242)	.130 (.297)	.040 (.034)	.320 (.085)	.035 (.032)	.070	.050 (.129)	.005 (.031)	.200	.103
15	Misc. molluscs/worms	-	-	-	-	-	-	-	-	-	-	- (.001)	- (.007)	.002	.010	.065	.059	.006	.170	.084	.179	.425
16	Sessile animals	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.025	.019	.011	.084	.861
17	Zooplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.800	.200	-	-
18	Decomposers/microfauna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.000

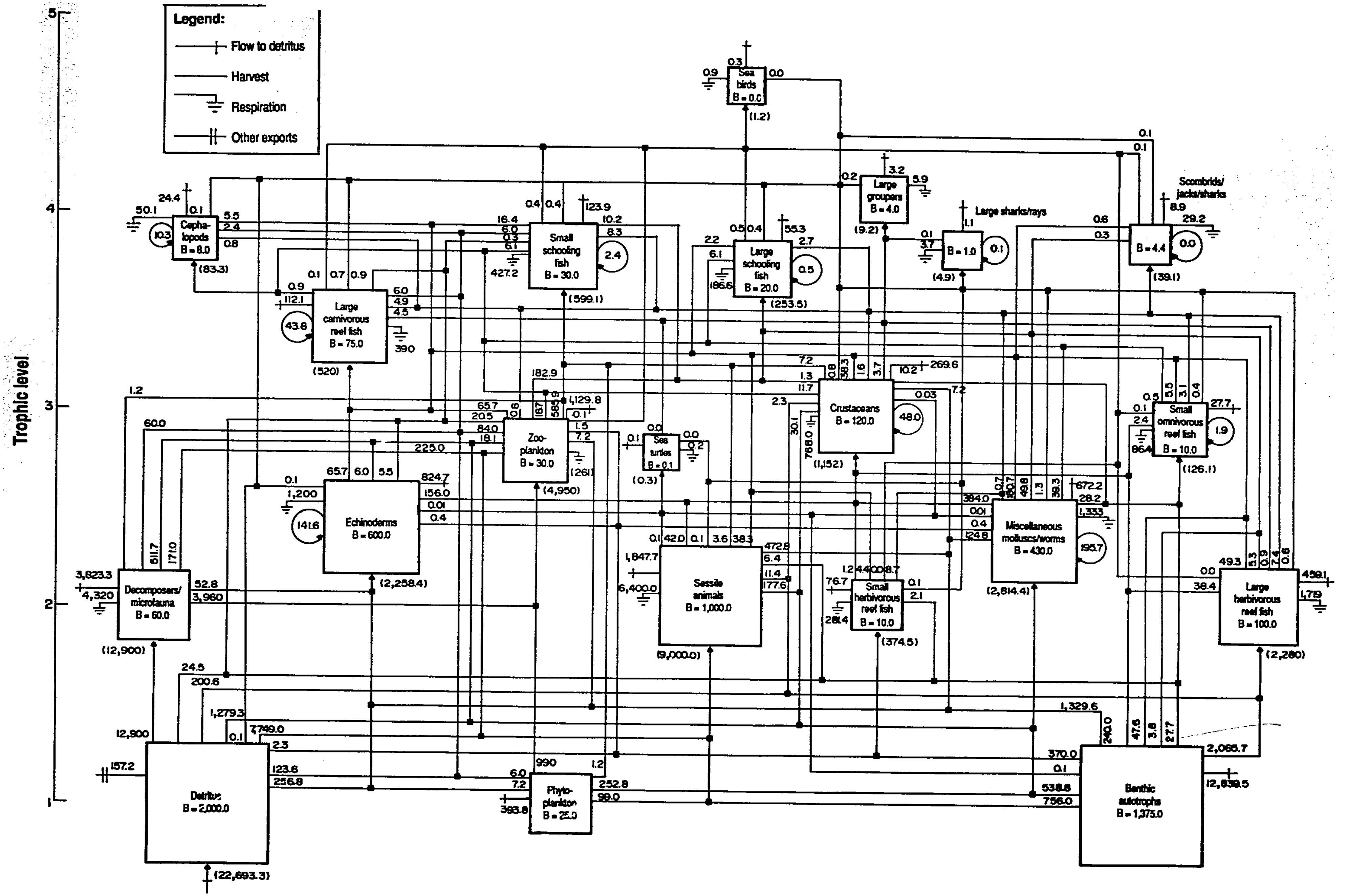

Fig. 2. Box model of a Caribbean coral reef ecosystem. The area of each box is proportional to the logarithm of the biomass (B; in g·m^{-2}) of each group. Values represent the average for all subsystems in Fig. 1. Flows are in g·m^{-2}·year^{-1}.

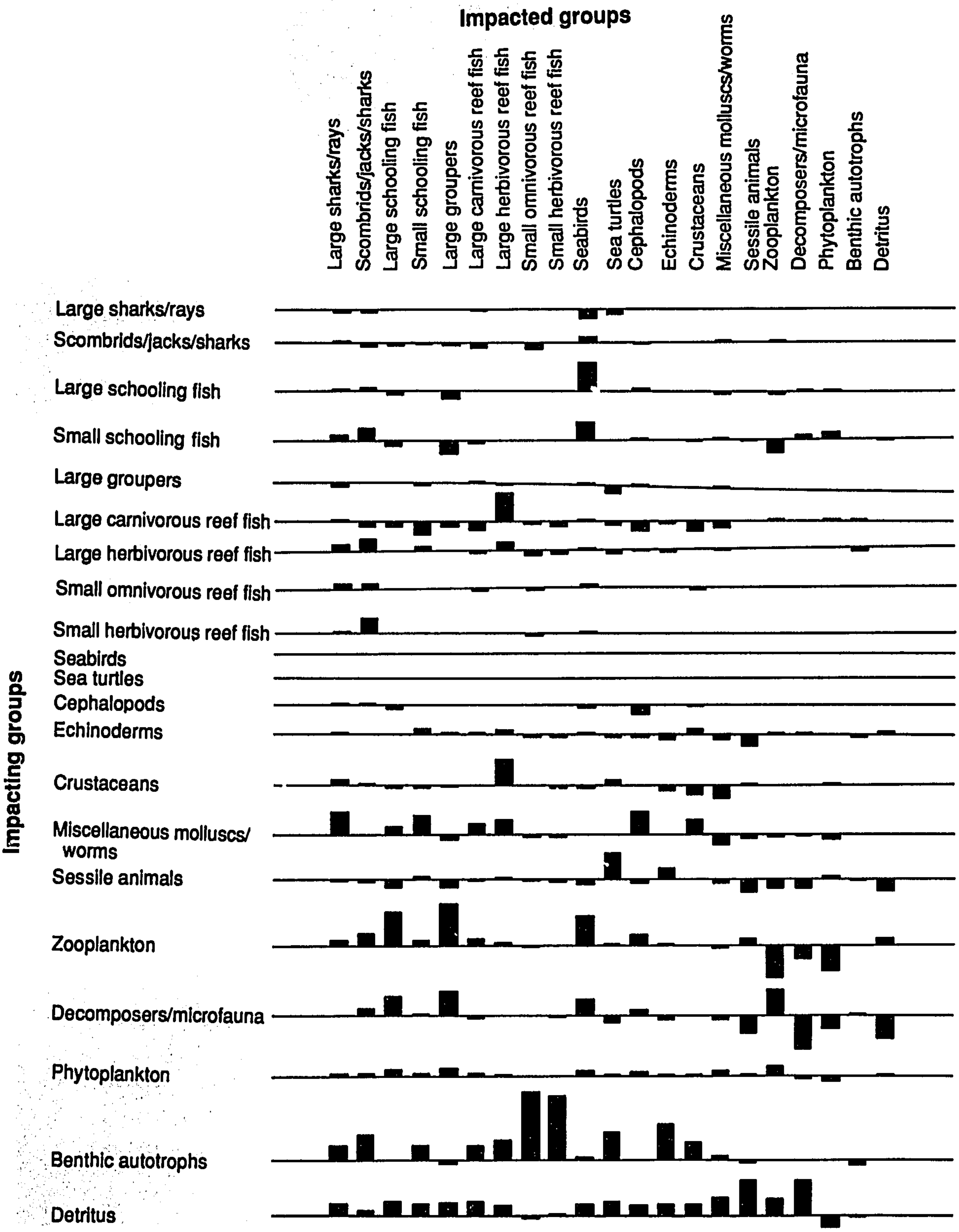

Fig. 3. Mixed trophic impacts in a Caribbean coral reef ecosystem. The impacts are relative and comparable between histograms.

facilitated, and this in turn creates guidelines for further research.

To improve further the reliability of the model the database on Caribbean coral reefs, especially, biomasses, and data on NFGs, has to be enhanced and completed. The aggregation of groups in general should not be based on taxonomies, but on size and/or diet.

A more detailed version of the model presented here may be found in Opitz (1991), pending its publication by ICLARM.

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SHELVES

Around 25% of global fish production comes from tropical shelves, including the large upwelling fisheries off Southern America and Africa. Of these catches nearly half (and more in monetary terms and in socioeconomic importance), or close to 12 million tons has been estimated to originate from the soft bottom shelf areas (Christensen et al. 1992).

A few decades ago, most of the shelf regions off the developing countries' coastlines were lightly or not exploited. Since then the introduction of industrialized fisheries has rapidly changed the status of most shelves, from areas with potential to overfished areas. The result of this is a large waste of resources through deployment of excessively large fleets and depletion of valuable stocks with less-valued, short-lived species dominating instead.

Due to the present, nearly total lack of management of trawl fisheries in the developing world, it is likely that the catches can be increased through proper management. To do so, it is essential to introduce new management strategies.

A development similar to and preceding the development in the tropical regions has led, in the northern temperate areas, to research focusing on models of species interaction and bioeconomic aspects. More traditional measures can also be effective; thus a new fishing regime, the main attribute of which was a 20% expansion of an already existing closed fishing season, led to a doubling of the total catches within a two-year period in the Cyprus trawl and inshore fisheries (Garcia and Demetropoulos 1986).

Fish stocks in the upwelling areas are very much affected by environmental conditions. This sometimes, not always in combination with severe overfishing, has led, for all the major stocks in upwelling areas, to total collapses of the fisheries.

To limit the risk of such collapses it is necessary to increase our understanding of how the environment influences fish populations. It has been shown that it is useful to develop models incorporating oceanographic features, species interaction and distribution of fleet deployment (Jarre et al. 1991). As adverse environmental conditions invariably occur, it is to some extent necessary to be able to control the large-scale upwelling fisheries, e.g., through protection of stocks if they drop below a critical minimum biomass, reducing recruitment. A management scheme incorporating such measures has long been used for the California anchovy fisheries (Radovich and MacCall 1979).

The ecosystems that have been modelled and which are presented in this section range from the tropics to Antarctica. The tropics are represented by four models from different parts of the Gulf of Mexico, one from the Caribbean, one from Southeastern Africa, and one from the South China Sea. In addition, there are two systems characterized by upwelling, a temperate sea, plus a first attempt to conceptualize a model of an Antarctic Sea.

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An Application of ECOPATH II to the North Continental Shelf Ecosystem of Yucatan, Mexico

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Abstract

The northern part of the continental shelf of Yucatan, as defined here, has a surface area of 100,000 km^2 and supports several important tropical fisheries resources (groupers, snappers, lobsters and shrimps, among others). This contribution provides a preliminary description of how this community is organized and its species linked by trophic flows. Analysis is centered on the application of the ECOPATH II model, which advantages and limitations are described, with emphasis on: (1) assumptions of model equations and (2) quality of information required.

Based on the results, about half of the energy used in the community comes from primary producers (benthic and phytoplankton); the rest is imported as detritus. Total production equals 2,049 g·m^{-2}·year^{-1} dry weight (dw); total respiratory flows are 602 g·m^{-2}·year^{-1} dw; and the total flows to the detritus, 395 g·m^{-2}·year^{-1} dw. ECOPATH II is a linear deterministic model that assumes steady-state conditions. Because of the biological basis of the model equations, ECOPATH II facilitates description of community processes and is useful for comparative studies of ecosystems. It could be modified, however, to consider the time delays inherent in ecosystem behavior as well as uncertainty in parameter estimation. Concerning input data, special attention must be given to stomach contents studies, which form the basis for analysis of trophic community structure and the study of energy flows.

Introduction

The north continental shelf of Yucatan is a large area, where many different fisheries operate. The bottom is mainly composed of rock and sand, and most of the commercially important species are characteristic of reef environments. Groupers, snappers, octopus and lobsters are the most important resource groups. Annual yields are around 26,500 t of which 74% comes from the above-mentioned groups (Arreguín-Sánchez et al. 1987b). The area (Fig. 1) is heavily influenced by a seasonal upwelling occurring at the northeast edge of the continental shelf (Ruíz and Merino 1989) during late spring and summer, and which impacts on the spatial behavior of species within the ecosystem, and their life strategies and reproduction processes (Arreguín-Sánchez 1989a). Exploitation of some of the most important species is currently close to maximum sustainable yield; this applies to the grouper (Seijo 1986; Arreguín-Sánchez 1989b; Arreguín-Sánchez et al. 1987a) and octopus (Solís and Arreguín-Sánchez 1984; Solís and Chávez 1986; Arreguín-Sánchez 1987; Seijo et al. 1987); while others, such as snappers (Torres 1987; Torres and Chávez 1987; Gonzalez et al. 1990) and lobsters (Seijo et al. 1990; Salas and Arceo 1988) may still be underexploited.

Arreguín-Sánchez et al. (1990) and Contreras et al. (1990) suggested important changes in the fish community structure after high mortalities on eggs, larvae and juveniles occurred during 1979-1980, probably due to human activity related to the oil industry. This hypothesis is partially supported by a substantial decrease of the biomasses of fishes during this time (Soberón-Chávez et al. 1988b), and because the recent catches of the regional fisheries also show changes in structure when they are compared with the catch composition in the previous decade. Beddington (1984) and Steele (1984) pointed out the importance of understanding how ecosystems respond to perturbations, including exploitation, to generate clear management strategies. This paper is a preliminary attempt to analyze the trophic structure of the Yucatan northern continental shelf ecosystem, with emphasis on the main commercially important species, and may be viewed as a case study of how coastal ecosystems change following perturbation.

Methods

The trophic community structure of the study area was analyzed through the application of the ECOPATH II model for ecosystems in steady state. Population changes and their interdependencies are described by deterministic and linear equations (Polovina and Ow 1983; Polovina 1984, 1985; Christensen and Pauly 1992a, 1992b). A generalized function of the system of equations is represented as follows:

$$B_i \cdot \left(\frac{P_i}{B_i}\right) \cdot EE_i - \sum_{j=1}^{n}\left(B_j \cdot \left[\frac{Q_j}{B_j}\right] \cdot DC_{ji}\right) - EX_i = 0 \qquad \text{...1)}$$

where B_i = biomass of group (i); P/B = production/biomass ratio of group (i); EE_i = ecotrophic efficiency of group (i); Q_j/B_j = consumption/biomass ratio of group (j); DC_{ji} = fraction of prey (i) in the average diet of predator(s) (j); EX_i = export out of the system (including fishing) of group (i); the summation denotes the total biomass of species i consumed by predators.

The data required by this model were obtained as follows:

Wet weights were converted to dry weights using a conversion factor of 20%.

Primary production data were taken from estimations reported in Soberón-Chavez et al. (1988a), and data on abundance of zooplankton, annelids and microcrustaceans from Batllori et al. (1987) and El-Sayed and Turner (1980).

Stomach contents of fishes were obtained from the literature for the main fish resources: red grouper (*Epinephelus morio*) and snappers, *Lutjanus campechanus, L. griseus, L. analis, L. synagris* and *Ocyurus chrysurus*, from Moe (1969), Claro (1981, 1983), Polovina and Ralston (1987); sharks, a group composed of several species and families, from Alvarez (1988) and Castro (1983); grunts (mainly *Haemulon plumieri* and *H. aurolineatum*) from Sierra (1983) and García (1976); king mackerel (*Scomberomorus cavalla*) from Berrien and Finan (1977), DeVane (1978), Naughton and Saloman (1981); herrings (with *Opisthonema oglinum* and *Harengula jaguana* as the more abundant species) from Finucane and Vaught (1986), Sierra and Díaz-Zaballa (1984); porgies and mojarras (mainly species of the genus *Calamus* spp.) from Salas (1984, 1986), Abarca-Arenas (1987) and Abarca-Arenas et al. (1982); seatrout and jacks from Sierra and Popova (1982), Sierra et al. (1986), Chávez et al. (1987), Cruz and Franco (1981) and Barba-Torres and Gaspar-Dillones (1987). Concerning the invertebrate groups, the literature reviewed was: for shrimps (several species of

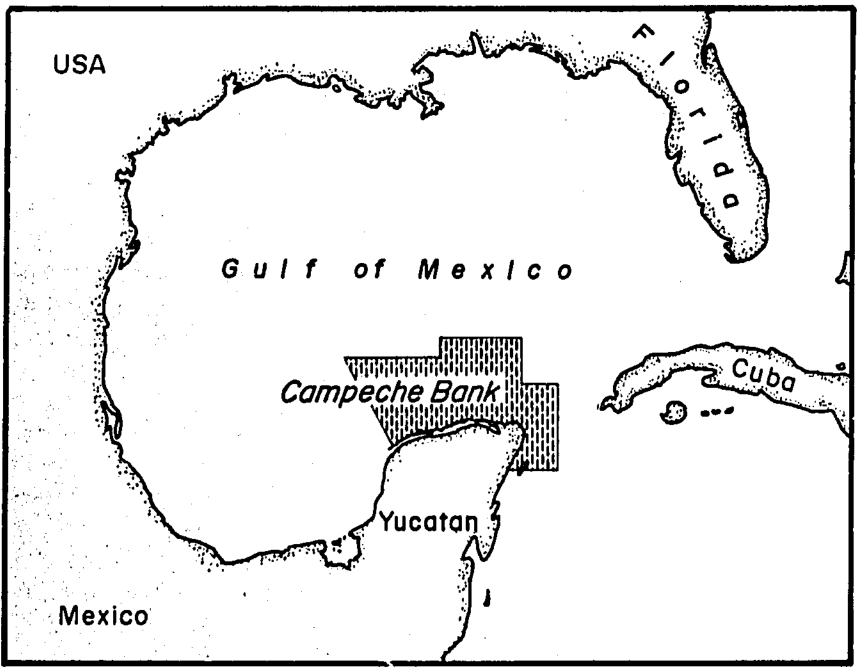

Fig. 1. The study area, the northern shelf of Yucatan, Mexico.

penaeids, the more abundant of which is the pink shrimp *Penaeus duorarum*) from García (1976) and Gracía (1989); lobsters (mainly the spiny lobster *Panulirus argus*) from Peacock (1974) and Kanciruck (1980); crabs (several species of *Callinectes* spp.) from Chávez and Fernandez (1976). For octopus, the most important species was *Octopus maya*, from Solís (1962, 1967), and other molluscs were from Batllori et al. (1987).

The north continental shelf of Yucatan was assumed to be the unit ecosystem for the present study. This assumption may not be correct for some species whose ranges extend beyond this area. For instance, the highest concentrations of shrimps occur in the southern Gulf of Mexico (Arreguín-Sánchez and Chávez 1985). Some grunts, porgies and sharks also have a larger distribution area (Stevenson 1982). Others, such as king mackerel are migratory species, but we considered that the average population size estimated represents the average population during the year. Under this scheme only catch data were considered as exports (EX_i). Catch estimates were based on data from the Ministry of Fisheries (SEPESCA 1987).

Values of the biomasses and P/B ratios (corresponding to the instantaneous rate of total mortality) were taken from several sources: for the red grouper from Arreguín-Sánchez et al. (1987a) and Contreras et al. (1990); for snappers from González et al. (1990), Torres and Chávez (1987), Mexicano-Cíntora (1985), Mexicano-Cíntora and Arreguín-Sánchez (1987); sharks from Alvarez (1988) and Alvarez and Arreguín-Sánchez (1990); grunts from Manooch (1976) and Manooch and Borans (1982); king mackerel from Cabrera (1986) and Cabrera-Vásquez and Arreguín-Sánchez (1987); herrings from Chávez et al. (1987) and Leonce (1990); porgies from Salas (1986); seatrout and jacks from Chávez (1981); shrimps from Arreguín-Sánchez and Chávez (1985); lobsters from Cabrera et al. (1990); crabs from Chávez and Fernández (1976) and Arreguín-Sánchez (1976); octopus from Solís and Chávez (1986); and other molluscs from Batllori et al. (1987).

Values of consumption/biomass (Q/B) ratios were obtained using the equation of Palomares and Pauly (1989)

$$\ln\left(\frac{Q}{B}\right) = -0.178 - 0.202 \log W_\infty + 0.612 \ln + A + 1.26F \quad ...(2)$$

where: W_∞ = asymptotic weight in g; T = mean habitat temperature in °C; A = aspect ratio of the caudal fin calculated from drawings in Guitart (1977) and Fischer (1978); and F = food type (= 0 in carnivores; 1 in herbivores and 0.5 for omnivores). The resulting estimates of Q/B (in % day^{-1}) were then converted to an annual basis. Specific inputs associated with estimations of Q/B ratio for use with equation 2 are given in Table 1.

Following the ECOPATH II default, it was assumed that 20% of the ingested food remained unassimilated, for all consumer groups, apart from zooplankton, for which 40% was used, such as to obtain a reasonable respiration/biomass ratio.

Table 1. Parameters used to estimate Q/B (consumption/biomass ratio) for carnivorous fishes of the northern continental shelf of Mexico.

Group	Asymptotic weight (W_∞, g)	Caudal fin aspect ratio
Red grouper	14,406	1.96
Snappers	9,631	1.46
Sharks	508	2.24
Grunts	1,618	2.50
King mackerel	10,629	6.20
Herrings	193	2.21
Mojarra	170	3.54
Seatrout	1,070	1.52
Jacks	3,503	5.10

T = 26°C, constant in all groups
F = 0 constant in all groups
W_∞ = maximum asymptotic weight, g
A = aspect ratio of the caudal fin

With parameters collected as mentioned above, a prey-predator matrix was then constructed. All inputs were standardized to $g \cdot m^{-2} \cdot year^{-1}$ dw. In some cases, when biomass estimations were not available or not specific for the area, they were estimated by the ECOPATH II model, using assumed values for the ecotrophic efficiencies as inputs.

Results and Discussion

The predator-prey matrix that was constructed is given in Table 2. Input values (without brackets) associated with catch, biomass, P/B and Q/B ratios, and gross efficiency are shown in Table 3, along with estimated parameters (in brackets). When ECOPATH II was applied, some adjustments in ecotrophic efficiency (EE_i) were made for the top predators, noting that they are not subjected to predation, only to exploitation.

Table 2. Predator-prey matrix from the northern continental shelf of Yucatan, Mexico.

					Predator				
Prey	1	2	3	4	5	6	7	8	9
1. Red grouper	-	-	0.19	-	-	-	-	-	-
2. Snappers	0.10	-	0.11	-	-	-	-	-	-
3. Sharks	-	-	-	-	-	-	-	-	-
4. Grunts	0.08	0.16	0.10	-	0.12	-	0.10	-	-
5. King mackerel	0.02	-	0.13	-	-	-	-	-	-
6. Herrings	-	0.12	0.07	-	0.46	-	0.05	-	0.02
7. Porgies	-	-	-	-	-	-	-	-	-
8. Mojarra	0.22	0.43	0.09	-	0.11	-	-	-	-
9. Seatrout	-	0.01	0.00	-	-	-	-	-	-
10. Jacks	0.08	-	0.08	-	-	-	-	-	-
11. Shrimps	0.18	0.01	0.07	0.15	0.25	0.14	0.10	0.20	0.10
12. Lobsters	0.06	0.05	0.01	-	-	-	-	-	-
13. Crabs	0.10	-	0.16	0.06	-	-	-	-	0.04
14. Octopus	0.15	0.22	-	0.08	0.07	-	0.05	0.07	0.05
15. Other molluscs	-	-	-	0.05	-	-	0.20	0.05	0.07
16. Microcrustaceans	-	-	-	0.18	-	0.35	0.29	0.50	0.35
17. Zooplankton	-	0.01	-	0.24	-	0.36	-	0.08	0.32
18. Annelids	-	-	-	0.25	-	0.08	0.06	0.10	0.05
19. Phytoplankton	-	-	-	-	-	-	-	-	-
20. Benthic producers	-	-	-	-	-	0.07	0.15	-	-
21. Detritus	-	-	-	-	-	-	-	-	-

					Predator				
Prey	10	11	12	13	14	15	16	17	18
1. Red grouper	-	-	-	-	-	-	-	-	-
2. Snappers	-	-	-	-	-	-	-	-	-
3. Sharks	-	-	-	-	-	-	-	-	-
4. Grunts	0.04	-	-	-	-	-	-	-	-
5. King mackerel	-	-	-	-	-	-	-	-	-
6. Herrings	0.29	-	-	-	-	-	-	-	-
7. Porgies	-	-	-	-	-	-	-	-	-
8. Mojarra	-	-	-	-	-	-	-	-	-
9. Seatrout	-	-	-	-	-	-	-	-	-
10. Jacks	-	-	-	-	-	-	-	-	-
11. Shrimps	0.36	-	0.08	0.20	0.05	-	-	-	-
12. Lobsters	-	-	-	-	0.15	-	-	-	-
13. Crabs	0.07	-	-	0.05	0.60	-	-	-	-
14. Octopus	0.10	-	-	-	-	-	-	-	-
15. Other molluscs	0.08	0.05	0.20	0.10	0.20	-	-	-	-
16. Microcrustaceans	0.06	0.20	0.40	0.30	-	0.05	0.05	-	0.05
17. Zooplankton	-	0.15	0.05	0.10	-	0.30	-	-	-
18. Annelids	-	0.50	0.20	0.15	-	0.05	0.15	-	0.05
19. Phytoplankton	-	-	-	-	-	0.20	0.30	0.95	-
20. Benthic producers	-	0.10	0.07	0.10	-	0.40	-	0.05	0.15
21. Detritus	-	-	-	-	-	-	0.50	-	0.75

To balance import to and output from the detritus box, an import of 150 g·m^{-2}·year^{-1} dw was needed. The import was assumed to be contributed by the seasonal upwelling on the east edge of the Yucatan continental shelf and export from the Lagoon of Terminos in the southern Gulf of Mexico (Yañez-Arancibia and Day 1988). Within the system, the groups representing the main sources of energy are those connected with the benthic environment, such as the microcrustaceans and annelids. For the balanced model, a diagram showing biomass flows was obtained (Fig. 2). The main ecosystem statistics are shown in Table 4.

The role of the fisheries within the system is equivalent to a predator which would occupy a mean trophic level of 5.1, slightly higher than the top predators, the sharks (4.9). Of the total system throughput, 29% was due to respiratory processes and 19% passed through the detritus, which supports 52% of the flows in the system.

The direct and indirect impacts of competition and predation can be explored using the Leontief matrix of ECOPATH II (Christensen and Pauly 1992b). In this ecosystem the most commercially important species are the red grouper, octopuses, herrings and porgies (Table 1). When the Leontief matrix routine was applied, the main

Table 3. Input data and estimated parameters (bracketed) used for the trophic model of the northern continental shelf of Yucatan, Gulf of Mexico. Flows are in g dw·m^{-2}·year^{-1}.

Group	Catches	Biomass	P/B	Q/B	EE	GE
Red grouper	0.031	0.18	0.50	4.60	(0.98)	(0.11)
Snappers	0.005	(0.30)	0.44	4.30	0.95	(0.10)
Sharks	0.005	(0.03)	0.32	9.70	0.50	(0.03)
Grunts	0.003	(1.32)	0.40	8.10	0.95	(0.05)
King mackerel	0.003	(0.10)	0.65	8.90	0.95	(0.07)
Herrings	0.013	(1.06)	1.10	11.70	0.95	(0.09)
Porgies	0.008	0.03	0.65	5.20	(0.35)	(0.13)
Mojarra	0.001	(0.82)	1.09	15.30	0.95	(0.07)
Seatrout	0.001	(0.01)	0.803	6.80	0.95	(0.12)
Jacks	0.000	(0.18)	0.39	10.00	0.95	(0.04)
Shrimps	0.001	(2.49)	5.38	19.20	0.95	(0.28)
Lobsters	0.001	(1.61)	0.90	8.20	0.95	(0.11)
Crabs	0.000	(2.58)	2.80	8.50	0.95	(0.33)
Octopus	0.015	(2.35)	1.10	3.50	0.95	(0.31)
Other molluscs	0.000	(4.30)	2.50	8.20	0.95	(0.31)
Microcrustaceans	0.000	(9.99)	7.01	27.14	0.95	(0.26)
Zooplankton	0.000	(1.70)	17.70	157.75	0.95	(0.11)
Annelids	0.000	(21.57)	4.60	15.90	0.95	(0.29)
Phytoplankton	0.000	(7.95)	45.50	0.00	0.95	-
Benthic producers	0.000	(6.60)	14.00	0.00	0.95	-
Detritus	-	(9.00)	-	-	0.99	-

impacted groups were as follows (Fig. 3): negative impacts of the red grouper on snappers and jacks; positive impacts of the octopus on snappers and sharks, and negative by the octopus on lobsters, crabs and octopus; positive impacts on king mackerel and jacks. An interesting case is the lobster, on which a fishery in the northern continental shelf of Yucatan has recently developed. For this group, the highest impact is negative on molluscs (other than octopus), with a smaller positive impact on sharks.

Table 4. Summary statistics (flows are in g·m^{-2}·year^{-1}; others, as given) for the ecosystem of the northern continental shelf of Yucatan.

Sum of all consumption	1,050.1
Sum of all exports	1.9
Sum of all respiratory flows	602.3
Sum of all flows into detritus	394.6
Total system throughput	2,049
Sum of all production	692
Total primary production/total respiration (-)	0.754
Net system production	-148.067
Total primary production/total biomass(-)	6.972
Total biomass/total throughput (year)	0.032
Total biomass (gm^{-2})	65.152
Total catches	0.087
Connectance index (-)	0.278

Conclusion

Although ecosystem statistics and energy flows may be considered reasonable as average values, it is necessary to consider these with care. The ecosystem is not closed: the distributions of species such as shrimps, grunts, porgies and sharks are not restricted to this area, and probably some inputs (or exports) relating to these species should be taken into account. However, there is no specific information about their seasonal movements in and out of the area. On the other hand, the seasonal upwelling has a heavy influence on the dynamics of the ecosystem, producing seasonal changes which may be very important to the trophic structure of the ecosystem and might influence conclusions relevant to management planning.

The input data were adapted from the literature and most of those rate or state estimates referred to different time periods. ECOPATH II assumes a steady state (because it is a condition to find a solution to the system of equations), and this is problematic when data stem from different time periods. Therefore, the results must be seen as giving only a preliminary picture of the trophic structure, and hard work should be devoted to update the information used here. Moreover, some values of the P/B ratio may be biased because estimations were made at different times, especially those that are related

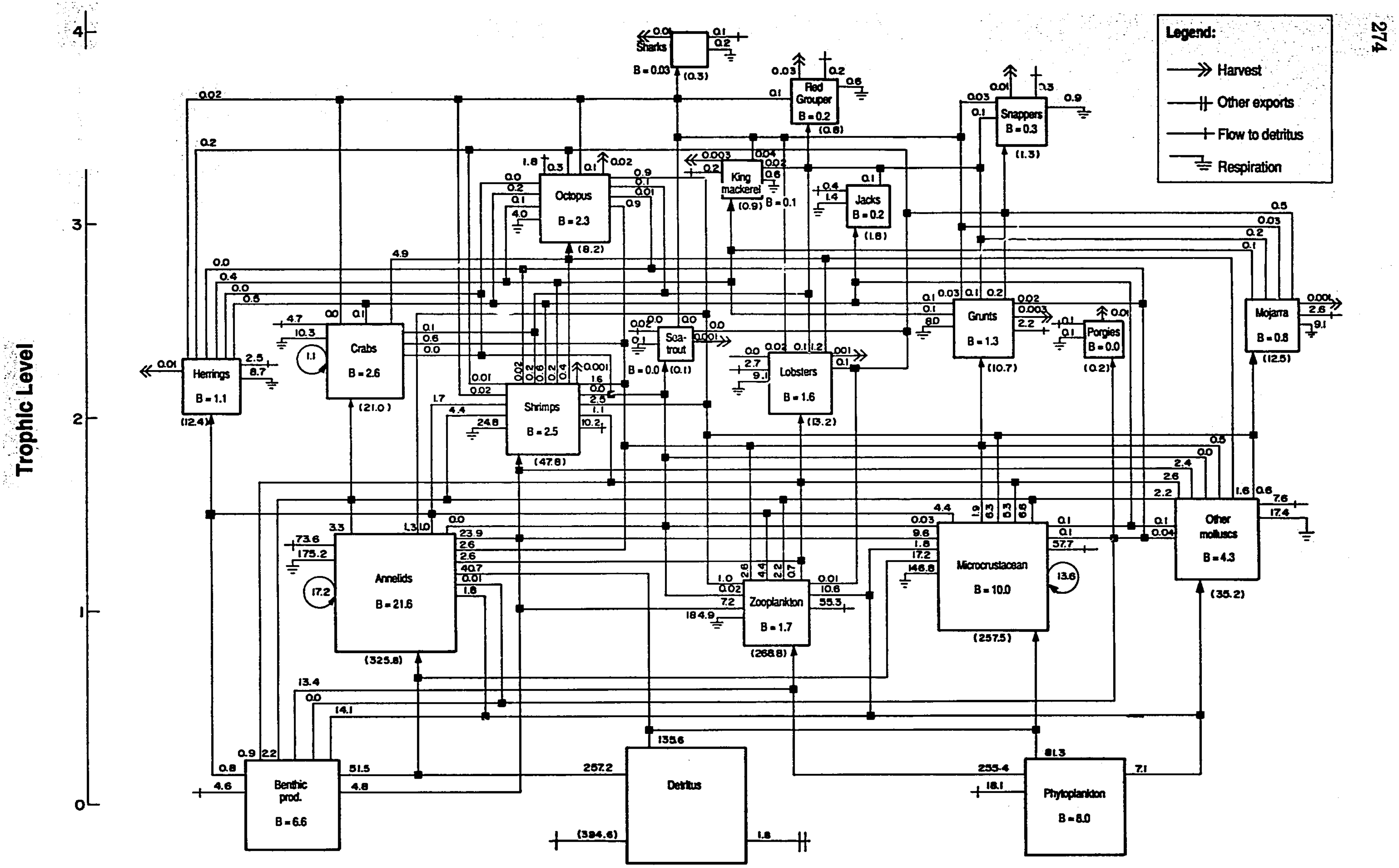

Fig. 2. Flow diagram for the model of the northern continental shelf of Yucatan, Mexico. Flows are in g dw·m^{-2}·year^{-1}.

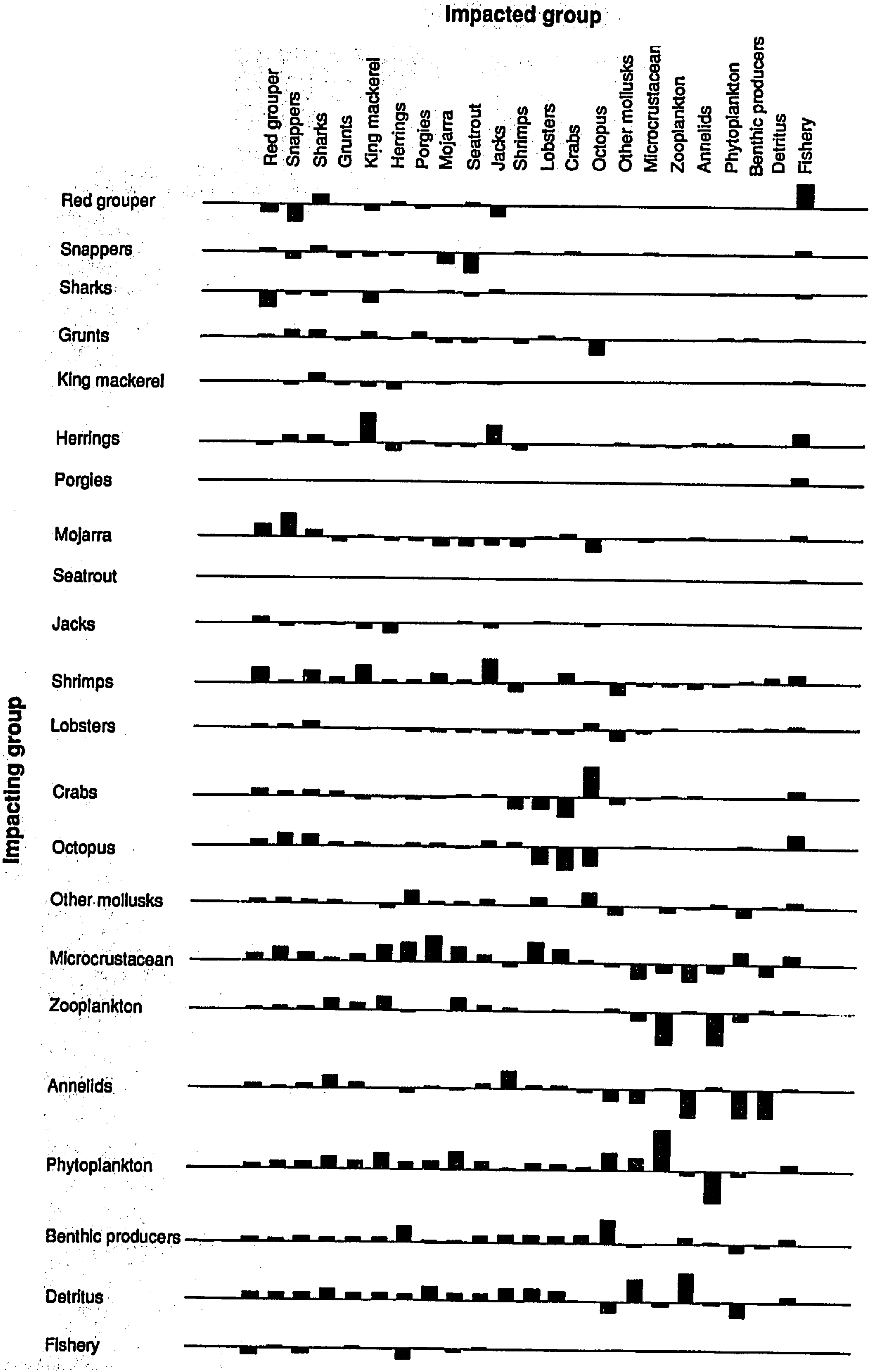

Fig. 3. Mixed trophic impacts of the groups in the ecosystem models of the northern continental shelf of Yucatan, Mexico.

to the dynamics of the whole system (i.e., the intensities of the predator-prey relationships are associated with relative abundances of the species at a given time).

Some limitations were observed for the main assumptions on the model; additional routines to deal with uncertainty and time delays in processes associated with ecosystem dynamics would be particularly useful (specially when perturbations are to be assessed). It is necessary to consider that when a perturbation is dissipated through the food web in the ecosystem, the effect on different trophic levels will not be simultaneous in time. Thus, to track such perturbation, an alternative possibility is to use analytical procedures other than ECOPATH II such as that provided by system analysis techniques, which, for some cases, may be powerful tools. Simulation modelling is a powerful tool for ecosystem analysis that allows change over time to be followed. On the other hand, the ECOPATH II model is an easy to use tool for ecosystem analysis; however, special care must be placed on confidence of input data, as this type of programs will always give results, even though they may not always be reasonable; the judgement of the model constructor is important, as for any other type of ecosystem models.

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A Pilot Model of the Gulf of Mexico Continental Shelf

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Abstract

Using the ECOPATH II software, a 15-compartment model was constructed to estimate biomass transfers in the Gulf of Mexico continental shelf ecosystem under steady-state conditions and using present, known catch rates. The purpose of the exercise was to evaluate the ecological realism of estimates of prey and predator biomasses that were made in a previous paper. The approach was to set manually biomass and consumption per unit biomass for most compartments based on the best available information and let the software calculate production per unit biomass and respiration per unit biomass. Since the software maintains conservation of matter, the plausibility of the modelling results gave an indication of the realism of the original biomass estimates. Results suggested that the original biomass estimates, except those for macrocrustaceans (shrimp and crabs), were reasonable.

