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TITLE XII
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WORKING PAPER SERIES

Working Paper No. 40

"The Significance of Physiologically Structured Models for Fish Stock Dynamics"

by
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The Fisheries Stock Assessment CRSP (sponsored in part by USAID Grant No. DAN-4146-G-SS-5071-00) is intended to support collaborative research between the U.S. and developing countries' universities and research institutions on fisheries stock assessment and management strategies.

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The present working document contains the initial papers of a series whose ultimate purpose is to provide a realistic basis for a fresh appraisal of both the surplus production and the dynamic pool approaches to fishery yield analysis.

The main idea is to *tighten the conceptual framework* of the "trinity" of recruitment, survival and growth, uncovering links among the three sectors by using recently developed physiologically structured models' methodology. There are good reasons to argue that this endeavour is appropriate and suitable for understanding tropical fisheries.

Paper I is a plain introduction to the general procedures for building physiologically structured models and the basic mathematical tools and results, mainly in the spirit of the Dutch school. In Paper II we lay out our strategy: to introduce and solve structured models in order to elucidate the underlying assumptions of simple production models. The case is made again for the use of size-structured models in tropical fisheries. Such a strategy demands a fair amount of work and the resolution of some paradoxes (cf. the treatment of Aldenberg's paradox in II, §6).

The decision to try to apply this type of modelling to stock-assessment problems in the context of CRSP was taken during a visit of J. M. Gracia-Bondía to the Chesapeake Bay Laboratory at Solomons in May 1986. These were gratifying, intense days of fecund discussions. We include here the memorandum then written with Brian J. Rothschild because we believe it keeps its programmatic value. Paper I was drafted in April 1987 and extensively revised in February 1988. Paper II was written in May 1987 and underwent some slight revisions later.

We gladly acknowledge our debt to many people: this is a kind of collective work, as it should be. Cluney Stagg provided much needed early encouragement at Solomons. Vincent Gallucci, Pat Sullivan and Han Lin Lai of Seattle provided instructive criticism. Manuel Murillo of CIMAR dexterously helped to keep alive our interest throughout.

José M. Gracia-Bondía thanks Odo Diekmann for inviting him to the Amsterdam meeting on the dynamics of physiologically structured populations in January 1988; to him and to Hans Metz also for a pleasant stay at the Centrum voor Wiskunde en Informatica at Amsterdam and the Institute of Theoretical Biology at Leiden. Thanks are also due to Andre de Roos for useful discussions. Last, but not least, Jerry Ault of Miami went with us through every paragraph of Paper II, perpetually forcing us to strive for greater clarity, precision and breadth.

José M. Gracia-Bondía and Joseph C. Várilly
San José, February 1988

Memorandum: On a class of mathematical models suitable to describe the Biodynamics of the Sea

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1. One of the requirements for an adequate theory of the biodynamics of the sea is that it should provide an explanation for the relative stability of marine populations. We do not deny, by any means, that large fluctuations of marine populations are sometimes observed. But, the purpose of the theory is precisely to relate these fluctuations to the fluctuations (periodic or otherwise) of the environmental parameters. We will tend to reject *a priori*, on these grounds, models which give unlimited growth, rapid decay or unwieldly oscillations, in constant environments.

2. It is a general principle that linear equations with *constant* coefficients are (almost) always exactly solvable and (generically) unstable. This is because the behavior of their solutions is governed (for $t \to \infty$) by the highest lying eigenvalue. If it is negative, we will ultimately have decay (after some oscillations perhaps). If it is positive, we will have unlimited growth. This is also true of the more sophisticated models that we are about to propose here: under fairly general conditions it is possible to prove that the "spectrum" of a linear operator (see below) has a highest lying eigenvalue, that the age structure incorporated in our model becomes stationary, but the total number of individuals undergoes unlimited growth or decay.

Of course, in a given problem, the highest lying eigenvalue could be exactly 0 and the number of individuals when $t \to \infty$ approaches a constant. But there is no *generic* stability: any change of the (physical, biological) parameters describing the problem, from which the eigenvalues are derived, will send the model down dangerous tracks. We cannot attach significance to this ocurrence.

There is another possible "trick", that is, to modulate the changes of the environment in such a way that the oscillations of the population are maintained within prescribed limits. We are now talking about linear equations with *variable* coefficients. This could be useful in specific situations. But, according to the general requirement outlined in §1, we have to conclude that linear models are not suitable to describe the biodynamics of the sea.

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3. Of course, we would expect *a priori* that a successful model of the biodynamics of the sea be a nonlinear one, because complicated feedback loops are an important characteristic of any complicated ecosystem. But we have to put some conceptual limits on the degree of complications that we are willing to consider, if we are to obtain any insight at all.

It should be possible to construct some general "statistical-mechanics-like" model for the entire ecosystem that we are studying, giving us some confidence that the system as a whole will function as a "reservoir" (in the thermodynamic sense) with respect to any one of its components. That is to say, we are neglecting the feedback of the fate of the species of interest on the whole system. To articulate this more concretely, consider predation, for example. The population of predators should be relatively insensitive to what is going on for the given particular species of interest, because that one is only a minute fraction of the pooled prey population; predators may "switch off and on" between possible kinds of prey. In another language, we would say that, even if the distribution of a given function changes with time (and we are bound to examine these phenomena, if we want to test asymptotic stability), the whole system, being composed of a large number of species, will remain in "equilibrium". Let us take that as a plausible assumption for the moment. From our point of view, the system as a whole is described by a number of parameters which couple with the physiology of the species in question. There is no reason to assume (and no interest, as we have seen) that this coupling is linear in the number of individuals of the species under consideration. Also, the parameters could vary with time.