Introduction

The Gulf of Mexico supports lucrative fisheries of both the United States and Mexico. Most of the harvest is taken on or near the continental shelf and is based on the biological productivity of estuarine and nearshore waters. Important commercial fisheries include those for menhaden, penaeid shrimp, snapper, grouper, yellowfin tuna, swordfish, and king and Spanish mackerel.

Harvested species are ecologically linked through prey-predator relationships and competition for the same food sources. Therefore, the harvest of one potentially could affect the harvests of others. Questions about the ecological interactions between fish species become highly relevant to fisheries management when traditional fisheries reach harvesting plateaus and exploitation expands to new species, as is now the case in the Gulf of Mexico. The first step in taking an ecosystem approach to fisheries management research in the Gulf of Mexico was to develop rough estimates of biomass and steady-state annual consumption rates of higher-trophic-level species in relation to the biomass of potential prey, as was done in Brown et al. (1991). The second step, taken in the present paper, is to evaluate the realism of those estimates in terms of fundamental physical laws such as conservation of mass-energy and of basic metabolic requirements for maintenance and growth. Brown et al. (1991) restricted their biomass estimates to the shelf, excluding the estuaries. Therefore, in using their estimates, this paper also excludes the estuaries.

The ECOPATH II software of Christensen and Pauly (this vol.) was used to prepare a biomass budget relevant to fisheries on the continental shelf of the Gulf of Mexico (US and Mexico combined). The generalized model is a compartment model with flows between compartments and conservation of matter and energy. It is a steady-state, or equilibrium, model in which the sum of primary production and imports is balanced by respiration and exports. The generalized model and model parameters are fully described in Christensen and Pauly (1992a and 1992b) and Pauly et al. (this vol.). The most important parameters in this discussion are as follows: biomass (B), production per unit biomass (P/B), consumption per unit biomass (Q/B), ecotrophic efficiency (EE) and export (EX). The value of EE is limited to the region from 0 to 1. Respiration (R) and respiration per unit biomass (R/B) are "passive" parameters of the ECOPATH II software that cannot be set directly but are important to observe in examining modelling results. This differs from the energy modelling approach of Odum (1983) in which consumption and respiration rate coefficients are set by the modeller and production rates are calculated in model execution. In ECOPATH, model structure must be defined by the modeller by means of an explicit prey-predator matrix indicating the percentage of consumption coming from each prey source.

Two of the three parameters B, P/B and EE must be set initially. The remaining will be computed by the software, first using some simple flow-balancing algorithms and then by a generalized inverse method. Particularly for some of the lower-trophic level organisms, EE sometimes is changed from its initial setting by the software, even when P or P/B are treated as initial unknowns. Q/B of a compartment also can be calculated by the software and treated as an unknown in initial parametrization, provided certain information is available for prey compartments.

Respiration for each trophic compartment is determined by the software as the difference between the digested food and the production. If unrealistically high or low, it indicates that initial parameter settings of the model were unrealistic.

Construction of the Model

A 15-compartment model was developed (Fig. 1). It consists of the following loosely defined trophic groups, arranged in the order numbered in the ECOPATH II model: (1) zooplankton, (2) benthos, (3) small pelagic fish and squid, (4) demersal fish, (5) crabs and shrimp, (6) small pelagic predators, (7) demersal predators, (8) mackerels and other coastal migratory pelagic predators, (9) tunas, (10) billfish, (11) sharks, (12) bottlenose dolphin, (13) phytoplankton, (14) benthic plants (everything from microalgae to macrophytes) and (15) detritus.

Fisheries harvests are included in the model and were the only exports from the system. As a simplifying assumption, the discards of shrimp trawls were considered as harvests and, therefore, exports, although, in actuality, most are returned dead to the system. In a previous paper (Browder 1983), I described results of a dynamic simulation model of biomass and nitrogen in which discards were returned to the system, but had little impact on system energetics.

One further simplifying assumption in the present model was that no imports to the system were included in initial model parametrization, even though the continental shelf receives some imports from rivers and coastal marshes. Terrigenous detritus is thought to be less important on the shelf than in the estuaries, which were excluded from the model.

The approach in this exercise was to set B and Q/B for all but the lowest trophic levels and let the software compute P/B and R/B. The Brown et al. (1991) estimates of biomass and consumption for fisheries species were used to set B for compartments 3 through 12 and Q/B for compartments 6 through 12. The consumption estimates in Brown et al. (1991) were based on respiration rate coefficients from the published physiological literature and total mortality estimates from recent fisheries assessments. Q/B was estimated for compartments 3 through 5 in the present study from similar sources.

Various literature sources were used to estimate the input parameters for the lower trophic groups (1, 3, 13, 14 and 15). Phytoplankton biomass for the Gulf of Mexico was estimated based on El-Sayed et al. (1972). The following conversions were used: chlorophyll *a* to carbon, 1 to 25; carbon to dry organic matter, 1 to 2.5; dry to wet weight organic matter to wet organic matter, 1 to 5 (Parsons et al. 1977). The latter two conversions were used elsewhere in this exercise wherever literature values were in units other than wet organic matter. Values of net primary production used in the model were within the range of average values reported for the Gulf of Mexico. Sources of these values were El Sayed et al. (1972), Platt and Subba Rao (1975) and Sklar (1976). Equations in Pauly et al. (this vol.) were used to estimate detrital biomass and initial EE for phytoplankton; however, the software recalculated the phytoplankton EE.

Zooplankton biomass specific to the Gulf of Mexico was obtained directly from Flint and Rabalais (1981). Zooplankton production per unit biomass was taken from Pauly et al. (this vol.) and Polovina (1984). Benthos B, P/B and Q/B were adjusted by hand in the modelling exercise using the lowest value of each that prevented R from becoming negative or EE from exceeding 1. Export was set equal to the fisheries harvest for compartments 3 through 11.

Information used to set the predation matrix was very rough. The best readily available information was for the mackerel group. Qualitative information was used for the other compartments.

Verification of the model and evaluation of the input values for B and Q/B were part of the same process. The steps in this process were (1) examination of R/B for each compartment except detritus, (2) examination of export from the detritus compartment, (3) examination of P/B for all compartments, (4) examination of B, P/B and Q/B for the benthos compartment and (5) examination of EE for phytoplankton compartment.

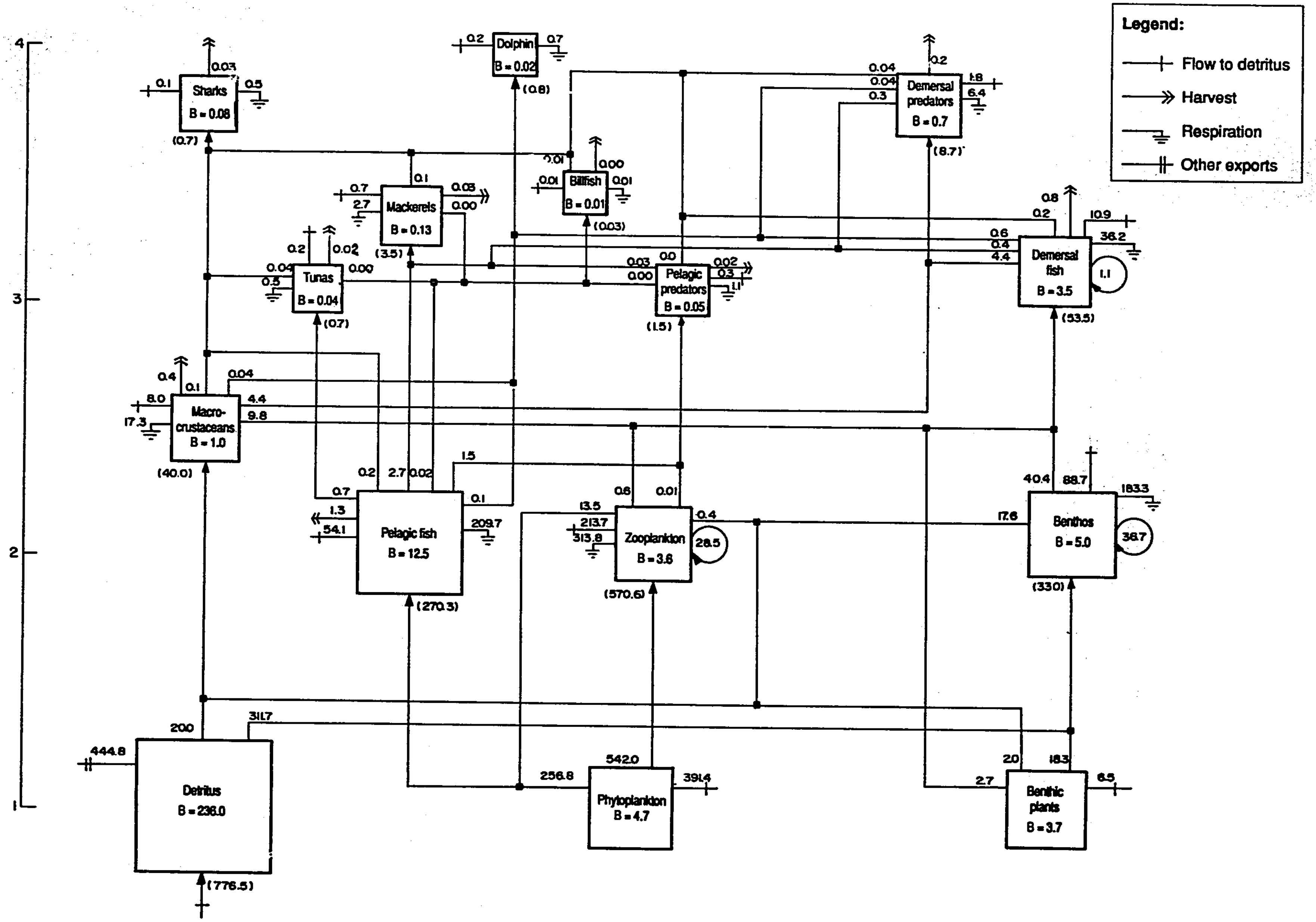

Fig. 1. Gulf of Mexico ecosystem model: trophic compartments and connecting pathways, with values used or calculated for biomass (B; $g{\cdot}m^{-2}$) and flows ($g{\cdot}m^{-2}{\cdot}year^{-1}$; on lines with arrows).

Evaluation of the Model

The calculated respiration for the macrocrustacean (crab and shrimp) compartment was negative in the first execution of the software. Modifying the input parameters, the biomass of this compartment was increased from approximately 0.3 to 1.0 g·m^{-2} and the prey-predator matrix was slightly revised, feeding demersal predator fish more benthos and less crabs and shrimp than in the first execution. This resulted in a more realistic macrocrustacean R/B being calculated.

R/B values first calculated by the software for most of compartments 6 through 12 were slightly low. In subsequent execution, Q/B was increased until the calculated RB roughly equaled the values that went into the original estimates of Q/B (Q/B, after all, must be the sum of respiration, predation and harvest rate coefficients in the steady-state systems). The adjustments were small, resulting in the difference of only 3% in total consumption for the six groups as a whole.

In initial parametrizations of the budget, the sum of detrital export and benthos respiration was unrealistically high in comparison to the B/R calculated from Nixon (1986). Hargrave's (1969) description of benthic respiration was another indication that the budget's initial detritus export value was much too high. The values of phytoplankton and benthic plant P/B influence the model's calculations of benthic respiration because of the software's constraints of mass balance and maintenance of steady state. Phytoplankton and benthic plants are an alternative food source to detritus at the base of the trophic pyramid. Therefore in subsequent model executions, phytoplankton and benthic plant P/Bs were adjusted until the sum of detritus and benthos respiration was of the same general magnitude as B/R calculated from the Nixon (1986) equation. The resultant net primary production, expressed in terms of carbon, was 97 g·C·m^{-2}·year^{-1}. Literature values for the Gulf of Mexico vary from 37 g·C·m^{-2}·year^{-1} for the gulf as a whole (El-Sayed et al. 1972) to 266 g·C·m^{-2}·year^{-1} for the gulf continental shelf (Platt and Subba Rao 1975), and 266 g·C·m^{-2}·year^{-1} for coastal waters off the Mississippi delta (Sklar 1976).

Evaluation of the Revised Budget

Input and model-calculated parameter values after the adjustments described above are shown in Table 1. Rates are shown in Table 2. The P/B values calculated by the software for trophic groups 5 through 12 seem reasonable, with three exceptions. Those for billfish and tuna compartments appeared unrealistically high based on qualitative information about these species. They have few predators as adults, although incidental evidence suggests they may be intensively preyed upon by both fish and oceanic birds when very young and small. On the other hand, the P/B value for the small pelagic fish and squid compartment was lower than expected and needs to be examined in relation to published figures for this trophic group in other ecosystems.

The values for the lower trophic compartments seemed reasonable. The zooplankton R/B calculated by the software seemed somewhat high - 88 times body weight per year, as compared to 40 times body weight per year obtained by Kiϕrboe et al. (1985) for mature *Acartia tonsa*. Benthos R/B was in the reasonable range, although B and P/B may have

Table 1. Model parameter values. Those imposed on the model are preceded by (*), those manually changed preceded by (@), and those imposed and reset by the software preceded by (&) (all other values were calculated by the software in interaction with the model). Biomass units are g·ww·m^{-2}.

Group	Biomass (B)	Harvest/B (EX = HB)	P/B (year^{-1})	EE	Q/B (year^{-1})	R/B (year^{-1})
Zooplankton	*3.57	-	*40.00	&0.30	160.00	88.00
Benthos	@5.00	-	@22.00	&0.86	@73.33	36.67
Pelagic fish	*12.48	1.31	0.52	1.00	21.67	16.81
Demersal fish	*3.46	0.81	2.17	1.00	*15.76	10.44
Macrocrustaceans	@1.00	0.38	14.68	1.00	@40.00	17.32
Pelagic predators	*0.05	0.02	1.06	&0.97	*32.13	24.65
Demersal predators	*0.68	0.20	0.86	&1.00	*12.92	9.48
Mackerels	*0.13	0.03	0.99	&1.00	*26.17	19.95
Tunas	*0.04	0.02	2.11	0.63	*15.46	10.25
Billfish	*0.01	0.00	2.43	&0.70	*6.00	2.37
Sharks	*0.08	0.03	0.50	&0.80	*7.93	5.84
Dolphin	*0.02	0.00	*0.10	0.00	*41.07	32.75
Phytoplankton	*4.69	-	254.06	&0.67	*0.00	-
Benthic plants	*3.69	-	8.00	0.78	*0.00	-
Detritus	*236.00	1.89	-	0.43	-	-

Table 2. Trophic levels and flow rates in the model. Flow units are $g \cdot ww \cdot m^{-2} \cdot year^{-1}$.

Group	Trophic level	Flow to detritus	Respiration rate	Food intake rate	Prod. * EE
Zooplankton	2.05	213.75	313.81	570.56	43.01
Benthos	2.11	88.67	183.33	366.67	94.66
Pelagic fish	2.05	54.06	209.71	270.32	6.55
Demersal fish	3.15	10.92	36.15	54.59	7.52
Macrocrustaceans	2.50	8.00	17.32	40.00	14.68
Pelagic predators	3.05	0.30	1.13	1.48	0.05
Demersal predators	3.82	1.75	6.41	8.73	0.58
Mackerels	3.35	0.70	2.67	3.51	0.13
Tunas	3.05	0.17	0.45	0.68	0.06
Billfish	3.45	0.01	0.01	0.03	0.01
Sharks	3.79	0.14	0.48	0.65	0.03
Dolphin	3.98	0.17	0.66	0.82	0.00
Phytoplankton	1.00	391.41	-	0.00	798.83
Benthic plants	1.00	6.46	-	0.00	23.06
Detritus	1.00	-	-	-	-

been too high. These latter parameters were roughly as low as they could be set without causing equilibrium adjustments by the software resulting in an EE greater than 1 or a negative R for benthos.

A further search of the literature is needed to determine the appropriateness of certain tenuous values entered into the model and some of the more questionable values that the software calculated. In particular, the biomasses of macrocrustaceans and the benthos and the P/Bs of small prey fish and squid need to be further researched.

With respect to this model, the ECOPATH II parametrization procedure is sensitive to changes in the prey-predator matrix, for which little quantitative data were used, except for the mackerel group as predators. Improved quantitative estimates of the diets of other predators are warranted.

There are many oppportunities to improve this budget in follow-up work. Greater realism might result from preparing a separate budget for each region, as there are substantial differences in fisheries, primary production and other ecosystem functions along the coast. Some of these regional differences could have caused the observed discrepancies. As an example, demersal and pelagic fish communities may be differently represented in the various regions. The northeastern gulf shelf may have a higher proportion of pelagic species than other regions, and demersal species may be better represented in north central and northwestern regions. Such regional differences could lead to differences in the relative consumption of benthic macrocrustaceans and small pelagic fish by higher trophic groups. These differences may have caused some of the unrealistic values resulting from the application of the ECOPATH II software to this model.

Conclusions

This modelling exercise suggests that the biomass and consumption estimates calculated by Brown et al. (1991) are reasonable for most compartments. They are both consistent with each other and of an order of magnitude that can be supported by the range of net primary production values that have been estimated. Certain unrealistic results suggest that a closer look is needed for the macrocrustacean and small pelagic prey compartments.

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A Preliminary Biomass Budget for the Northeastern Venezuela Shelf Ecosystem

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Abstract

The northeastern Venezuela shelf ecosystem (30,000 km^2) is the most productive fishing area in the country. Marine biological productivity is associated with wind-induced upwelling in the dry season (November through May) and river runoff in the rainy season (May through November). Considering its regional socioeconomic and scientific importance, available information was analyzed in order to study biomass production and flow by means of the ECOPATH II steady-state trophic model. The system was divided into 16 species or species groups: small sharks, scombrids and barracudas, snappers and groupers, squids, croakers, carangids, grunts, catfish, mackerel, other demersal fishes, small pelagics, heterotrophic benthos, zooplankton, phytoplankton, benthic producers and detritus.

Introduction

Marine biological production on the shelf along the northernmost coast of South America is highly correlated with wind-induced upwelling in the dry season (November-May) and river runoff in the rainy season (June-October). Main terrigenous inputs are associated with the Orinoco and Magdalena Rivers, as well as the large estuarine Lake Maracaibo-Gulf of Venezuela system. Main regional upwelling events occur on the Colombian coast of the Guajira Peninsula, the western coast of the Paraguana Peninsula in the Gulf of Venezuela and, especially, along the northeastern Venezuela coast (Longhurst and Pauly 1987; Muller-Karger and Varela 1988). These systems sustain regionally important fisheries of demersal and pelagic resources.

The northeastern Venezuelan shelf (Fig. 1) is located within 62°W - 66°W and 10°N - 11°30'N. The shelf narrows abruptly west of 66°W to become almost nonexistent at 66°30'W in the Venezuelan central marine province. Maximum shelf width of about 110 km is reached north of Margarita Island; the wide shelf continues east towards Trinidad and Tobago, but the hydrological regime there is different, due to the influence of the Orinoco River and the absence of upwelling. Bottom sediments are variable, with mud, originated from the plume of the Orinoco and transported westwards, predominating along the northern Paria coast. The Tortuga Bank, from Los Testigos Islands to Cabo Codera at its western limit, is covered with sandy sediments and numerous areas of hard bottoms. South of Cariaco, Trench and in the Gulf of Cariaco, mud sediments predominate.

The pelagic resources in the area are mostly exploited by small-scale fishers. The most important species are Spanish "sardine" (*Sardinella aurita*), king mackerel (*Scomberomorus cavalla*), little tunny (*Euthynnus alleteratus*) and Atlantic bonito (*Sarda sarda*). Demersal resources are exploited by both small-scale fishers and commercial trawlers. Main species are shrimps (*Penaeus* spp.), grunts (Haemulidae), snappers (Lutjanidae), groupers (Serranidae), molluscs (Cephalopoda and Bivalvia) and croakers (Sciaenidae).

Many fisheries biologists have dealt with exploited marine living resources using the traditional single-species approach (Beverton and Holt 1957; Ricker 1975). Even though early authors acknowledged the need to account for environmental

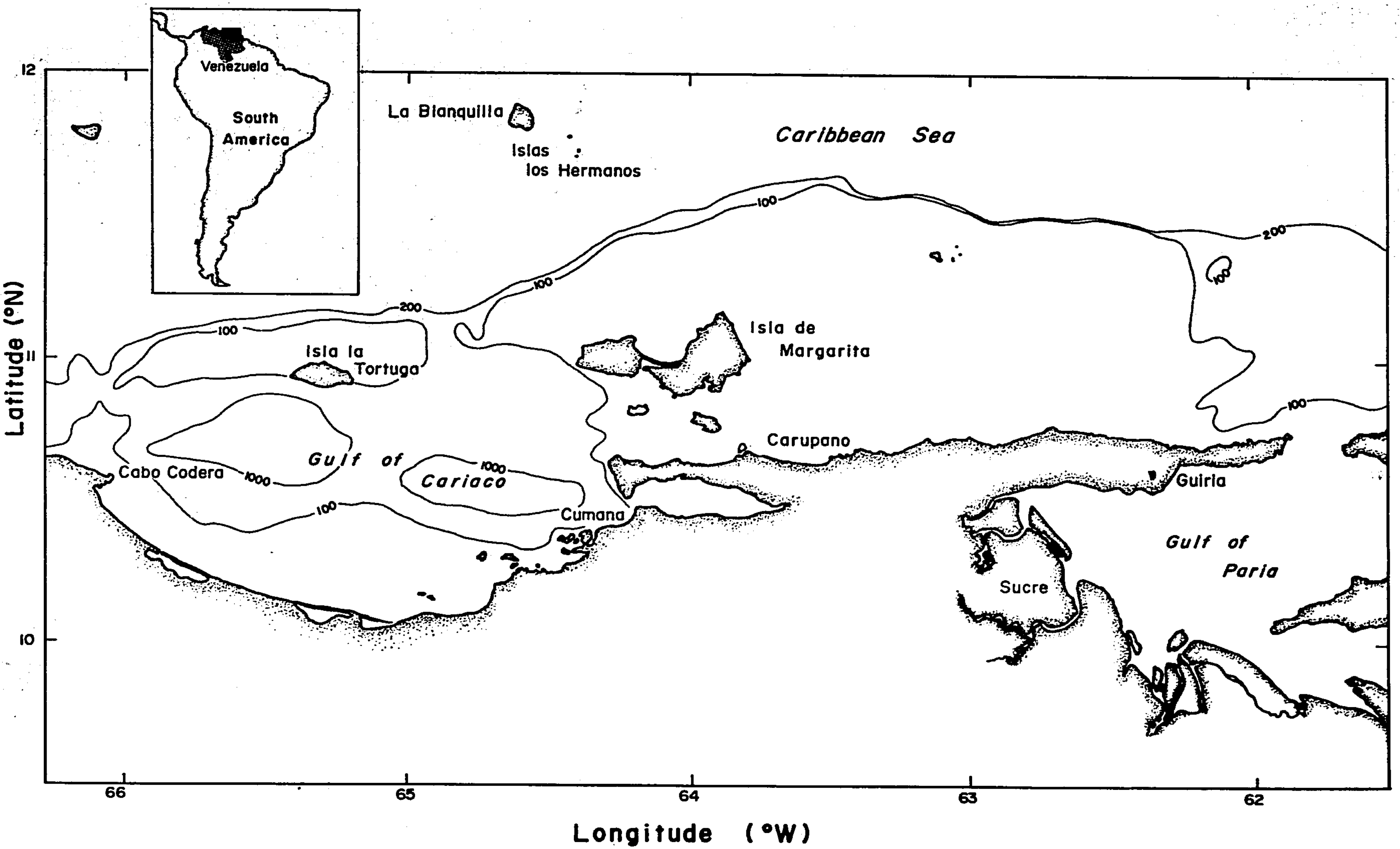

Fig. 1. The northeastern Venezuela shelf. Depth contours are in meters.

variables and species interactions (Smith 1988), it has been only recently that pertinent models have been developed (Andersen and Ursin 1977; Laevastu and Larkins 1981; Walsh 1981; Pauly and Murphy 1982; Polovina 1984). Some of these models are very data demanding and have therefore limited applicability, especially in tropical developing countries.

Polovina (1984) developed a simple steady-state trophic box model known as ECOPATH, in which an ecosystem is partitioned into species groups and, given a set of parameters as inputs, and which produces estimates of mean annual biomass, annual biomass production and annual biomass consumption for each of the species groups. These groups are defined based on the similarity of their life history parameters, common physical habitat and similar diet. This approach was further expanded upon by Pauly et al. (this vol.) and Christensen and Pauly (1992a, 1992b).

Considering the need to gain insight into the functioning of the trophic food web in the shelf ecosystem of northeastern Venezuela, I have found it useful to gather available information in order to sketch a preliminary biomass budget for this important marine area. This approach is particularly relevant considering that no previous modelling effort of this sort has been attempted in this shelf region. Most studies have been aimed at describing the ichthyological fauna (Cervigon 1966) and the general characteristics of the system within the fisheries context (Gines 1972).

Materials and Methods

In the present study, the ECOPATH II model (Christensen and Pauly 1992a and 1992b) has been applied in order to produce a balanced steady-state description of the northeastern Venezuela shelf ecosystem. First a brief outline of the model is given, followed by the different techniques and data sources used to satisfy model input requirements.

The ECOPATH II Model

As described in Pauly et al. (this vol.) and Christensen and Pauly (1992a, 1992b), the ECOPATH II model is derived from the ECOPATH program of Polovina and Ow (1983) and Polovina (1984).

Basically, the approach is to model an ecosystem using a system of simultaneous linear equations [one for each (group of) species i]:

Production by (i) - all predation on (i) - nonpredation losses of (i) - export of (i) = 0, for all i.

or,

$$B_i \cdot \frac{P_i}{B_i} - \sum_{j=1}^{n} B_j \cdot \frac{Q_j}{B_j} \cdot DC_{ji} - \frac{P_i}{B_i}(1-EE_i) - EX_i = 0$$

(Christensen and Pauly 1992b) where

B_i = biomass of (i);

P_i/B_i = production/biomass ratio of (i), which under steady-state conditions, is equal to the instantaneous coefficient of total mortality Z (Allen 1971);

EE_i = ecotrophic efficiency is the part of production that goes to predation, catches and exports to other systems;

B_j = biomass of predator j;

Q_j/B_j = consumption/biomass ratio of predator j;

DC_{ji} = is the fraction of prey (i) by weight in the average diet of predator j;

EX_i = sum of fisheries catches of (i) plus emigration to adjacent ecosystems.

Data Sources and Parameter Estimation Techniques

BIOMASS ESTIMATES

Hydroacoustic and demersal trawl surveys have been used in this area to evaluate fish and invertebrate biomass over the past decade (Gerlotto and Elquezabal 1986; Gines and Gerlotto 1988; Anon. 1989). Overall fish biomass for the region has apparently remained relatively stable at around 1.4 x 10^6 t. The report presented by the Institute of Marine Research, Bergen (Anon. 1989) presents relatively detailed data for the most important pelagic and demersal species groups. The biomass estimates were transformed to $t \cdot km^{-2}$ using a value of 30 x 10^3 km^2 for the shelf area (Gines 1972; Anon. 1989).

PRODUCTION/BIOMASS RATIOS

I have used catch data provided by the Fisheries and Aquaculture Directorate of the Ministry of Agriculture and Husbandry (Direccion General Sectorial de Pesca y Acuicultura del Ministerio de Agricultura y Cria - DGSPAMAC) to estimate fishing mortality. That is: $F = Y/B$ (Gulland 1969).

Natural mortality (M) has been estimated using Pauly's (1980) empirical formula:

$$\ln M = -.0152 - .279 \ln L_\infty + .6543 \ln K + .463 \ln T$$

where L_∞ and K are von Bertalanffy growth parameters and T represents average ambient temperature. For this last variable, we have chosen 24°C (Gines 1972).

Finally, the P/B ratio, i.e., Z was estimated from F + M.

Otherwise, I have used data available in the literature for species groups to which the above methods were not applicable.

CONSUMPTION/BIOMASS RATIOS

The consumption/biomass ratios were obtained by species groups using the empirical formula of Palomares and Pauly (1989):

$$\ln Q/B = -.1775 - .2018 \ln W_\infty + .6121 \ln T + .5156 \ln A + 1.26\,F$$

where

W_∞ = asymptotic weight (in g);
T = average ambient temperature (24°C);
A = aspect ratio of caudal fin (calculated from photographs in Gines (1972) and drawings in Cervigon (1966));
F = food type variable (= 0 in carnivores and 1 in herbivores).

DIET COMPOSITION

A non-negligible amount of work has been done in the area on diet composition of numerous fish species, mainly as university degree requirements. Most of these studies are of a qualitative nature. However, as demonstrated by MacDonald and Green (1983), there is a high level of redundancy in the different variables applied in diet composition analysis. Nevertheless, educated guesswork is required when the size distributions of prey differ markedly. Furthermore, in many of these studies, fish are often lumped together as a single dietary item. Considering the catholic taste of many tropical fish, I have used biomass estimates and general habitat characteristics to partition consumption of fish species as prey items. In other cases when local diet compositions were not available, or insufficient, data from the literature were used.

ECOTROPHIC EFFICIENCY

No data were available concerning this parameter. It was assumed for most groups that ecotrophic efficiencies were greater than 0.9 and less than 1. In this preliminary stage a conservative value of 0.75 was assumed for phytoplankton.

PRIMARY PRODUCTION

Phytoplanktonic primary production was intensively studied in the area during the 1960s (Curl 1960; Ballester and Margalef 1965; Hammer 1967; Gines 1972). The average values observed in the Gulf of Cariaco were approximately 1,800 $mg{\cdot}C{\cdot}m^{-2}{\cdot}day^{-1}$. North of Araya Peninsula and north and northwest of Margarita island average observations were 500-600 $mg\ C{\cdot}m^{-2}{\cdot}day^{-1}$. North of Paria and around Los Testigos Islands average values were about 360 $mg\ C{\cdot}m^{-2}{\cdot}day^{-1}$. North of Cariaco Trench around La Tortuga Island observed average production was relatively low, approximately 280 $mg{\cdot}C{\cdot}m^{-2}{\cdot}day^{-1}$. There were no observations in the coastal waters south of Cariaco Trench. An overall average of 450 $mg\ C{\cdot}m^{-2}{\cdot}day^{-1}$ for the entire shelf was estimated. An additional 20% was added to the primary production estimate to account for benthic production and coastal phytoplanktonic production south of Cariaco Trench. A conversion factor of .06 gC = 1 g ww (Walsh 1981) was employed for transformation. Input average total primary production for the system was set at 3,300 $t{\cdot}km^{-2}{\cdot}year^{-1}$.

SPECIES GROUPS

The model includes a total of 16 groups and relies heavily on the exploited part of the ecosystem. Thus, 12 of the groups are exploited commercially, 10 of these being fish groups. The four remaining groups are zooplankton, phytoplankton, benthic producers and detritus.

Small sharks. The most important species in this group are smooth dogfish (*Mustelus canis*), Caribbean sharpnose (*Rhizoprionodon porosus*) and small-eye smooth hound (*Mustelus higmani*). The smooth dogfish presented the highest relative abundance during the surveys; it was therefore considered as representative of this group. Overall biomass was estimated at 2,800 t and catches at 500 $t{\cdot}year^{-1}$.

Maximum observed length for *M. canis* is 1,500 mm (Compagno 1984). L_∞ was approximated using $L_{max}/0.95$ (Pauly 1983), which equalled 158 cm. A conservative value of K = .24 $year^{-1}$ was estimated using information on *Mustelus* spp. from Francis (1981). The Q/B ratio of 4.5 was taken from Polovina (1984). The diet composition for this group was determined using information from Russo (1975) and Gomez and Bashirullah (1984).

Scombrids and barracudas. The group is formed by king mackerel (*Scomberomorus cavalla*), little tunny (*E. alleteratus*), Atlantic bonito (*Sarda sarda*), the guachanche barracuda (*Sphyraena guachancho*) and the southern sennet (*Sphyraena picudilla*). King mackerel was taken as the representative species. Group biomass was estimated at 16,000 t and catches at 5,500 $t{\cdot}year^{-1}$.

Growth parameters were obtained from Beaumariage (1973). Diet composition information was available for this group from Etchevers (1976), Anon. (1983a), Torres (1986), Bashirullah and Acuna (in press).

Snappers and groupers. This group is composed of lutjanids (essentially *Lutjanus* spp., *Pristipomoides macrophthalmus* and *Rhomboplites aurorubens*) and serranids. Lutjanids were by far the most abundant during the surveys. The yellowtail snapper (*R. aurorubens*) was considered as group representative. Biomass was estimated at 22,600 t and catches at 5,250 t·year^{-1}.

Growth parameters were obtained from Grimes (1976). Diet composition data for this group were obtained from Garcia and Bashirullah (1976); Grimes (1979); Anon. (1983b); Munro (1983); and Lorenzo (1985).

Squid. Main species are *Loligo plei* and *Loligo pealei*. Biomass was estimated at 8,000 t and catches at 1,600 t·year^{-1}.

Growth parameters and natural mortality are from Pauly (1985). The Q/B ratio was established on the basis of a 10% body weight ingestion per day (Amaratunga 1983). The latter author also provides information on the dietary habits of these species.

Carangids. This group contains rough scad (*Trachurus lathami*), scads (*Decapterus* spp.), bumper (*Chloroscombrus chrysurus*), big-eye scad (*Selar crumenophthalmus*), look-downs (*Selene* spp.) and others. Biomass was estimated at 200,000 t and catches at 9,200 t·year^{-1}. Rough scad represented more than 85% of the biomass and was chosen as group representative.

Approximate growth parameters were estimated on the basis of information provided by Munro (1983), Rodriguez (1987) and Widodo (1988).

Food habits of this group were approximated from Anon. (1983b), Munro (1983) and Rodriguez (Instituto Oceanografico, Universidad de Oriente, Cumana, pers. comm.).

Mackerel. The only species present is *Scomber japonicus*. Biomass was estimated at 24,000 t and catches at 600 t·year^{-1}.

L_{max} observed during the surveys was 30 cm and L_∞ was estimated from $L_{max}/0.95$ (Pauly 1983). The growth performance index ϕ' (Munro and Pauly 1983) was estimated from data in Morales-Nin (1988), which permitted to establish a preliminary value of K.

Local diet composition studies have not been carried out. Data from Muck and Sánchez (1987) were used to estimate the diet vector for this species.

Croakers. This group contains mainly weakfish (*Cynoscion* spp.) and whitemouth croaker (*Micropogonias furnieri*). This last species was chosen as group representative. Biomass was estimated at 6,900 t and catches at 2,800 t·year^{-1}.

Growth parameters are from Rodriguez (1968). Diet composition data were obtained from Moreno (1985), Ruiz (1985) and Isaac (1988).

Grunts. This group contains species of the family Haemulidae, mainly *Haemulon* spp. and *Orthopristis ruber*. Biomass was estimated at 14,300 t and catches at 3,840 t·year^{-1}. *Haemulon steindachneri* was chosen as group representative.

Growth parameters were estimated by Barreto (1990). Food habits in the area have been studied by Gonzalez (1981), Guzman (1989) and Barreto (1990).

Catfish. Main species in this group are *Bagre marinus* and *Cathorops spixii*. This last species was chosen to represent the group.

Biomass was estimated at 11,400 t and catches at 2,170 t·year^{-1}. Growth parameters were estimated by Etchevers (1978). Diet composition was based on Arias and Bashirullah (1984).

Other demersals. This is a very heterogenous group of demersal fishes. The most abundant families are Mullidae, Priacanthidae, Sauridae, Sparidae, Gerreidae, etc. Biomass was estimated at 25,400 t and catches at 25,000 t·year^{-1}. The goatfish, *Mulloidichthys martinicus* (Mullidae), was elected as group representative.

Approximate growth parameters are from Munro (1983). The diet composition of this group was tentatively established based on the studies by Vasquez (1977), Fradique (1981), Fernandez (1982), Munro (1983), Granado (1985) and Franco (1987).

Small pelagics. This group contains engraulids and clupeids. The Spanish "sardine", *Sardinella aurita,* comprised more than 80% of total group abundance. Overall biomass was established at 1,000,000 t and catches at 80,000 t·year^{-1}.

Growth parameters and natural mortality are from Fréon (1988). Diet composition data are from Anon. (1984), Huq (1984), Parra and Leon (1984) and Medina-Gaertner (1988).

Heterotrophic benthos. This group contains all benthic invertebrates including shrimps and crabs. Catches were estimated at 20,400 t·year^{-1}. The P/B ratio value of 3 was taken from Polovina (1984). A tentative diet vector was approximated from general knowledge of food habits of benthic invertebrates (Barnes 1974) and from Polovina (1984).

Zooplankton. This group includes fish larvae. Following Polovina (1984), the P/B ratio was set at 40 and the diet vector was based on phytoplankton and some cannibalism.

Phytoplankton. The P/B ratio was set at 70 (Polovina 1984) and the EE at 0.75.

Benthic producers. The P/B ratio of 12.5 was taken from Polovina (1984).

Detritus. There was no available information regarding the biomass of this component in the area studied. I have used the empirical relation established by Pauly et al. (this vol.) to obtain a rough estimate of this parameter , i.e.,

$$\log D = .954 \log PP + .863 \log E - 2.41$$

where D is detrital biomass in $g \cdot C \cdot m^{-2}$, PP is primary production in $g \cdot C \cdot m^{-2} \cdot year^{-1}$ and E is the euphotic layer depth. Values entered were 182.5 for PP and 40 for E.

Assimilation in all cases was set at 80% of consumption, which is the default value in the ECOPATH II model, based on the work of Winberg (1956) on fishes.

Results and Discussion

Table 1 presents input values and estimates of biomass, catches and the instantaneous rate of fishing mortality for the different species groups.

In most cases we used average biomass estimates as provided by the four hydroacoustic and swept area surveys during 1988 (Anon. 1989). Acoustic results pertain to small pelagics, carangids, mackerels, and scombrids and barracudas; the species composition having been determined by midwater trawling. Naturally, gear selectivity by size and species may introduce an important bias regarding the true species composition. It is hard to say in which sense the results may be biased, although the above cited report considers that mackerel and scombrid and barracuda abundance may be overestimated due to their relatively high catchabilities. For most demersal resources, biomasses based on swept area are probably underestimates considering that catchability of all species was set at 1. The only significant change introduced in the data provided was to double the small sharks component biomass, which was considered in the report to represent a "gross underestimate," due to their pelagic nature.

Table 1. Biomasses ($t \cdot km^{-2}$), catches ($t \cdot km^{-2} \cdot year^{-1}$) and instantaneous rate of fishing mortality (F; $year^{-1}$) for species groups in the northeastern Venezuela shelf.

	Group	Biomass	Catches	F
1.	Small sharks	0.082	.017	.21
2.	Scombrids/barracudas	0.550	.183	.33
3.	Snappers/groupers	0.750	.175	.23
4.	Carangids	6.670	.307	.05
5.	Mackerel	0.800	.020	.02
6.	Squid	0.267	.053	.20
7.	Other demersal fishes	0.850	.833	.98
8.	Catfish	0.380	.072	.19
9.	Grunts	0.480	.128	.27
10.	Croakers	0.230	.093	.40
11.	Small pelagics	33.300	2.667	.08
12.	Zooplankton	8.160	-	-
13.	Heterotrophic benthos	13.400	.680	.05
14.	Phytoplankton	45.000	-	-
15.	Benthic producers	11.200	-	-
16.	Detritus	135.000	-	-
Total		257.119	5.228	

Additionally, fisheries catch statistics in Venezuela are of poor quality, especially in the case of the coastal small-scale fisheries. Several studies in the northeastern area [Mendoza et al. 1987; Mendoza and Fréon, in press (a), in press (b)] indicate that official statistics may underestimate landings by more than a 100%.

Therefore several empirical adjustments were necessary in order to account for deficiencies in the data. Globally, 50% was added to official landings of fish species landed by small-scale fishers. This relatively low-value adjustment was used in order to account for the fact that biomass estimates do not cover the 0-20 m depth range and that most demersal resources are probably underestimated (see above). On the other hand, the trawl fisheries landing statistics for both shrimp and fish species are of better quality. However, allowance must be made for discards of noncommercial fish and invertebrates (basically other demersal fishes and heterotrophic benthos), which may represent between two and three times the amount landed.