4. Admittedly, the description of the "state" of a population merely by the number of its individuals is too crude. Furthermore, it makes for a poor connection of population dynamics with the other levels of biological science (such as the study of the behavior of individual organisms and even of systems of organs), because in general it is difficult to justify the *ad hoc* mathematical terms on a biological basis.

Also, if we are to recognize structure (age, length, etc.) in the given species of interest, we have to avoid ordinary differential equations, because *they describe instantaneous transitions* between life stages and are in this sense self-defeating. As a matter of fact, with ordinary differential equations we are not able to follow the histories of particular individuals and, as a consequence, there is no clear way of maintaining adequate bookkeeping for the populations through the different stages. The whole point of having different life stages is lost.

5. The "continuum distribution population dynamics" models are flexible anough to incorporate the relevant physiological information which may be available.

Let us describe the models. The physiological state of each individual is represented by a vector, i.e., a point x in a state space. If we need n variables to describe a state, the state space is a subset $\mathcal{D}$ of $\mathbb{R}^n$. It is important to appreciate that x might incorporate not only age, but length, weight, geographic location, gonad content, whatever we think is important.

The individual trajectories are described by a differential equation:

$$\frac{dx}{dt} = v(x).$$

Of course, v reflects the influences that have affected the individual given its species, age, length, sex, ... We have not emphasized in the notation that v includes parameters relating the individual to the environment; if the latter is variable, v would depend on time as well. The description at the individual level is too detailed to be useful; we shall choose to describe the state of the population as a whole by a continuous distribution function (it would be perhaps more accurate to talk of a continuous density function) that we shall call $n(x;t)$. The meaning is the following: $n(x;t)\,\Delta x$ gives the number of individuals whose physiological state is described by a point of the state space inside a cube of volume $\Delta x = \Delta x_1 \ldots \Delta x_n$ centered at $x = (x_1, \ldots, x_n)$, at a given time t.

It is clear that this is the same type of description that one finds in the kinetic theory of gases. The continuity equations of hydrodynamics, that we borrow, assure systematic bookkeeping:

$$\frac{\partial n}{\partial t} + \operatorname{div}(nv) = \text{births} - \text{deaths} \tag{1}$$

We recall here that the operator div, applied to an n-dimensional vector function $\beta = (\beta_1, \ldots, \beta_n)$ of n variables $(x_1, \ldots, x_n)$ yields:

$$\operatorname{div}\beta = \frac{\partial \beta_1}{\partial x_1} + \frac{\partial \beta_2}{\partial x_2} + \cdots + \frac{\partial \beta_n}{\partial x_n}.$$

At any time, the total number of individuals of the species of interest, with state in a given subset of $\mathcal{D}$, say $\mathcal{D}_0$, is:

$$N_{\mathcal{D}_0} = \int_{\mathcal{D}_0} n(x;t)\,dx.$$

We may see now (1) as a dynamical equation, which gives the evolution of n with time, provided that we specify $\mathcal{D}$, v and the rates of birth and of death corresponding to each value of x. Usually births will appear as boundary conditions.

The description is deterministic, in the sense that the behavior of populations is related to the (predictable) behavior of individuals in the state space. There is an inherent stochasticity related to the birth and death processes; we approximate it by describing these chance occurrences in terms of rates.

6. A better understanding of the flexibility of the model may be gained from some examples.

i) Suppose that we take x to represent only the age a. In this case $v = \frac{da}{dt} = 1$. Suppose furthermore that we know that the average fraction of fish which die during the time interval dt, at age a, is $\gamma(a)$, and that the age-specific birth-rate is $\beta(a)$. Then (1) reduces to the "von Foerster equation":

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} + \gamma(a)n = 0 \tag{2}$$

which may be solved explicitly (in conjunction with the birth condition

$$n(0,t) = \int_{a_{\min}}^{a_{\max}} \beta(a)n(a;t)\,da$$

and the arbitrarily given initial ($t = 0$) age distribution) to obtain $n(a;t)$ at all times. This is done on pp. 63 and following of the book by Nisbet and Gurney and will not be repeated here.

We remark that (2) is a linear equation and so the general considerations of §2 apply.

ii) To illustrate the formalism, consider a population of monocellular beings which do not die, but divide into two identical cells when its "size" s is inside a given range. Let us call $d(s)$ the rate of division. Then (1) gives:

$$\frac{\partial n(s;t)}{\partial t} + \frac{\partial}{\partial s}(v(s)n(s;t)) + d(s)n(s;t) - 4d(2s)n(2s;t) = 0. \tag{3}$$

In this case individuals "jump" instantaneously from one point in the state space to another; birth may happen "everywhere" and not as a boundary condition.

iii) Let us look at more-to-the-point examples. Let us consider fish whose behavior in state space is described by two parameters, age and length. Then we have $x = (a, l)$. We have, as before, $\frac{da}{dt} = 1$. Now the evolution of the length of the individuals with time should be related to the length already reached and—here is the coupling with the "external reservoir"—with the availability of food.