Naturally, errors in the biomass estimates and catches will reflect upon the value of the fishing mortality coefficient. Unfortunately, at this time there are no available independent estimates to compare with the results obtained. The particularly low values for carangids, mackerels and small pelagics are explained by the very low fishing pressure being exerted upon these groups. Overall, there is no reason to believe, however, that the results presented are not reasonable approximations to the value of this parameter.

The biomass values presented for phytoplankton, zooplankton, benthic producers and heterotrophic benthos are steady-state equilibrium estimates determined by the ECOPATH II model. The values obtained for the phytoplanktonic and zooplanktonic compartments are comparable with observed values in the area (Ferraz-Reyes 1983; Urosa 1983). There are no published data on biomasses of benthonic autotrophs and heterotrophs in this shelf. However, the value estimated for the heterotrophic benthos compartment is very similar to observed biomasses in the western Gulf of Guinea tropical shelf (Longhurst 1959, in Longhurst and Pauly 1987). Moreover, the estimate of detrital biomass obtained from the empirical relation of Pauly et al. (this vol.) is a reasonable approximation for the northeastern Venezuela shelf area (W. Senior, Departamento de Oceanografia, Instituto Oceanografico, Universidad de Oriente, Cumana, pers. comm.).

Table 2 presents growth parameters and natural mortality estimates for the representative species in this study. It is important to underline the fact that

Table 2. Growth parameters and natural mortality on a yearly basis for chosen representatives of species groups in the northeastern Venezuela shelf.

	Species	L_∞ (cm)	W_∞ (g)	K (year^{-1})	M (year^{-1})
1.	*M. canis*	158.0	-	.24	.22
2.	*S. cavalla*	110.0	9,411	.21	.23
3.	*R. aurorubens*	62.6	2,982	.26	.26
4.	*T. lathami*	53.9	478	.40	.40
5.	*S. japonicus*	31.6	416	.54	.58
6.	*L. plei*	23.0	207	.95	1.50
7.	*M. martinicus*	30.0	459	.40	.94
8.	*C. spixii*	33.9	622	.34	.43
9.	*H. steindachneri*	34.9	586	.20	.30
10.	*M. furnieri*	68.0	3,144	.18	.23
11.	*S. aurita*	27.4	201	1.20	1.05

most growth parameter estimates, except for *C. spixii* and *H. steindachneri*, are from studies relating to other tropical and subtropical areas. Unfortunately, the amount of work on growth and ageing in the northeastern Venezuelan shelf is scanty. Furthermore, work by Heald and Griffiths (1967) and Gonzalez (1985) on otoliths and scales, respectively, of Spanish "sardine" (*S. aurita*) and otolith readings by Rodriguez (1987) on rough scad (*T. lathami*) were not included, mainly because their relatively low values of K led to production estimates which were incompatible with the predatory pressure exerted upon these groups (see below). Therefore, the model may be useful in testing gross discrepancies in input parameters.

Table 3 presents the estimated P/B and Q/B ratios, as well as the ecotrophic efficiencies (EE). The P/B ratio for most species groups is dependent on the estimates of F and M, hence the errors and limitations that affected the estimation of these parameters will be added in the estimation of production. As stated earlier, the Q/B ratios for the ichthyofauna were based on the empirical formula of Palomares and Pauly (1989) and are comparable for most species groups with data presented by these authors and by Pauly (1989) for a number of tropical and temperate species. However, the estimates obtained for snappers/groupers and other demersals may slightly overestimate consumption. This would be basically explained by the relatively high aspect ratio (A) of the caudal fin of selected group representatives, the yellowtail snapper *R. aurorubens* and the goatfish *M. martinicus*, respectively. The values presented for zooplankton and heterotrophic benthos are model estimates, which are very close to the values obtained by Polovina (1984).

Table 3. Production/biomass (P/B; year^{-1}) and consumption/biomass (Q/B; year^{-1}) ratios in t·year^{-1}·km^{-2} and ecotrophic efficiency (EE) per species group in the northeastern Venezuela shelf. The EE estimates were calculated by the program.

	Group	P/B	Q/B	EE
1.	Small sharks	.40	4.5	.83
2.	Scombrids/barracudas	.57	5.9	.83
3.	Snappers/groupers	.49	5.6	.87
4.	Carangids	.45	7.6	.93
5.	Mackerel	.60	9.0	.91
6.	Squid	1.70	36.5	.96
7.	Other demersal fishes	1.92	8.4	.92
8.	Catfish	.62	7.2	.93
9.	Grunts	.57	6.7	.95
10.	Croakers	.64	4.9	.92
11.	Small pelagics	1.13	9.8	.93
12.	Heterotrophic benthos	3.00	12.5	.97
13.	Zooplankton	40.00	279.9	.97
14.	Phytoplankton	70.00	0.0	.75
15.	Benthic producers	12.50	0.0	.61

Estimated ecotrophic efficiencies were kept deliberately high, between .9 and 1, for most species groups. It is reasonable to assume that most of the production in an exploited ecosystem will be predated upon or fished. This of course may not be the case for top predators. In our case, top predators sustain important catches and, moreover, there is a certain amount of unaccounted predation on these groups by tunas and large sharks, which were not included in this preliminary stage due to inadequate data. Therefore, estimates were held at values ranging from .8 to .9. The value of .75 retained for phytoplankton may be considered as a conservative value for this parameter. Walsh (1983) determined for a number of temperate and subtropical marine systems that the export of phytoplanktonic production into the detritus was 50% or more. However, considering the protracted period of relatively low intensity upwelling that occurs in the tropical northeastern Venezuelan shelf, it may be reasonable to assume that phytoplanktonic production is more efficiently used. This assumption is partially sustained by the fact that carbon/nitrogen ratios in the sediments of this area show an important component of terrigenous origin (Bonilla-Ruiz et al. 1985). The value of .61 estimated by the model for benthic producers may be considered an overestimate if only macrophytic producers are taken into account (Christensen and Pauly 1992a). Nonetheless, there is likely to be an important production by benthic microalgae upon which the predatory pressure is certainly much higher. Finally, the low ecotrophic efficiency of the detrital component (.03) indicates that an important amount of input is being buried into the sediments.

Table 4 shows the estimated diet matrix for the different components used in this model. As stated earlier, most of the food habit studies carried out in this area have been of a qualitative nature. Therefore

Table 4. Diet composition matrix for species groups in the northeastern Venezuela shelf ecosystem. The diet compositions sum to 1 (vertically).

	Predator												
Prey	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Small sharks	.03	-	-	-	-	-	-	-	-	-	-	-	-
2. Scombrids/barracudas	.03	.02	-	-	-	-	-	-	-	-	-	-	-
3. Snappers/groupers	.06	.01	.02	-	-	-	-	-	-	-	-	-	-
4. Carangids	.15	.10	.08	.04	-	-	-	-	-	-	-	-	-
5. Mackerel	-	.06	.01	-	.03	-	-	-	-	-	-	-	-
6. Squid	-	.02	.02	-	-	.02	-	-	.01	-	-	-	-
7. Other demersal fishes	.06	.00	.03	-	-	-	.05	.01	.05	.02	-	-	-
8. Catfish	.02	.01	.02	-	-	-	-	-	-	-	-	-	-
9. Grunts	.02	.01	.02	-	-	-	-	-	-	-	-	-	-
10. Croakers	.07	.00	-	-	-	-	-	-	-	-	-	-	-
11. Small pelagics	.25	.74	.40	.37	.39	.41	.18	.26	.23	.20	-	-	-
12. Zooplankton	-	-	-	.50	.59	.46	.06	.11	.10	.10	.56	.04	.05
13. Heterotrophic benthos	.32	.02	.40	.10	-	.11	.62	.58	.61	.68	-	-	.13
14. Phytoplankton	-	-	-	-	-	-	-	-	-	-	.44	.95	.20
15. Benthic producers	-	-	-	-	-	-	.08	.02	-	-	-	.01	.37
16. Detritus	-	-	-	-	-	-	.02	.02	-	-	-	-	.25

educated guesswork was required to adjust values to quantitative (by weight) estimates of diet composition. Basically, once the initial diet vectors were determined, the approach consisted in adjusting these vectors individually in order to satisfy the preestablished limits on ecotrophic efficiencies and other model inputs. Fortunately, there was no need to modify substantially the initial estimates of percentage consumption. In most cases, minor adjustments of the order of .05% to 5% were applied to satisfy model requirements. Still, the diet vectors per species group should only be considered indicative of dietary preferences.

Table 5 presents some important component parameters estimated by the ECOPATH II model. Details of the calculation procedure for these parameters may be found in Christensen and Pauly (1992a). As expected, most of the consumption of biomass is associated with the pelagic compartments: zooplankton, small pelagics and, to a lesser degree, carangids. There is also an important consumption of biomass on the part of the benthic heterotrophs. These four components consume around 75% of the production within the system and contribute around 95% of the total flow to the detritus box. In addition, several groups with relatively low biomass levels play a significant role in the consumption of production, namely squid, mackerel and other demersals.Most of the assimilated consumption is respired, particularly in the case of carangids,

Table 5. Estimates of food intake (FI), assimilation (AS), respiration (RS), flow to detritus (FD) and net efficiency (NE) per species group in the northeastern Venezuela shelf. All values, except NE, are in t·km^{-2}·year^{-1}.

Group	FI	AS	RS	FD	NE
1. Small sharks	0.37	0.29	0.26	0.08	0.11
2. Scombrids/barracudas	3.27	2.61	2.30	0.71	0.12
3. Snappers/groupers	4.20	3.36	2.99	0.89	0.11
4. Carangids	50.70	40.56	37.56	10.34	0.08
5. Mackerel	7.22	5.78	5.30	1.49	0.09
6. Squid	9.75	7.80	7.34	1.97	0.06
7. Other demersal fishes	7.10	5.68	4.05	1.56	0.23
8. Catfish	2.73	2.19	1.95	0.56	0.11
9. Grunts	3.21	2.56	2.29	0.65	0.10
10. Croakers	1.13	0.90	0.75	0.24	0.16
11. Small pelagics	327.01	261.60	223.98	67.91	0.15
12. Heterotrophic benthos	167.00	133.60	93.40	34.51	0.30
13. Zooplankton	2,284.00	1,827.20	1,500.80	465.15	0.18
14. Phytoplankton	-	-	-	802.92	
15. Benthic producers				54.78	

mackerel and squid. This is reflected in the relatively low values of the net efficiencies for these groups, which, however, considering their particularly active nature, the relatively low production of mackerel and carangids (associated with a very low level of exploitation) and the high Q/B ratio in squid, appear to be reasonable estimates. Otherwise, the estimated net efficiencies for other components are well within accepted limits (Jones 1982; Polovina 1984).

Fig. 2 presents major biomass flows as estimated by the ECOPATH II program. As might be expected, most of the biomass and production is contained within the pelagic domain. The main flow is determined by the interaction between phytoplankton, zooplankton, small pelagics and carangids. In the bentho-demersal domain, most of the biomass and production is associated with the detritus, benthic producers and heterotrophic benthos compartments.

The total estimated biomass, excluding detritus, was 122 t·km^{-2} of which 78% corresponded to the pelagic components and 22% to benthic and demersal compartments. Total biomass production was around 3,700 t·km^{-2}·year^{-1} of which around 95% was pelagic. Furthermore, there is a non-negligible amount of direct demerso-pelagic coupling. The consumption of pelagic production by benthic and demersal components was approximately 66 t·km^{-2}·year^{-1}, essentially phytoplankton, zooplankton and small pelagics. In the opposite direction consumption was approximately 45 t·km^{-2}·year^{-1}, mainly heterotrophic benthos.

At this stage, results must be viewed as a preliminary approximation to the interactions occurring within the system. It is important to stress that the model is incomplete in the sense that apex predators (such as large sharks and tunas) and avian fauna were not included due to lack of adequate data and, for the former, due to their limited role within this neritic environment. Most likely, the main impact of these groups would be upon the pelagic compartment (mainly small pelagics and carangids) and upon the small sharks, scombrids and snapper groups. Nevertheless, I feel that the major pathways depicted in Fig. 2 would not be significantly altered, except probably for the relatively high levels of cannibalism within the carangids and small shark compartments that were required to balance the system equations.

Another shortcoming stems from the fact that imports and exports (apart from catches) are not known. However, biomass estimates (Anon. 1989) for species groups from adjacent areas are more than an order of magnitude lower than in the study area. The assumption was therefore made, as a first approximation, that interactions with adjacent ecosystems were negligible.

In addition, the ECOPATH II model provides important information (Table 6) that may allow to establish the "status" of an ecosystem in terms of maturity and to compare different systems on the same grounds (see Christensen and Pauly 1992a and Christensen, in press for details). The total system throughput is equal to the sum of all flows (consumption, exports, respiratory flows and flows into the detritus) within an ecosystem. The value of 8,078 t·km^{-2}·year^{-1} obtained for the northeastern Venezuelan shelf determines an intermediate-sized ecosystem in terms of flow per unit area, when compared to data presented by Pauly et al. (this vol.). An important amount of this throughput is linked to the flow into the detritus and its subsequent export into the sediments.

The other summary statistics, which are meant to express the relative degree of maturity of an ecosystem, give a somewhat ambiguous picture. On the one hand, the relatively low value of the primary production/respiration ratio and the relatively high estimate of the connectance index indicate a certain level of system maturity. On the other hand, the relatively high net system production and total primary production/biomass ratio and the relatively low total biomass/total throughput ratio are indicative of an immature ecosystem. Notwithstanding the possible errors and limitations of the dataset, this apparent ambiguity may be partially explained by certain characteristics of this particular ecosystem. Mainly, most of the biomass and production is related to a lightly exploited and dominant pelagic subsystem, which has multiple trophic links, over an extensive and relatively shallow shelf, to a bentho-demersal subsystem that is moderately to intensively exploited. This characteristic can also be appreciated by examining the network flow indices (Table 7) based on the theory developed by Ulanowicz (1986, in Christensen and Pauly 1992a and 1992b). Despite the fact that the ecosystem is pelagically driven, the important

Table 6. Summary statistics of the northeastern Venezuela shelf ecosystem. Flows are in t·km^{-2}·year^{-1}.

Sum of all consumption (t·km^{-2}·year^{-1})	2,868
Sum of all exports (t·km^{-2}·year^{-1})	1,417
Sum of all respiratory flows (t·km^{-2}·year^{-1})	1,883
Sum of all flows into detritus (t·km^{-2}·year^{-1})	1,454
Total system throughput (t·km^{-2}·year^{-1})	7,621
Total primary production/total respiration	1.752
Net system production (t·km^{-2}·year^{-1})	1,417
Total primary production/total biomass (year^{-1})	27
Total biomass/total throughput (year^{-1})	0.016
Total biomass (t·km^{-2}·year^{-1})	122.1
Total catches (t·km^{-2}·year^{-1})	5.2
Connectance index	0.32

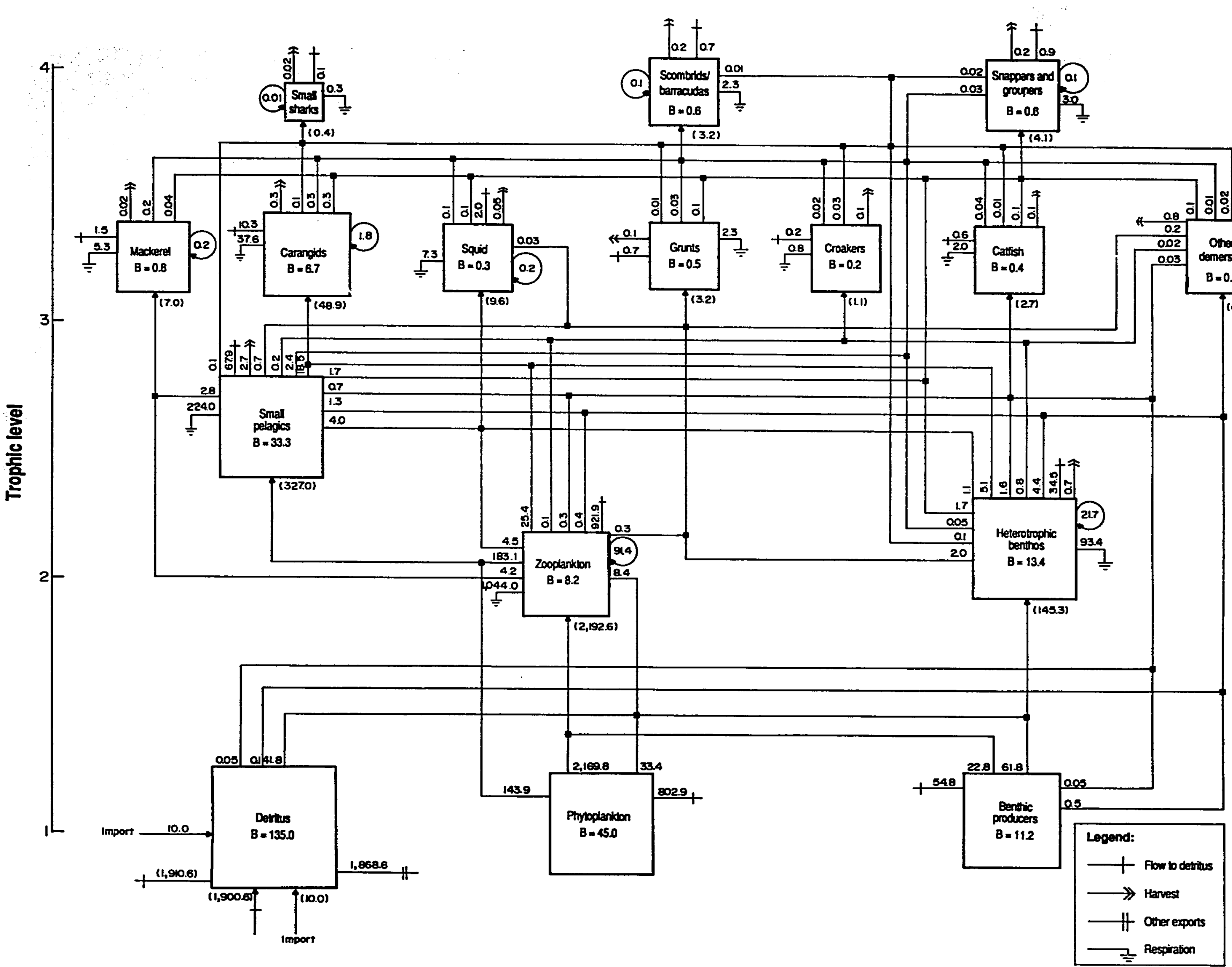

Fig. 2. Biomass pathways in the northeastern Venezuela shelf. B is biomass (t·km^{-2}), all flows are in t·km^{-2}·year^{-1}.

Table 7. Network flow indices as determined by the ECOPATH II model for the northeastern Venezuela shelf ecosystem.

	Ascendency		Overhead		Capacity	
Source	Flowbits	%	Flowbits	%	Flowbits	%
Import	20.8	0.1	75.8	0.3	96.6	0.4
Internal	4,025.7	15.9	11,811.8	46.5	15,837.4	62.4
Exports	3,858.0	15.2	156.1	0.6	4,014.1	15.8
Respiration	2,158.2	8.5	3,274.3	12.9	5,432.6	21.4
Total	10,062.7	39.6	15,318.0	60.4	25,380.7	100.0

Total system throughput = 8,078 t·km^{2}·year
Throughput cycled = 128 t·km^{2}·year
Cycling index = 1.6 (%of throughput)

number of links between groups determine a relatively large overhead on internal flows which would confer an important amount of stability to the system.

The ECOPATH II model also estimates the overall fisheries trophic level which, in this case, is equal to 3.80, that is at approximately the same level as the small sharks and scombrids/barracudas groups. Its gross efficiency (total catch/primary production) is estimated at 0.0016. Furthermore, the estimated primary production to sustain the system was 3,290 t·km^{-2}·year^{-1} as opposed to an input value of 3,300 t·km^{-2}·year^{-1}.

Finally, it is apparent from the dataset that the pelagic component (especially small pelagics, carangids and mackerel) suffers from only a small amount of fishing pressure. The existence of a relatively large unexploited biomass of pelagic species, as determined by hydroacoustic surveys over the past decade (Gerlotto and Elquezabal 1986; Gines and Gerlotto 1988; Anon. 1989), is generally recognized within the scientific, governmental and enterpreneurial communities in Venezuela.

Interest has been focused on the possible increase in exploitation of the Spanish "sardine". However, there is considerable concern about the effects this may have on ecosystem functioning and exploitation of other species (Anon. 1990). Considering the social and economic needs of Venezuelan society it is necessary to understand the possible effects increased exploitation may have on ecosystem functioning. Some straightforward manipulation of the input data indicates that catches of the small pelagics group may be increased by approximately 50% while retaining system balance, mainly at the expense of the ecotrophic efficiency of this group. Another observable effect is the increase of flow to the detritus box from reduced predation on planktonic organisms.

The ECOPATH II model (version 2.0+) also contains a routine for the analysis of the mixed trophic impact of biomass variations of component groups (Christensen and Pauly 1992a). As might be expected, the results (not shown here) indicate that small pelagics are the exploited component that has the largest effect on other groups. This effect is particularly marked in the case of top predators, especially the scombrids and barracudas group and squid. Interestingly, a reduction of small pelagic abundance has a positive effect upon itself by means of reduced competition. Furthermore, the main impact of variations in the carangids group is felt within the group (cannibalism) and upon the small pelagics. It appears from these results that the most adequate exploitation strategy for the ecosystem, within the constraints of the model, would be to exploit small pelagics and carangids simultaneously.

In conclusion, the ECOPATH II model is a powerful tool for understanding ecosystem functioning and for fisheries management. In a data limited situation, such as the one presented here, a coherent picture of the shelf area was obtained. Obviously, further research is required in order to improve input data and to sustain or dismiss the results presented in this preliminary model. It is hoped that future fisheries assessment work in the area incorporates model requirements and interdisciplinary feedback, in order to complement the more traditional approach and, also, exploit some additional model possibilities that were not explored in this study.

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Energy Flow Model of the North Sea Ecosystem

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Abstract

This paper analyzes the major trophic flows in the North Sea covering the late 1970s and early 1980s and shows that there is enough food for North Sea fish, even if trophic efficiency is assumed to be 10%. Some major knowledge gaps are presented.

Introduction

Jones (1984) developed models of energy flow through the North Sea ecosystem and, like Steele (1974), concluded that there was insufficient primary production to satisfy the food requirements of the fish if the efficiency of energy transfer to each trophic level was no higher than 10%. This brief communication attempts to bring these models up to date.

Revised Model

Fig. 1 follows the structure of Jones' model but uses a revised estimate of net primary production (growth minus autocatabolism) of 200 $g \cdot C \cdot m^{-2} \cdot year^{-1}$ derived by the 14C method (Reid et al. 1991) and assumes a 10% trophic transfer efficiency throughout. Partitioning of energy flow between the demersal and pelagic branches has also been modified slightly. Fish biomass estimates (Daan et al. 1990) were derived from English Groundfish Survey data for 1977-1986. The amount of food eaten is assumed to be 3.8 times the fish biomass (Jones 1984). About 20% of the total biomass of the demersal fish is assumed to be 0-groups, which are classed as planktivores. Energy flow and food requirements in the model have been expressed in tons of carbon per year for the North Sea as a whole. This was for convenience since primary production is usually expressed in units of carbon and the carbon content of fish is known. There is uncertainty over the biomass of young demersal fish in the pelagic phase. In general, young fish will have higher relative feeding rates and exhibit higher conversion efficiencies than older fish.

Conclusion

The model indicates that there is sufficient food for North Sea fish, even if trophic transfer efficiency is assumed to be 10%.

Triangular routes in the energy flow allow differential transfer efficiencies between trophic

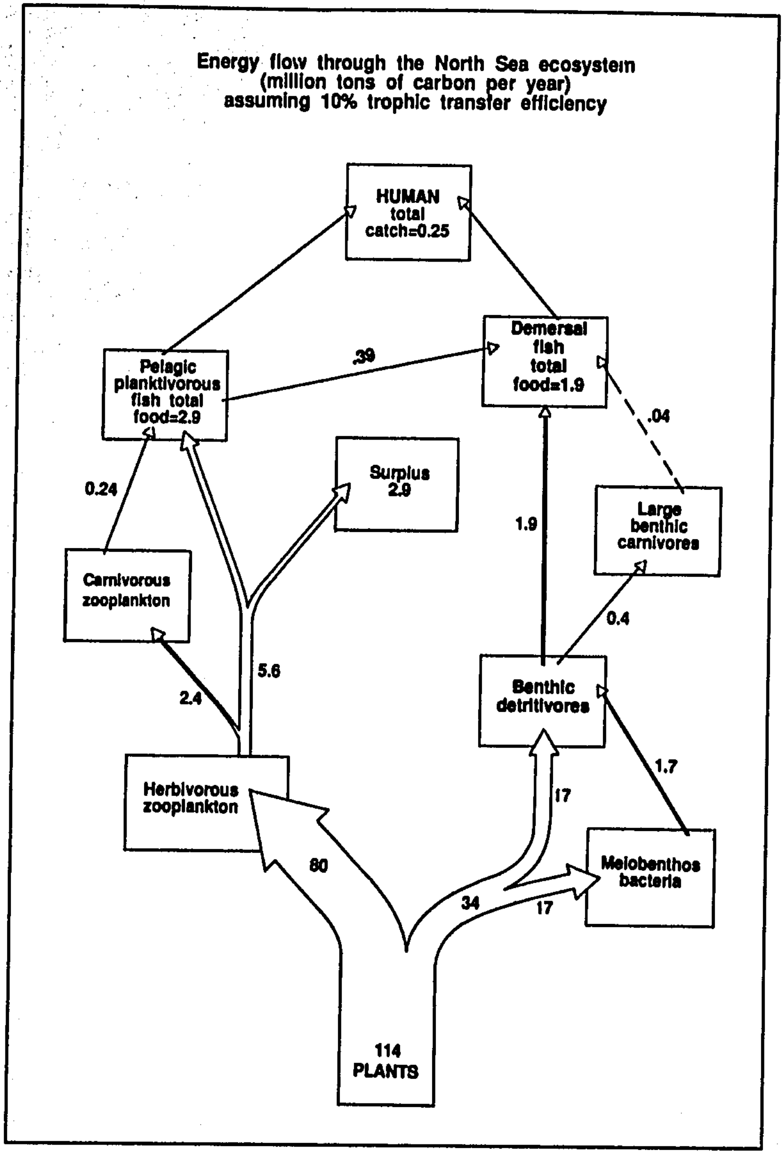

Fig. 1. Energy flow through the North Sea ecosystem (million tons of carbon per year) assuming 10% trophic transfer efficiency.

levels. Even in this simplistic diagram, three such structures exist and in a more detailed representation, many more triangular energy shunts would be revealed. Yet even simple models can generate ideas about the mechanisms which mediate the flow of energy through the ecosystem, and they expose gaps in our knowledge.

It would be useful to have an idea of the extent to which there is interchange of energy between the two main branches of the ecosystem.

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Preliminary Trophic Model of the Coastal Fisheries Resources of Brunei Darussalam, South China Sea*

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SILVESTRE, G., S. SELVANATHAN and A.H.M. SALLEH. 1993. Preliminary trophic model of the coastal fisheries resources of Brunei Darussalam, South China Sea, p. 300-306. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Abstract

A steady-state trophic model of the coastal fisheries ecosystem of Brunei Darussalam is derived via ECOPATH II using selected parameters from studies conducted in the area and the available literature. Biomass estimates of various groups so derived are consistent with independent estimates from demersal trawl and pelagic acoustic surveys conducted in Brunei waters. These estimates of biomass combined with fisheries catches give exploitation rates (E) between 0.011 and 0.191, confirming independent assessments which indicate the coastal fisheries resources to be lightly fished. Selected summary statistics relevant to efficiency of the system are given together with recommendations for research towards refinement of the preliminary model presented.

Introduction

Brunei Darussalam (Fig. 1) has a long tradition of fishing and one of the highest per capita consumption (40 kg/person/year) of seafood in Southeast Asia. Between 1985 and 1988, roughly 5,300 t·year^{-1} was caught in the country's coastal waters, 40% of which was sold through the fresh fish markets and the rest went to subsistence consumption. About 1,900 t·year^{-1} of fisheries products was imported during the same period. The small-scale fisheries sector comprises 560 full-time and 1,700 part-time fishers, while the semi-industrial fleet comprise seven trawlers and two purse seine vessels. Even though the capture fisheries is small by regional standards, its sustainability is deemed significant by local planners. This is in view of (1) its importance to local fresh food supply and security, (2) efforts to diversify the economy from the dominant oil and natural gas industry and (3) the nation's long fishing tradition and current food preferences. Local authorities, therefore, have taken vigorous interest in sustainable development and improved management of the fisheries.

In line with such interest, improvement of the biological input in the fisheries development and management process has been identified as a major constraint. In this regard, demersal trawl and pelagic acoustic surveys were initiated in mid-1989 to complement previous assessment studies in Brunei Darussalam waters (see Chua et al. 1987 for a profile of available assessments). Initial results from the demersal survey indicate low exploitation rates of available resources [viz., (1) mean yield to biomass

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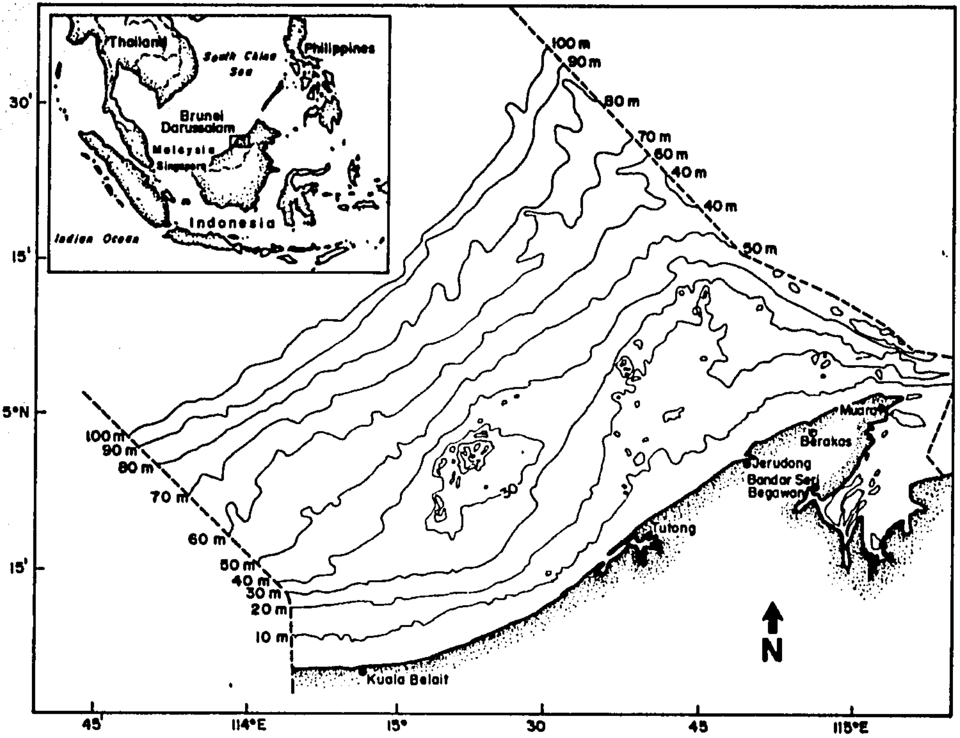

Fig. 1. Brunei Darussalam coastal area.

(Y/B=F) ratio of 0.08 for the fisheries, and (2) mean exploitation ratio (E=F/Z) of 0.15 for the more abundant demersal species based on ELEFAN analyses, Gayanilo et al. 1989]. The present contribution, part of demersal investigations currently in progress, attempts to verify estimates of biomass and exploitation rates obtained thus far using an ecosystem box model (ECOPATH II, Christensen and Pauly 1992) and available information on the various resource groups. Moreover, it attempts to illustrate the nature of available information on Brunei coastal fisheries resources and research areas requiring attention.

Materials and Methods

The approach used here to derive a steady-state trophic model of the coastal fisheries resources of Brunei Darussalam relies primarily on the ECOPATH model (Polovina and Ow 1983, 1985) as modified by Christensen and Pauly (1992). In the absence of site-specific food studies, the trophic groupings and food composition data given by Liew and Chan (1987) and Chan and Liew (1986) for a similar tropical ecosystem (off Terengganu, Malaysia) were utilized. Table 1 gives a summary of input parameters to ECOPATH II used in the present study. Biomass estimates as obtained from demersal (Silvestre et al., unpubl.) and pelagic surveys (DOF 1989) conducted in Brunei Darussalam waters (7,396 km^2 from the shoreline to 100 m depth) were partitioned into the various trophic groups as shown in Table 2. However, given the confidence limits associated with the biomass estimates from such surveys and the variation in catchability and escapement ratios characteristic of each group, only the biomass estimates for demersal zoobenthos feeders (assumed to be the best sampled) were utilized.

Production to biomass ratios (P/B=Z or instantaneous total mortality) for groups 6-9 were obtained from length-based assessments (via ELEFAN) using demersal survey data (see Table 3). Apart from these, the rest of the entries in Table 1 were taken from literature values, as follows: (1) phytoplankton and detritus biomass and phytoplankton P/B from Linden et al. (1989) and Pauly et al. (this vol.); (2) P/B and Q/B ratios from Liew and Chan (1987) and Polovina and Ow (1983); (3) catches from statistics of the Fisheries Department, Brunei Darussalam (Silvestre et al., unpubl.) adjusted for subsistence consumption and discarding practices; and (4) ecotrophic efficiency (EE) assumed to be 0.95 for groups 1 to 8 (see Polovina 1984). Table 4 gives a summary of food composition ratios used as input to ECOPATH II in the present study. All entries are from Liew and Chan (1987) with minor modifications to reflect relative prey abundance/availability in Brunei waters.

Table 1. Summary of input parameters used to derive (via ECOPATH II) a preliminary steady-state trophic model of the coastal fishery resources of Brunei Darussalam. P/B gives the production/biomass ratio and Q/B, the consumption/biomass ratio. EE is the ecotrophic efficiency , i.e., the proportion of the production that is utilized in the system.

Group no.	Group	Biomass ($t \cdot km^{-2}$)	P/B[d] ($t \cdot km^{-2} \cdot year^{-1}$)	Q/B[d] ($t \cdot km^{-2} \cdot year^{-1}$)	Catch[e] ($t \cdot km^{-2} \cdot year^{-1}$)	EE
1.	Zooplankton	-	67.00	280.00	-	0.95
2.	Small molluscs/worms	-	6.85	27.40	-	0.95
3.	Small crustaceans	-	62.00	310.00	-	0.95
4.	Large crustaceans	-	4.00	21.90	0.174	0.95
5.	Heterotrophic benthos	-	3.00	12.50	0.003	0.95
6.	Demersal zooplankton feeders	-	3.40[f]	14.00	0.005	0.95
7.	Demersal zoobenthos feeders	5.579[a]	2.15[f]	10.75	0.131	0.95
8.	Small pelagics	-	2.37[f]	7.90	0.283	0.95
9.	Intermediate predators	-	1.74[f]	8.70	0.060	0.50
10.	Large zoobenthos feeders	-	0.40	6.10	0.120	0.50
11.	Large predators	-	0.60	9.50	0.058	0.50
12.	Phytoplankton	12.825[b]	71.15[b]	0.00	-	-
13.	Detritus	120.000[c]	-	-	-	-

[a] From demersal trawl survey conducted in 1989-1990 (Silvestre et al., unpubl.) covering 7,396 km^2 of shelf area from the shoreline to the 100-m isobath.

[b] Based on Linden et al. (1989).

[c] Based on equation A5 of Pauly et al. (this vol.).

[d] Based on figures used by Liew and Chan (1987) and Polovina and Ow (1983) unless otherwise indicated.

[e] From catch statistics of Fisheries Department, Brunei Darussalam, adjusted for subsistence consumption and discards.

[f] From length-frequency data collected in the area analyzed using ELEFAN (Silvestre et al., unpubl.).

Table 2. Checklist of families/groups occurring in demersal and pelagic catches in Brunei Darussalam, distributed among trophic groups used by Liew and Chan (1987).

Large predators
    Carcharhinidae, Scombridae (excluding *Rastrelliger* but including, Thunninae)
Large zoobenthic feeders
    Dasyatididae, Rhynchobatidae, Ephippidae, Rajidae, Gymnuridae
Intermediate predators
    Carangidae (excluding *Decapterus, Selar, Alepes, Selaroides, Megalaspis*), Sciaenidae, Synodontidae, Ariidae, Lutjanidae, Trichiuridae, Psettodidae, Rachycentridae, Serranidae, Sphyraenidae, Fistularidae, Paralichthyidae, Muraenesocidae, Scorpaenidae, Chirocentridae
Small pelagics
    Carangidae (e.g., *Decapterus, Selar,* etc.), Clupeidae, Loliginidae, *Rastrelliger*, Engraulidae
Demersal zoobenthos feeders
    Leiognathidae, Mullidae, Nemipteridae, Haemulidae, Ariommatidae, Priacanthidae, Theraponidae, Balistidae, Tetraodontidae, Platycephalidae, Lactaridae, Bothidae, Apogonidae, Triglidae, Dactylopteridae, Lethrinidae, Monocanthidae, Sparidae, Stromateidae, Triacanthidae, Polynemidae, Siganidae, Ostraciidae, Labridae, Cynoglossidae, Sillaginidae, Diodontidae, Gobiidae, etc.
Demersal zooplankton feeders
    Gerridae, Centriscidae
Heterotrophic benthos
    Sepiidae, Octopodidae, echinoderms, sponges, large molluscs
Large crustaceans
    Scyllaridae, Portunidae, Penaeidae, Palinuridae, etc.

Results and Discussion

The steady-state trophic model for the Brunei Darussalam coastal fisheries ecosystem as derived using ECOPATH II is illustrated in Fig. 2. A summary of selected output statistics is given in Table 5. Note that the system is largely driven by the large detritus flows occurring off Brunei. Similar flows were assumed by Liew and Chan (1987) for the coastal waters of Terengganu, Malaysia. The biomass estimates (B) obtained via ECOPATH II are consistent with those (i.e., B') obtained from demersal trawl and pelagic acoustic surveys conducted in Brunei waters during the 1989-1990 period. The B' estimates for large crustaceans, heterotrophic benthos, small pelagics and large zoobenthos feeders are believed to be underestimates for reasons of low catchability and above-average escapement from the trawl used for the demersal surveys, and the fact

Table 3. Estimates of P/B ratios for selected trophic groups as derived from length catch curve estimates of Z(year^{-1}) on selected trawl-caught species in Brunei Darussalam (Silvestre et al., unpubl.). Values in parentheses are estimates based on literature values.

Group no.	Group/family/genera	Representative genera/species	% of group biomass	Z (= P/B)
9.	Intermediate predators		81.7	1.74
	Carangidae	*Carangoides malabaricus*	29.4	2.07
	Sciaenidae	*Johnius coitor, Pennahia macrophthalmus*	23.2	2.13
	Synodontidae	*Saurida tumbil*	14.4	14.4
	Ariidae	*Arius thalassinus*	11.1	11.1
	Psettodidae	*Psettodes erumei*	3.6	0.85
8.	Small pelagics		100.0	2.37
	Carangidae	*Decapterus, Selar*	50.3	(2.08)
	Clupeidae	*Sardinella*	42.1	(2.70)
	Loliginidae	*Loligo*	3.4	(2.05)
	Rastrelliger	*Rastrelliger*	2.7	(3.04)
	Engraulidae	*Stolephorus*	1.5	2.26
7.	Demersal zoobenthos feeders		82.8	2.15
	Leiognathidae	*Leiognathus splendens, L. bindus, L. elongatus, L. equulus, Secutor insidiator, Gazza minuta, L. smithursti*	43.4	2.32
	Mullidae	*Upeneus sulphureus U. tragula*	12.3	2.21
	Nemipteridae	*Nemipterus japonicus, N. hexodon, N. nematophorus, N. virgatus*	11.7	1.74
	Haemulidae	*Pomadasys argyreus, P. maculatus*	10.5	2.02
	Priacanthidae	*Priacanthus tayenus, P. macracanthus*	3.4	1.62
	Theraponidae	*Therapon theraps*	1.5	1.88
6.	Small demersal zooplankton feeders	-	3.4	
	Gerridae	*Pentaprion longimanus*	-	3.40

Table 4. Summary of food composition ratios of various trophic groups as used in ECOPATH II to derive a steady-state model of the coastal fisheries resources of Brunei Darussalam. Data from Liew and Chan (1987) with minor modifications indicated by entries in parentheses. (See Table 1 for group names/definitions; dashes imply zero occurrence).