We try to manufacture an example with plausible assumptions. First of all, the rate of food intake may be considered proportional to the area of the digestive apparatus, and then to l^2. Second, let y be the perceived food density. The maximum food intake would be in principle proportional to y. Let us call α the constant of proportionality. If the food availability is very big, the fish could become satiated at the maximum, so we model ingestion by a function that it is nearly proportional to y when y is small and nearly equal to a constant when y is large: for instance $g(y) = \dfrac{\alpha y}{1+y}$. So we have: ingestion $= \dfrac{\alpha y}{1+y} l^2$.

The ingested resources are used in (i) maintenance, (ii) reproduction, and (iii) growth. We may suppose that maintenance is proportional to weight, and then to l^3. Let δ be the fraction of ingested resources allocated to maintenance divided by the energy cost of growth. We have, finally:

$$\frac{dl^3}{dt} = \frac{\delta\alpha y}{1+y} l^2 - \mu l^3; \qquad 3l^2\frac{dl}{dt} = \frac{\delta\alpha y}{1+y} l^2 - \mu l^3; \quad \text{or}$$
$$\frac{dl}{dt} = \frac{\delta\alpha y}{3(1+y)} - \frac{\mu l}{3} =: f(l;y) \qquad \text{(by definition).}$$

We must keep in mind that y is the *perceived* quantity of food, which is a function of physical environment (turbulence of water, temperature, irradiance, ...) as well as a function of the *real* density of food z.

The continuity equation gives now:

$$\frac{\partial}{\partial t}n(a,l;t) + \frac{\partial}{\partial a}n(a,l;t) + \frac{\partial}{\partial l}(f(l;y)n(a,l;t)) = -\gamma(a,l)n(a,l;t). \quad (4)$$

In order to solve it, we have to specify births as boundary conditions, presumably relating them to age and length, as above; we will not go into that now. As before, γ is the mortality rate, which depends mainly on age a for natural mortality and on length l for mortality due to fishing.

Equation (4) still seems linear in n. But we need not consider y to be merely a given external parameter, because y is dynamically dependent on consumption. This can provide the nonlinear term we are looking for.

7. To summarize, the continuum distribution population dynamics are appropriate to incorporate any relevant biological information that we may happen to have about the species under consideration; that is what we have attempted to show, rather clumsily, with the previous examples. This is perhaps the main advantage of method; practical biologists may be apt to feel that this kind of models fits better to their concerns than the usual *ad hoc* machinery of population specialists.

On the other hand, it is indisputable that we are pushing mathematics for biology here to a new degree of sophistication: as the spaces where distribution functions $n(x;t)$ "live" are infinite-dimensional, we are bound to use "functional analysis", the type of analysis characteristic of the twentieth century, in order to study deeply equations like (1). The Hille-Yosida theorem of semigroup theory gives the essential tools for that in the linear case but the nonlinear one is, as usual, much more difficult. It appears to be philosophically wrong to expect great breakthroughs in the biodynamics of the sea without developing a mathematical panoply suitable for treating the real-life complications in a theoretically realistic way.

8. Realistic models should be elaborated to take account of the following:

i) Other physiological traits of interest.
ii) Specified assumptions about food consumption and its relation to environmental characteristics; also to birth and mortality rates.
iii) Effects of variable environments.
iv) Change of feeding habits during the life history of a species.

9. Finally, we should pay attention to the possibility of justifying the idea outlined in §3 if not on a first-principle basis, at least in a self-consistent way.

Bibliographical Note. Chapter 3 of Nisbet and Gurney's book *Modelling Fluctuating Populations* (Wiley, New York, 1982) is concerned with single-species models with age structure. However, it does not explain that its "von Foerster equation" is an instance of the continuum equation of hydrodynamics: the fact that the state space could contain other parameters different from age is not sufficiently stressed. When it comes to seek regulatory (non-linear) effects to stabilize the populations, it postulates a relationship between the total number of individuals and the birth and death rates very different in spirit from our treatment of food availability.

A good place to look for the appropriate methodology is Nieuw Archief voor Wiskunde 4 (2), 1984.

The Significance of Physiologically Structured Models for Fish Stock Dynamics. I

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1. GENERAL CONSIDERATIONS

The classical models of population dynamics are of the lumped type: all individuals are treated as identical units and it is hoped that the gross features of the population under study are captured in a very small number of global parameters.

In opposition to lumped models, *structured* models purport to take account of differences among individuals of a given population—mainly with respect to developmental stages—in the hope of a more detailed confrontation of the models with real data.

At first sight, the physiologically structured models we treat below appear full of promise at the i-level (see §2); practical biologists may well feel that this kind of models fits better to their concerns than the usual opaque *ad hoc* machinery of "population mathematicians".

However, any modelling methodology will entail drastic simplifications, compromises made in search of mathematical tractability and, indeed, sources of insight. Before we decide to apply structured population models to a given class of fisheries, we have to critically examine the worth of this effort.

We can do no better than to refer to the classic of marine biology [**1**]. Hardy vividly illustrates there the consequences for the fishery of different age structures in the stock. This exercise was done for populations in a steady state; it is clear that these differences in structure are more significant in transient modes of the population.