	Prey											
Predator	1	2	3	4	5	6	7	8	9	10	12	13
1.	0.100	-	-	-	-	-	-	-	-	-	0.650	0.250
2.	0.300	0.050	0.050	-	-	-	-	-	-	-	0.100	0.500
3.	0.150	-	-	-	-	-	-	-	-	-	0.050	0.800
4.	0.005	0.250	0.180	-	0.190	-	(-)	-	-	-	0.010	(0.365)
5.	0.100	0.060	0.070	0.010	0.020	-	-	-	-	-	0.100	0.640
6.	0.883	0.062	0.055	-	-	-	-	-	-	-	-	-
7.	0.008	(0.260)	0.536	(0.006)	0.154	0.005	0.012	0.014	-	-	-	(0.005)
8.	(0.700)	-	0.050	-	-	(-)	0.050	(0.010)	-	-	(0.190)	-
9.	-	-	0.043	(0.047)	0.006	(0.004)	(0.815)	(0.041)	(0.044)	-	-	-
10.	-	(0.170)	0.664	(0.013)	(0.153)	-	-	-	-	-	-	-
11.	-	-	-	-	0.050	(0.005)	(0.340)	(0.500)	(0.100)	(0.005)	-	-

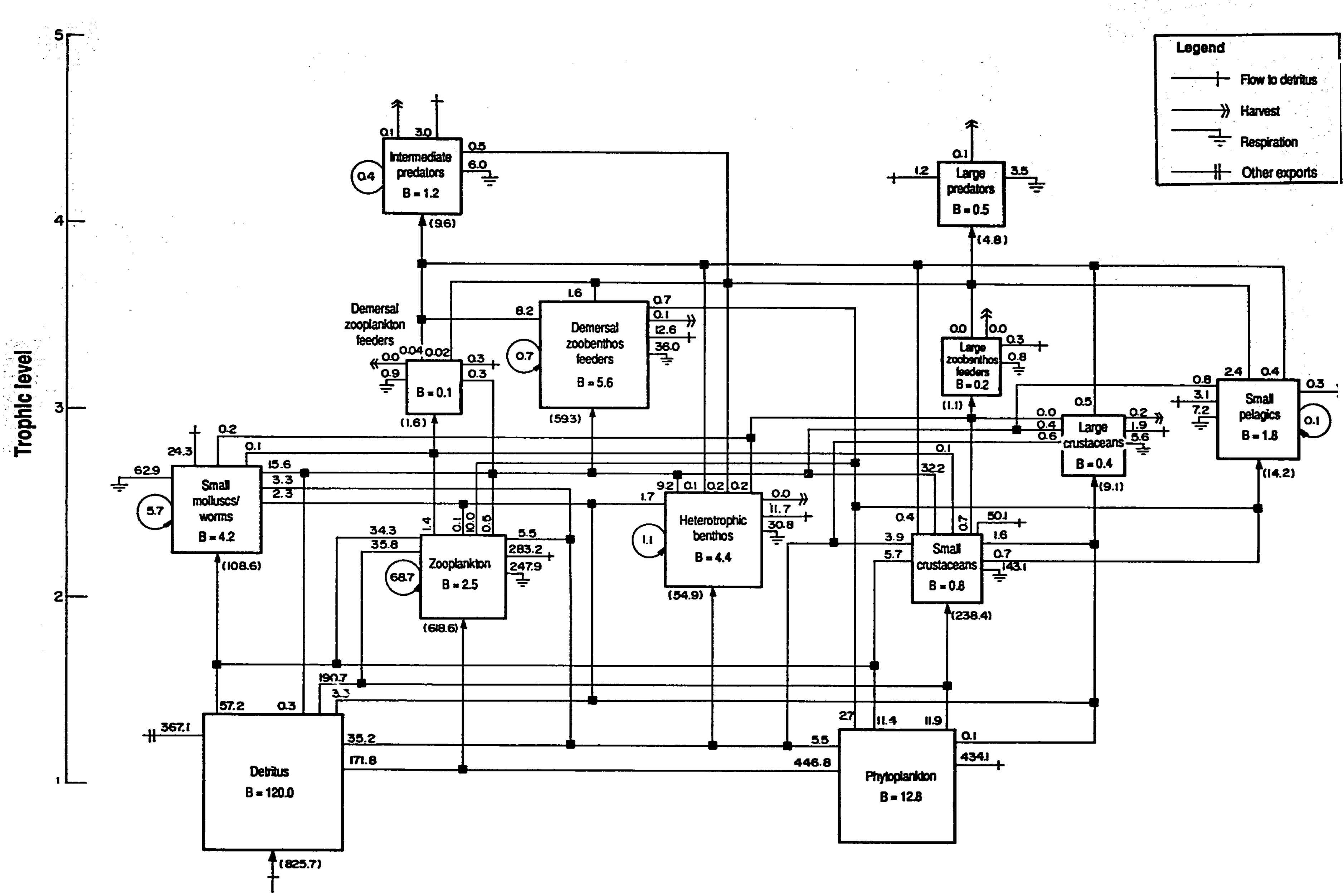

Fig. 2. Steady-state trophic model of the coastal fisheries resources of Brunei Darussalam as obtained using ECOPATH II. See Tables 1 and 2 for input parameters and Tables 3 and 4 for summary output statistics. Units are in t·km^{-2}·year^{-1} for an area of 7,396 km^2.

that the pelagic acoustic survey data available were only for a period when pelagic biomass was below average (i.e., June 1989 or mid-southwest monsoon period). The B estimates for the other groups (i.e., demersal zooplankton feeders, intermediate predators and large zoobenthos feeders) are consistent with those obtained via the surveys, albeit at the lower end of the 95% confidence limits of B'. Overall, the biomass outputs from ECOPATH II for the various groups are consistent with those available in the literature for similar ecosystems.

The B values obtained via ECOPATH II together with estimates of fisheries catch given in Table 1 imply low exploitation rates (E). These vary from E=0.011 for demersal zoobenthos feeders to E=0.191 for large predators. The range of values is consistent with those observed in other fisheries wherein the larger and more valuable target species are more heavily exploited and are, in fact, the first to be overexploited. Moreover, the E values obtained here confirm independent assessments cited above that Brunei Darussalam coastal fisheries resources are relatively lightly fished.

The other statistics given in Table 5 for the various groups considered here are consistent with similar estimates available in the literature (see Christensen and Pauly, this vol. and Jφrgensen 1979). Ecotrophic efficiency (EE) and gross efficiency (GE) are low for groups high in the food chain (e.g., large predators) and vice-versa (e.g., zooplankton). The omnivory index is a measure of the variance in trophic level of the prey of a given group (Christensen and Pauly, this vol.) which in this study varies from 0.007 for demersal zooplankton feeders (which feeds almost solely on zooplankton) to 0.427 for large crustaceans (which feed on a wide variety of prey groups in fairly similar proportion). Further, Table 6 and Fig. 3 give selected summary statistics for the Brunei Darussalam coastal fisheries ecosystem as used by Christensen and Pauly (this vol.) for comparison with other ecosystems.

The present contribution illustrates the type of insights that can be derived from ecosystem approaches (albeit steady-state) on fisheries systems such as those in the coastal waters of Brunei Darussalam. It also shows, however, the amount of

Table 5. Summary of selected output statistics obtained via ECOPATH II for the Brunei Darussalam coastal fisheries ecosystem. Estimates in brackets are input parameters. B is ECOPATH-derived biomasses while B' is biomasses from survey.

Group no.	Group	B (t·km^{-2})	B'^{a} (t·km^{-2})	E (=F/Z)	EE^{b}	Mean GE^{c} level	Trophic level	Omnivory index
1.	Zooplankton	2.455	-	-	(0.950)	0.239	2.11	0.111
2.	Small molluscs/worms	4.173	-	-	(0.950)	0.250	2.47	0.330
3.	Small crustaceans	0.769	-	-	(0.950)	0.200	2.17	0.157
4.	Large crustaceans	0.413	>0.087	0.105	(0.950)	0.183	2.83	0.427
5.	Heterotrophic benthos	4.395	>0.064	-	(0.950)	0.240	2.33	0.310
6.	Demersal zooplankton feeders	0.114	0.112- 0.348	0.013	(0.950)	0.243	3.14	0.007
7.	Demersal zoobenthos feeders	(5.579)	4.380-	0.011	(0.950)	0.200	3.30	0.049
8.	Small pelagics	1.812	≥1.273	0.066	(0.950)	0.300	2.97	0.293
9.	Intermediate predators	1.156	1.042- 3.225	0.030	0.489	0.200	4.25	0.112
10.	Large zoobenthos feeders	0.180	0.170- 0.433	0.167	0.500	0.066	3.25	0.018
11.	Large predators	0.505	>0.234	0.191	0.191	0.063	4.18	0.177
12.	Phytoplankton	(12.825)	-	-	0.524	-	1.00	-
13.	Detritus	(120.000)	-	-	0.555	-	1.00	-

[a] From demersal trawl survey using "swept area" method and initial results of pelagic acoustic survey (DOF 1989).
[b] Ecotrophic efficiency (proportion of fishing plus predatory mortality to total mortality).
[c] Gross efficiency = production/food consumption.

Table 6. Selected summary statistics for Brunei Darussalam coastal fisheries ecosystem for comparison with other ecosystems (see Christensen and Pauly, this vol.). Units in t·km^{-2}·year^{-1} unless indicated otherwise.

Sum of all production (including export)	1,196
Sum of all imports	0
Sum of all respiratory flows	913
Sum of all flows into detritus	826
Total system throughput	2,934
Throughput cycled	331
Finn's cycling index (cycled to total throughput)(%)	11.3

progress that is still needed in understanding such systems. The extensive recourse to the literature and approximations used herein emphasize the need for increased research efforts into the food consumption and composition of the various species/resource groups in Brunei waters. Improvement of the fisheries catch statistics also appears to be in order, given that only marketed fish are being presently monitored. This information should lead to a refinement of the preliminary model presented here (incorporating more boxes/groups better suited for management purposes ultimately leading on to simulation models) towards better management and sustainable development of the fisheries resources.

Acknowledgements

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Seasonal Changes in the Peruvian Upwelling Ecosystem*

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Abstract

A set of twelve balanced steady-state models is presented which quantify the seasonal changes in biomass and food consumption among major fish stocks of the Peruvian upwelling ecosystem, *Engraulis ringens*, *Sardinops sagax*, *Scomber japonicus*, *Trachurus murphyi* and *Merluccius gayi*, as well as three species of guano birds and three groups of marine mammals. The results are based on published series of monthly biomasses and vital statistics, covering the years 1973 to 1979, a period which did not include major El Niño events. The seasonality of network flow indices computed from these models is discussed, following the theory of R.E. Ulanowicz.

Introduction

The Peruvian ecosystem is one of the world's large upwelling ecosystems. During the 1960s it supported a huge industrial fishery for anchoveta *Engraulis ringens*, which collapsed in the early 1970s. The anchoveta fishery has however continued to the present on a reduced level, and was in part replaced by fisheries on other species such as sardine *Sardinops sagax* for reduction purposes, and mackerel *Scomber japonicus*, horse mackerel *Trachurus murphyi* and hake *Merluccius gayi* for human consumption. Data compiled and results published in the course of various research efforts in the 1970s and 1980s (among others: Dickie and Valdivia 1981, Arntz et al. 1985, Pauly and Tsukayama 1987, Salzwedel and Landa 1988, Pauly et al. 1989) have now enabled us to model species interactions in this ecosystem. In the frame of an investigation of time series available from 1953 to 1982, and based on three models averaging the periods 1953-1959, 1960-1969 and 1973-1979 (Jarre et al. 1991), this contribution attempts to quantify monthly changes during the years 1973 to 1979, a period which did not include major El Niño events, and in which conditions were stable enough to allow the use of a steady-state approach.

Materials and Methods

The area included in this analysis extends along the Peruvian coast from 4 to 14°S, to about 55 nautical miles offshore, thus covering the main area of anchoveta distribution (see

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*ICLARM Contribution No. 649.
CEOS Contribution No. 34.

contributions of Pauly and Tsukayama 1987b, and Pauly et al. 1989). The ECOPATH approach originally developed by Polovina (Polovina 1984; 1985) and extended as ECOPATH II by D. Pauly and associates (Pauly et al., this vol.; Christensen and Pauly 1992a, this vol.) was used to quantify the interactions of a total of 20 boxes, including major components of the system with emphasis on the commercial fish species (Fig. 1). For each group, monthly averages of biomass, mortality, consumption/biomass rate and catch were entered into the program, as was the diet composition for each component. Primary production, zooplankton biomass and biomasses of anchoveta and its most important predators, as well as some vital statistics were computed from the data made available in Pauly and Tsukayama (1987) and Pauly et al. (1989), and from other statistics and estimates of diet composition from the available Peruvian literature (see Tables 1 and 2 for details). Average values of the above statistics were used where seasonal data were not available. The program's default values of 20% of the consumption for unassimilated food were accepted. We further assumed no imports to the system and no exports from it, apart from fishery catch. For brevity's sake the input data are not listed in this paper in detail but are included in the files distributed with this volume (see Appendix 4).

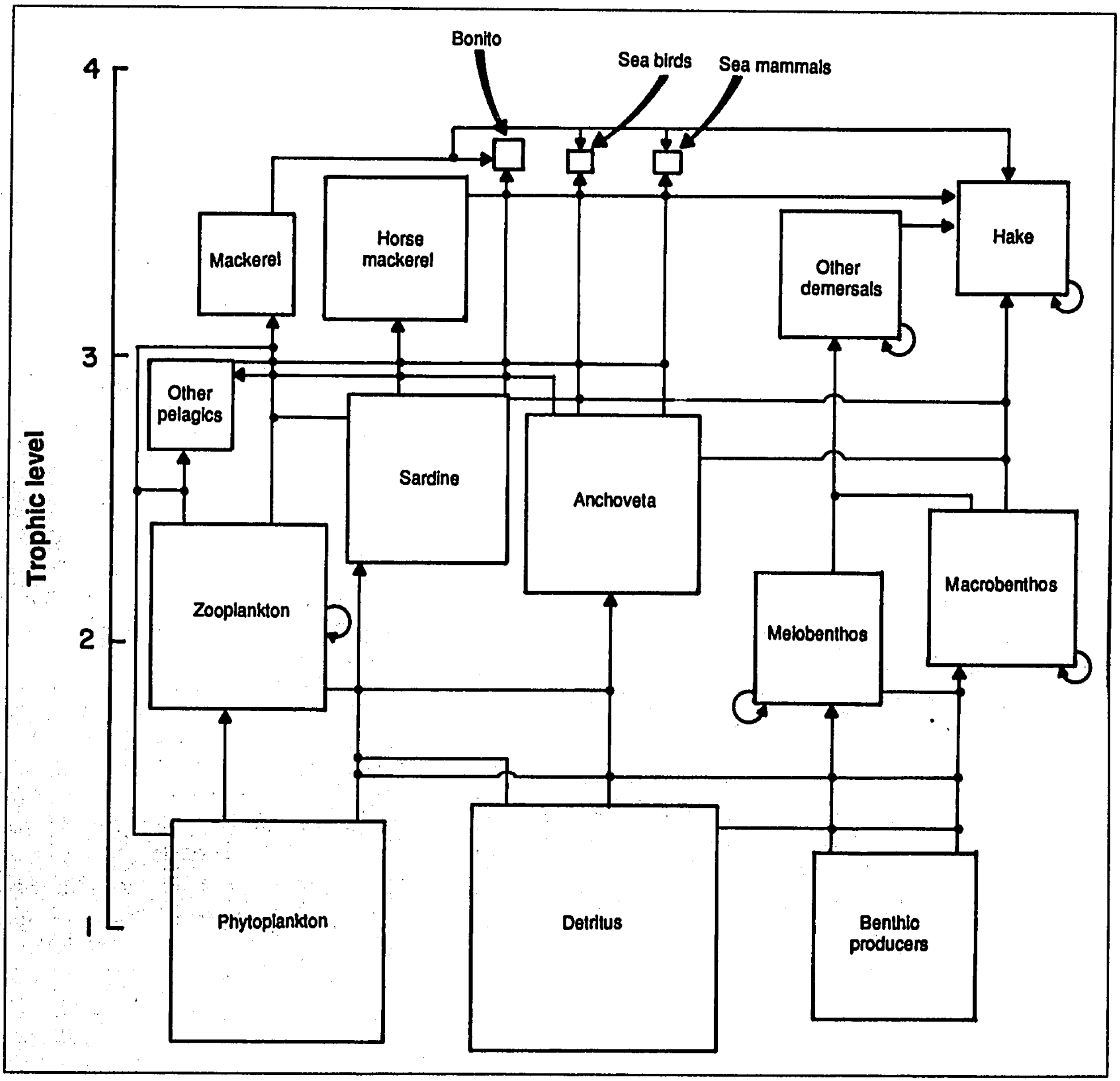

Fig. 1. Overview of the boxes used for the 12 monthly ECOPATH II models described in the text, arranged according to average annual trophic level. Note that the box "sea birds" is comprised of cormorants, boobies and pelicans which are computed with separate parameters, and the box "sea mammals" is comprised of sea lions, fur seals and other mammals also kept separate in model construction.

Table 1. Sources for biomass, mortality and catch inputs for ECOPATH II models of the Peruvian upwelling ecosystem.

Group	Biomass	P/B or mortality	Catch
Zooplankton	Carrasco and Lozano (1989)	Shushkina et al. (1978)	-
Meiobenthos	guesstimate	Gerlach (1971)	-
Macrobenthos	Rosenberg et al. 1983, Arntz et al. 1991	Walsh (1981)	IMARPE (1987)
Anchoveta	Pauly and Palomares (1989)	Pauly and Palomares (1989)	Tsukayama and Palomares (1987), Castillo and Mendo 1987
Sardine	Muck and Sánchez (1987) and Serra and Tsukayama (1988)	Serra and Tsukayama (1988)	Serra and Tsukayama (1988)
Mackerel	Muck (1989b and unpubl. data)	Jarre et al. (1991), based on Muck and Sánchez (1987)	IMARPE (1987)
Horse mackerel	Muck (1989b and unpubl. data)	Jarre et al. (1991), based on Muck and Sánchez (1987)	IMARPE (1987)
Bonito	Muck (1989b)	Jarre et al. (1991), based on Muck and Sánchez (1987)	IMARPE (1987)
Hake	Espino and Wosnitza-Mendo (1989) and Muck (1989a)	Espino and Wosnitza-Mendo (1989)	Espino and Wosnitza-Mendo (1989)
Other pelagics	guesstimate, based on IMARPE (1987)	guesstimate (Jarre et al. 1991)	IMARPE (1987)
Other demersals	guesstimate, based on IMARPE (1987)	guesstimate (Jarre et al. 1991)	IMARPE (1987)
Cormorant	Muck and Fuentes (unpubl. data), based on Tovar et al. (1987)	Laugksch and Duffy (1984)	-
Booby	Muck and Fuentes (unpubl. data), based on Tovar et al. (1987)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	-
Pelican	Muck and Fuentes (unpubl. data), based on Tovar et al. (1987)	Jarre et al. (1991, based on Lindstedt and Calder (1981)	-
Sea lion	Muck and Fuentes (1987)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	guesstimate, based on Majluf and Reyes (1989)
Fur seal	Muck and Fuentes (1987)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	guesstimate, based on Majluf and Reyes (1989)
Other mammals	guesstimate (Jarre et al. 1991)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	guesstimate, based on Majluf and Reyes (1989)
Phytoplankton	computed output; production values from Mendo et al. (1989)	Polovina (1985)	-
Benthic producers	computed output	Polovina (1985)	-
Detritus	regression in Pauly et al. (this vol.)	-	-

The models were balanced using the ecotrophic efficiencies computed by the program (i.e., the proportion of the production that is consumed by predators or taken by the fishery, and the value of which, for obvious reasons, must be between zero and one), and computed values of Ivlev's electivity index (Ivlev 1961, Parsons and LeBrasseur 1970). The Q/B estimates of the anchoveta predators from the literature were reduced by 10%; further adjustments for balancing the models were achieved exclusively by changes in the diet composition matrix.

Summary Statistics

In an attempt to derive some system-level generalizations from steady-state models, a number of ecosystem attributes and goal functions have been proposed (Odum 1969; Mejer and Jφrgensen 1979; Ulanowicz 1986; Jφrgensen 1992). Discussions have recently occurred as to the appropriateness of those proposed attributes and goal functions to actually describe ecosystem maturity and stability (Baird et al. 1991; Jarre-Teichmann 1992; Christensen, in press). This

Table 2. Sources of consumption rate and diet composition inputs for ECOPATH models.

Group	Consumption/biomass	Diet composition
Zooplankton	Polovina (1985)	guesstimate
Meiobenthos	Walsh (1981)	guesstimate
Macrobenthos	Walsh (1981)	guesstimate
Anchoveta	Alamo (1989), Rojas de Mendiola (1989), Jarre et al. (1991)	Alamo (1989), Rojas de Mendiola (1989)
Sardine	Jarre et al. (1991)	Alamo et al. (1988)
Mackerel	Jarre et al. (1991), based on Muck and Sánchez (1987)	adapted from Muck and Sánchez (1987)
Horse mackerel	Jarre et al. (1991), based on Muck and Sánchez (1987)	adapted from Muck and Sánchez (1987)
Bonito	Palomares (unpubl. data)	guesstimate
Hake	Muck (1989a), based on Espino and Wosnitza-Mendo (1989)	guesstimate, based on Muck (1989a)
Other pelagics	guesstimate, between anchoveta and sardine	guesstimate
Other demersals	guesstimate	guesstimate
Cormorant	Muck and Pauly (1987)	guesstimate, based on Muck and Pauly (1987)
Booby	Muck and Pauly (1987)	guesstimate, based on Muck and Pauly (1987)
Pelican	Muck and Pauly (1987)	guesstimate, based on Muck and Pauly (1987)
Sea lion	Muck and Fuentes (1987)	guesstimate, based on Muck and Fuentes (1987) and Majluf and Reyes (1989)
Fur seal	Muck and Fuentes (1987)	guesstimate, based on Muck and Fuentes (1987) and Majluf and Reyes (1989)
Other mammals	guesstimate of Jarre et al. (1991)	guesstimate, based on Muck and Fuentes (1987) and Majluf and Reyes (1989)
Phytoplankton	-	-
Benthic producers	-	-
Detritus	-	computed output

shall, however, not be elaborated further in the present contribution but will instead be investigated in a larger context (Jarre-Teichmann and Christensen, in press). For the present contribution, we focus on the network flow indices based on Ulanowicz (1986): based on the "maximum power principle" (Odum 1983). Ulanowicz proposed to link the size of an ecosystem, computed as the sum of all flows in the ecosystem, with its internal structure, computed as a "factor of average mutual information" from the distribution of flows in this ecosystem. This factor of average mutual information is a probability by nature, and describes the reduction in uncertainty associated with a given unit of flow being channelled in a flow network. The product of these two parameters, i.e., of total system throughput and average mutual information, is called ascendency. As Ulanowicz (1986) based his studies on the attributes of ecosystem maturity described in Odum (1969), he postulated that ecosystems evolving towards maturity optimize this goal function.

For mathematical-theoretical as well as for biological-practical reasons, there exists an upper bound of ascendency, named development capacity. This bound is based on the reasoning that the total throughput of a given system, being limited by the inputs to the system, cannot exceed certain limits, and the number of components cannot increase without limits either: a high humber of compartments would necessarily result in low throughput per compartment and, consequently, in high vulnerability to random environmental perturbations. The difference between development capacity and ascendency is called system overhead, and may be understood as a measure of a system's ability to cope with random perturbations.

As a measure for the importance of cycling in an ecosystem, an index giving the fraction of the total throughput that is recycled in the system (Finn 1976) is commonly used. This index is strongly dependent on the way a particular model is constructed (i.e., on the number of compartments included and/or the degree of resolution of the model), and can only be compared between similarly structured models, as is the case here.

In order to be able to compare the efficiency of biomass transfer in the system at different points in time, it is useful to look at discrete trophic levels *sensu* Lindeman (1942). An algorithm that, after removal of all cycling in the system, assigns each predator to (several of) these discrete trophic levels according to its diet composition has been proposed by Ulanowicz and Kemp (1979) and Ulanowicz (in press) and is applied to illustrate the structure of energy flows throughout the different seasons, in the Peruvian upwelling ecosystem.

Results and Discussion

Species Interactions

The annual cycles of sea surface temperature and primary production are given in Fig. 2a and the annual course of zooplankton biomass and the fraction of zooplankton consumed by anchoveta in Fig. 2b. The results show a clear seasonality of temperature and production, the former with a maximum in (southern) summer and a seasonal temperature difference of about 4°C, the latter with a maximum in winter, where monthly production is about 2.5 times higher than in the summer months. The seasonality of zooplankton biomass roughly follows the temperature trajectory, and is reflected in the diet of anchoveta. Fig. 2c gives the seasonal biomass fluctuations of major fish species in the system, and Fig. 2d shows the amounts of anchoveta consumed by its major predators, and taken by the fishery (note that the fishery was usually closed during the months June to September, hence the strong seasonality of catches). Natural predation on anchoveta as estimated in the relevant papers in Pauly and Tsukayama (1987), however, is considerably lower than the inputs that were necessary to balance the models, given the biomasses and vital

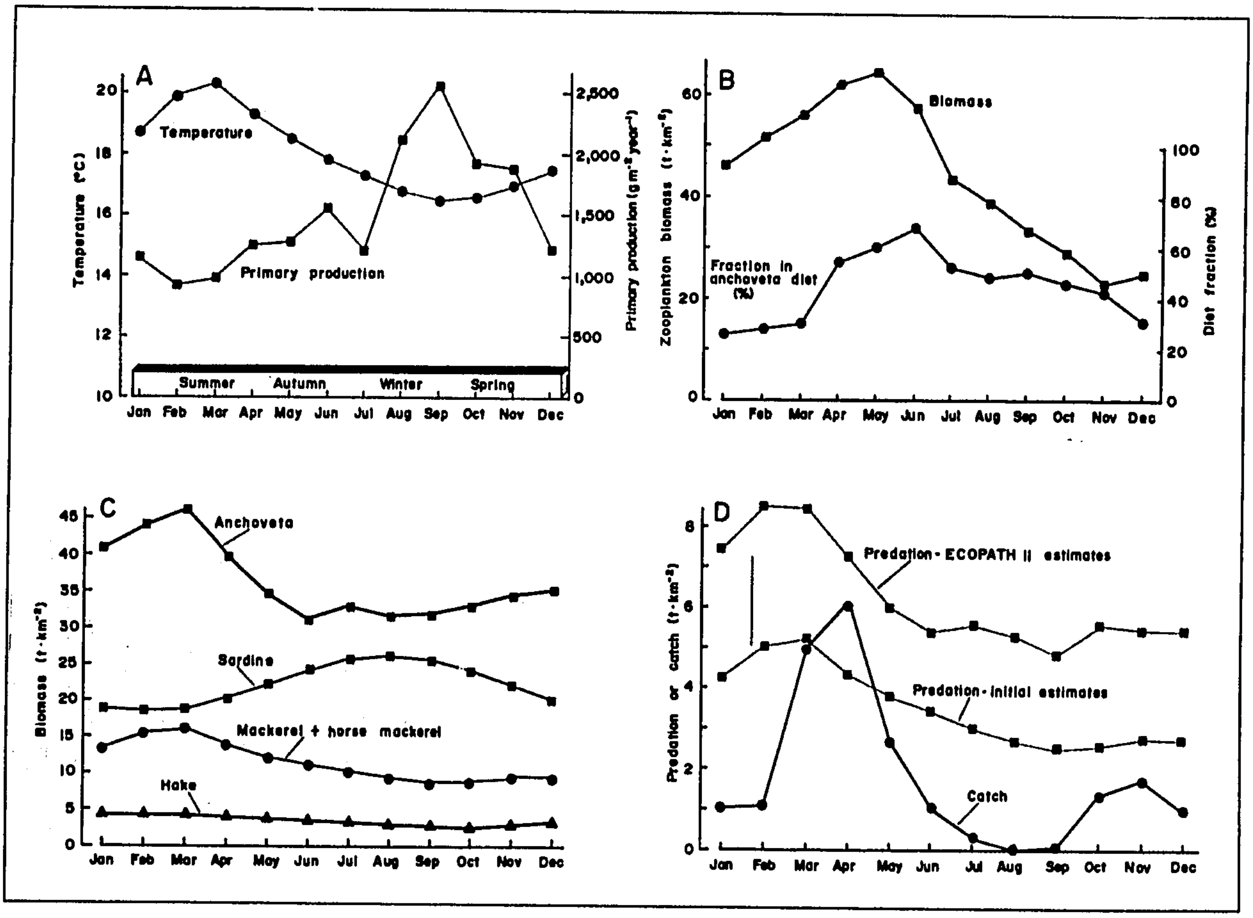

Fig. 2. Seasonal temperature and primary production changes in the Peruvian upwelling ecosystem, 1973-1979. Sea surface temperature averaged from Pauly and Tsukayama (1987b, Table 2). New primary production (g wet mass·m^2·month^{-1}) based on Mendo et al. (1989) (variable depth model, mean of coastal and oceanic estimates), using a conversion factor of 13.6 from carbon to wet mass.

a. Temperature and primary production.
b. Zooplankton biomass and fraction of zooplankton on the diet of anchoveta.
c. Biomass of dominant fishes; note contrary courses of sardine and anchoveta, and temperature-dependence of hake and mackerel, due to their usual location at the thermal periphery of the system.
d. Total predation and catch of Peruvian anchoveta, *Engraulis ringens*, 4-14°S.

statistics of other species which could have replaced the anchoveta as prey items, mainly in the diets of horse mackerel and hake. Assuming that the consumption rates of these species are of the right order of magnitude, we therefore have to conclude that either the anchoveta fraction in the diet of its predators has been larger than assumed before (i.e., an average fraction of about 40% as compared to about 26% estimated earlier), or sardine and "other pelagics'" biomass and production values have been considerably higher. The following discussion of summary statistics assumes the former to be true.

Summary Statistics

The seasonality of system throughput, ascendency and development capacity are given in Fig. 3 and roughly follow the trajectory of primary production with a maximum in winter. Fig. 3 shows the annual course of ascendency normalized by total system throughput, the factor of "average mutual information" (Ulanowicz 1986, equation 6.9) with a bimodal seasonality (one maximum in late summer, the second in spring). As the value of this factor changes only slightly, we conclude that the system's content of mutual information is roughly constant throughout the year, and that the change of ascendency is mainly due to changes of the size of the ecosystem, based on the seasonality of primary production. This corresponds well to the findings of Baird and Ulanowicz (1989) for Chesapeake Bay.

The seasonality of cycling in the Peruvian upwelling ecosystem as computed by Finn's cycling index (Finn 1976), however, is more pronounced (Fig. 3). This index is generally low (less than 10%), but clearly indicates a higher fraction of cycling in the system in summer (when upwelling is low) than in winter (when

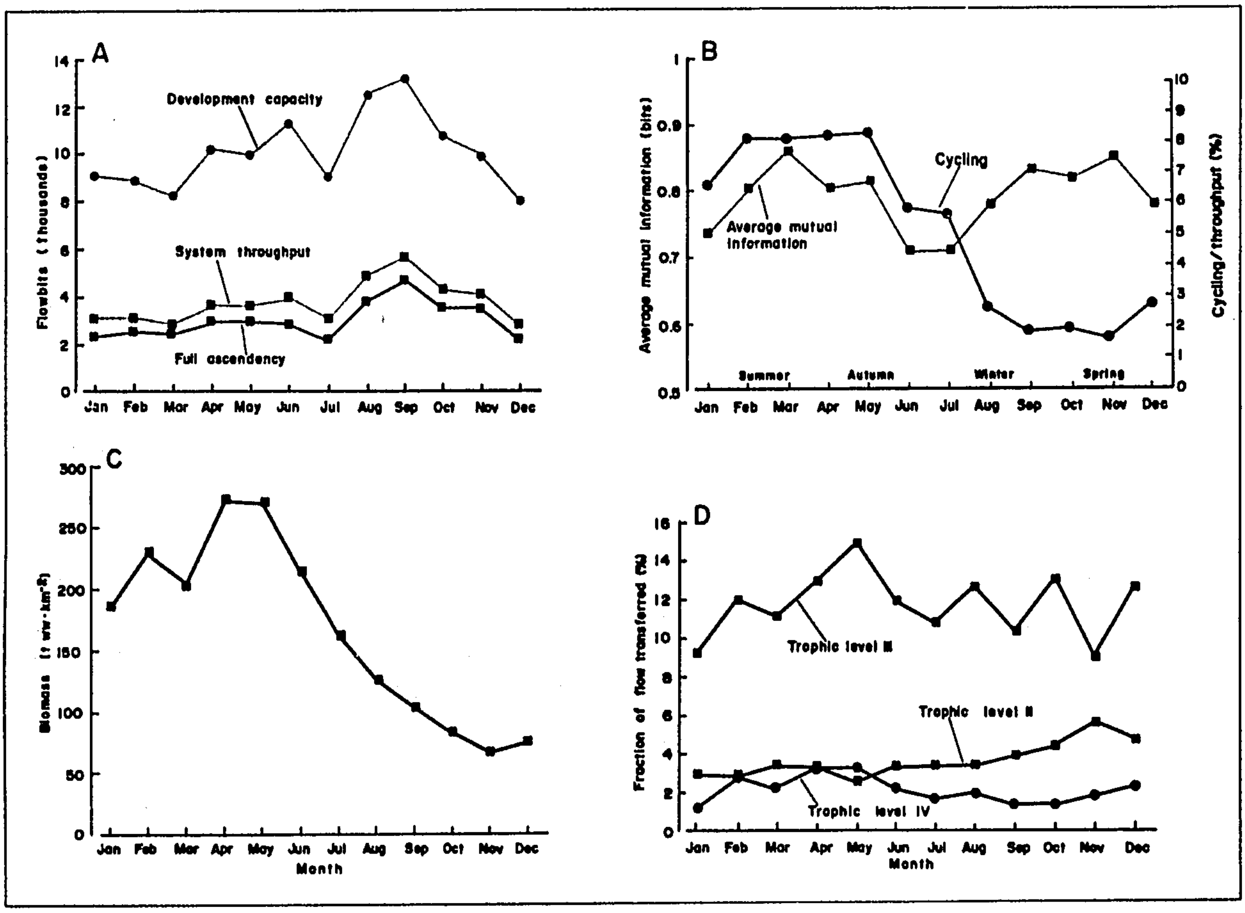

Fig. 3. Seasonality of basic features of the Peruvian upwelling ecosystem, 4 to 14°S, 1973 to 1979:
A. Summary statistics of the 12 ECOPATH II models constructed in this paper, following the theory of Ulanowicz (1986).
B. Seasonality of the factor of "average mutual information" (Ulanowicz 1986), i.e., full ascendency divided by system throughput, and seasonal changes of the Finn cycling index (Finn 1976), i.e., the fraction of total throughput that is recirculated within the system.
C. Seasonality of cycling in the Peruvian upwelling ecosystem as constructed in the 12 ECOPATH II models.
D. Monthly transfer efficiencies computed from the 12 ECOPATH II models, flows based on producers and on detritus combined.

upwelling is high). This increase in the Finn's cycling index is not only due to the increased system throughput (the denominator of this index) in winter, but also to the reduced amount of organic matter cycled in the system in winter and spring (Fig. 3), due to the seasonal decrease in biomass and activity of zooplankton and benthos as the principal consumers of detritus.

The transfer efficiencies of all flows as computed using ECOPATH II and shown in Fig. 3D range from 1% for trophic level IV (in October) to 15% for trophic level III in May; a clear seasonal pattern is not apparent. Whereas the monthly transfer efficiencies from trophic level II to level III average at about 12%, corresponding very closely to the 10% literature "rule of thumb," the transfer efficiencies from level II to III and III to IV appear rather low. As the transport from levels II to III is dominated by zooplankton, a closer look at this box reveals that the largest fraction of its ecotrophically efficient production is consumed within the box itself and hence does not enter the computation of transfer efficiency as used here. Although a certain decrease in trophic efficiency with trophic level is observed in many ecosystems (see, e.g., Baird and Ulanowicz 1989), the low value of the transfer efficiency of the other levels (III to IV) can be additionally explained with the fact that the activity of the fishery (trophic level about 3.6) as an export, is not included in the computation but may account, e.g., in the case of the anchoveta, for up to 83% (April) of the withdrawals from the system.

Summarizing, our results indicate that the Peruvian upwelling ecosystem shows a clear seasonality not only as far as the vital parameters of each of its components are concerned, but also on the system level. This seasonality is mainly expressed in the change of system throughput (dominated by the upwelling intensity) but also, albeit to a less extent, in a change in the topology of the system.

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An Ecosystem Model of Monterey Bay, California

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Abstract

A preliminary ecosystem trophic structure model was built for Monterey Bay, California, USA, and analyzed using the ECOPATH II program. The model has fifteen living boxes plus one box for detritus. Three different primary production values were used to evaluate the model. They correspond to: (1) winter low, (2) mean high upwelling and (3) occasional very high upwelling production observed in the bay. Biomass, ecotrophic efficiencies, flows to detritus and respiration/assimilation estimated by the model were in agreement for values measured in the bay and/or similar environments. This suggests that even though the model is in a preliminary stage, it possesses characteristics of the natural system.

Introduction

Models, whatever their form, are intended to mimic a larger entity. In the natural sciences they are used to gauge the level of understanding of system function and structure. In oceanography, as in many other disciplines, they are frequently used to "fill in" gaps resulting from the current capabilities for observing the system. With the ever increasing human pressure on the environment, models are being looked at to predict the effects of natural and anthropogenic climate variability on ecosystems. Even though models are valuable and necessary tools for scientists, care needs to be exercised with their use and interpretation because an infinite number of solutions to a model are possible. A set of observations, that partially define the model characteristics and boundaries, are required before a model can be trusted. Modelling and observing exercises are therefore intertwined in the study of system function and structure.

The physics, chemistry and biology of Monterey Bay have been and continue to be studied extensively making it an ideal site for work devoted to developing ocean ecosystem models. A myriad of scientific institutions ring the bay (Fig. 1) and it has been the focus of research since the early 1930s including work by the California Cooperative Oceanic Fisheries Investigations program (CalCOFI). Most of the work carried out in the bay, however, has been within specialized fields with little integration of disciplines. The opportunity arises, therefore, for integrating the existing information into some form of ecosystem model. This contribution is a preliminary attempt at this integration. The long-term goal of our modelling effort is geared at providing a tool that can be used to: (1) broaden our understanding of system function and structure; (2) test new concepts and hypotheses, as well as evaluate the consequences of climate and ocean variability; and (3) define an optimal long-term sampling strategy.