This first paper seeks only to delineate the basic framework and fundamental theorems pertaining to a population dynamics theory which incorporates the description of dynamical, ecological processes at the individual level; detailed specific models and applications are dealt with in subsequent papers, referred to as **II** and **III**. Here we include:

a) An introduction to the state-representations, at the i-level (§2) and the p-level (§3). The basic partial differential equations of the theory are derived in §3.

b) A detailed review of the simplest case of age-structured populations, including full solutions and a sketch proof of the "ergodic theorem" (§4).

c) An analysis of the size-structured case, which, we believe, is of direct relevance for tropical fisheries. The concept of age-equivalent representation is introduced and a generalized ergodic theorem is discussed (§5).

d) Considerations of stochasticity in the variables and parameters used in the description of the i-space and some mathematical questions are touched upon in §6 and §7.

2. THE i-STATE REPRESENTATION

To obtain a measure of biological realism in physiologically structured models we must work at the level of the individual description, or i-state representation. The individuals are considered as input-output systems, the input being given by the interface with the environment. The variables employed to describe the state of the system may be very diverse, depending of the focus of interest in our study: age, size, geographic location, sex, epidemiological state, concentration of toxic chemicals, gonad content, ..., whatever we think is relevant.

The larger the number of variables introduced, the greater the penalty we will have to pay in terms of mathematical and computational difficulties. Our variables should be judiciously chosen so as to minimize their number, with the constraint that the following necessary qualifications should be met:

i) The i-state at a given moment should be completely determined by the i-state at a previous moment and the intervening environmental history;

ii) The "behavior" (output) of the system at time t should be determined by the values of the variables characterizing the i-state at t.

As an example, if we can argue that the offspring production, feeding rate, and probability of dying of an individual fish, all depend just on its size (and on the current environmental conditions), then size alone is enough to describe the i-state.

We shall denote by $\mathcal{D}$ the space of the possible i-states. In practice, $\mathcal{D}$ will always be a subset of $\mathbb{R}^k$, the ordinary k-dimensional space. Let us denote by x a point of $\mathcal{D}$. The models we have in mind are deterministic: two individuals with the same value of the system variables and experiencing the same circumstances will follow their life histories in a predetermined, indistinguishable way. It goes without saying that this assumption (called the "strong" form of the i-state description) restricts the class of populations to which the present modelling philosophy can be reasonably applied. We will consider in §6 how the deterministic condition can be relaxed; as it stands for the moment, it means in practice that the individual 'trajectory' is governed by a differential equation:

$$\frac{dx}{dt} = v(x;t). \tag{1}$$

Here v reflects the influences that affect the individual, given its present state; if the environment is variable, it will depend on time.

3. THE p-STATE REPRESENTATION

We have then the picture of a multitude of identical individuals, flowing inexorably in their state space forward in time. We must also incorporate birth and death, which are inherently random processes at the i-level. The point, however, is that we want to address questions to the model at the population level: such as, how much fish biomass is present at a given t between certain ages; what is the probability of dying in a given period for fishes of a certain size; what is the expected offspring of our population; and so on. In order to do so, *we define the p-state as a frequency distribution over the space $\mathcal{D}$ of i-states*: this is the ideal counterpart of the natural population under study. We make implicitly the assumption that the numbers characterizing the population are very large, so births and deaths—and other stochastic "jumps" in the i-state space, see II, §6—play a role in the p-state dynamics only through their averages.

It is clear that this is the same type of description that one finds in microscopic theories of fluid motion. One is not interested in following the motions of particular molecules or microscopic parts of the fluid, but in the properties and dynamics of the whole. However, and this is the point we want to emphasize next, once the "microscopic theory" (i.e. the workings of i-state level system) is specified, we have no freedom of choice in regard to the p-level dynamics. In fact, that dynamics is given by the hydrodynamical continuity or mass balance equation, assuring automatic bookkeeping (in this picture, births can be thought of as "sources" and deaths as "sinks").

From the mathematical point of view, the simplest available deduction of our transport equation uses the Gauss divergence theorem: let $n(x;t)\,dx_1 \ldots dx_n$ give the number of individuals whose physiological state is described by a point of the state space inside the hypercube of sides $(x_1, x_1 + dx_1; x_2, x_2 + dx_2; \ldots; x_n, x_n + dx_n)$, at time t. Then n represents a p-state. Let $\mathcal{D}_0$ be a subdomain of $\mathcal{D}$ with (a piecewise smooth) boundary $\partial\mathcal{D}_0$. At each point of $\partial\mathcal{D}_0$ we may identify the flux vector φ: the number of individuals which are transported across the boundary at point $x \in \partial\mathcal{D}_0$ per unit of "area" on $\partial\mathcal{D}_0$ and per unit of time is $\nu \cdot \varphi$, with ν the outward pointing normal at x.

Clearly, the total number of individuals with state belonging to $\mathcal{D}_0$ at time t is

$$N_{\mathcal{D}_0}(t) = \int_{\mathcal{D}_0} n(x;t)\, dx.$$

Conservation of the individuals forces is to write (we suppress arguments of functions in the formulae that follow):

$$\frac{d}{dt}\int_{\mathcal{D}_0} n\, dx + \int_{\partial\mathcal{D}_0} \nu \cdot \varphi\, d\sigma = 0 \tag{2}$$

where $d\sigma$ denotes measure of "area" on $\partial\mathcal{D}_0$.

Gauss's divergence theorem states:

$$\int_{\partial\mathcal{D}_0} \nu \cdot \varphi\, d\sigma = \int_{\mathcal{D}_0} \operatorname{div}\varphi\, dx. \tag{3}$$

So we find:

$$\frac{d}{dt}\int_{\mathcal{D}_0} n\, dx + \int_{\mathcal{D}_0} \operatorname{div}\varphi\, dx = \int_{\mathcal{D}_0}\left(\frac{\partial n}{\partial t} + \operatorname{div}\varphi\right) dx = 0.$$

Since $\mathcal{D}_0$ is arbitrary this implies:

$$\frac{\partial n}{\partial t} + \operatorname{div}\varphi = 0$$

which is the desired equation.

We note that this way of reasoning is the equivalent of the Eulerian approach in fluid dynamics theory (see A.III.3 in [**2**]). We prefer it to the alternative Lagrangian approach because it remains valid when there are random components in the i-state movement (as will be briefly considered in §6). Straining the fluid dynamics analogy a bit, it means that the argument is still good for a kinetic theory of the microscopic motion. In the present deterministic framework, one has simply $\varphi = nv$, v being the same as in (1).

The less mathematically-minded reader in referred to [**3**, Chapter 5] for a lower-brow treatment, which is of course tantamount to an intuitive argument in support of (3).

If we take into account the probability of death, we end up with:

$$\frac{\partial n}{\partial t} + \operatorname{div}(nv) = -\mu n, \tag{4}$$

where $\mu(x;t)$ is a mortality rate which is always strictly positive. We suppose that births occur only at the boundary of the state space, so they enter the theory as a boundary condition for (4), which is our fundamental dynamical equation.

As it stands, equation (4) is linear, which is an important mathematical asset but, as recalled in the previous memorandum, a biological liability. Nonlinearities can be introduced via the feedback coupling of the environment with the system.

4. AGE STRUCTURE

Chronological-age-dependent population dynamics models have been around for a long time. Although they are not directly relevant in our context, they are important as giving the simplest examples of structured models, and also for theoretical reasons, as will be explained in §5. This theory started in the classical paper by Sharpe and Lotka [4] under the guise of the linear renewal equation (10). The ergodic theorem was disbelieved by their contemporaries. Equation (5) was written down first by McKendrick [5] and forgotten; it was rediscovered (33 years later!) by von Foerster [6], whose name it usually carries. The deterministic linear theory embodied in equations (5) and (10) forms the basis of modern standard human demography [**7**,**8**,**9**]. Sinko and Streifer [**10**] introduced size jointly with (chronological) age; Oster and Takahashi [**11**] considered variable (periodic) environments in some detail. A mathematically heavygoing book, working rigorously with nonlinearity in the pure age-dependent context is [**12**]. For the generalization of the ergodic Sharpe-Lotka theorem, one should mention [**13**]. The general theoretical framework is, as rightly argued by the main authors in [**2**], *in statu nascendi*. However, that book itself shows some signs of maturity already in progress.

Next we derive the main formulas of the standard theory of age-structured populations. We concentrate on the relevant ideas behind the formalism and refer for technical details to [**14**]. Let us denote age by a. As $\frac{da}{dt} = 1$, equation (4) reduces to:

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} + \mu n = 0. \tag{5}$$

Let us suppose, for the time being, that the mortality rate does not depend on t. If $n_0(a) := n(a;0)$ is the initial population, equation (5) has the solution:

$$n(a;t) = n_0(a-t)\exp\left(-\int_0^t \mu(a-t+s)\,ds\right) \tag{6}$$

valid for $a \geq t$. It clearly represents the dying off of the original members of the population. To calculate the solution for $a < t$, we need to specify the birth rate $b(t) = n(0,t)$. Let us give names: $\phi(a)$, the *birth kernel*, is the expected number of offspring that an individual will beget from birth until age a; $\beta(a)$, the *maternity function*, is the mean number of offspring produced by an individual aged a; and $\mathcal{F}(a)$, the *survival function*, is the probability that an individual survive to age a. We have here $\phi(a) = \beta(a)\mathcal{F}(a)$ with $\mathcal{F}(a) = \exp\left(-\int_0^a \mu(a')\,da'\right)$ and the *renewal condition*:

$$n(0;t) = b(t) = \int_0^{a_{\max}} \beta(a)n(a;t)\,da. \tag{7}$$

The remaining half of the solution to (5) is then:

$$n(a;t) = \exp\left(-\int_0^a \mu(a')\,da'\right)\int_0^{a_{\max}} \beta(a')n(a';t-a)\,da', \tag{8}$$

valid if $a \lesssim t$. Note the compatibility condition $n_0(0) = b(0)$.

It is supposed that relevant p-outputs can be calculated from the p-state n, using appropriate kernels:

$$F_{\mathcal{D}_0}(t) = \int_{\mathcal{D}_0} f(a)n(a;t)da. \tag{9}$$

Here, for example, f could denote the i-space feeding rate; F is then the total feeding rate, for individuals inside a given age-class represented by $\mathcal{D}_0$.