The Setting

Monterey Bay is located at the edge of the California Current, on the eastern boundary of the

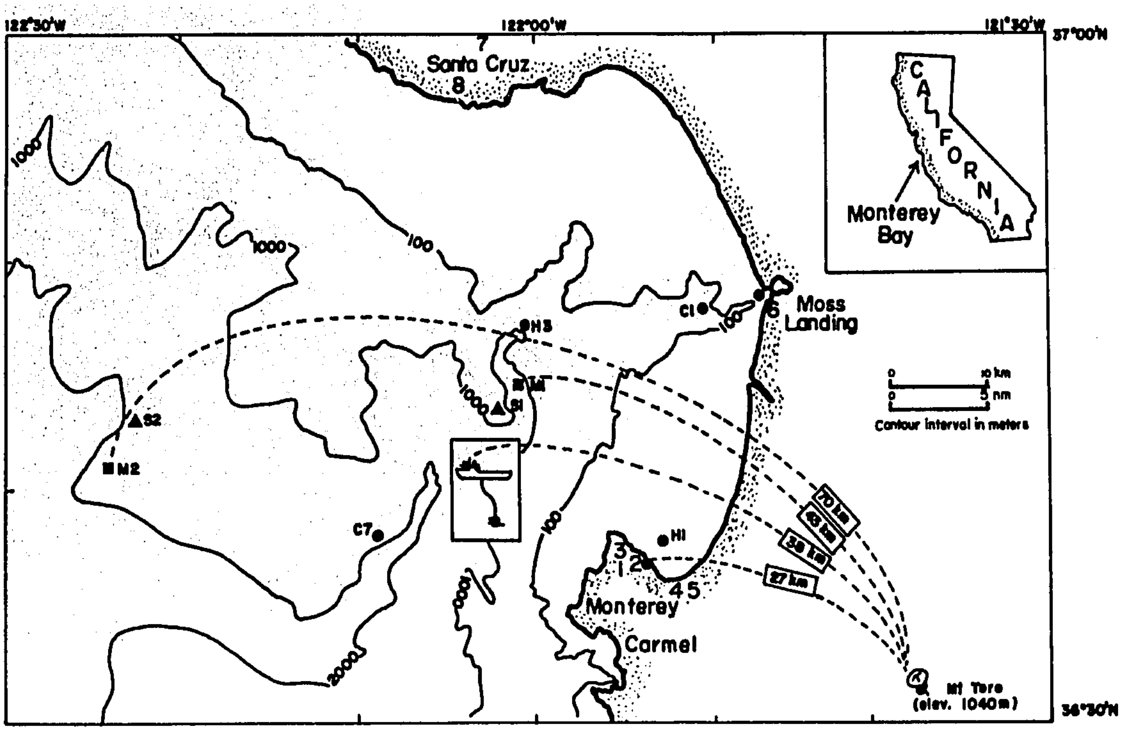

Fig. 1. MBARI oceanographic sampling stations in Monterey Bay; hydrocast stations (●), ATLAS mooring (■ M1 and M2) capable of real time data acquisition and telemetry, and sediment traps moorings (•S1 and S2); and location of marine research institutions: (1) MBARI, (2) Monterey Bay Aquarium, (3) Hopkins Marine Station, Stanford University, (4) US Naval Postgraduate School, (5) US National Marine Fisheries Center, (6) Moss Landing Marine Lab, California State University, (7) Institute of Marine Science, University of California Santa Cruz, (8) Long Marine Lab, University of California Santa Cruz.

North Pacific gyre. Northwesterly upwelling-favorable winds prevail over most of the year with their strongest intensity during the late spring (Nelson 1977; Strub et al. 1987). Three oceanographic seasons have been defined for Monterey Bay: (1) upwelling, (2) oceanic and (3) Davidson (Skogsberg 1936; Bolin and Abbott 1963) and these are evident in the time series of temperature structure from the inner ATLAS mooring (Fig. 2). Cold water is often found in the central and outer portions of the bay during the upwelling season, while warm water is found inside the bay in a narrow band nearshore (Bigelow and Leslie 1930; Skogsberg 1936; Bolin and Abbott 1963). The fall, as is the spring, is a transition time between the "upwelling" regime and the winter period when horizontal and vertical thermal gradients are reduced and the Davidson Current flows over the shelf and slope in a predominantly northward direction along the central California coast (Skogsberg 1936; Hickey 1979; Chelton 1984). Recent studies at the Monterey Bay Aquarium Research Institute (MBARI) show that the physical cycle results in a clear biological cycle of phytoplankton production in Monterey Bay (Fig. 3). The cycle has two marked seasons: (1) a winter, low productivity season from October through February and (2) an upwelling, high productivity season from March through August.

This high productivity combined with diverse habitats such as kelp forest, rocky shores, sandy beaches and a deep submarine canyon results in an abundance of living resources that have made Monterey Bay an important commercial fishing site on the coast of California. During 1989 over 7,150 t of squid, 2,100 t of rockfish, 900 t of anchovies and 450 t of salmon were landed in or around the bay (Wild 1990). The bay and surrounding waters also maintained, during the first half of the century, a strong sardine fishing industry until its collapse in the late 1940s and early 1950s. The anchovy replaced the sardine as the important clupeid species along California but it has never been harvested like its predecessor.

The primary production cycle in Monterey Bay can be approximated with a simple simulation model that we have generated (Fig. 4). This model uses the monthly mean wind speed, isotherm depths and irradiance levels to calculate values of primary production. Although the simulation requires added complexity it compares well with field values. To complement this model and to understand better the fate of the primary production, a trophic ecosystem box model was built for the bay and subsequently evaluated using the ECOPATH II software (Polovina 1984; Christensen and Pauly 1992; Pauly et al., this vol.).

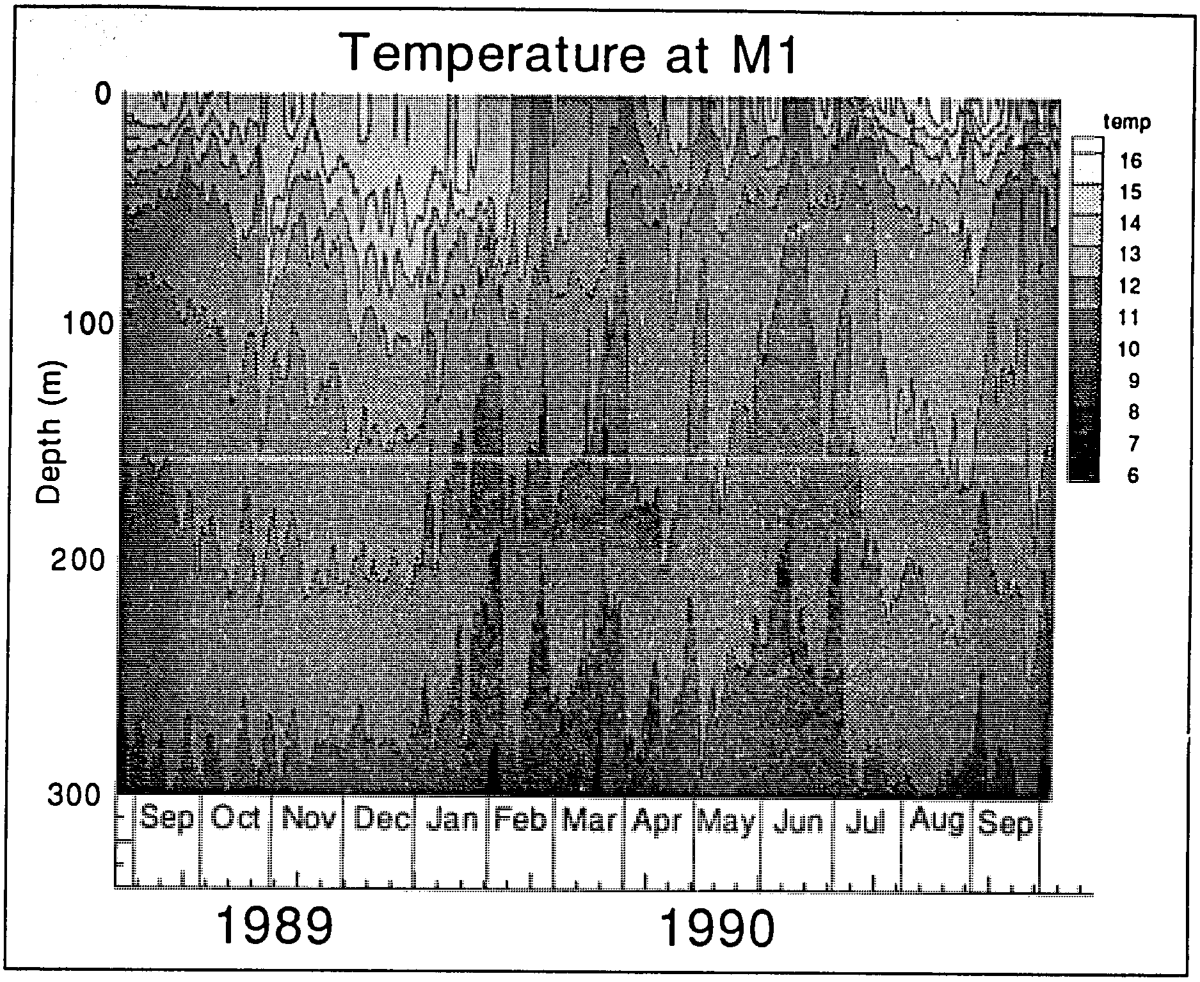

Fig. 2. Time series of temperature structure at the M1 (see Fig. 1) ATLAS mooring. Data for January to March 1990 were from M2 due to electronic failure of M1. Three oceanographic seasons are evident: (1) Davidson period with deep mixed layer from October to January, (2) upwelling period with raised isotherms from February to June and (3) oceanic season with warmer surface temperatures, increased surface stratification and deeper isotherms from July to September.

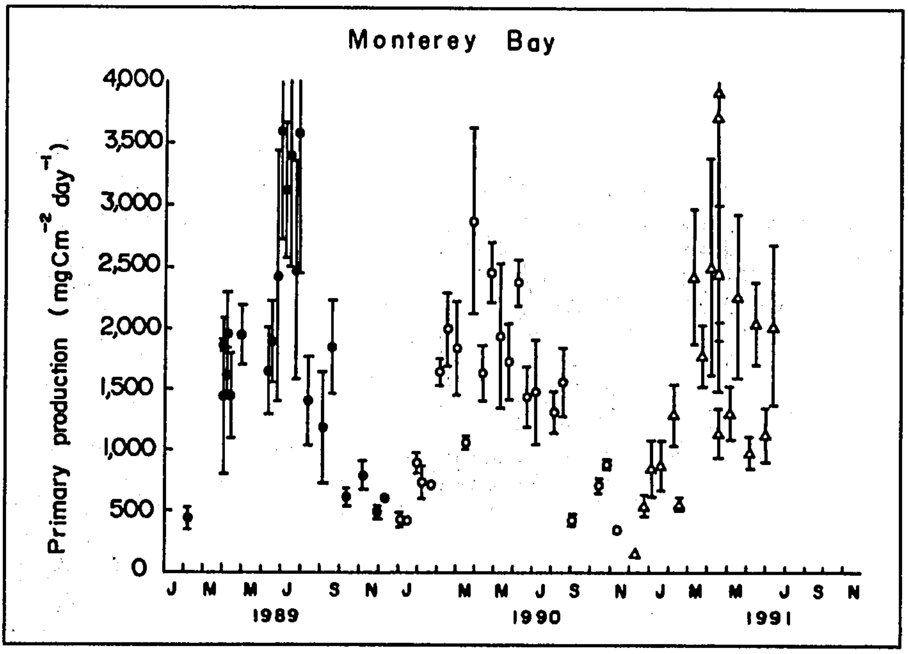

Fig. 3. Measurements of primary production in Monterey Bay, California, from February 1989 to June 1991. Values are means with standard errors for 3 to 4 stations. Evident is annual cycle of production with highest levels between May and July.

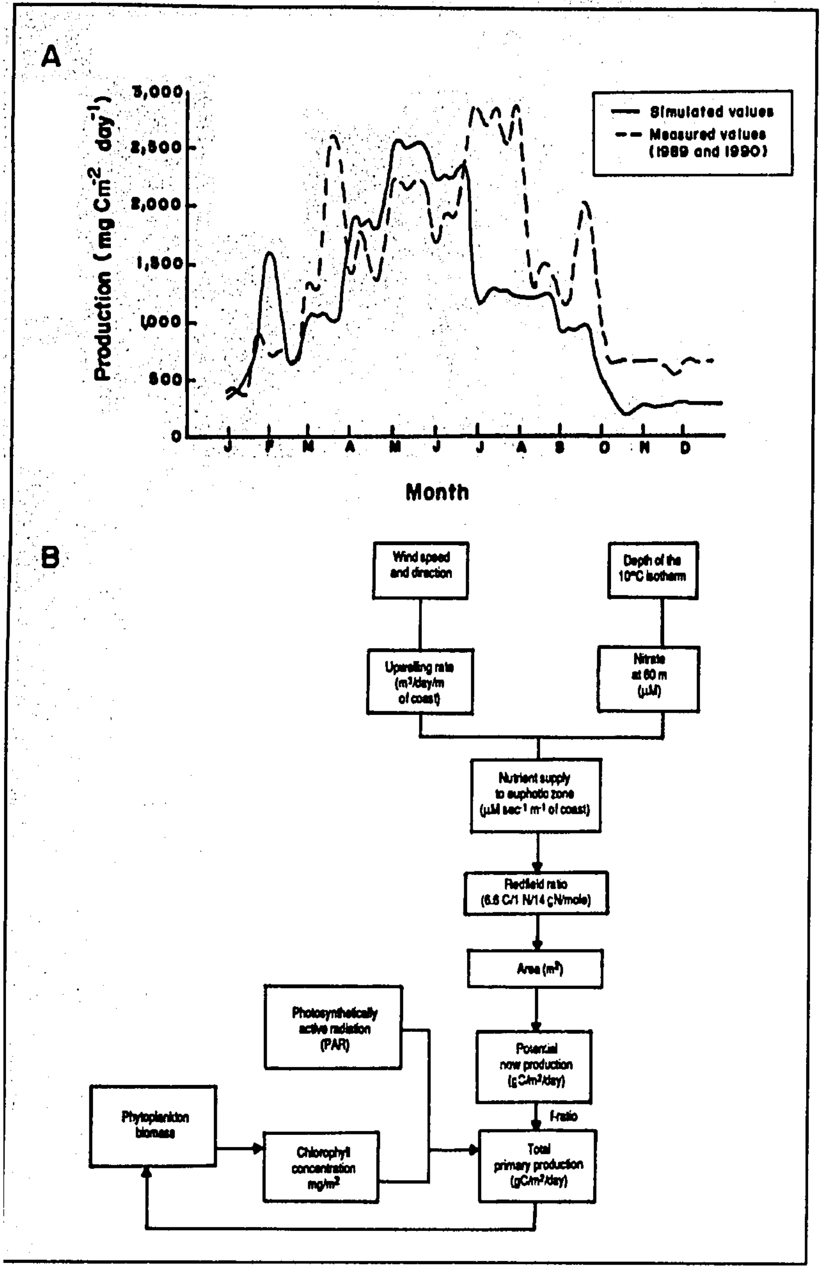

Fig. 4. A. Comparison between simulated and measured values in Monterey Bay, California. Correlation between simulated and measured values was 0.7. B. Flowchart of the simulation model of primary production in Monterey Bay. The model is an outgrowth of potential new production for the Peruvian upwelling system described in Chavez et al. (1989) to which the photosynthetic active radiation (PAR) component has been added.

Materials and Methods

The model was built with fifteen compartments (Fig. 5), each representing organisms with similar size and ecology (Table 1), plus one box for detritus. Biomass were in mg·C·m^2 and rates were assumed to be on an annual basis. To keep the model as simple as possible, the export and import were assumed to be zero. Ecotrophic efficiencies (EE) for most groups were set at 0.9, which oversimplified and somewhat constrained the model's accuracy but allowed for a better understanding of how the ECOPATH II software operated. This preliminary contribution was therefore partially a study of the ECOPATH II model as well as a study of the Monterey Bay ecosystem.

Input values for the model were either from field data or gleaned from the literature. When no published data for Monterey Bay or even the California Current are available, values from regions with similar physical regimes were used. The model was run with three different annual values for primary production, representing: (1) the upwelling, high primary productivity season from March through August with mean levels of about 2,250 mg·C·m^2·day^{-1}; (2) the occasional very high primary productivity events with levels of around 3,500 mg·C·m^2·day^{-1}; (3) the winter, low primary productivity season from October through February with primary production levels of about 500 mg·C·m^2·day^{-1}. The diet composition (Table 2) and, as a consequence, the structure of the system, was kept unchanged for both seasons. For all runs, the primary producer biomass and production/biomass ratio (P/B) and the top predator (marine mammals and seabirds) biomass, P/B and consumption biomass ratio (Q/B) were fixed. The P/B and Q/B for the remaining boxes were also fixed. We then analyzed the estimated biomass, EE, respiration/assimilation rate and flow to detritus for primary producers and consumers

Results and Discussion

For the upwelling, high primary productivity run some of our results were consistent with observations while others were apparently not. For example, the EE for the benthic producers suggests that nearly all of the production goes directly to the detritus pool (Table 3). This compares well with Newell (1984, in Mann 1988), who gave values close to 87% for kelp in an energy flow model of the West Coast of the Cape Peninsula in South Africa and with Gerard (1976, in Foster and Schield 1985) who estimates that about 70% of the *Macrocystis* production goes into the consumers as drift material. For zooplankton, if we assume 6.8% of

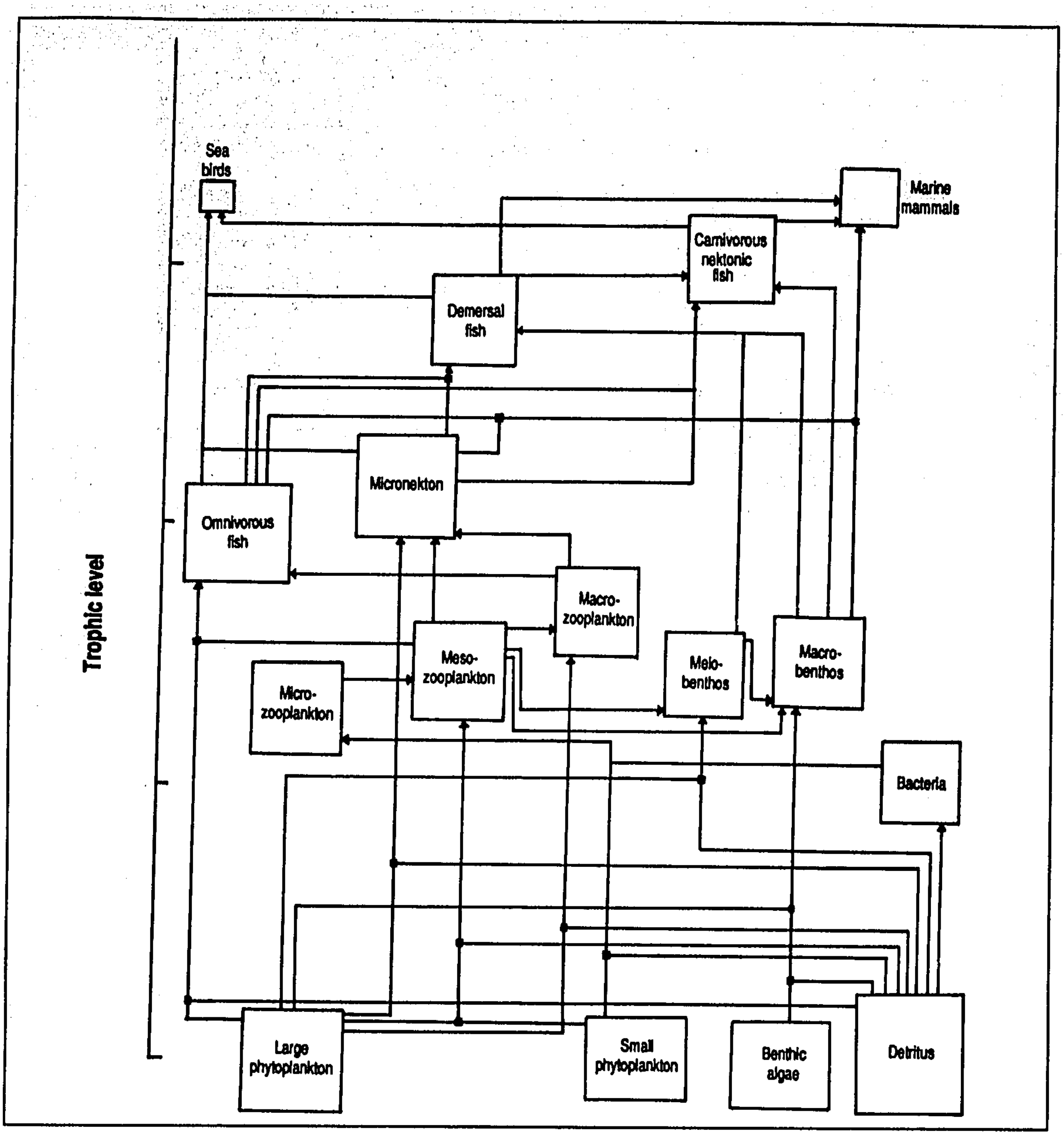

Fig. 5. Preliminary box model of the Monterey Bay ecosystem, California. Values for fluxes are omitted as this is a general representation that can be applied to high and low productivity situations. Also omitted are backflows to detritus.

wet weight is carbon, the biomass (macro + meso) was somewhat higher, but within the range of values reported for the Southern California Bight (Smith and Eppley 1981). When comparing the biomass of omnivorous fish to the anchovy biomass reported in the previous reference, if 7.2% of wet weight is carbon (Chavez et al. 1989), we found a somewhat lower value but within the range reported. The demersal fish biomass was nearly as high as the one for omnivorous fish, and even though we do not have evidence to refute this, we suspect it might be an overestimate. However, oxygen limitation (the oxygen minimum off Monterey is at 700 m with levels of 0.25 $mlO_2 \cdot l^{-1}$) is not as severe as in other eastern boundary systems (i.e., Peru) so an independent control of the estimate would be very interesting. Errors in demersal fish biomass may be the result of errors in P/B and Q/B or diet composition and/or Q/B of their predators. An interesting result is the prediction that almost 80% of the primary production of the large phytoplankton flows directly to detritus implying a very inefficient system. This is in agreement with the concept that an upwelling system "like any system under stress, works with leaks ... carbon (is) passed (directly) to the sediment" (Margalef 1978).

The very high run, which increased the biomass and production of the large phytoplankton and

Table 1. List of boxes used in the model and their inputs. All rates are annual.

1. Marine mammals: Dolphins, seals, sea lions and sea otters. A biomass of 24 mg·C·m^{-2} was used based on one 160 kg/animal/km^2 and 0.15 carbon/weight. A Q/B of 30 was approximated from data in Muck and Fuentes (1987) and Sakamoto et al. (1989).
2. Sea birds: Terns, shearwaters, gulls, brown pelican, etc. A biomass of 2 mg· C·m^{-2} was estimated assuming 0.5 kg/bird, 25 bird/km^2 (approximated from values in Schneider and Hunt 1982 for the Bering Sea) and 0.15 carbon/weight ratio. A Q/B of 62 was calculated from values in Muck and Pauly (1987).
3. Carnivorous nekton fish: Sharks, salmon, jack mackerel, tunas, etc. with a P/B of 0.6 (for pelagics in Mills and Fournier 1979) and Q/B of 6.2 (average from similar groups in Pauly et al., this vol.).
4. Demersal fish: Flatfish, hake, rockfish, bottom sharks, etc. with a P/B of 0.3 (Mills and Fournier 1979) and Q/B of 3.6 (for bottom fish in Pauly et al., this vol.).
5. Omnivorous fish: Anchovies and sardines, with a P/B of 2 and Q/B of 36 (approximated from values in Shannon and Field 1985).
6. Micronekton: Lanternfish, squid, large gelatinous and some large crustaceans. A P/B of 5 and Q/B of 15 were used as an approximation due to the lack of observation.
7. Macrobenthos: Invertebrates with a P/B of 3.2 (midpoint of values in Mills and Fournier 1979) and Q/B of 10.
8. Meiobenthos: Invertebrates with a P/B of 10 and Q/B of 30 were used, as they are expected to have somewhat higher values than the macrobenthos (Valiela 1984).
9. Macrozooplankton: Large copepods and euphausids with a P/B of 25 and Q/B of 70. The P/B for zooplankton can range from 10 to 73 (in Shannon and Field 1985).
10. Mesozooplankton: These are smaller copepods, pteropods, etc. The P/B was set at 50 and Q/B at 140, values higher than the ones for macrozooplankton.
11. Microzooplankton: Ciliates and other small heterotrophs. A P/B of 100 and Q/B of 300 were used due to their fast turnover.
12. Bacteria: P/Bs reported from bacteria are between 100 and 400 (Valiela 1984). We used here a value of 100, with a consumption rate of 300 year^{-1}.
13. Small phytoplankton: Cells less than 5 µm including cyanobacteria and flagellates. A P/B of 125 was used for the low productivity calculation and 255 for mean and high.
14. Large phytoplankton: Large diatoms with the same P/B as the small phytoplankton.
15. Benthic algae: The bulk of this group are kelps with a P/B of 10.3 (C. Harold, pers. comm.).

Table 2. Diet composition matrix for Monterey Bay ecosystem model, California. Bacteria were not included; it was assumed that they feed exclusively on detritus.

		Predator										
	Prey	1	2	3	4	5	6	7	8	9	10	11
3.	Carnivorous nekton fish	0.15	0.10	-	-	-	-	-	-	-	-	-
4.	Demersal fish	0.15	0.10	0.10	-	-	-	-	-	-	-	-
5.	Omnivorous fish	0.30	0.40	0.45	0.25	-	-	-	-	-	-	-
6.	Micronekton	0.35	0.40	0.35	0.25	-	0.05	-	-	-	-	-
7.	Macrobenthos	0.05	-	0.10	0.30	-	-	0.05	-	-	-	-
8.	Meiobenthos	-	-	-	0.20	-	-	0.15	0.05	-	-	-
9.	Macrozooplankton	-	-	-	-	0.30	0.40	-	-	0.05	-	-
10.	Mesozooplankton	-	-	-	-	0.30	0.30	0.10	0.10	0.055	0.05	-
11.	Microzooplankton	-	-	-	-	-	-	-	-	-	0.20	0.10
12.	Bacteria	-	-	-	-	-	-	-	0.05	-	-	0.25
13.	Small phytoplankton	-	-	-	-	-	-	-	-	-	0.10	0.50
14.	Large phytoplankton	-	-	-	-	0.30	0.20	0.10	0.20	0.30	0.55	-
15.	Benthic producers	-	-	-	-	-	-	0.30	-	-	-	-
16.	Detritus	-	-	-	-	0.10	0.05	0.30	0.60	0.10	0.10	0.15

retained the original top predator parameters, resulted in even lower EE for the phytoplankton and identical biomass for the remaining boxes (Table 2). This is in accordance with the previous run which showed that the production of the large phytoplankton was underutilized. If the biomass of the top predators is increased until the EE of the large phytoplankton is near 0.5 the model predicts extremely large biomass for the intermediate trophic levels. This result also highlights the sensitivity of the ECOPATH II model to top predators numbers. Again this low EE may reflect a real phenomenon in nature. Mass sinking of intact phytoplankton cells has been observed after high productivity events (see Smetacek 1985 for a review).

For the low productivity condition we reduced the biomass and productivity of the large phytoplankton and the productivity of the small phytoplankton, consistent with our observations in the field. Keeping the original top predator biomass for the low productivity run resulted in an EE for large phytoplankton which exceeded 1.00. We therefore reduced the biomass of the marine mammals by a factor of four. This resulted in a structure that only sustained about 40% of the biomass calculated with the higher primary

Table 3. Estimated parameters for three models of the Monterey Bay upwelling ecosystem. B indicates biomass (in mg C m^{-2}) and EE ecotrophic efficiency.

Group	Parameter	Winter low productivity	Summer upwelling mean productivity	Summer upwelling high productivity
3. Carnivorous nekton fish	B	73	223	223
4. Demersal fish	B	313	958	958
5. Omnivorous fish	B	332	992	992
6. Micronekton	B	145	430	430
7. Macrobenthos	B	165	508	508
8. Meiobenthos	B	63	194	194
9. Macrozooplankton	B	235	700	700
10. Mesozooplankton	B	359	1,070	1,070
11. Microzooplankton	B	167	499	499
12. Bacteria	B	141	419	419
13. Small phytoplankton	EE	0.24	0.35	0.35
14. Large phytoplankton	EE	0.59	0.21	0.11
15. Benthic producers	EE	0.05	0.07	0.07
16. Detritus	EE	0.33	0.24	0.14

production values (Table 3). If this is true, then resource limitation may partially explain the migration and reproductive cycle of many groups along the California coast that seems to be in phase with the production cycle. Interestingly the ecotrophic efficiency of the large phytoplankton increases, which is what we might expect in more mature, open ocean, systems (Margalef 1978).

The comparison of the flow to detritus from the phytoplankton during the upwelling and winter simulations is of interest and may reflect processes occurring in nature. The ratio of large phytoplankton primary production from high to low is close to 8. On the other hand, the ratio of the flow to detritus is closer to 16, almost twice the previous rate. A similar relationship was reported by Jahnke et al. (1990) between primary productivity and benthic fluxes on a transect offshore of Monterey. They show that the productivity changed by a factor of 3-4 while the benthic flux changed by a factor greater than 20. We get a different perspective, however, if we take into consideration the change in productivity and flux to detritus for the small and larger phytoplankton together. In this case, the ratio of the change for both the productivity and flow to detritus is around 4. This suggests that even though the total change in detritus production is almost identical to the change in primary production, the sources of the detritus differ dramatically with season. The composition of the so-called detritus pool probably also varies with season. We might expect changes in the proportion of dissolved vs. particulate fraction. In the future it will probably be necessary to partition the detrital pool in the ECOPATH II model into the previous mentioned fractions. These observations, coupled with the model predictions, are among the first data that support the concept that the composition of the primary producers (i.e., small vs. large phytoplankton) has significant impact on the rate of particulate flux (Michaels and Silver 1988).

Another set of results that are within expected values are respiration/assimilation rates. A 55% respiration/assimilation rate for zooplankton was estimated by the model, which is almost identical to the 56% estimated by Fasham (1985). Also, the same rate for the top predators is very close to 1, as suggested by Christensen and Pauly (1992). These observations suggest realistic estimates for the input parameters.

What we report here is a preliminary effort in modelling the Monterey Bay ecosystem. Verification of the model assumptions and results with observations of biomass and rates is clearly needed. However, due to the obvious limitations of ECOPATH II, we cannot expect more than general agreement. Most of the difficulties lie in the fact that ECOPATH II assumes a steady state so it cannot incorporate time-varying changes. In coastal upwelling systems, like Monterey Bay, physical biological variability is high (Figs. 2 and 3). What this implies is that many of the grazers need to be omnivorous feeders and instantaneous observations do not reflect changes in diet making it difficult to establish the mean (closest to steady-state) value in nature. We clearly need more information regarding the diet composition of the consumers within the model. A sensitivity analysis was not done on the model, however small modifications in diet composition resulted in major changes in the model output. At this time the same diet composition is used for the low and high production runs, but this should change as a result of variation in the relative abundance of the different groups within the model. Another area that needs better definition is the role of the bacteria as primary producers, consumers of detritus and dissolved organic matter (DOM) and as a prey for higher trophic levels. This could be critical for the low production season. We also plan to incorporate into the model results from ongoing MBARI research regarding the use of marine snow and fecal pellets as food source for grazers and to compare the model outputs with detailed fisheries information from the bay.

In order to circumvent the steady-state limitations of ECOPATH II, it is necessary to add temporal and spatial components to the model. A new generation of ecosystem models (see Sarmiento et al. 1989) deals with this issue by merging physical models, which have time and space information, with ecosystem models. In the future we expect to see models of the California Current, like those of O'Brien and students (Parez-Sierra and O'Brien 1989), merged with ecosystem models like those of Fasham et al. (1990) or even ECOPATH II.

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Towards a Conceptual Model of the Weddell Sea Ecosystem, Antarctica*

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Abstract

An attempt was made to construct a conceptual model of the biomasses at and energy flows through, the various trophic levels and compartments in an Antarctic marine ecosystem, comprising pelagic, benthic, as well as ice habitats.

Although many scientific papers concerning the marine environment in the Antarctic have been published, especially in the last decade, there still are major gaps in the present day knowledge of Antarctic marine ecology. Moreover, spatial and temporal variability in both structure and functioning of the food web is considerable and seriously hampers the construction of a general model.

As the Southern Ocean spans 11 to 22% of the world ocean, depending on its definition, and includes many very different shallow areas and deep basins, we confined this first modelling effort to the Weddell Sea proper as an example of *an* Antarctic marine ecosystem.

The flexibility of Antarctic ecosystems is large and stocks and flows in the various compartments of these systems exhibit great variability. In fact different subsystems can be recognized, both in time and space. We therefore chose to present ranges rather than averages in the properties of the various subsystems. The Weddell Sea model presented here is far from complete and gives an indication of the trophic relations between the most important compartments as they are known now. However, a large number of the energy fluxes between the subsystems and compartments remain largely unknown. Gaps in present knowledge are pointed out as areas for future investigations.

Introduction

The Antarctic Ocean comprises the southern parts of the Atlantic, Indian and Pacific Oceans. Depending on the northern boundary chosen, the Southern Ocean covers an area of approximately 11 to 22% of the world ocean (Kort et al. 1965; Hellmer and Bersch 1985), including three large ocean basins: the Weddell Basin, the South India Basin and the Southeast Pacific Basin, separated by the Antarctic Peninsula, the Kerguelen Plateau and a southward branch of the Mid Ocean Ridge, south of New Zealand. The Antarctic waters thus consist of several subsystems. As a consequence the generalized term "the Antarctic marine ecosystem" from a geographical, hydrographical and biological point of view should be applied with caution.

The Weddell Sea (ca. 2.3 x 10^6 km^2, Hellmer and Bersch 1985) comprises a large gyral system with a rotation speed of about six years. Its western boundary is the Antarctic Peninsula, in the north it is separated from the Scotia Sea by the Circum-Antarctic Current and a distinct hydrographic front system. Towards the east the gyre flattens and is squeezed between the northward extending landmass of Dronning Maud Land in the south and the waters of the Circum-Antarctic Current in the north. In the west, the Weddell Sea extends beyond 80°S, and below the permanent Filchner-Ronne ice shelf.

The centre of the Weddell gyre is a relatively stable system, as in other gyral water masses, while at its borders, disruption of the hydrography occurs due to landmasses (the continental shelves and ice shelf) in the south, southeast and west or due to contact with other water masses (Circum-Antarctic Current in the north). The northern boundary, the Scotia Front and Confluence Zone, has no fixed position and meanders (Foster and Middleton 1980; Patterson and Sivers 1980). Exchange of water between the Scotia and Weddell Seas probably takes place during occasional events in the form of eddies and lenses breaking through the front (Cederlϕf et al. 1989).

These disruptions in hydrography are reflected by the biology in the water column, and ultimately also by the bottom fauna. This leads to a differentiation in two types of marine ecosystems. In the stable center a "fully" regenerating type of pelagic system is found, characterized by low biomasses at all trophic levels and extreme low sedimentation rates ("retention system"). The boundaries on the other hand are areas of high but very variable activity at the different production and consumer levels, characterized by large temporal phytoplankton (diatom) blooms, which are superimposed upon a regenerating type of system (Smetacek et al. 1991). Extensive krill stocks are found in these regions, and large salp blooms occur there which are reflected in the high (and variable) peaks of vertical particle flux ("export system"), see Fig.1.

The ice cover on the Weddell Sea varies from year to year. A general feature is that a part of the southwestern Weddell Sea is covered by

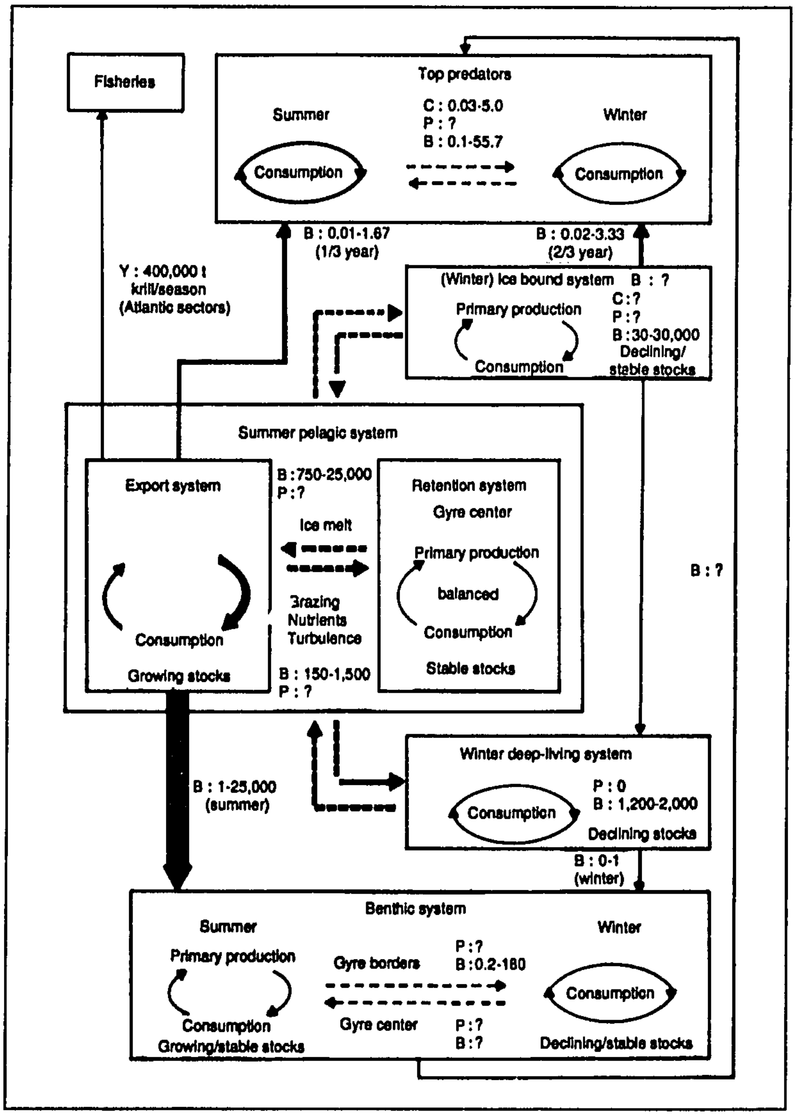

Fig. 1. Components of the Weddell Sea ecosystem model, Antarctica (see Figs. 2-5 for amplifications of components). C = Consumption (mgC m^{-2} year^{-1}); P = Production (mgC m^{-2} year^{-1}); and B = Biomass (mgC m^{-2}).

multi-year ice throughout the year as a result of the concentrating effect of the gyral currents in this area. The northwestern part experiences different degrees of ice cover, depending on the season and yearly variations. The melting ice-edge causes a local disruption of the hydrographical conditions and generates changes in the structure and biological activity in the ecosystems (Ross and Quetin 1986; Smith and Nelson 1986; Garrison et al. 1986; Daly and Macaulay 1988; Frixell and Kendrick 1988; Schalk 1990). This results in a complicated and heterogeneous picture of local events, superimposed upon the general effects of the overall hydrography.

There is much more heterogeneity in macro-nutrient concentrations (phosphate and nitrate) on both temporal and spatial scales than expected some years ago (Jacques and Tréguer 1986); hence macro-nutrient depletion may be a limiting factor for primary production in certain regions, especially in coastal and continental shelf areas (Tréguer and Jacques 1992).

In addition to the primary production of phytoplankton, the second major source for carbon fixation are the micro-algae living in the sea ice that seasonally covers a large portion (> 5,830,000 km^2) of the Southern Ocean.

Almost all biological activity in the water column and related vertical fluxes are restricted to the spring/summer period (some four months). In winter the pelagic system reverts to a retention system and segregates into an "ice-associated system," a community subsisting on the ice algae production at the underside of the sea ice, and a "deep system," consisting of hibernating stocks and their predators (Fig. 1).

The benthic system as well as the "top predators" (birds, seals and whales) are more persistent factors (biomass, consumption) in the Weddell Sea system. The benthos depends almost entirely on the short spring/summer pulse for the sedimentation of organic matter produced by the export systems (Clarke 1988; Arntz et al. 1992). Despite this, epifauna (mostly suspension feeders such as sponges and bryozoans but also including some motile elements as amphipods, isopods and shrimps) is surprisingly rich and diverse in most continental shelf and slope areas (Mühlenhardt-Siegel 1988; Gerdes et al. 1992). However, present day knowledge on structure and processes in the deep benthic systems on the vast abyssal planes of the central Weddell Sea and its links to vertical fluxes is limited. The top predators subsist on both pelagic export systems as well as on ice-bound systems and feed on these resources throughout the year.

Thus the Antarctic is characterized by a complex of linked ecosystems. This paper is a first attempt to depict the different Antarctic systems as distinguished in the Weddell Sea and some of their links and estimated fluxes. The result is a model (Fig. 1) which as yet is incomplete, but should serve as a focus for future research.

Summer Pelagic System

The Antarctic pelagic system was earlier generally considered to be highly productive with a short simple food chain based on brief but productive summer periods dominated by extensive diatom blooms, efficiently grazed by the main consumer krill, which is eaten by whales, seals and penguins (Tranter 1982). Recently it has become clear that the ice-free period is *not* exceptionally productive and that the sparse flagellate community is more characteristic of this period than the phytoplankton blooms of large diatoms which occur (temporarily) in restricted areas such as frontal systems, shelf areas, or the ice edge region (Sakshaug and Holm-Hansen 1984; Heywood and Priddle 1987). Next to krill other zooplankton grazers (salps, copepods) can also be of importance and there are significant pelagic predators (squid, fish) that prey on the zooplankton stock (Boysen-Ennen et al. 1991). Differently structured pelagic systems exist at various spatial and temporal scales, their patchiness and functioning depending on history and local events.

Essential are the differences between pelagic systems based on new production (export systems in Fig. 1) or regenerated production (retention systems in Fig. 1) for the level of primary producers, consumers and carbon export (Smetacek et al. 1991).

Export systems (Fig. 2) are dominated by large diatoms, high primary production rates (up to 3,000 mgC m^{-2}day^{-1}, Table 1), high biomasses of grazers (200-4000 mgC m^{-2}, Table 2), of small predators (15-130 mgC m^{-2}, Table 2) and large predators ($\leq$ 840 mgC m^{-2}, Table 2). Diel consumption rates are estimated to $\leq$ 1,100 mgC m^{-2}day^{-1} in grazers and to $\leq$ 10 mgC m^{-2}day^{-1} in small predators, whereas a considerable export of carbon may take place ($\leq$ 1300 mgC m^{-2}day^{-1}, Table 4, Fig. 6). The large predators, fish and squid, feed on krill mainly (Permitin 1970; Tarverdiyeva and Pinskaya 1980; Kock 1985; Williams 1985; Nemoto et al. 1985).

Retention systems (Fig. 3) are characterized by small flagellates, low primary production rates

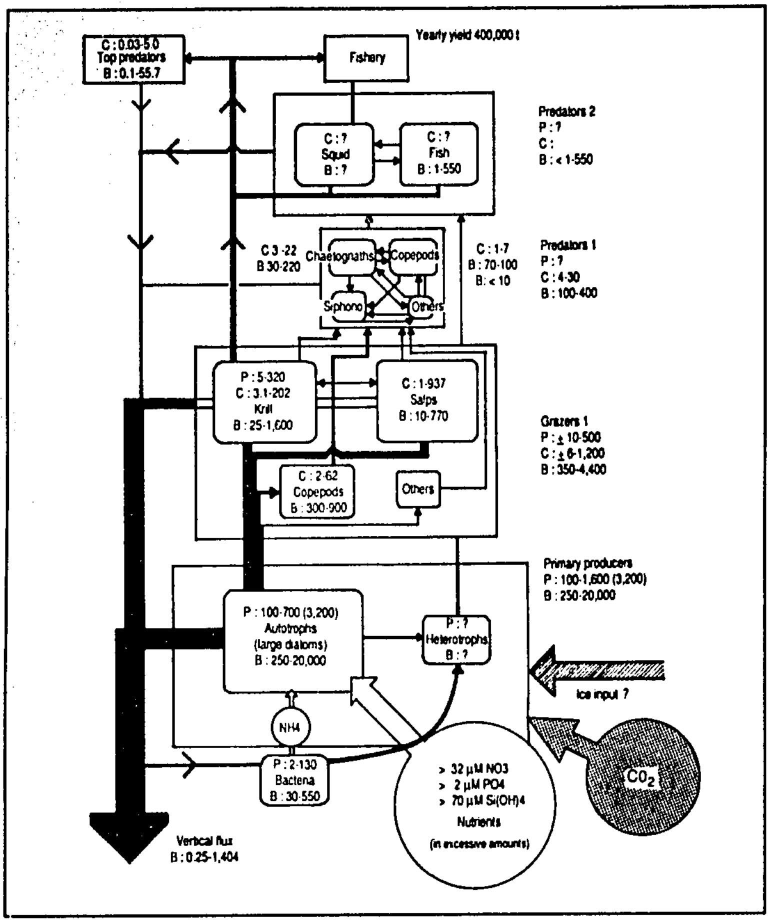

Fig. 2. The pelagic export system component of the Weddel Sea ecosystem model, Antarctica (see also Fig. 1). C = Consumption (mgC m^{-2} day^{-1}); P = Production (mgC m^{-2} day^{-1}); and B = Biomass (mgC m^{-2}). Consumption estimates for salps based on Ikeda and Mitchell (1982), Huntley et al. (1989), Schalk (1990); for copepods on Schalk (1990), Schalk and Schiel (in press); for chaetognaths on Feigenbaum (1982), Sameoto (1987), Schneider (1989), Oresland (1990), Schalk (1990); for krill on Schalk (1990).

Table 1. Annual primary production in Weddell Sea waters and adjacent areas. Daily production during the productive period can be estimated roughly by annual flux / 100 (Holm-Hansen et al. 1977, Smith and Nelson 1986)[a]. Geographical zones according to Tréguer and van Bennekom (1991); PFZ: Polar Front Zone; POO: Permanent Open Ocean; SIZ: Seasonal Sea-Ice Zone; PSIZ: Permanent Sea-Ice Zone.

Area	Annual production gC m^{-2} year^{-1}	Reference
Central Weddell Sea PSIZ	0.3	Jennings et al. (1984)
N central Weddell Sea SIZ	10.4	El-Sayed and Taguchi (1981)
NW Weddell Sea SIZ	10.5	von Bröckel (1981)
NW Weddell Sea SIZ	23.2	*fide* von Bröckel (1985)
N Weddell Sea SIZ	54.0	El-Sayed and Mandelli (1965)
E Weddell Sea SIZ	18.0	El-Sayed and Mandelli (1965)
SE Weddell Sea SIZ	40.1	El-Sayed and Taguchi (1981)
SE Weddell Sea SIZ	67.4	von Bröckel (1985)
S Weddell Sea SIZ	53.0	El-Sayed and Mandelli (1965)
S Weddell Sea SIZ	70.6	El-Sayed (1971)
Weddell Sea SIZ	69.0	El-Sayed and Mandelli (1965)
Weddell Sea SIZ	0.7	Wefer and Fischer (1991)
Weddell Sea SIZ	13.2-37.8	Jennings et al. (1984)
Weddell Sea (60-78°S)	63.8 [1]	Hayes et al. (1984)
Weddell Sea POO	3.0-40.0	Wefer and Fischer (1991)
Polar Front PFZ	83.5	Wefer and Fischer (1991)
SE Weddell Sea Shelf	26.0-33.0	von Bodungen et al. (1988)
Coastal zone	10-170	Wefer and Fischer (1991)
Near Signy Island	300	Horne et al. (1969)
Near Deception Island	362	Mandelli and Burkholder (1966)
Drake Passage	173.0	Wefer and Fischer (1991)

[a] Values estimated from production measurements in mgC m^{-3} hour^{-1} by multiplying with a factor 19.7 for productive period per day and a factor 18.3 to integrate over the water column (relations drawn from data in El-Sayed and Mandelli 1965).

Table 2. Depth ranges and biomasses of zooplankton, squid and fish in Antarctic areas. Conversion factors dry mass -> carbon follow Schneider (1989): (1) CP: closed pack ice; (2) TZ: transitional zone; (3) OW: open water.

Group	Area	Time	Depth range (m)	Biomass (mgC m^{-2})	Reference
Grazers					
Copepods	W Weddell Sea	Mar	0-1,000	441.6	Hopkins and Torres (1988)
	Central gyre	Feb-Mar	0-300	557.7	Boysen-Ennen et al. (1991)
	NE shelf	Feb-Mar	0-300	1,669.2	"
	S shelf	Feb-Mar	0-300	189.0	"
	N Weddell Sea CP	Oct-Nov	0-60	2.5	Siegel et al. (1992)
	N Weddell Sea TZ	Oct-Nov	0-60	3.5	"
	N Weddell Sea OW	Oct-Nov	0-60	190.7	"
Salps	Antarctic Peninsula	Mar	0-200	49-671	Huntley et al. (1989)
	Antarctic Peninsula	Jan-Feb	?	1-200	Witek et al. (1985)
	Central gyre	Feb-Mar	0-300	39.6	Boysen-Ennen et al. (1991)
	NE Weddell Sea	Feb-Mar	0-300	12.3	"
	S Weddell Sea	Feb-Mar	0-300	21.3	"
	W Weddell Sea	Mar	0-200	11.1	Lancraft et al. (1989)
	N Weddell Sea CP	Oct-Nov	0-60	0	Siegel et al. (1992)
	N Weddell Sea TZ	Oct-Nov	0-60	0.4	"
	N Weddell Sea OW	Oct-Nov	0-60	19.6	"
Euphausiacea	W Weddell Sea	Mar	0-1,000	16.7	Hopkins and Torres (1988)
(mainly *E. superba*)	Central gyre	Feb-Mar	0-300	111.0	Boysen-Ennen et al. (1991)
	NE Weddell Sea	Feb-Mar	0-300	50.5	"
	S Weddell Sea	Feb-Mar	0-300	1.1	"
	W Weddell Sea	Mar	0-200	257.5	Lancraft et al. (1989)
	N Weddell Sea CP	Oct-Nov	0-60	172.2	Siegel et al. (1992)
	N Weddell Sea TZ	Oct-Nov	0-60	7.2	"
	N Weddell Sea OW	Oct-Nov	0-60	2.5	"
Predators 1					
Copepods (mainly	Central gyre	Feb-Mar	0-300	39.6	Boysen-Ennen et al. (1991)
Euchaeta spp.)	NE Weddell Sea	Feb-Mar	0-300	41.0	"
	S Weddell Sea	Feb-Mar	0-300	11.1	"
Chaetognaths	W Weddell Sea	Mar	0-1,000	16.8	Hopkins and Torres (1988)
	Central gyre	Feb-Mar	0-300	58.7	Boysen-Ennen et al. (1991)
	NE shelf	Feb-Mar	0-300	21.0	"
	S shelf	Feb-Mar	0-300	17.8	"
	N Weddell Sea CP	Oct-Nov	0-60	0.2	Siegel et al. (1992)
	N Weddell Sea TZ	Oct-Nov	0-60	3.1	"
	N Weddell Sea OW	Oct-Nov	0-60	1.6	"
Coelenterates	W Weddell Sea	Mar	0-1,000	5.9	Hopkins and Torres (1988)
	Central gyre	Feb-Mar	0-300	29.5	Boysen-Ennen et al. (1991)
	NE Weddell Sea	Feb-Mar	0-300	2.4	"
	S Weddell Sea	Feb-Mar	0-300	8.8	"
	W Weddell Sea	Mar	0-200	28.2	Lancraft et al. (1989)
	N Weddell Sea CP	Oct-Nov	0-60	0.1	Siegel et al. (1992)
	N Weddell Sea TZ	Oct-Nov	0-60	0.4	"
	N Weddell Sea OW	Oct-Nov	0-60	<0.1	"
Predators 2					
Squid	?			?	
Fish	SE Weddell Sea shelf	Jan-Feb	200-670 (d)	20-460	Ekau (1990)
	S. Georgia shelf		demersal	600-820	Sosinski and Skora (1988)
	SE shelf and slope	Feb	0-850 (pel)	10-150	Hubold and Ekau (1987)

Table 3. Chlorophyll and organic carbon content of Weddell Sea ice samples.

Area	Season	Ice type	mg Chl a m^{-2}	mg C m^{-2}	Reference
NW	Summer	Pack ice	9.6	355	Garrison and Buck (1982)
NW to SE	Summer	Pack ice	1.4	52	Ackley et al. (1979)
E	Summer	Fast ice	137.5	5,088	G. Dieckmann unpubl.
E	Winter	Pack ice	0.6	22	Clarke and Ackley (1984)
E	Winter	Pack ice	1.6	58	G. Dieckmann unpubl.
E to SE	Spring	Pack ice	5.5	203	G. Dieckmann unpubl.
NW	Spring	Pack ice	6.5	241	G. Dieckmann unpubl.
Average (excl. fast ice)			4.1	151	

Table 4. Measured and estimated annual vertical flux in Antarctic waters. Daily flux during the productive period can be estimated roughly by annual flux / 100. Estimation of annual carbon flux (export) at 100 m water depth using the equations of Martin et al. (1987) and measured carbon flux rates at the various sampling depths derived from sediment trap experiments reported in the literature cited. Geographical zones according to Tréguer and van Bennekom (1991): PFZ: Polar Front Zone; POO: Permanent Open Ocean; SIZ: Seasonal Sea-Ice Zone; PSIZ: Permanent Sea-Ice Zone.

Area	Water depth [m]	Annual flux measured gC m^{-2} $year^{-1}$	Calculated annual $C_{flux\ at\ 100m}$ g C m^{-2} $year^{-1}$	Source
Drake Passage	965	5.41	37.80	Wefer et al. (1982)
Drake Passage	2,540	4.78	76.70	Wefer et al. (1982)
Bransfield Str.	100	8.7-130[a]	8.7-130	von Bodungen et al. (1986)
Bransfield Str.	494	7.7	30.32	Wefer and Fischer (1991)
Bransfield Str.	693	0.35	1.84	Wefer and Fischer (1991)
Bransfield Str.	687	1.1	5.75	Wefer and Fischer (1991)
Bransfield Str.	150	10.3[a]	14.50	Dunbar (1984)
Weddell Sea SIZ	863	0.021	0.133	Wefer and Fischer (1991)
Polar Front PFZ	700	2.86	15.19	Wefer and Fischer (1991)
Maud Rise SIZ	4,456	0.17	4.42	Wefer and Fischer (1991)
Maud Rise SIZ	360	2.28	6.84	Wefer and Fischer (1991)
Maud Rise SIZ	352	0.16	0.47	Wefer and Fischer (1991)
Weddell Sea Shelf SIZ	100	2.4[a]	2.40	von Bodungen et al. (1988)
Weddell Sea Shelf SIZ	250	1.9[a]	4.17	Bathmann et al. (1991)
Coastal zone	100	?	2-30	Wefer and Fischer (1991)
Coastal zone	100	?	13.00	Bathmann et al. (in press)
Lutzow-Holm Bay SIZ	100	9.3[a]	9.30	Fukushi and Sasaki (1981)
Lutzow-Holm Bay PSIZ	23	8.29[a]	2.35	Matsuda et al. (1987)
Ross Sea SIZ	225	3.18[a]	6.38	Dunbar (1984)

[a] Daily rates recalculated.

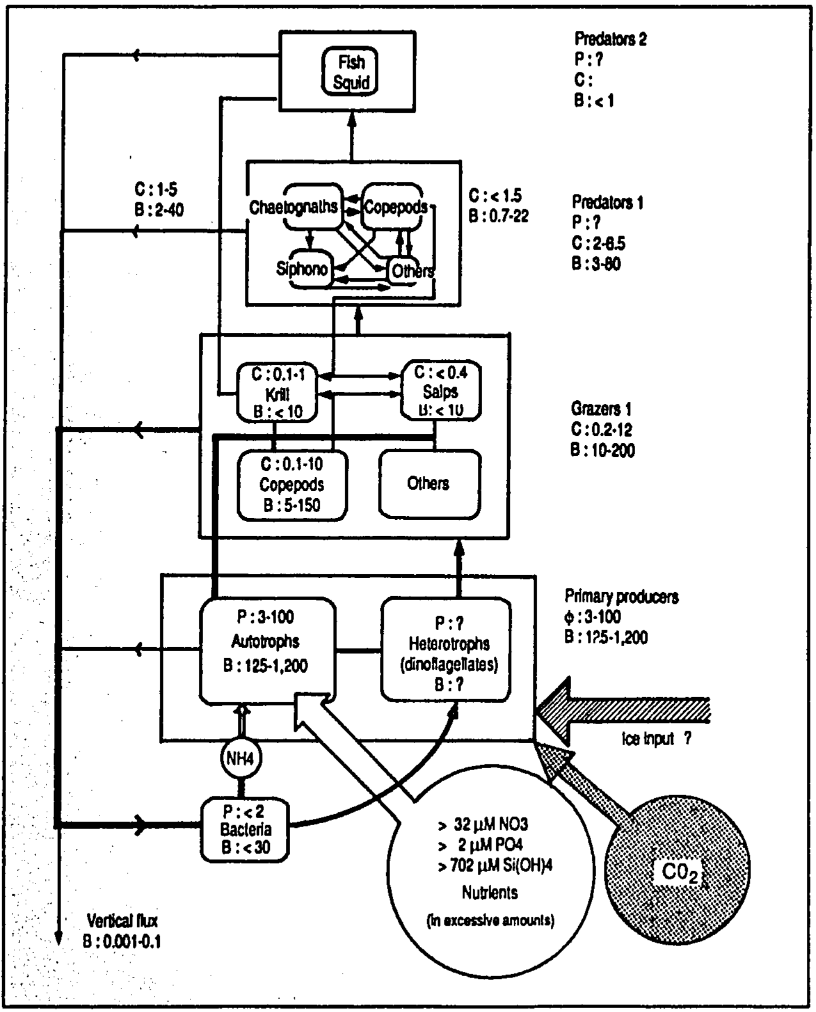

Fig. 3. The pelagic retention system component of the Weddel Sea ecosystem model, Antarctica (see also Fig. 1). C = Consumption (mgC m^{-2} day^{-1}); P = Production (mgC m^{-2} day^{-1}); and B = Biomass (mgC m^{-2}). Consumption estimates for salps based on Ikeda and Mitchell (1982), Huntley et al. (1989), Schalk (1990); for copepods on Schalk (1990), Schalk and Schiel (in press); for chaetognaths on Feigenbaum (1982), Sameoto (1987), Schneider (1989), Oresland (1990), Schalk (1990); for krill on Schalk (1990).

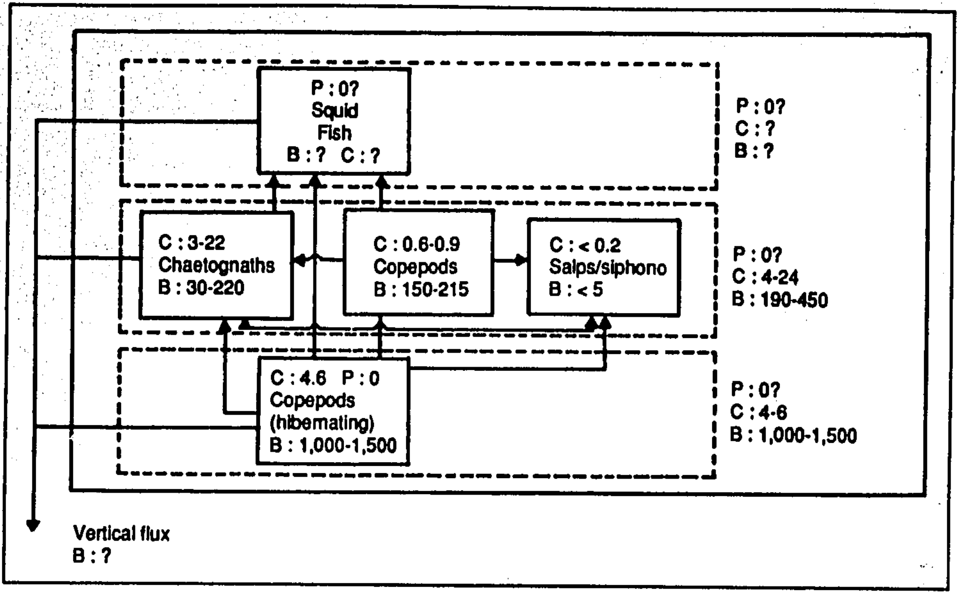

Fig. 4. The winter deep-living system component of the Weddel Sea ecosystem model, Antarctica (see also Fig. 1). C = Consumption (mgC m^{-2} day^{-1}); P = Production (mgC m^{-2} day^{-1}); and B = Biomass (mgC m^{-2}).

(< ±100 mgC $m^{-2}day^{-1}$, Table 1), low biomasses of grazers (10-200 mgC m^{-2}, Table 2) as well as small (3-80 mgC m^{-2}, Table 2) and large predators (< 1 mgC m^{-2}, Table 2). Accordingly, consumption rates are low, and carbon is recycled almost without any export (± 1 mgC $m^{-2}day^{-1}$, Table 4, Fig. 6).

Export systems may occur in frontal areas at the northern part of the Weddell gyre, the shelf areas in the south and southwest, near islands, and in the wake of the melting ice edge. They change into relatively poor retention systems due to (micro)nutrient exhaustion, vertical mixing in the photic layer and/or heavy grazing pressure by various heterotrophs and vice versa as a result of water column stabilization, ice-edge seeding or mixing of water masses. As a consequence of this switching, the export vertical flux to the deep-sea and bottom communities has a pulsed character, with main peaks in the spring/summer period (November-February, Fig. 6).

Thus the structure of the pelagic food webs varies in space and time as biomass and energy flows through the various compartments change. Present day knowledge is limited to a few areas only, and some seasons of the year and a majority of the ecosystem compartments still have to be studied.

Winter Pelagic System

Pelagic primary production is confined to the short spring/summer period (ca. four months); during the remainder of the year the water column

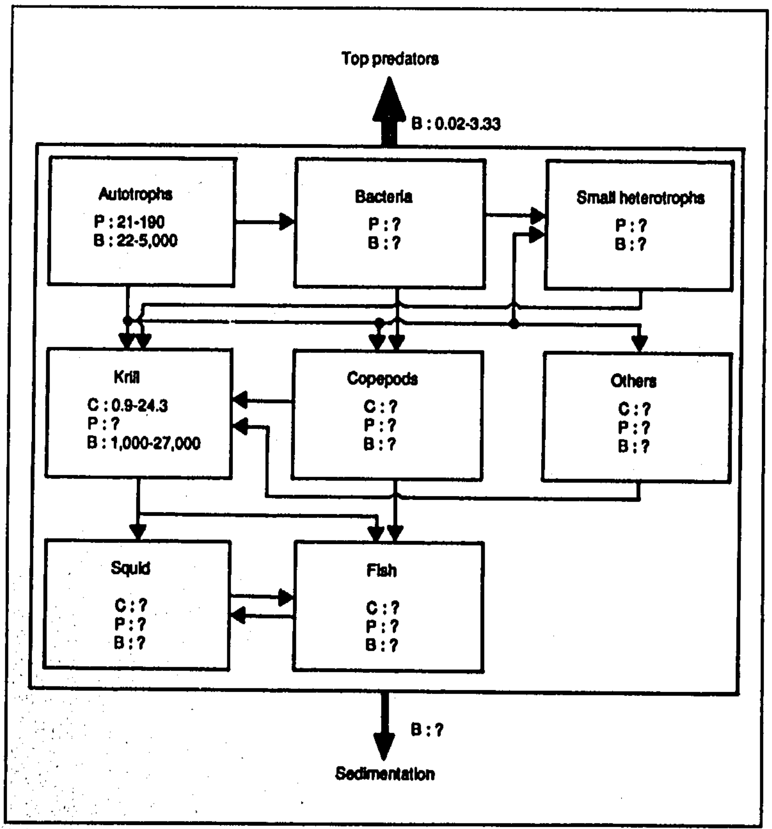

Fig. 5. The ice bound system component of the Weddel Sea ecosystem model, Antarctica (see also Fig. 1). C = Consumption (mgC m^{-2} day^{-1}); P = Production (mgC m^{-2} day^{-1}); and B = Biomass (mgC m^{-2}).

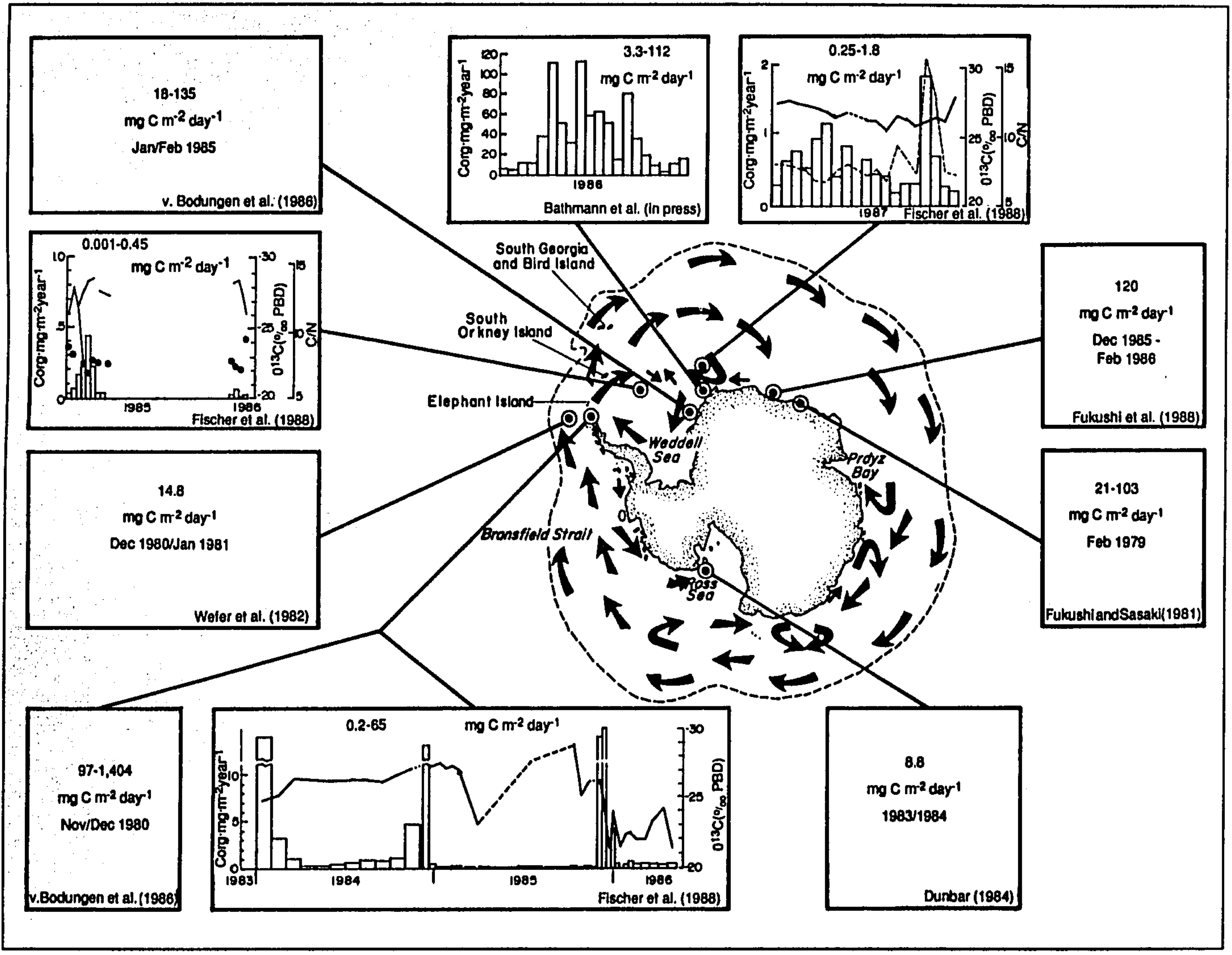

Fig. 6. Observed vertical particle flux in the Weddell Sea (mgC m^{-2} day^{-1}) and adjacent systems.

is low in primary producers. There are several strategies for the pelagic zooplankton community to "overwinter":

1. reduce biomass (e.g., salps, siphonophores);
2. reduce metabolic demand (e.g., the majority of herbivorous copepods);
3. continue feeding on another energy source (e.g., krill, some herbivorous copepods, carnivorous copepods, chaetognaths); and
4. migrate out of the area (e.g., mesopelagic fishes).

As a result the pelagic zooplankton community disperses in winter into a deep-living community and a surface- and ice-bound community (Marín 1988; Marschall 1988; Strech et al. 1988; Schnack-Schiel et al. 1991). Grazers which maintain a more or less constant biomass throughout the year and have an insufficient capability to reduce metabolic demand (krill, some copepods) switch to ice algae in the sea ice system (Table 3); some predators follow (Kottmeier and Sullivan 1987). A majority of the herbivorous copepods migrates to deeper water layers (> 500 m) and "hibernates" (Voronina 1972, 1978), followed by predators (e.g., chaetognaths, siphonophores). The two grazers (krill and salps) which may occur in high densities in the summer pelagic system have the capability to switch to a carnivorous diet (Boyd et al. 1984; Price et al. 1988; Huntley et al. 1989). For salps this is necessary to maintain a minimum stock during winter in the deeper water layers where only copepods are available as a food source. Krill has to maintain a relatively large stock throughout the year and when summer pelagic or winter ice algal production is insufficient they switch to carnivory to cover their metabolic demand (Boyd et al. 1984; Price et al. 1988).

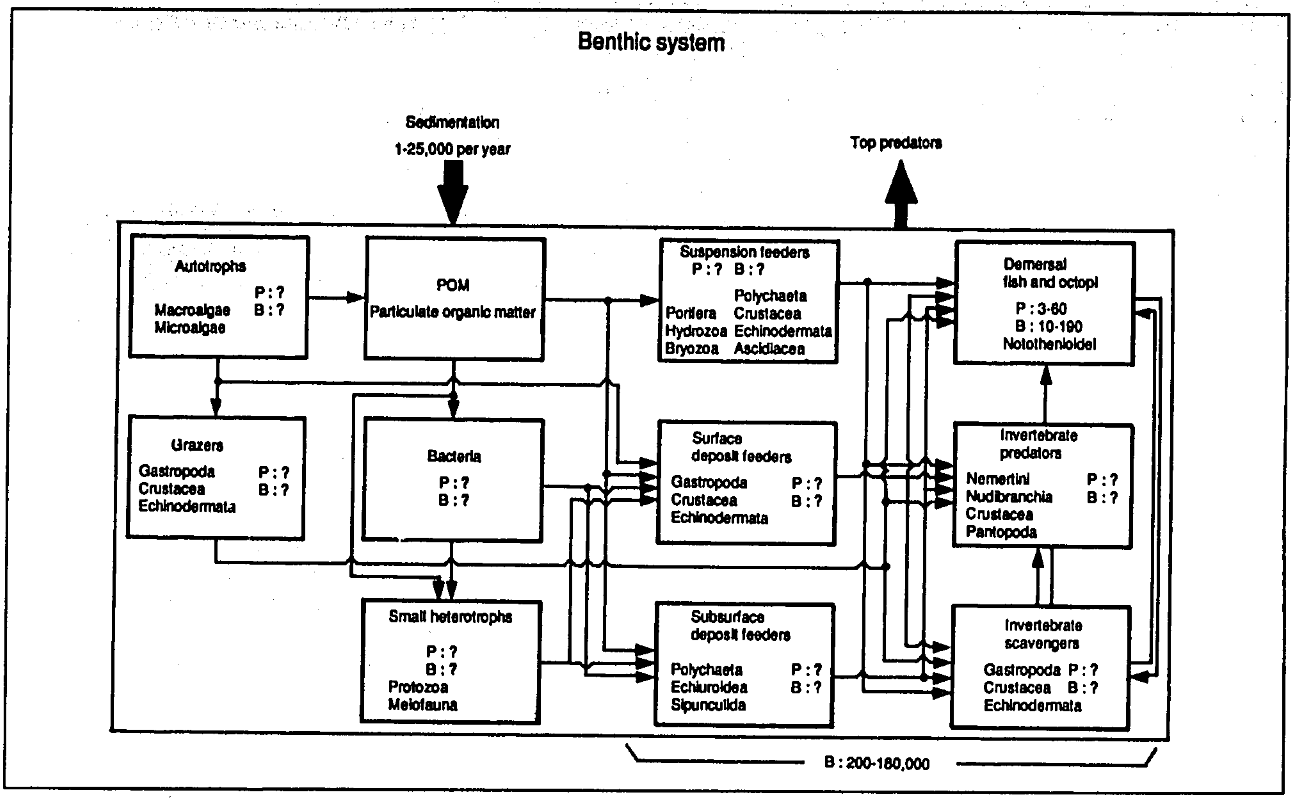

Fig. 7. The benthic component of the Weddel Sea ecosystem, Antarctica (see also Fig. 1). C = Consumption (mgC m^{-2} day^{-1}); P = Production (mgC m^{-2} $year^{-1}$); and B = Biomass (mgC m^{-2}).

Sea Ice System

The sea ice is an extremely diverse and heterogeneous substratum, the result of different ice formation processes varying on a spatial and temporal scale. The northeastern Weddell Sea has the largest annual variability in ice-cover, with the maximum extent in August ($4.36 \cdot 10^6$ km^2) and the minimum in February ($1.14 \cdot 10^6$ km^2). In addition an annual residual of $0.8 \cdot 10^6$ km^2 multi-year sea ice remains in the western Weddell Sea during summer.

A variety of organisms, ranging from bacteria to small metazoan copepods (Adriashev 1968; El-Sayed 1971; Spindler et al. 1990) are incorporated into the sea ice during its formation (algae) or actively invade it after its formation. A major portion of the sea ice organisms (those forming internal assemblages) is not available or accessible to large pelagic grazers until the ice melts in spring (Horner et al. 1992). However, algae growing on submerged and exposed sea ice surfaces, at the ice-water interface, are potentially available throughout the year, their growth being limited mainly by light (Table 3).

The sea ice cover can be regarded as an important component of the pelagic system as it influences and governs critical factors such as hydrography and light regime in the water column and supports an algal stock and energy resource for grazers during winter. Primary production figures of the sea ice system are scant; however, the annual production attributed to the Antarctic sea ice cover is estimated to be from 0.66 to $0.83 \cdot 10^{14}$ $gCyear^{-1}$, which is about 30% of the total Antarctic primary production (Legendre et al. 1992). Since the Weddell Sea ice cover, at its maximum extent, represents approximately 22% of the overall Antarctic ice cover (Ropelewski 1983), the contribution to the annual primary production by sea ice in the Weddell Sea lies between 0.15 and $0.18 \cdot 10^{14}$ gC $year^{-1}$, (i.e., 15-18 $gC \cdot m^{-2} year^{-1}$).

Vertical Particle Flux

A very limited amount of data concerning the vertical particle flux is available for the Antarctic (Table 4, Fig. 6). Especially year-round data are scarce. The pattern of vertical flux rates and amount and composition of the particles vary considerably in space and time.

In the Bransfield Strait regular patterns in the vertical particle flux were observed with maximum rates from December to January, but the total flux differed between years (Wefer 1989). Krill grazing is considered to be responsible for that variability. In contrast to the shelf area of Kapp Norvegia, krill seemed to play only a minor role in the particle transport from shallow to deeper water layers (Bathmann et al. 1991). In that area during the time of ice melting, first a flux of ice algae occurs, followed by krill pellets, minipellets, diatom aggregates, oval and round pellets, indicating a succession in composition and functioning of the pelagic ecosystem (Bathmann et al. 1991). Thus, the vertical flux differs by at least one order of magnitude between the Bransfield Strait and other shelf areas (Table 4).

For the central gyres of the Antarctic, little is known about the amount and pattern of the vertical particle fluxes. In the central Weddell Sea gyre, the world's lowest sedimentation rates (0.001-0.45 $mgC \cdot m^{-2}day^{-1}$) were recorded (Fischer et al. 1988). The pelagic system has adapted completely to the relatively stable hydrography in the gyre and as a result organic matter is retained in the upper water layer throughout the growing season by a regenerating type of plankton community. Some sinking occurs at the end of the growing season in March/April (Fischer et al. 1988). At the border of the gyre sedimentation is much higher and rates from 3.3 to 135 $mgC \cdot m^{-2}day^{-1}$ occur at the shelf off Kapp Norvegia in the productive season.

Even for the Weddell Sea, by far the best known of all Antarctic waters, it would be difficult to derive a mathematical model relating pelagic production to vertical particle flux. Knowledge of the life cycles of the various species involved in primary and secondary production, as well as of the hydrographical situations and the impact of ice as a habitat and boundary force, is urgently needed before attempts are made to model fluxes.

Benthic System

Recent reviews on Antarctic marine benthos agree that the level of energy flow through Antarctic benthic communities is low, although community biomass is often very high (Clarke 1983; White 1984; Picken 1985; Arntz et al. 1992). The extraordinary diversity and complexity of most of these communities are the main obstacles for a rapid analysis of food webs and energy flow patterns (Fig. 7).

As the pelagic system, the Antarctic benthic ecosystem cannot be treated as a single system. Broadly, the Weddell Sea benthal can be divided into three depth-related compartments (Knox and Lowry 1977; Johnson et al. 1981; Picken 1985): (1) the ice-affected shallow littoral and sublittoral (above approx. 30 m) around the tip of the Antarctic peninsula and the islands in the north (South Shetland Island, South Orkney Island); (2) the narrow continental shelf and slope (down to about 3,000 m) along the Antarctic continent and around the islands; and (3) the deep sea compartment, which is situated partially below the central Weddell Sea gyre.

With the exception of the shallow areas in the north, where benthic primary producers are present, the Weddell Sea benthos depends on food supply from the pelagic zone. Sedimentation rates are high from the export systems in the northern and southern border areas and extremely low in the centre of the gyre (see previous chapter). The food supply via sedimentation is a strong, brief and likely to be the main limiting factor for Antarctic benthic ectotherms (Clarke 1988).

Along the northern borders of the Weddell Sea gyre, a variety of benthic communities has been described from shallow sites around the various islands, which depend on substrate type and hydrodynamic regime mainly (Hardy 1972; White and Robins 1972; Platt 1979; Richardson 1979; Jazdzewski et al. 1986; Mühlenhardt-Siegel 1988). There is a partially rich algae cover in the sublittoral zones of the islands down to about 30 m water depth with macroalgal biomasses up to 80 $gC \cdot m^{-2}$ (White and Robins 1972; Richardson 1979). Macrozoobenthic biomass up to 180 $gC \cdot m^{-2}$ has been reported. Growth and reproduction show strong seasonal oscillations (Thurston 1970; Bone 1972; Bregazzi 1972; Picken 1979, 1980; Richardson 1979; Luxmoore 1982), and annual somatic production/biomass ratios are in the range of 0.1 to 1.8 (see Brey and Clarke, in press). Latitudinal clines (north-south) in growth and reproduction of several species have been reported, too (Wägele 1987; Brey and Hain 1992; Clarke and Gore 1992; Gorny et al. 1992; and others).

Along the continental borders of the Weddell Sea gyre, several distinct communities were recognized (Voß 1988), of which structure and distribution are similar to other Antarctic regions such as the Ross Sea (Bullivant 1967; Dayton et al. 1970; Dell 1972) or parts of the Indian Ocean sector (Ushakov 1963; Belyaev 1964; Gruzov et al. 1967; Adriashev 1968). Biomass estimates range from <0.1 to >180 $gC\ m^{-2}$ above 1,200m water depth, whereas at about 2,000 m <0.8 $gC\ m^{-2}$ were found (based on wet mass data of

Gerdes et al. 1992). Reproduction, larval development and growth of benthic invertebrates from the southern shelf seem to be extremely slow in general, and productivity seems to be very low (0.07 - 0.31 year^{-1}, see Wägele 1987; Hain 1990; Brey 1991; Brey and Hain 1992; Arntz et al. 1992).

The fauna of the Antarctic deep sea is fragmentarily known only, especially quantitative data are scarce (e.g., Ushakov 1963). Biomass is much lower than on the shelf and upper slope (Gerdes et al. 1992; Brey and Clarke, in press), but most likely higher than in the Arctic deep sea (George 1977).

The available data allow only for speculations on the energy flow through the benthic systems of the Weddell Sea:

For a shallow bay at Signy Island, Everson (1970) estimated about 11 gC m^{-2} of benthic secondary production to be required to maintain the actual stock of the system key predator, the demersal fish *Notothenia neglecta*.