The simplest example is the total population number

$$N(t) = \int_0^{a_{\max}} n(a;t)\,da.$$

We have reached a formally complete solution of the linear problem for age-structured population in a constant environment. However, for many purposes an alternative approach is to be preferred. From (7) and (8) it is clear that we can calculate any linear functional of the p-state, if we know the initial distribution n_0 and can solve for the birth rate b. This is indeed feasible: we clearly have from (6), (7) and (8):

$$b(t) = \int_0^t b(t-a)\phi(a)\,da + g(t) \tag{10}$$

where $g(t)$ is the rate of births into the population which are not daughters of individuals born after $t = 0$:

$$g(t) = \int_0^{a_{\max}} n_0(a)\beta(a+t)\frac{\mathcal{F}(a+t)}{\mathcal{F}(a)}\,da. \tag{11}$$

(It is instructive and left to the reader to derive (10) and (11) from first principles.) We write $b = \phi * b + g$, with $*$ denoting convolution.

Equation (10) is an inhomogeneous Volterra equation of the second kind (the argument of the unknown function appears as the limit of the integral) that can be solved by Laplace transforms: defining

$$\tilde{b}(s) := \int_0^\infty e^{-st} b(t)\,dt, \quad \tilde{\phi}(s) := \int_0^\infty e^{-st}\phi(t)\,dt, \quad \text{etc.},$$

we have, by the convolution theorem [**15**]:

$$\tilde{b} = \tilde{b}\tilde{\phi} + \tilde{g}, \tag{10'}$$

so:

$$\tilde{b} = \frac{\tilde{g}}{1-\tilde{\phi}} = \tilde{g}(1 + \tilde{\phi} + \tilde{\phi}^2 + \dots)$$

It can be shown that the expansion is convergent. We conclude that:

$$b = g + g * \phi + g * \phi * \phi + \dots$$

The solution makes sense, as it easy to see that $\phi * \cdots * \phi$ (n times) is the mean rate at which nth generation births happen. Uniqueness of the solution is guaranteed by Titchmarsh's theorem [**15**, 2.15, Sätze 11 and 12].

From here to the ergodic (Sharpe-Lotka, renewal) theorem it is just a short step. We start by removing the initial moment of the population to $t = -\infty$, so we have to solve:

$$b(t) = \int_0^{a_{\max}} b(t-a)\phi(a)\,da.$$

Substituting a trial solution of the form $b(t) = Ce^{rt}$, we find the equation:

$$\tilde{\phi}(r) = 1. \tag{12}$$

Now $\phi(a) \geq 0$. This seemingly trivial observation implies that for s real, the Laplace transform is a (smooth) monotonically decreasing function with $\tilde{\phi}(+\infty) = 0$. Moreover, if, as usual, the Laplace transform is defined for $\Re e\, s > \sigma$, and $\lim_{s\downarrow\sigma}\tilde{\phi}(s) \geq 1$ (this last inequality will be true in any reasonable biological context), then (12) has a unique solution, called the *intrinsic rate of natural increase* associated with the birth kernel ϕ.

The ergodic theorem asserts that r is greater than the real part of the remaining roots of (12). From this it follows that the birth rate and the population must grow or decay exponentially with a time constant $\frac{1}{r}$, asymptotically reaching a stationary relative distribution. Moreover, the conclusion still applies under some suitable technical assumptions, if we reintroduce g into the picture. This was first proved rigorously and in full detail by Feller [16], and so ended the controversy surrounding the paper [4].

Note that $\tilde{\phi}(0) \gtrless 1 \iff r \gtrless 0$; $\tilde{\phi}(0)$ is the *net reproductive number*, the mean number of offsping that an individual is expected to bear during its lifetime (more on that in II, §5).

We conclude this section with a remark: the integral (Sharpe-Lotka) form of the (McKendrick-von Foerster) partial differential dynamical equation exists even in the absence of constant environmental conditions; but of course the ergodic theorem no longer applies in this general case. For the nonlinear problem, the integral form still exists in some cases, and an example will be presented in III.

5. SIZE-STRUCTURED POPULATIONS, AGE-EQUIVALENT REPRESENTATIONS AND GENERALIZED ERGODIC THEOREMS

Age is a variable of minimal physiological significance in fisheries. Other variables, size in particular, are more appropriate as building blocks of an i-state representation. It is a relatively trivial matter to rewrite equation (4) adapted to the case at hand. However, a general theory for solving the resulting equation in closed form does not exist. We can show by an example what the relevant problems are and what pitfalls should be avoided. We choose a length-based model that will be examined in more depth in II. For constant death rate, the dynamical equation that we read from (4) is:

$$\frac{\partial}{\partial t}n(l;t) + \frac{\partial}{\partial l}(g(l;x)n(l;t)) = -\mu n(l;t). \tag{13}$$

Here g denotes the right hand side of the differential equation for fish growth:

$$\frac{dl}{dt} = g(l;x), \tag{14}$$

where x is a collective name for parameters which describe the (possibly variable) state of the environment. The precise form of g, whether it corresponds to von Bertalanffy's law or otherwise, need not concern us here.

Now, the birth rate *is not the same* as the frequency distribution of length at birth (as should be clear from dimensional considerations).