On the southeastern shelf, annual sedimentation is in the range of 2-50 gC m^{-2} (Bodungen et al. 1988; Bathmann et al. 1991; Bathmann et al., in press). Assuming an ecological efficiency (production/consumption) of 15%, average annual macrobenthic production could be in the range of 0.3-7.5 gC m^{-2}. The annual production of demersal fish in this area is estimated to roughly 0.03 gC m^{-2} (e.g., Ekau 1990). If the ecological efficiency of these fish is about 5% (Everson 1970), 0.6 gC m^{-2} of benthic production is required to maintain the present stocks. Both approaches estimate the annual export from the macrobenthic compartment on the shelf to be in the range of a few grams C m^{-2}.

Top Predators and Fisheries

Seabirds, seals and whales are the top predators in the Antarctic marine ecosystem (Laws 1977). Bird and seal communities are highly variable in different areas and seasons (Laws 1977; Ainley 1985). In general, tube-nosed birds (Procellariiformes) dominate the open waters, whereas penguins are most abundant in the marginal sea ice zone and in areas of closed pack ice (Plötz et al. 1991a). Evidently such a pattern will be disrupted in nearshore ecosystems around sub-Antarctic islands supporting huge penguin populations foraging in almost ice-free water. The same applies to seals. The terrestrial breeding of fur- and elephant seals will limit their pelagic distribution, whereas crabeater-, leopard- and Ross seals breed in oceanic pack ice areas and the Weddell seal prefers continental fast ice. Whales are temporary guests in Antarctic waters. Baleen whales for example migrate south during Austral summer and feed for a short period extensively on krill and squid

Table 5. Biomass and energy requirements for the top predators based upon data obtained during the EPOS expedition in the Scotia-Weddell Sea Confluence zone (Franeker 1989, 1992). Conversion factors: C = 0.1·wet mass, 1 gC = 41.8 kJ.

A. Biomass (mgC m^{-2})

Zone	Birds	Seals	Whales	All predators
Subantarctic	0.08	-	-	0.1
Scotial Sea	0.50	-	-	0.5
Confluence zone	0.97	-	30.7	31.7
Weddell Sea	1.18	-	2.9	4.1
Outer marginal ice zone	2.87	7.6	9.6	15.0
Inner marginal ice zone	5.57	14.1	29.4	49.1
Pack ice zone	4.48	34.6	16.6	55.7
Average	2.37	6.8	15.3	24.5

B. Energy requirements (mgC m^{-2} day^{-1})

Zone	Birds	Seals	Whales	All predators
Subantarctic	0.024	-	-	0.024
Scotial Sea	0.177	-	-	0.177
Confluence zone	0.514	-	1.134	1.648
Weddell Sea	0.273	-	0.151	0.424
Outer marginal ice zone	0.737	0.883	0.778	2.398
Inner marginal ice zone	1.199	1.316	1.376	3.891
Pack ice zone	0.969	3.254	0.775	4.998
Average	0.524	0.780	0.603	1.907

to build up fat reserves. A further complicating factor in assessing the role of top predators in the pelagic ecosystem is the limited knowledge on their diet. Diets vary with location and season and neither of these variables is sufficiently known to give adequate overall figures (see e.g., Croxall and Prince 1982).

Krill, *Euphausia superba*, seems to be the overall main food of the top predators around the islands in the north and in the seasonal pack ice zone of the East Wind Drift (Dodge and Croxall 1985; Croxall et al. 1985). Further south *E. superba* becomes sparse in many areas and is replaced by *E. crystallorophias* in the shallow coastal waters of the permanent pack ice zone (Hempel 1985). *E. crystallorophias* is the preferred food of the midwaterfish *Pleuragramma antarcticum* (Hubold 1985) and of the squid *Psychroteuthis glacialis* (Kear 1992), which are the main food items of Weddell seals (Plötz 1986; Plötz et al. 1991b) and of emperor penguins (Klages 1989).

The impact of top predators shows distinct spatial and seasonal differences as the ice cover has a major influence on distributions. However, the overall energy demand of the krill feeding penguins and seals will be more or less constant throughout the year. During winter this will be met mainly by the overwintering krill stocks residing directly under the ice cover, while during summer their metabolic demand is (partly) covered by krill production in the pelagic system. Overall biomass and consumption of top predators in the Scotia-Weddell Sea Confluence zone are estimated to 24.5 mgC m^{-2} and 1.79 mgC $m^{-2}day^{-1}$, respectively (Table 5).

Commercial krill fisheries were established in the early 1970s. Since 1984, fishing efforts have concentrated in the Atlantic sector and shifted from the area off Elephant Island, to the South Orkneys and more recently to South Georgian waters. The seasonal catch rates have been more or less constant in the last five years and amount to some 400,000 t per season (FAO), i.e. about 0.04 mgC $m^{-2}day^{-1}$ per total Weddell Sea. Also for squid there are commercial fishing activities. However, no catch rates were available to us up to now.

We hope that the data that are gradually becoming available on the dynamics of the various components of the Antarctic ecosystem will enable our partial models as well as different seasonal representations to be linked, such as to obtain a more integrated representation of that system.

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Flow Characteristics of Aquatic Ecosystems*

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Abstract

This contribution examines various flow measures based on analysis of 41 quantified models of trophic interactions in aquatic ecosystems. System productivity/biomass ratio is shown to relate to ecosystem maturity and to the degree of cycling in the systems. Distinct patterns or clusters are observed for different types of resource systems with respect to average path lengths and residence times. Examination of the average trophic transfer efficiencies shows efficiencies of 10-11% for herbivores/detritivores and first-order predators, and lower efficiencies for higher trophic levels. The overall average transfer efficiency is 9.2%, and thus confirms the often assumed value of approximately 10% for transfers from one trophic level to the next. An approach for estimation of the amount of primary productivity that is required to produce the biomass which directly or indirectly contributes to the fisheries catches is presented and applied to some of the systems.

Introduction

This paper presents some generalizations based on a selection of the models in this volume along with a number of published ECOPATH models as adopted for comparisons by Christensen (in press). A number of different measures are examined, notably measures discussed by previous authors, and as such, this paper somewhat resembles a collage. Our main intention, however, is to provide some material for comparisons for ecosystem modellers wishing to interpret model characteristics, and for this the present approach seems appropriate. We do not seek to give comprehensive descriptions of all attributes, as the present paper is intended to supplement the contributions of Christensen and Pauly (1992a, b), and Christensen (1992, in press), not to duplicate them.

Methods and Materials

A total of 41 models were used for comparisons in this paper (Table 1). The majority of these are presented in this volume, while a few have been adapted from previously published ECOPATH models (see Appendix 4). The selection of models, along with a few modifications, follow Christensen (in press). Brief descriptions of all models can be found in the same paper. A table giving a summary of the key data can be found in Christensen (1992) though some of the models were updated between that publication and the present.

Very few changes had to be made to the models to facilitate comparison. The models were standardized to using $g \cdot m^{-2}$ wet weight on an annual basis as standard unit, which nearly all also did beforehand. In addition, bacterial activity

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Table 1. Models used for analysis of flow patterns within ecosystems. The model number and filename are used for reference in subsequent tabulations (see also Appendix 4). Where no publication year is indicated under "Source" the reference is to publications included in this volume.

Type and system	Filename	Source
Ponds, lakes and rivers		
1. Mulberry Carp Pond, China	china	Ruddle and Christensen
2. Laguna de Bay, Philippines, 1968	bay68	De los Reyes
3. Laguna de Bay, Philippines, 1980	bay80	De los Reyes
4. Lake Kinneret, Israel	kinneret	Walline et al.
5. Lake Chad, Africa	chad	Palomares et al.
6. Lake Turkana, Kenya, 1973	turk73	Kolding
7. Lake Turkana, Kenya, 1987	turk87	Kolding
8. Lake Victoria, Africa, 1971-1972	victor71	Moreau et al.
9. Lake Victoria, Africa, 1985-1986	victor85	Moreau et al.
10. Lake Tanganyika, Africa, 1974-1976	tanga75	Moreau et al.
11. Lake Tanganyika, Africa, 1980-1983	tanga81	Moreau et al.
12. Lake Malawi, Africa	lmalawi	Degnbol
13. Lake Kariba, Africa	kariba	Machena et al.
14. Lake Ontario, North America	ontario	Halfon and Schito[a]
15. Lake Aydat, France,	aydat	Reyes-Marchant et al.
16. River Garonne, France	garonne	Palomares et al.
17. River Thames, England	thames	Mathews
Coastal areas		
18. Etang de Thau, France	thau	Palomares et al.
19. Tamiahua Lagoon, Gulf of Mexico	tamiahua	Abarca-Arenas and Valero-Pacheco
20. Coast, Western Gulf of Mexico	wgmexico	Arreguín-Sánchez et al.
21. Campeche Bank, Gulf of Mexico	campeche	Vega-Cendejas et al.
22. Shallow areas, South China Sea	thai10	Pauly and Christensen (1993)
23. Lingayen Gulf, Philippines	lingayen	Pauly and Christensen (1993)
24. Schlei Fjord, Germany	schlei	Christensen and Pauly (1992b)
25. Mandinga Lagoon, Mexico	mandinga	de la Cruz-Aguero
Coral reefs		
26. Bolinao reef flat, Philippines	bolinao	Aliño et al.
27. French Frigate Shoals, Hawaii	ffs	Polovina (1984)
28. Virgin Islands, Caribbean	virgin	Opitz
Shelves and seas		
29. Yucatan shelf, Gulf of Mexico	yucatan	Arreguín-Sánchez et al.
30. Gulf of Mexico continental shelf	gomexico	Browder
31. Northeastern Venezuela shelf	venezuel	Mendoza
32. Brunei Darussalam, South China Sea	brunei	Silvestre et al.
33. Kuala Terengganu, Malaysia	terengga	Christensen (1991)
34. Gulf of Thailand, 10-50 m	thai50	Pauly and Christensen (1993)
35. Shelf of Vietnam/China	vietnam	Pauly and Christensen (1993)
36. Deep shelf, South China Sea	deepscs	Pauly and Christensen (1993)
37. Peruvian upwelling system, 1950s	peru50	Jarre et al. (1991)
38. Peruvian upwelling system, 1960s	peru60	Jarre et al. (1991)
39. Peruvian upwelling system, 1970s	peru70	Jarre et al. (1991)
40. Monterey Bay, California	monterey	Olivieri et al.
41. Oceanic waters, South China Sea	oceanscs	Pauly and Christensen (1993)

[a] As modified by Christensen (in press).

was excluded from all models, as they dominated the flows of the five systems in which they were originally included.

The number of groups in the different models and their distribution by trophic level have not been standardized in the present comparisons as this was not necessary for the kind of analyses here (Christensen, in press).

Results and Discussion

System Primary Production/Respiration

Odum (1971) described how the ratio between total primary production and total system respiration (P_p/R) would develop as systems become more mature. For immature systems, he assumed that primary production would grossly exceed total respiration (e.g., for upwelling systems); he also suggested that the ratio would move toward unity as systems mature. For systems where remineralization is a dominant pathway, respiration was expected to exceed primary production, e.g., for systems receiving large amount of organic pollution. H.T. Odum summarized his description in graphical form, represented here as Fig. 1.

Based on the models given in Table 1, the primary production/respiration ratio can be quantified. However, we found that the estimates were not as nicely distributed around the 1:1 P_p:R line, as one might perhaps have expected (Fig. 2). For the majority of the models primary productivity exceeds respiration. This, however is not surprising as primary production is known to exceed respiration in both oceanic systems (Quiñones and Platt 1991) and coral reefs (Lewis 1981). Table 2 presents a comparison of the literature estimates reported by Lewis (1981) with the estimates from the present study; as might be seen, the two data sets display the same trend, with the bulk of the models having P_p/R ratios in the range from 0.8 to 3.2. However, some of the ECOPATH models show higher values and this warrants a closer examination.

The seven models with the highest P_p/R ratio (numbers 14, 26, 15, 2, 16, 40, 39) are the only ones for which the ratio between total export and the system throughput exceeds 0.3. This points to respiration as the culprit, i.e., to a parameter which, in ECOPATH models is estimated as the difference between consumption and the sum of production and egestion. Quantification of egestion (or of its converse, assimilation) is often quite uncertain; higher egestion leads to lower respiration and results in a higher production of detritus. As export from the detritus box in ECOPATH models is approximated as the difference between the flow into the detritus box and the flow out of the detritus box, an increased egestion will lead to increased export of detritus. Export of detritus is the only important export for practically all models. Therefore it is evident that the diverging P_p/R ratios are due to problems in model parametrization, specifically problems with quantification of assimilation rates and hence indirectly of respiration.

Adding to the problem of generally high P_p/R ratios is the omission of bacterial activity. Not all the detritus here assumed to be exported will indeed leave the system. Rather, a large fraction of the detritus will be reutilized by bacteria (which respire!) and thus again made available to the systems. Therefore omission of bacterial activity will lead to an underestimation of respiration (and of total throughput). One can thus conclude that ECOPATH-type models from which bacterial activity is excluded, can be expected to overestimate the P_p/R ratios.

System Productivity and Biomass

The ratio of system productivity over biomass (P/B) varies; developing systems tend to have a high P/B ratio, due to low biomasses and high productions, while developed systems tend to

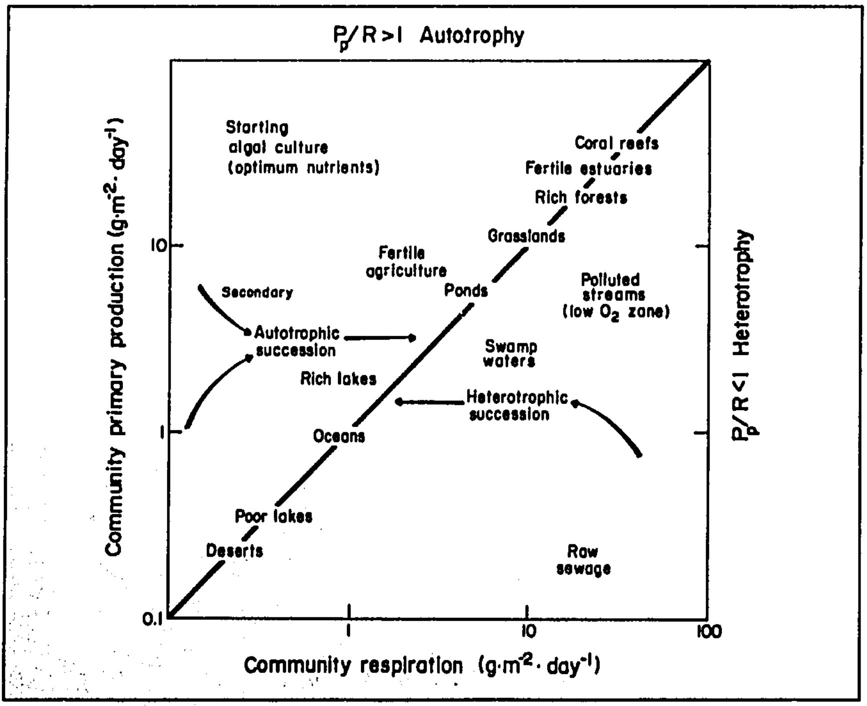

Fig. 1. Position of various community types in a classification based on community metabolism. Gross primary production (P) exceeds community respiration (R) on the left side of the diagonal line (P/R > 1 = autotrophy), while the reverse situation holds on the right (P/R < 1 = heterotrophy). The latter communities import organic matter or live on storage or accumulation. The direction of autotrophic and heterotrophic succession is shown by the arrows. Over a year's average, communities along the diagonal line tend to consume about what they make, and can be considered to be metabolic climaxes. (Redrawn from Odum 1971).

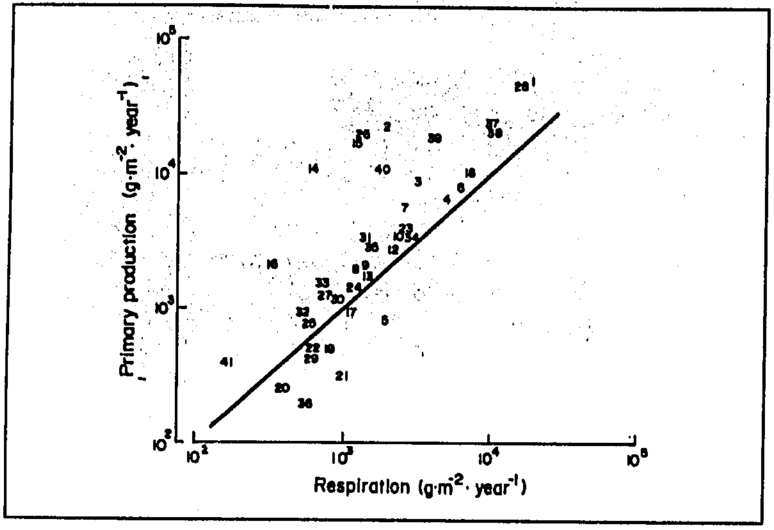

Fig. 2. Total primary production *vs* total respiration for the 41 models in Table 1, to which the numbers refer. The 1:1 line is indicated.

Table 2. Ratio between total primary production and population respiration as reported by Lewis (1981) and in the present study.

P_p/R	Number of systems within the range	
Range	In Lewis (1981)	In this study
<0.8	1	5
0.8-1.6	9	16
1.6-3.2	12	13
3.2-6.4	3	2
>6.4	0	5

have high biomasses and lower production rates, giving a lower P/B ratios. This relationship was discussed by Margalef (1968) who, working with marine phytoplankton, found that perturbations or fluctuations in the environment cause a shift toward a state resembling earlier phases of ecosystem development.

These findings are however in contrast to those of Baird et al. (1991) who could not identify any relationship between P/B and ascendency (with ascendency assumed to be a measure of maturity). Christensen (in press) found that the system P/B ratio was useful as one out of eight attributes for derivation of a maturity ranking. Following Christensen's (in press a) approach, a measure of ecosystem maturity was derived. To obtain some independence, the maturity ranking in the present analysis was, however, derived excluding the system P/B ratio as an attribute. The result is shown in Fig. 3; there is a strong correlation between the two measures; using Spearman's rank correlation gives a highly significant coefficient $r_s = -0.73$.

The maturity ranking was shown by Christensen (in press) to be strongly correlated with total system overheads, which are themselves complementary to relative ascendency. This means that there are no contradictions in the findings of the three studies discussed.

Pimm (1982) examined the relationship between total primary production and system biomass and found a positive correlation. The analysis of the 41 ecosystem models compared here shows a pattern similar to that found by Pimm (Fig. 4).

Connectance and System Omnivory Index

Connectance is a measure of the observed number of food links in a system relative to the number of possible links (Gardner and Ashby 1970). It has been assumed that there exists an optimum degree of connectance and that this optimum is dependent on the size of the system (Pimm 1982). Other findings suggested that the stability of linear systems decreases as the connectance increases (Martens 1987). Overall the interpretation of connectance is ambiguous.

The system omnivory index expresses the variance in the trophic levels of the consumers prey groups (Pauly et al., this vol.) and can be seen as an alternative to the connectance index. The two indices are here found not to be significantly correlated, and none of them are correlated with ecosystem maturity, as shown by the Spearman rank correlation coefficients, which are not significant.

Pimm (1982) showed that, as the number of groups in a system increases, connectance will decrease. For the present data set, regression analysis gives

$$C = \exp(-0.62 - 0.04 * N),$$

where C is the connectance and N the number of groups in the system. The regression is significant (0.1%), $r^2 = 0.25$. This supports Pimm's findings, but also illustrates that only a small proportion (1/4) of the variability of the connectance can be explained by the number of groups in the system.

Cycling

Cycling is assumed to increase as systems mature (Odum 1969), and can be quantified using Finn's cycling index (FCI, Finn 1976),

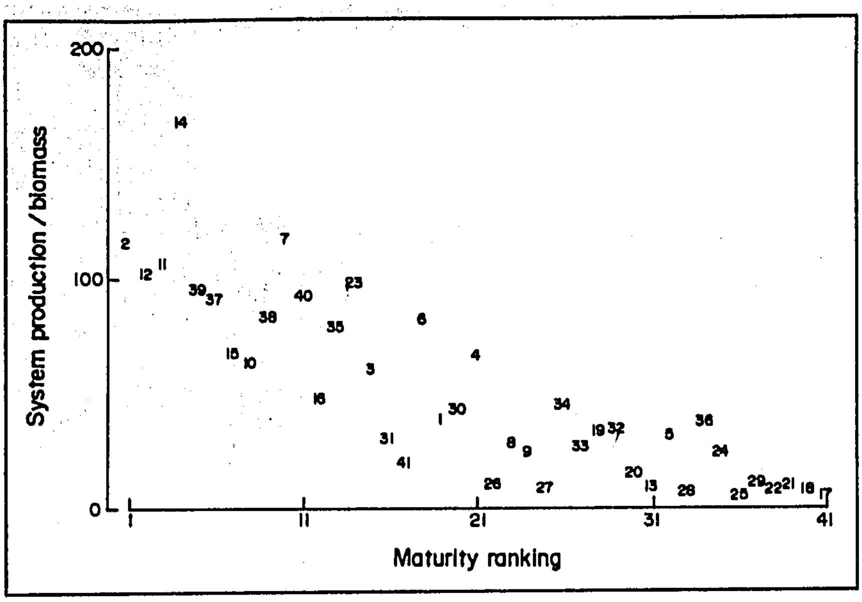

Fig. 3. Relationship between system production/biomass ratio and ranking after maturity *sensu* Odum. The ranking used here was derived without using production/ biomass as input.

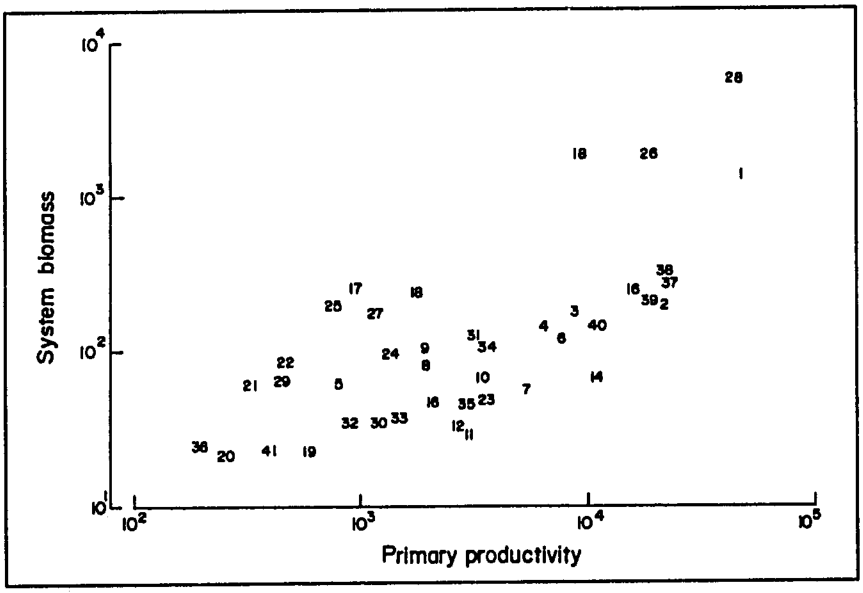

Fig. 4. System biomass as a function of the total primary production for 41 ecosystem models.

which expresses the percentage of the total throughput that is actually recycled. The FCI was not used by Christensen (in press) for quantification of maturity due to its perceived strong dependence on model specification, which makes intersystem comparisons difficult.

However, ranking the systems after both maturity and FCI leads to strong rank correlation ($r_s = 0.56$, $P < 0.1\%$). We conclude from the present analysis that FCI expresses something that is related to maturity.

Richey et al. (1978) compared four North American lakes with different degree of eutrophication in an effort to evaluate differences in cycling indices, which were found to vary between 0.03 and 0.66. While some of the factors regulating the system structure were apparent, no clear explanations for the varying degree of cycling could be found, suggesting that cycling in itself is not a clear descriptor of ecosystem development.

Wulff and Ulanowicz (1989) and Baird et al. (1991) were more conclusive: in comparisons of ecosystems these authors concluded that FCI was more likely to be an index of stress than of maturity. In both studies, however, it was

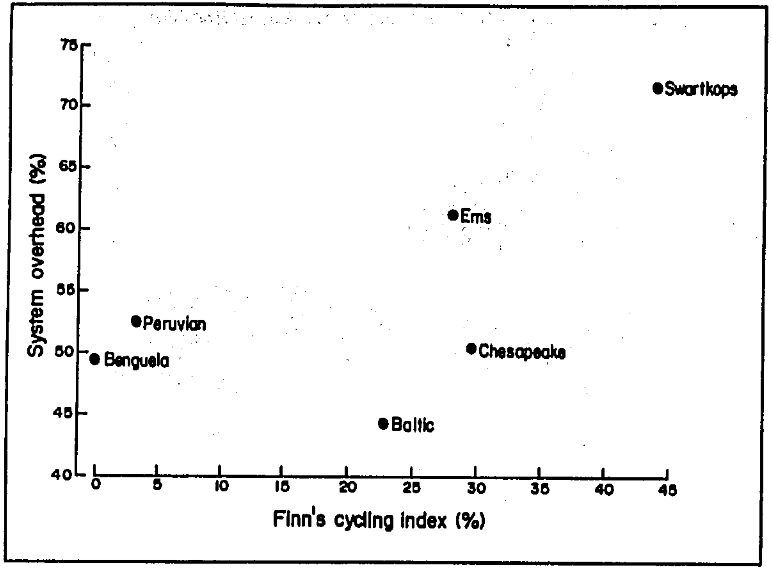

Fig. 5. System overheads (ecosystem stability) *vs* Finn's cycling index for the six ecosystems studied by Baird et al. (1991).

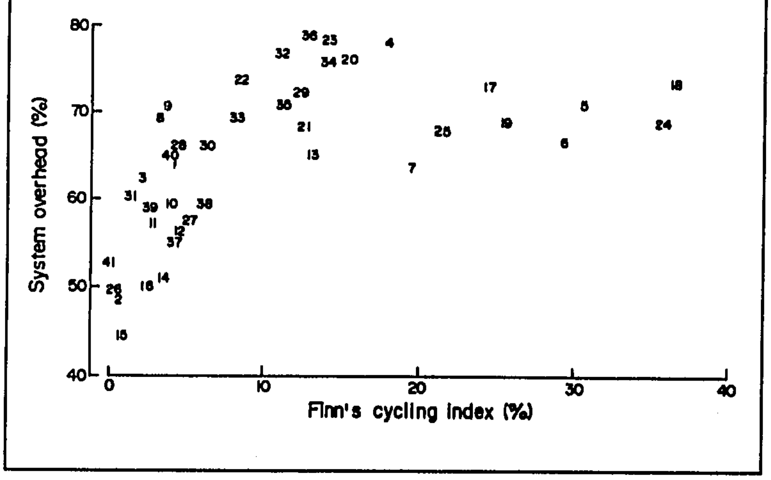

Fig. 6. System overhead (ecosystem stability) *vs* Finn's cycling index for the 41 ecosystems in Table 3.

assumed that relative ascendency was itself a measure of maturity, following Ulanowicz (1986).

In contrast, the present analysis suggests that FCI may be related to maturity *sensu* Odum. As maturity was shown by Christensen (1992) to be related to stability *sensu* Rutledge et al. (1976), i.e., to the system overhead (Ulanowicz 1986), one can assume that the FCI also should relate to system overhead.

To study this possibility further, we have first regressed system stability *sensu* Rutledge et al. (1976) against FCI for the six systems studied by Baird et al. (1991).

As can be seen from Fig. 5, this leads to inconclusive results even if the plot indicates that there may be a correlation between FCI and stability. The inconclusiveness is not unexpected, as only six ecosystems are included, not enough to override the variability of FCI estimates. Cycling is mainly a function of the degree of detritivory and zero-order cycles ("cannibalism") in a system, and both are difficult to quantify.

Studying a larger number of ecosystems can be of interest. Therefore Fig. 6 shows a similar plot for the 41 ecosystems analyzed in this study. There is some correlation between cycling index and system overhead (i.e., ecosystem stability *sensu* Rutledge et al. 1976). The relationship is perhaps parabolic, and suggests that system overheads (stability) decrease at high values of the cycling index. An interpretation may be that ecosystems with low cycling (e.g., upwelling systems) are highly dependent on energy rapidly passing through and as such rather unstable and vulnerable to changes in nutrient input (e.g., through El Niño events). On the other hand, systems with a very high cycling may be less stable because of the need to maintain an intricate pattern of internal flows. Values intermediate of these extremes may well be optimal from a stability point of view.

Cycling and System Overhead

It was demonstrated above that there is a correlation between cycling and system overheads (i.e., ecosystem stability). It is however not clear if this is due to a direct influence of cycling on the system overheads. To study this we have included a simulation based on the Schlei Fjord ecosystem model (Table 1, No. 24.)

First we removed all cycles from the model, and allocated consumption of detritus to phytoplanktivory. Then we gradually increased the diet component of detritus for zoobenthos from 0 to 60% (the FCI thereby increased from 0 to 22%), by increasing the diet component of detritus for zooplankton from 0 to 60% (the FCI increased from 22 to 26%), and finally increasing the diet component of detritus for both groups from 60 to 99% (the FCI then increased 26 to 31%). This led to the results shown in Fig. 7.

It is clear that there is a relationship between the degree of cycling and these measures. System overhead first increases with cycling, levels off, and finally decreases, to some

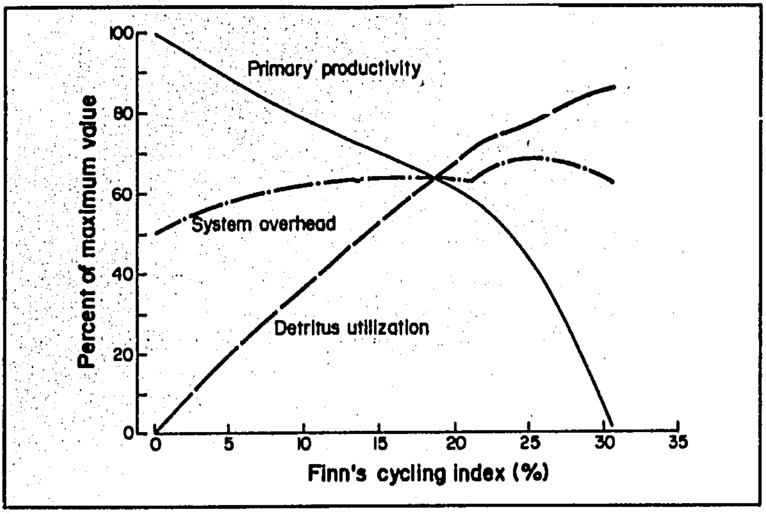

Fig. 7. Relationship among system overhead, primary productivity and detritus utilization, upon the degree of cycling (FCI, all values in %).

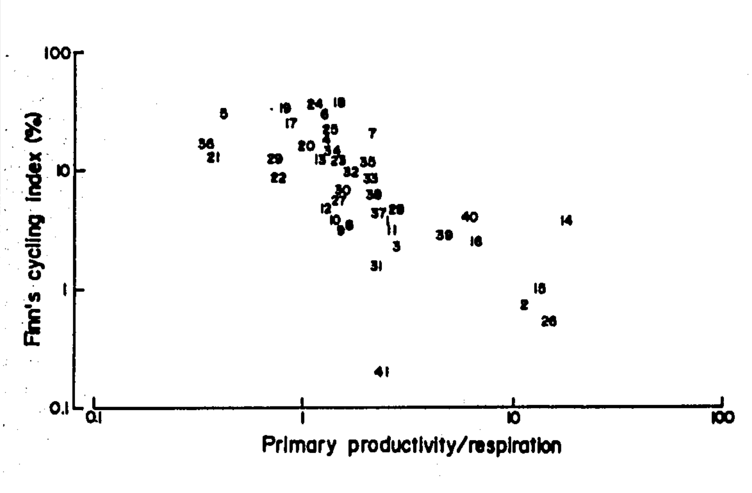

Fig. 8. Finn's cycling index *vs* primary productivity/respiration ratio for the 41 ecosystem models in Table 1.

extent as on Fig. 6. As primary productivity in trophic models depends on the food consumption of the primary consumers, primary productivity will gradually decline when these consumers shift towards detritivory.

The findings may at first seem alarming because of the lack of robustness that they seem to imply but it should be recognized that unrealistic parametrization is very likely to be detected by careful analysis of the model diagnostics. In the present simulation, primary productivity provides limits for how much cycling can be allowed to vary. It is our conclusion that the results mainly serve to increase our understanding of network indices behavior, and that they do not invalidate the previous findings. This is also supported by the previously reported result of a strong correlation between the path length and the straight-through path length (Christensen 1992 and see below).

Cycling, Primary Productivity and Respiration

It may be of interest to compare FCI with the primary productivity/respiration (P_p/R) ratio as, based on Eppley (1981), there is an inverse relationship between these indices. A close relationship between FCI and P_p/R does exist (see Fig. 8), and that the only outlier is the model of the oceanic part of the South China Sea (No. 41), a deep (4,000 m) ecosystem dominated by biomasses flow from the surface towards the bottom (sedimentation) with very little recycling.

Fig. 8 shows that groups with a high P_p/R ratio display a low degree of recycling, which is in line with the findings reported above: P_p/R moves toward unity and FCI increases as systems mature. Perhaps the main conclusion to be drawn here is that this indicates robustness and mutual consistency of Odum's (1969) attributes of maturity.

As another system descriptor, we have estimated the average path length for all 41 systems. The path length is defined as the average number of groups that a flow passes through and is calculated as the total throughput divided by the sum of the exports and the respiration (Finn 1980). It appears that average path length is strongly correlated with FCI (Fig. 9). The relationship between cycling rate and path length is not simply a causal relationship from cycling on path length. Christensen (1992) found a strong correlation between path length and straight-through path length for the same 41 models. As the straight-through path length is calculated without reference to cycling this means that the correlation between path length and cycling rate is due to other aspects of the models' structure.

Baird et al. (1991), who compared six ecosystems found that the upwelling systems they studied had short average path lengths; these were longer in the estuarine systems. Fig. 10 was assembled to allow comparisons of the 41 systems studied here.

The majority of the models in Fig. 10 have average path lengths between 2 and 3; 4 have

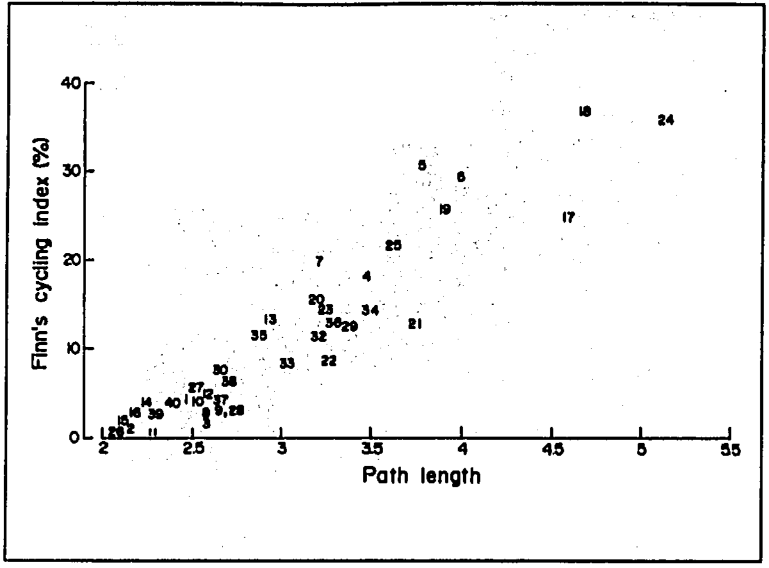

Fig. 9. Finn's cycling index *vs* average path length for the 41 ecosystem models in Table 1.

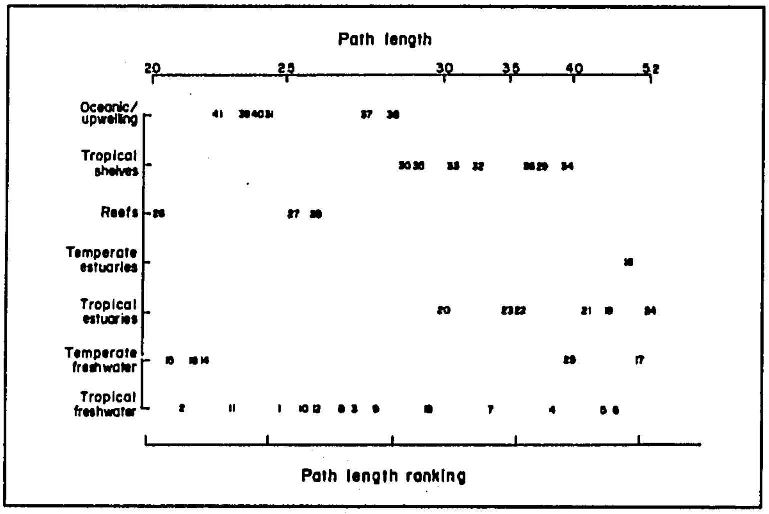

Fig. 10. Tropical and temperate ecosystems ranked after path length.

path lengths between 3 and 4 and only 4 models have path lengths that exceed 4. The estuaries and shelves have long path lengths, and the reefs and upwelling/oceanic systems have short path lengths, which is in agreement with the findings of Baird et al. (1991). The freshwater systems spread out over the scale probably because of "lumping" of ecosystems; the marine systems would do the same had they been pooled in one big "seawater group".

Maximum Chain Length and Trophic Levels

Schoener (1989) discussed the importance of maximum chain length i.e., the number of links in the longest food chain in a system, when one moves from primary producers or detritus to a top predator. Schoener found from a review of 75 aquatic food webs that only three webs included food chains longer than six steps.

Schoener's results are summarized in Fig. 11 (A-D); this figure also includes maximum chain lengths as calculated from ECOPATH II using the 41 models compared here (E-H). It is evident that the maximum chain lengths in the present study exceed those in Schoener's study.

The differences between the two studies can to some extent be explained by the inclusion of a number of very small systems in Schoener's study, e.g., small rockpools and springs. In contrast the present study includes larger ecosystems. Another reason may be related to how detailed the included diet compositions are in the models that are discussed. Schoener stated, "I see as probably the major problem with web description the decision to draw a link or not. Many species have broad ranges of prey types included in their diet but concentrate on only a few. At what percent occurrence should a prey no longer be counted as such?"

In the models included here, all preys that play a quantitative role (based on weight/volume, not on occurrence) are included. This to some extent reduces the implied degree of subjectivity, but also increases the maximum chain lengths. It is, however, likely that one more explanation must be added to explain the differences: many of the present models are made by biologists with interest in fish population dynamics, and the upper part of the trophic systems are therefore better described in the present models than in the rockpools and other microsystems in Schoener's study.

The maximum chain length is not always easy to find when the search for food webs is by trial-and-error. Fig. 12 shows the total number of pathways going from phytoplankton to all top predators for the 41 ecosystem models as a function of the number of groups in the systems.

One system shows remarkably many pathways, the Virgin Islands coral reef ecosystem, which includes 107,618 different pathways from the phytoplankton. This astronomical number illustrates that the more one studies diet compositions, the more detailed

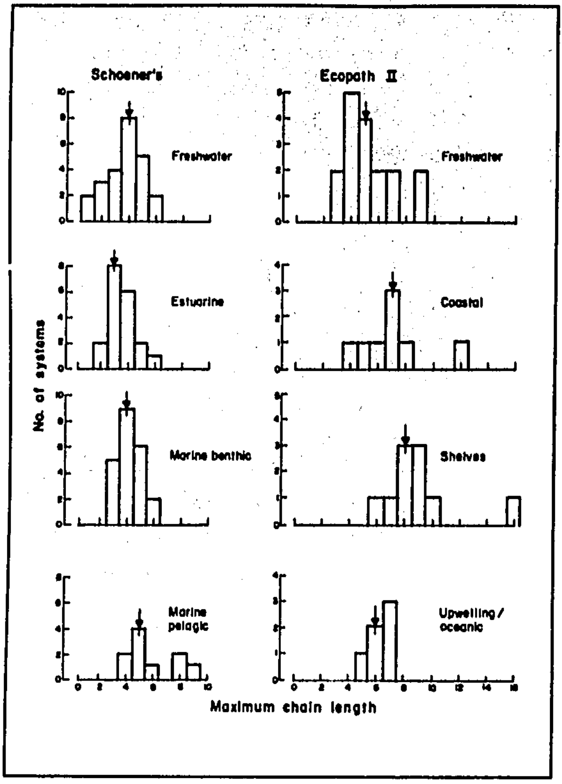

Fig. 11. Distribution of maximum chain length in aquatic systems. The models on the left are adapted from Schoener (1989), while those on the right are based on the 41 models in Table 1. The vertical arrows indicate the median chain length by resource system type.