Assuming that all individuals have the same length at birth, the correct boundary condition which replaces the first equality in (7) is:

$$b(t;x) = n(l_b;t)g(l_b;x) \tag{15}$$

with b of the form $\int_{\mathcal{D}} \beta(l;x)n(l;t)\,dl$.

The main theoretical question relative to a physiologically structured model is whether there exists an age-equivalent representation. A necessary condition for that, which turns out to be sufficient in most practical cases, is the

"Principle of natal democracy": *all individuals are born equal.*

(In other words, l_b is the same for all fish under consideration.)

Let us write, as an example, the age-equivalent representation for the system described by (13) and (15). We suppose for the time being that the environment is constant. The idea is to attack (13) by integrating it along the characteristics, in other words, by integrating the ordinary differential equation (14). Suppose that $g > 0$ always, and that the solution of (14) is given by $l = L(a)$ (the parameter along the characteristics is just age); here $l_b = L(0)$. Using this expression, we can perform a change of variables from l to a in (13) and we get a similar equation for the age distribution $m(a;t)$:

$$\frac{\partial m}{\partial t} + \frac{\partial m}{\partial a} = -\mu m \tag{16}$$

with the birth rate $b(t) = \int_0^{a_{\max}} \beta(L(a))m(a;t)\,da$.

Then it is possible to go to the integral representation of the age-equivalent problem (16) and the ergodic theorem applies. Retracing our steps, we obtain the generalized ergodic theorem that we will use in **II**: the solutions of the linear problem (13) with suitable boundary conditions given by (15) tend asymptotically to an exponentially growing or decaying solution, with a stationary relative frequency distribution in the *length* variable.

For a form of von Bertalanffy growth depending on the feeding rate, this distribution is exhibited in **II** in full detail.

So we have generally *three* representations for the p-state dynamics of a physiologically structured model: the original form which comes from (4), the representation derived from integration along the characteristics of (4), and the integral form given at the end of §4. If "natal democracy" does not apply, we can still distinguish cohorts of individuals born with different i-states x_b, and then go over to an integral equation for the birth rate. So, although we can no longer speak of an age-equivalent representation, we have in any case three forms of the dynamics, among which we may choose according to their ease of use in various applications [17].

Also, if the environment is no longer constant, equation (16) is not enough to describe the dynamics, as the characteristics of (13) change over time. But this is easily fixed by introducing a supplementary equation to (16):

$$\frac{\partial l}{\partial t} + \frac{\partial l}{\partial a} = g(l; x) \tag{17}$$

which will update g as needed.

6. WEAK i-STATES

The conceptual framework laid down in §2 does not really demand the rigid determinism we have adhered to so far. Provided we are prepared to accept an interpretation of p-states as mere probability distributions, we can allow stochastic "motions" at the i-state level and work out the corresponding flux φ. Nor is one committed to Markov diffusion processes, contrary to what is asserted in [2, III B].

We can roughly distinguish among "internal" and "external" stochasticity, depending on whether we consider the variables of the system or the input as the random variables. In some sense the latter is more fundamental, as we can think of the former as a superposition of deterministic problems of the kind we have already faced.

§7. A WORD ON MATHEMATICS

We believe that the foregoing sections show that one need not be a mathematician to formulate and to deal with physiologically structured population models. What matters most here is an abstract pattern of reasoning: going from a picture of the i-behaviour, by good use of the fluid dynamics analogy (some prefer a conveyor belt analogy) to the p-state dynamics.

Underneath there is of course a deep mathematical theory, namely, the theory of semigroups in Banach spaces: a fine exposition is to be found in [18]. Works like [12] make heavy use of it. In fact we can see the evolution of n as the result of applying a semigroup of operators on an infinite-dimensional Banach space to the "initial condition" n_0; the differential "generator" of that semigroup is specified by our biological assumptions; and it often happens that mathematical difficulties in determining conditions for existence and uniqueness of the solutions of our equation—the main concern of mathematicians—turn out to hinge on hidden compatibility conditions. Also, the satisfactory solution of subtle paradoxes like that of Aldenberg (**II**, §6) demands the use of tools of operator theory. The renewal ergodic theorem is in fact a result of *spectral theory* in the infinite-dimensional context.

However, in order to fruitfully manipulate formulas, these questions are not usually a problem as long as we are able to develop the necessary "common sense". And so, we can safely leave them to mathematicians, for whom the theory of physiologically structured models is already proving an attractive hunting ground.

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The Significance of Physiologically Structured Models for Fish Stock Dynamics. II

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1. USE AND ABUSE OF MODELS

The conventional wisdom in fish stock assessment is to keep separate, up to a point, the stock-recruitment relationship aspect and the production aspect. It is only sensible not to mingle excessively a relatively reliable model with a highly doubtful one, provided that doing so does not strain reality too much. Sometimes, in practice, this is tantamount to using constant recruitment as an input for the production model. Still, total yields may be predicted if average recruitment and equilibrium yield per recruit are susceptible of calculation. There are also many models which do mix production and recruitment, but in a completely *ad hoc* way.

When addressing the problem of tropical fisheries, this conventional wisdom runs aground. For one thing, many tropical fish spawn continuously in time. Concepts and methods like yield per recruit and following of the cohorts through time become difficult to grasp.