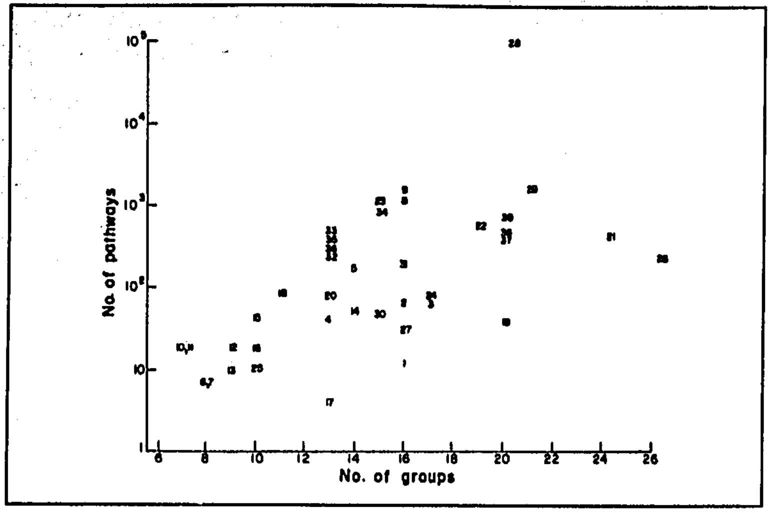

Fig. 12. Number of pathways from phytoplankton to all top predators as a function of number of groups included in description of 41 ecosystem models in Table 1.

they will become. For the Virgin Islands system the diet composition was originally based on a very detailed diet matrix with more than 200 different groups, subsequently aggregated to the present 20 box system (Opitz 1991, this vol.).

Given the preceding considerations, it can also be assumed that the more one studies diet compositions, the more trophic levels will appear. Not knowing how much effort the different authors have put into establishing their diet compositions, we have used an indirect approach to examine this relationship: we assume that the degree of effort is reflected in the number of groups in the model descriptions. This led to Fig. 13, where the number of trophic levels has been calculated so that only trophic levels with a throughput of at least 0.1 g·m^{-2}·year^{-1} are included.

It can be seen that there is a relationship, albeit a weak one, between the two measures. However, none of the systems has more than six trophic levels, which is much in line with Pimm (1982), who could not find systems with more than six trophic levels in the literature. On the other hand the present investigation produced considerably longer food chains than reported by either Schoener (1989) or Pimm (1982), and it is likely that this is best explained by the generally larger size of the ecosystems considered here, along with more detailed descriptions of food compositions.

The distribution of number of trophic levels for models belonging to different resource systems is presented in Fig. 14. The average number of trophic levels is lowest in the freshwater systems and increases from coastal systems over reefs to shelf systems, and declines for the upwelling systems. Nothing much is available for comparison with these findings, but Ryther (1969) found that food chains in upwelling areas are shorter than in open oceans systems. This trend is not found in the present study, where the number of trophic levels, and the maximum and average food chain lengths of the upwelling systems exceed those of the oceanic systems. This may well be explained by the more detailed description of trophic interactions in upwelling areas included here, compared to previous descriptions.

Pimm (1982) made several "predictions" for testing purposes. One of these was that "sites with high primary productivities should have more trophic levels than those with low productivities." Pimm reviewed the available cases and refuted the prediction. This is also the result of analysis of the 41 ecosystem models in this study. There are no indications at all of a correlation between productivity and the number of trophic levels in a system.

Residence Time

Overall residence time of particles or energy in the system can be estimated from the ratio of

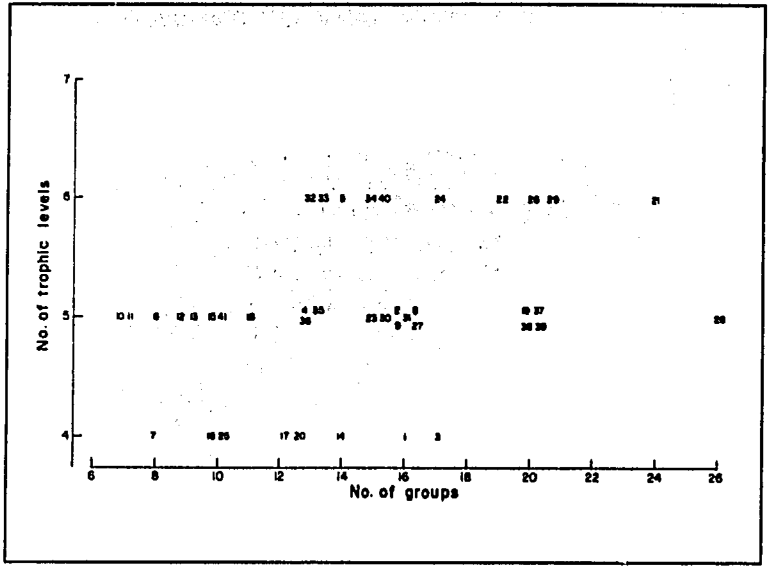

Fig. 13. Number of trophic levels as a function of number of groups in the model descriptions for the ecosystems included in this study.

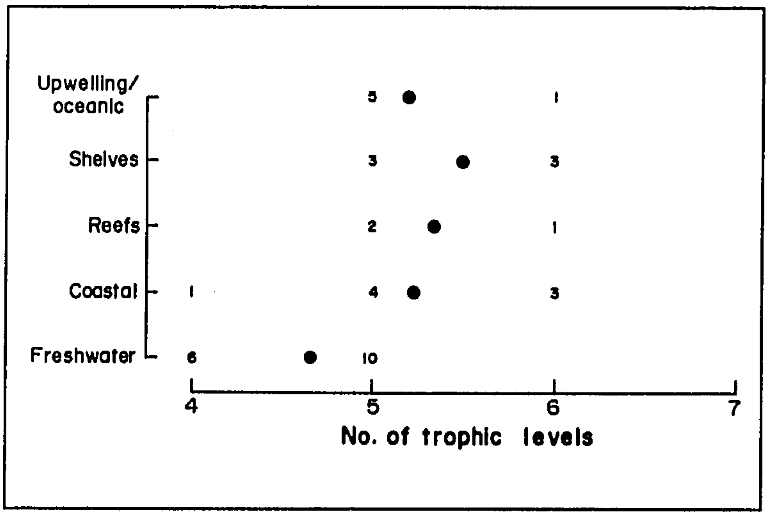

Fig. 14. Number of systems with a given number of trophic levels, by resource system type. The dots indicate means.

total system biomass to the sum of all respiratory flows and all exports (Herendeen 1989). It has been assumed that the residence time of particles on energy in a system increases to a maximum during succession as a result of increasing ecological organization (Cheslak and Lamarra 1981).

Overall residence time has been estimated for the 41 models compared here, and used for quantification of ecosystem maturity (Christensen, in press a). The residence times for the models (Fig. 15) vary from a few days to a quarter of a year.

To help in the search for patterns in residence times Fig. 15 also shows the ecosystems ranked after increasing residence time, and grouped in different resource types. This suggests that upwelling systems generally have a short residence time, while shelves generally show long residence times. The coral reefs also have long residence times, along with most of the estuarine systems, while the freshwater systems dominate the short residence time end of the ranking.

Trophic Transfer Efficiencies

Since Lindeman (1942), it has often been assumed that trophic transfer efficiencies in ecosystems vary around 10%, so that one-tenth of the energy that enters a trophic level is transferred to the next trophic level; and that the trophic transfer efficiencies gradually decrease on the higher trophic levels due to increased respiration (Lindeman 1942; Burns 1989).

Numerous approaches have been suggested for calculation of trophic transfer efficiencies. Originally, they were calculated as net energy intake less respiration relative to the net energy intake (Lindeman 1942, based on G.E. Hutchinson, unpubl.); alternatively they may be based on ratios such as total transfer to the next higher trophic level over total transfer from the previous lower trophic level.

In the present analysis a definition intermediate between the above two has been adopted: the ratio between the summed exports and predation, and the energy throughput (total consumption) on a given trophic level (Christensen and Pauly 1992b). Following this definition only the proportion of the production that is lost to the detritus is excluded from the calculation, and fishery or harvesting activities are treated as "predators" in the system. Efficiencies for the producers, trophic level 1, are not quantified in the present analysis, as all models are on a wet weight basis, and their (solar) energy input is therefore not quantified.

Using the trophic aggregation routine in ECOPATH II (Christensen and Pauly 1992a) the flows in a system can be distributed by trophic levels and the transfer efficiencies can be estimated. The approach follows one originally described by Ulanowicz (in press).

The trophic transfer efficiencies depend strongly on how the efficiencies of the groups in a system are described. High gross food

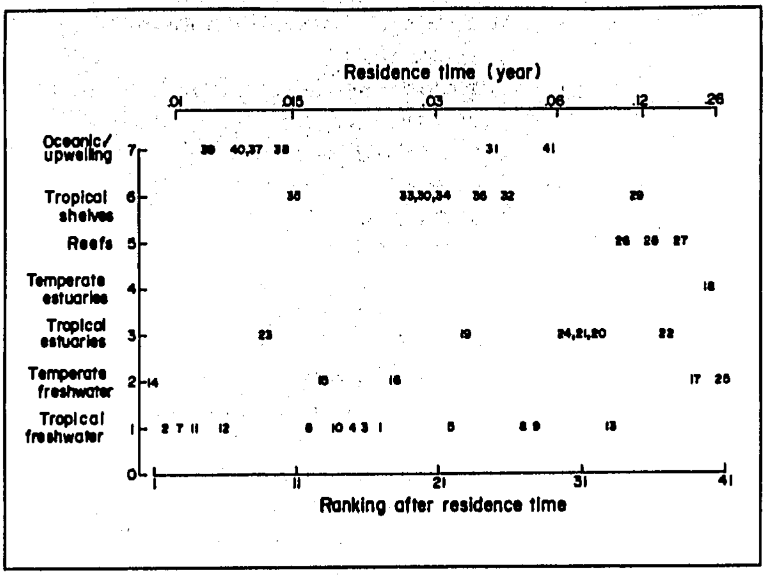

Fig. 15. Residence time for 41 ecosystem models ranked after increasing residence time. The distribution of each of the models on resource systems is indicated.

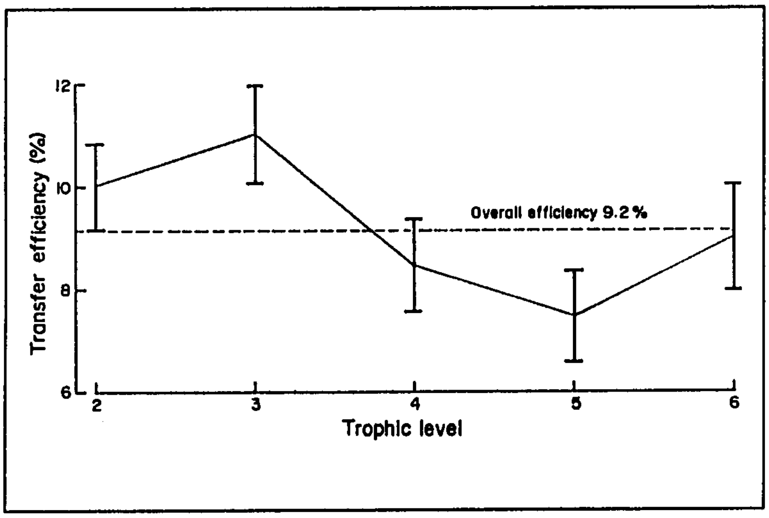

Fig. 16. Average trophic transfer efficiencies (%) by trophic level based on 37 of the models included in the analysis. The vertical bars are ± 1 standard error.

conversion efficiencies, GE, corresponding to high production/consumption ratios, lead to high efficiencies. The gross efficiencies for groups in different models are not standardized; one must therefore expect that the transfer efficiencies as they appear here will be highly variable. Also, the transfer efficiencies show no correlation at all with the degree of cycling in the systems.

The analyses were based on the majority of the ecosystems described earlier. Systems known to include fisheries but in which that element was not included (most often because of lacking catch data) were excluded from the analysis. The new findings are summarized in Table 3.

From Table 3, a high variability is apparent for the non-African freshwater systems. For the Chinese pond system, the efficiency on the herbivore/detritivore level is low (5%) as expected, and much higher on the two next levels. The low efficiency on level 2 is due to the inefficient grass carps ("manure-machines") feeding on low-quality food in the ponds. Lake Ontario shows a constant low efficiency of some 5%. Lake Aydat has a low efficiency at all levels, apart from on trophic level 4, where there is a peak. The two river systems show the same pattern, around 10% for the herbivores/detritivores, with rapidly declining efficiencies at level 3, and nothing at the higher levels. For the two models of Laguna de Bay the patterns are also similar: from level 2 to 3 the efficiencies tend to increase, and then to remain constant. It seems that the cultivation of phytoplanktivorous milkfish (*Chanos chanos*) resulted as might be expected, in increased efficiencies on the lower trophic levels.

The efficiency in Lake Victoria increased with the introduction of Nile perch, while the herbivore/detritivore efficiency in Lake Turkana decreased radically from 1973 to 1987.

The African lakes to some degree separate out in low and high efficiency systems, the former represented by Lake Tanganyika, Lake Victoria (post-Nile perch) and Lake Chad and the latter by Lake Kariba, Lake Turkana, Lake Malawi and Lake Victoria (pre-Nile perch). Most of the systems are characterized by rather high efficiencies at trophic level 2, and gradually declining efficiencies at the higher levels.

Most of the coastal systems, including lagoons, have rather similar efficiencies of the order of 10 to 15%. The efficiencies for Lingayen Gulf are far too high, probably indicating problems with model parametrization.

The overall efficiencies for the three coral reef models are seen to vary more between than within systems. The transfers are most effective in the Bolinao model, which is the only one that incorporates exploitation of the resources. Noting that the exploitation rate is very high in this system, it seems reasonable that the derived efficiencies should be in the range 9 to 13%. The

Table 3. Trophic transfer efficiencies (%) for a number of ecosystem models. Only trophic levels with a throughput of at least 0.01 g m^{-2} year^{-1} and quantified fisheries catches are included.

Trophic level	System								
	1 Pond China	2 Laguna 1968	3 Laguna 1980	4 Kinneret Israel	5 Chad Africa	6 Turkana 1973	7 Turkana 1987	8 Victoria 1971-72	9 Victoria 1985-86
2	5.3	9.8	5.6	19.6	8.8	8.7	4.4	16.0	15.9
3	12.4	23.1	19.4	8.4	12.6	1.6	5.4	12.3	18.6
4	13.9	16.7	18.2	3.8	11.5	2.6	0.8	7.0	10.5
5	-	16.9	-	3.2	9.8	0.8	-	5.4	10.8
6	-	-	-	-	8.5	-	-	-	-

Trophic level	10 Tanganyi. 1974-76	11 Tanganyi. 1980-83	12 Malaŵi	13 Kariba	14 Ontario N.America	15 Aydat France	16 Garonne France	17 Thames England	18 Thau France	20 Coast Mexico
2	18.3	13.8	16.9	5.4	4.7	6.6	10.1	8.3	5.3	17.5
3	8.6	11.5	2.5	6.5	5.6	2.9	5.3	1.4	13.9	18.6
4	10.1	11.0	1.6	2.0	4.2	14.1	0.2	0.0	17.3	12.9
5	11.2	11.3	0.0	2.2	-	5.6	-	-	16.4	10.0
6	-	-	-	-	-	-	-	-	-	8.0

Trophic level	21 Campeche Mexico	22 Coast SCS	23 Lingayen Phil.	24 Schlei Germany	26 Bolinao Phil.	27 FFS Hawaii	28 Virgin Island	29 Yucatan Mexico	30 G.o. Mexico	31 Venezuela
2	18.4	6.3	9.4	4.9	9.1	10.1	15.7	15.7	7.6	10.5
3	16.8	3.6	10.9	10.3	11.9	4.0	9.5	19.7	15.1	9.1
4	13.6	14.6	24.0	8.2	10.3	4.1	6.2	17.6	8.1	4.1
5	12.2	15.8	26.8	-	10.8	3.3	6.1	15.4	4.9	6.0
6	11.7	-	29.6	-	-	-	7.7	8.3	-	-

Trophic level	32 Brunei D.	33 Malaysia	34 G.o. Thailand	35 Vietnam	36 Deep SCS	37 Peru 1950s	38 Peru 1960s	39 Peru 1970s	41 Ocean SCS
2	15.9	22.7	7.2	3.5	10.8	2.6	2.9	9.3	9.2
3	18.7	17.8	15.5	11.7	12.4	9.8	10.6	15.1	12.1
4	12.2	14.0	9.7	10.3	9.0	1.8	1.9	7.0	8.0
5	6.6	16.2	10.8	7.5	9.0	1.0	0.1	2.4	7.2
6	3.5	17.5	13.6	-	-	-	-	-	-

two unexploited reef systems show highest efficiencies for the herbivores/detritivores, and lower on the higher trophic levels.

For the tropical shelf areas some of the models from Southeast Asia show high transfer efficiency. This is partly due to high exploitation rates, but it may also be caused by similarities in model construction; this is most apparent for the Malaysian model, whose parameter values were used in a number of the other models from the region, including the Lingayen model mentioned earlier to have excessively high efficiencies.

The transfer efficiencies for the upwelling systems and the oceanic system in Table 3 suggest a pattern of low herbivore transfer efficiencies, higher efficiencies on trophic level 3 and lower efficiencies on the higher levels. It is noteworthy that the transfer efficiencies of the Peruvian system increased from the 1950s, over the 1960s, to the 1970s. This increase may be due to the collapse of the anchoveta (*Engraulis ringens*) and the high exploitation rate (see Jarre-Teichmann 1992 for further discussion).

The two offshore South China Sea models show the same patterns, but as expected the efficiencies are higher in the model covering the more shallow part (Deep SCS). The match between the trends is not likely to be caused primarily by similarities in the model descriptions, but more likely reflects the actual situation.

Based on the system and trophic level specific transfer efficiencies the average transfer efficiencies for the different systems can be estimated (as geometric mean, weighted after flow). As expected the African lakes fall in two groups: high and low efficiency systems, with average efficiencies of 10-15% and of 2-8%

respectively. The distribution of systems on these groups is as discussed above.

The three temperate systems, rivers and fjords have rather low average efficiencies, from 3 to 7%, while the single temperate lagoon has an average efficiency within the range of the tropical lagoons and coastal systems, i.e., between 10 and 14%. Two coastal areas/shelves, Lingayen Gulf, and Kuala Terengganu, Malaysia, both have very (unrealistic) high efficiencies, 17-18%, probably because of similarities in the model descriptions. These systems are not used in the later generalizations.

The coral reef systems have average efficiencies in the range of 5-10%, while the models for the deeper tropical shelf areas generally have average efficiencies of 5 to 10%, only the deeper part of the Gulf of Thailand has a higher efficiency (12%).

The deeper part of the South China Sea and especially the Peruvian upwelling models are also to be found below the 10% efficiency line.

It is difficult to present conclusions regarding overall trends for ecosystems based on the very variable observed efficiencies. One overall system level property can however be estimated: the overall average transfer efficiencies by trophic level based on the 36 models that are discussed here. Fig. 16 shows an average efficiency of 10% for the herbivores/detritivores, 11% for the next trophic level and lower efficiencies (7.5-9.0%) on the higher trophic levels. The grand mean transfer efficiency for all trophic levels in all systems is 9.2%, so Lindeman was not far off.

It can be concluded that the trophic transfer efficiencies are variable, because of both system- and model-specific characteristics. Generally, the trophic efficiencies at lower levels (2, 3) tend to be higher than at higher levels (4-6). In addition, the grand mean trophic transfer efficiency is found to be very close to the often assumed, but rarely estimated, general rule of 10% per step up the trophic ladder.

Primary Production Required for the Fisheries

For terrestrial systems, it has been shown by Vitousek et al. (1986) that nearly 40% of the potential terrestrial net primary productivity is used directly or indirectly by human activities. Similar estimates for aquatic systems are not available though a rough estimate was presented in the same publication. The figure given was 2%, i.e., much lower than the estimate for the terrestrial systems. It was based on the assumptions that the "average fish" feeds two trophic levels above the primary producers; and that the average food conversion efficiency is 10% at each trophic level.

The crudeness of the approach for the aquatic systems is due to lack of information especially on the trophic positions of the various organisms harvested by humans. Models of trophic interactions may, however, help to alleviate the situation, and we suggest here an alternative approach based on network analysis, for quantification of the primary productivity needed to sustain harvest by humans.

This approach is based on quantified descriptions of trophic flows in ecosystem networks. First, all cycles are removed from the diet compositions, and all paths in the flow network are identified using the method suggested by Ulanowicz (in press). For each path the flows are then raised to primary production equivalents using the product of the catch, the consumption/production ratio of each path element times the proportion the next element of the path contributes to the diet of the given path element. For instance for a path,

$$\text{Primary producer} \xrightarrow{100} \text{Herbivore} \xrightarrow{12} \text{Carnivore} \xrightarrow{1.2} \text{Fishery},$$

the primary production equivalents corresponding to the catch of 1.2 units are: $1.2 \cdot [(12/1.2) \cdot 1] \cdot [(100/12) \cdot 1] = 100$, as expected for this simple straight food chain.

This approach (which will be implemented in future releases of ECOPATH II) was applied to some of the ecosystems analyzed in this volume, and the results follow.

For the Peruvian upwelling ecosystem, the harvest in the 1950s required 2% of the available primary productivity (PP). In the 1960s, the fishery expanded drastically (14 times) while the primary productivity requirements (PPR) increased to 5%. The relatively small increase in PPR is mainly caused by the increased catch being predominantly anchoveta which is phytoplantivorous, and thus require comparatively less PP than organisms on higher trophic levels. The model estimate for the model for the Peruvian system in the 1970s pointing to this model being parametrized with an unrealistically low production/biomass estimate for bonito (0.03 year^{-1}). This indicates that the present analysis may be used as a sensitive tool for model diagnosis.

For the Laguna de Bay models, total PPR increased slightly from the late 1960s to the early 1980s (from 892 to 941 t ww km^{-2} year^{-1}). Total PP, however, decreased considerably due to the milkfish's consumption of phytoplankton resulting in an increase in utilization of PP from 4 to 11%.

In Lake Victoria, the proliferation of Nile perch resulted in a threefold increase in PPR, to sustain the catches, from some 242 t ww km^{-2} year^{-1} in the model from the early 1970s to 742 t ww km^{-2} year^{-1} in the model for the mid-1980s.

For many of the coastal tropical ecosystems the PPR is of the order of a few percentage of the total PP, e.g., for the Brunei, Bolinao and Vietnam models and for the shallow part of the Gulf of Thailand ecosystem. Interestingly, the PPR is higher for the offshore part of the South China Sea (up to as high as 32% for the deep South China Sea models). The catches in the offshore regions are mainly of large pelagics high in the food web, and thus indirectly requiring a large fraction of primary productivity.

The method we are proposing here for study of PPR to sustain catches to some extent parallels a methodology and a concept for valuation of flows in an ecosystem: emergy, short for **em**bodied en**ergy**, developed by Odum (1988). Using the emergy concept, it is possible to assign a value to all transfers and for instance compare how export and import of natural resources from a country compare. The basic principle is that using flow specific transfer coefficients all flows are given in a common currency expressing how much energy was used to generate the flows. The currency in the applications we know of has been solar energy equivalents, see e.g., Brown et al. (1988), and Brown and McClanahan (1992).

The present cursory treatment only gives a first rough introduction to what can be achieved from studies of that part of primary productivity that is used by humans. We anticipate that further studies will be of use for strategic considerations related to our global use of ecological resources.

Conclusion

The present analyses have shown that it is possible, based on quantified ecosystem models, to estimate characteristics of flow patterns in aquatic ecosystems. We hope that this preliminary study will encourage new studies aimed at further refining the analyses, and placing these in a context where the information can be utilized in a management context. Most notably the question of how ecosystems are best utilized needs proper attention. For this, estimation of ecosystem flow patterns is of prime concern.

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Appendix 1

Proximate Analysis of Selected Organisms Important for Constructing Trophic Models of Ecosystems[a]

Construction of trophic ecosystem models requires the use of a common "currency," often organic carbon or energy (i.e., cal or j).

Except for a few cases where the same research group has estimated all important flows and biomasses in a system, this standardization requires conversion of disparate measures into that common currency, e.g., from wet weights to energy contents.

A few documents exist which present conversion factors that can be used for this, notably Jϕrgensen et al. (1991); however, most of the relevant literature is widely scattered.

Pending the release and dissemination of the new version (3.0) of ECOPATH II, which will contain a large number of appropriate empirical ecological relationships, a number of constants and conversion factors is presented below to assist would-be modellers in standardizing required outputs.

To assure conformity with the "Système International," all measures of energy formally expressed in calories (cal) or kilocalories (1 kcal = 1,000 cal) were converted to Joules (1 cal = 4.19 J; 1 J = 0.239 cal). The original sources should be consulted for details.

Group	Species	n	J/mgDW	J/mgAFDW	J/mgWW	Water %	Ash %	Other information	Source
Algae	*Dilylus brightwelli*		7.84	17.50			55.24		E
	Hymenosonas elongata							13.1µm diam.; C = 585.7µg/ind.; N = 60.0µg/ind.	D
	Phaedactylus tricomutus							14.09µm diam.; C = 18.52%DW; N = 3.04%DW	D
	various species (see ref.)								C
Protozoans	*Tetrahymena pyriformis*			24.86					K
Porifera		8 spp.	6.10						B
Hydrozoans	*Chlorohydra viridissima*			23.99					K
	Hydra littoralis			25.26					K
Anthozoans	*Duva multiflora*	2	12.88		2.07	83.0			C
Polychaetes	*Aphrodita hastata*	3	14.39		2.03				C
	Axiothella sp.	2	14.86		2.32	84.0			C
	Luabrinereis fragilis	3	28.34		4.43	78.0			C
	Nepthys ciliata	3	17.00		3.13	61.0			C
	Niochamache sp.	1	14.91		2.59	83.0			C
	Pectinaria hypoborea	3	13.57		2.61	81.0			C
	Pherusa plumosa	3	11.14		1.94	82.0			C
	Phascolion stroabl	2	14.19		2.49	82.0			C
	Stemaspis fossor	3	8.91		2.25	75.0			C
	various species	43 spp.	18.79						B
		27 spp.		23.33					B
Oligochaetes	various species	5 spp.	22.36						B
Starfishes	*Asterias vulgaris*	3	10.68		2.65	75.0			C
	Ctenodiscus crispatus		7.65		2.55	67.0			C
Cumaceans	*Diastylis rathkei*			16.90				3.54-4.9 mm	J
				18.70				1.0-7.5 mm	J
				19.00				6.5-7.5 mm	J
				16.40				6.5-7.5, -eggs	J
Euphausids	*Euphausia superba*		19.76		3.73	81.0	21.00	20-50 mm, 0.41 g; lipid = 7.4%DW; protein = 69%DW	M

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[a] Compiled by V. Sambilay, Jr., International Center for Living Aquatic Resources Management, MCPO Box 2631, 0718 Makati, Metro Manila, Philippines.

Group	Species	n	J/mgDW	J/mgAFDW	J/mgWW	Water %	Ash %	Other information	Source
Ascidians	various species	11 spp.	7.13						B
		11 spp.		19.66					B
Hyperiids				2.51					M
Salps				0.17					M
Copepods	*Acartia tonsa*		17.91	22.39			19.96	DW = 10.86%WW	E
	Calanus helgolandicus			22.61					K
	Cyclops vernalis	3	23.82	24.36			2.30		C
	Mesocyclops edax			22.94					C
	Trigriopus californicus			23.09					K
Amphipods	*Anisogammarus pugettensis*		12.54		2.48			DW = 19.6%WW	L
	Crangonyx richmondensis	4	18.27	22.12			26.40		C
	Gammarus duebeni	5	18.47	21.50		74.0	26.00		C
	Gammarus minus	6		22.50					C
Isopods	*Asellus brevicaudus*	2		18.11					C
	Sphaeroma rugicauda	7	12.58	19.06		75.0	56.00		C
Decapods (Crabs)	*Uca pugilator*	2	8.69						C
	Uca pugnax	2	10.53						C
(Shrimps)	*Artemia* sp. (*nauplii*)			28.21					K
	Metapenaeus monoceros		22.00						N
		69				75.8			O
	Palaemon debilis	24	17.90				24.50	DW = 24.1%WW; lipid = 2.9%DW	F
	Palaemon elegans	26	18.60				22.00	DW = 25.3%WW lipid = 3.6%DW	F
		6	16.83	20.08		71.0	17.00		C
	Pandalus hypsinotus		21.36		4.98			DW = 23.3%WW	L
	Pandalus platyceros		20.59		5.02			DW = 24.4%WW	L
	various crustaceans	53 spp.	15.31						B
		46 spp.		22.74					B
Sea cucumbers	*Chirodota laevis*	2	10.76		1.11	90.0			C
	Cucumaria frondosa	3	12.87		0.94	93.0			C
	Malpadia oolitica	3	7.05		0.74	90.0			C
Sea urchins	*Strongylocentrotus drombachiensis*	3	3.70		1.20	68.0			C
	various species	25 spp.	9.48						B
		20 spp.		22.74					B
Ctenophores	various species				0.17				M
Squids	*Dosidicus gigas*	2	23.73	24.88	4.22	82.2	4.60	beaks removed	I
	Loligo opalescens	4				78.8		lipid = 19.1%DW or 4.4%WW; TL = 160 mm, 53.2 g	H
	Symplectoteuthis ovalaniensis	3	21.86	23.64	5.59	74.5	7.50	beaks removed	I
Gastropods	*Natica clausa*	2	18.39		3.31	82.0			C
	Thais lamellosa	4		24.47			8.00		C
	Thais lapillus	2	19.24		1.85	82.0			C
	various species	59 spp.	18.24					shells removed	B
		57 spp.		23.27					B
Pelecypods	*Ensis minor*			14.65					C
	Clinocardium ciliatum	3	18.64		1.57	92.0			C
	Modiolus sp.	3	19.26						C
	Scobicularis plana	60		21.34			12.20		C
	Yoldia sapotilla	3	20.01		2.88				C
	Yoldia thraciaeformis	3	20.03		2.13	89.0			C
Bivalves	various species	43 spp.	18.85					shells removed	B
Opisthobranchs	*Scaphander punctostriatus*	3	13.97		1.75	90.0			C
Nudibranchs	*Acanthodoris rhodoceras*	4		22.77			41.00		C
	Aegires albopunctatus	3		22.23			43.00		C
	Aglaja diomedea	7		23.26			27.00		C
	Bulla gouldiana	5		26.60			25.00		C
	Dendrodoris albopunctata	4		21.60			41.00		C
	Dirona picta	4		27.95			41.00		C
	Flabellina iodinea	7		20.70			30.00		C
	Haminea virescens	6		22.34			27.00		C
	Hermissenda crassicornis	9		26.99			28.00		C
	Hopkinsia rosacea	7		25.15					C
	Navanax inermis	11		25.09			36.00		C
		4	3.86						C
	Polycera atra	8		23.78			28.00		C
	Triopha maculata	19		23.62			27.00		C
Mysids	various species				3.77				M
Fishes	*Raja orinaca*			23.45					C
	Brevoortia tyrannus		26.12	29.32			10.94	DW = 33.4%WW	E

Continued

Group	Species	n	J/mgDW	J/mgAFDW	J/mgWW	Water %	Ash %	Other information	Source
	Clupea harengus	1	26.63		8.07				C
	Clupea harengus pallasi		25.90		8.34			DW = 32.2%WW	L
	Stolephorus purpureus	4				76.2		lipid = 18.0%DW or 4.3%WW; FL = 40 mm, 0.4 g	H
	Hypomesus pretiosus	4				76.2		lipid = 23.6%DW or 5.5%WW; FL = 126.0 mm, 17.8 g	H
	Vinciguerria lucetia	3	22.12	24.35	5.15	76.1	11.60		I
	Exocoetus volitans	6	19.72	23.33	5.35	73.8	15.50		I
	Oxyporhamphus micropterus	6	19.96	23.21	5.54	72.2	14.00		I
	Epinephalus aeneus					77.8		% fat = 0.57; TL = 30-80 cm	G
	Remora remora	2	19.93	24.18	5.27	73.6	17.60		I
	Coryphaena equisalis	2	22.27	23.81	4.81	72.9	6.40	bones removed	I
	Lethrinus nebulosus							% fat = 2.6; % protein = 22.4	A
	Tautogolabrus adspersus	1	20.43						C
	Auxis thazard	2	22.48	24.03	4.63	70.6	6.50	bones removed	I
	Euthynnus lineatus	2	21.97	23.30	4.27	72.4	6.10	bones removed	I
	Scomber japonicus	7				73.7		lipid = 30.7%DW or 8.1%WW; FL = 188 mm, 62.9 g	H
	Cubiceps panciradiatus	7	19.92	22.67	4.80	75.8	11.65		I
	Canthidermis maculatus	2	23.68	25.11	3.84	74.8	5.70	bones removed	I
	Lactoria diaphanus	2	20.74	24.26	5.28	74.6	14.50		I

A = Aldonov and Druzhinin (1978).
B = Brey et al. (1988).
C = Cummins and Wuycheck (1971).
D = Debs (1984).
E = Durbin and Durbin (1981).
F = Fonds et al. (1981).
G = Mikhail et al. (1982).
H = Olson and Boggs (1986).
I = Peterson (1979).
J = Rachor et al. (1982).
K = Slobodkin and Richman (1961).
L = Smith et al. (1986).
M = Tarverdiyeva (1972).
N = Ramadhas and Sumit-Vijayaraghavan (1979).
O = Royan et al. (1977).

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Appendix 4

Datafile Description[a]

The ECOPATH II files used to generate the models presented in this book, plus a few more models (see below) are available from ICLARM in the form of one 3½" diskette, for US$10.00 to cover material and shipping costs.[b]

The MSDOS files listed below,[c] are provided—as suggested by Pauly (1993) and with the consent of all contributors to this book—to enable colleagues to replicate the results presented here, and to go beyond them. We look forward to interacting with colleagues who have extracted more from these files than we have been able to so far.

	Type and system	Filename	Filesize (KB)	Source
	Ponds, lakes and rivers			
1.	Lake Ontario food web	ontario	1.8	Halfon and Schito (this vol.); Christensen (in press)
2.	Mulberry carp pond, China	china	1.9	Ruddle and Christensen (this vol.)
3.	Ricefield nitrogen model, without fish	rice	1.1	Lightfoot et al. (this vol.)
4.	Ricefield nitrogen model, with fish	ricefish	1.4	Lightfoot et al. (this vol.)
5.	Napier grass-fed pond, Malaŵi	malawi	1.1	Van Dam et al. (this vol.)
6.	Laguna de Bay, Philippines, 1968	bay68	1.9	delos Reyes (this vol.)
7.	Laguna de Bay, Philippines, 1980	bay80	2.1	delos Reyes (this vol.)
8.	Lake Veli, India	veli	1.5	Aravindan (this vol.)
9.	Lake Aydat, France (original model)	aydat	1.2	Reyes-Marchant et al. (this vol.);
10.	Lake Aydat, France (revised model)	aydat2	1.3	Reyes-Marchant (1993)
11.	Lake Kinneret, Israel	kinneret	1.5	Walline et. al (this vol.)
12.	Lake Malaŵi, Africa	lmalawi	0.9	Degnbol (this vol.)
13.	Lake Turkana, Kenya, 1973	turk73	0.8	Kolding (this vol.)
14.	Lake Turkana, Kenya, 1987	turk87	0.8	Kolding (this vol.)
15.	Lake George, Uganda	george	1.6	Moreau et al. (this vol.)
16.	Lake Kariba, Zimbabwe	kariba	1.0	Machena et al. (this vol.)
17.	Lake Tanganyika, Africa, 1974-76	tanga75	0.7	Moreau et al. (this vol.)
18.	Lake Tanganyika, Africa, 1980-83	tanga81	0.7	Moreau et al. (this vol.)
19.	Lake Victoria, Africa, 1971-72	victor 71	2.1	Moreau et al. (this vol.)
20.	Lake Victoria, Africa, 1985-86	victor85	2.1	Moreau et al. (this vol.)
21.	Lake Chad, Africa	chad	1.8	Palomares et al. (this vol.)
22.	River Thames, England	thames	1.4	Mathews (this vol.)
23.	River Garonne, France	garonne	1.0	Palomares et al. (this vol.)
	Coastal areas			
24.	Tamiahua Lagoon, Gulf of Mexico	tamiahua	1.5	Abarca-Arenas and Valero-Pacheco (this vol.)
25.	Celestun Lagoon, Mexico	celestun	1.2	Chavez et al. (this vol.)
26.	Mandinga Lagoon, Mexico	mandinga	2.5	de la Cruz-Aguero (this vol.)
27.	Coast, Western Gulf of Mexico	wgmexico	3.8	Arreguín-Sánchez et al. (this vol.)
28.	Campeche Bank, Gulf of Mexico	campeche	2.6	Vega-Cendejas et al. (this vol.)
29.	Maputo Bay, Mozambique	maputo	1.0	Paula e Silva et al. (this vol.)
30.	Etang de Thau, France	thau	1.2	Palomares et al. (this vol.)
31.	Shallow areas, South China Sea	thai10	1.8	Pauly and Christensen (1993)
32.	Lingayen Gulf, Philippines	lingayen	2.1	Pauly and Christensen (1993)
33.	Schlei Fjord, Germany	schlei	1.1	Christensen and Pauly (1992)

Continued

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[b] Payment (payable to ICLARM) should be in US$ by international money order, bankdraft or UNESCO coupons. We can accept US$ checks only if from a US-based bank due to high clearance fees of other banks.

[c] All datafiles have the extension ".EII".

	Type and system	Filename	Filesize (KB)	Source
	Coral reefs			
34.	Bolinao reef flat, Philippines	bolinao	4.0	Aliño et al. (this vol.)
35.	Virgin Islands, Caribbean	virgin21	3.1	Opitz (this vol.)
36.	French Frigate Shoals, Hawaii	FFS	2.1	Polovina (1984); Pauly et al. (this vol.)
	Shelves and seas			
37.	Yucatan Shelf, Gulf of Mexico	yucatan	2.9	Arreguín-Sánchez et al. (this vol.)
38.	Gulf of Mexico continental shelf	gomexico	1.8	Browder (this vol.)
39.	Northeastern Venezuela shelf	venezuel	2.1	Mendoza (this vol.)
40.	Brunei Darussalam, South China Sea	brunei	1.6	Silvestre et al. (this vol.)
41.	Peruvian upwelling system, 1950s	peru50	2.8	Jarre et al. (1991)
42.	Peruvian upwelling system, 1960s	peru60	2.8	Jarre et al. (1991)
43.	Peruvian upwelling system, 1970s	peru70	2.9	Jarre et al. (1991)
44.	Monterey Bay, California	monterey	1.9	Olivieri et al. (this vol.)
45.	Kuala Terengganu, Malaysia	terengga	1.6	Christensen (1991)
46.	Gulf of Thailand, 10-50 m	thai50	1.4	Pauly and Christensen (1993)
47.	Shelf of Vietnam/China	vietnam	1.5	Pauly and Christensen (1993)
48.	Deep shelf, South China Sea	deepscs	1.5	Pauly and Christensen (1993)
49.	Oceanic waters, South China Sea	oceanscs	1.0	Pauly and Christensen (1993)

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Appendix 5

Author Index[a]

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[a] Compiled by R.A. Gayosa, International Center for Living Aquatic Resources Management, MCPO Box 2631, 0718 Makati, Metro Manila, Philippines.

Appendix 6

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[a] Compiled by F.S.B. Torres, Jr., International Center for Living Aquatic Resources Management, MCPO Box 2631, 0718 Makati, Metro Manila, Philippines.

Appendix 7

Index of Taxa, Functional Groups and Their Trophic Transfers[a]

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[a] Compiled by F.S.B. Torres, Jr., International Center for Living Aquatic Resources Management, MCPO Box 2631, 0718 Makati, Metro Manila, Philippines.