The purpose of this series of papers is precisely to test the usefulness of (physiologically) structured models for gaining understanding about the dynamics of tropical fisheries. This kind of models is well suited for continuously spawning populations.

This does not mean that we intend to incorporate structured models for biological sector calculations in fisheries management modules as a matter of course. We want to keep things as simple as possible. It has been pointed out, in a somewhat different context, that simple stock-production models give results which are no worse than structured models,for instance for calculating optimum fishing effort [1].

One obvious reason for that is the difficulty of parameter estimation in the more elaborate model. We will show later how some of the parameter indeterminacy may be removed. At any rate, we believe that simple production models, having number or biomass as the sole variable, should be used as long as it is feasible. Of course a "biological realist" would argue that the same biomass consisting of juvenile fish or of mature adults will show very different growth and reproduction patterns. For a deeper reason, however, this is almost irrelevant in usual circumstances. The population-dynamics process is a highly redundant self-stabilizing one [2]. Suppose you have a fish population in a pond and you reduce drastically the food supply. You will get stunted fish and for a while a highly transient mode will occur, such as to need a structured population model to be followed in some detail. But sooner or later the population will stabilize itself at a lower level: fish will tend to regain their usual weight and number will be as good an indicator as it had always been [3].

Our strategy is then to use structured models as ancillary to the building of (hopefully) simple production models.

It is only too easy, in this latter kind, to introduce equations and parameters devoid of physical underpinning. Throughout the construction of structured models we force ourselves to think rigorously about the problem at hand, to take account of biological interactions, to uncover paradoxes, and so on.

Formulating the state space dynamics is, as we will see, a healthy way to bring out into the open the hidden assumptions and to eliminate (or to alleviate at least) the inconsistencies in the conception of the vital mechanism one is trying to represent. This process of formulation, understanding and simplification underlines our basic line of approach.

Now there follows the usual preview. For this paper we will focus on:

a) A derivation of the Ricker stock-recruitment relationship from first principles (§2).
b) The basic model for length-structured, continuous-time dynamics (§§3–5).
c) An example of a general procedure to calculate production, incorporating more precise physiological information (§6).
d) Outlook (§7).

2. RICKER'S FORMULA AND CANNIBALISM

Now we set out to work out a concrete example in some detail, in order to illustrate the program outlined in §1.

One of the factors that make for the difference between birth rate and actual recruitment rate is, of course, predation at an early stage of the life cycle. We are going now to examine an idealized model of this phenomenon and use it to derive the well-known relationship of Ricker [4].

Let us write the dynamical equations for the prey in the age-structured format:

$$\frac{\partial n(a,t)}{\partial t} + \frac{\partial n(a,t)}{\partial a} = -\mu(a,t)n(a,t). \tag{1}$$

Here $n(a,t)$ is the density of population per class of age and μ is the mortality rate, as usual.

Assuming a Lotka-Volterra-type interaction, we have

$$\mu(a,t) = \gamma(a)p(t) \tag{2}$$

where $\gamma(a)$ is the age-specific mortality coefficient and $p(t)$ is the density of predators.

The vulnerability of the prey is thought to differ from zero only for $0 \leq a \leq \epsilon$, with ϵ small. Our idealization consists in letting ϵ go to zero, without changing the global intensity of predation θ (defined below). This is appropriate for egg-eating cannibals, and it is neat also in that it avoids the introduction of a multiplicity of parameters. In mathematically pedantic terms, we choose for γ a δ-convergent net. We can avoid the use of δ-function arguments by passing to the limit carefully. We set

$$\gamma(a) = \frac{1}{\epsilon}\zeta(\frac{a}{\epsilon}) \tag{3}$$

where $\zeta(x) = 0$ unless $0 \leq x \leq 1$.

We denote $\theta := \int_0^1 \zeta(\tau)\,d\tau = \int_0^\epsilon \gamma(a)\,da$, the intensity of predation.

Suppose now that we follow a "cohort" of neonates submitted to the mortality given by (2) and (3):

$$n(a,t) = b(t-a)\exp\left(-\int_0^a \frac{\zeta(\alpha/\epsilon)}{\epsilon}p(t-a+\alpha)\,d\alpha\right).$$

Here $b(t)$ is the birth rate, as usual. Taking limits for $\epsilon \downarrow 0$ and $a \downarrow 0$ (in that order!) we get

$$n(0+,t) = b(t)e^{-\theta p(t)}. \tag{4}$$

This is a most important formula: it gives the recruitment (survival) rate as modified by early predation. It is amazing how the first proponents of models of newborn predation [5,6] failed to derive such a relationship. They simply wrote down a rate of prey disappearance of the form $b(t)p(t)$. Small wonder that sometimes recruitment becomes negative. Small wonder also that they found a destabilizing effect of this kind of predation, when nature and more serious models [7] point in the opposite direction (the mistake found its way into the textbooks: see [8]).

Now, suppose that we have cannibalism, so the predators are the adults themselves. Suppose further that we are in a stationary age distribution, so $b(t)$ and $p(t)$ are proportional to the total number of fish

$N(t)$. If reproduction occurs in a single "pulse", the adult population has no time to age nor to die in the meanwhile. Then we get the following stock-recruitment relationship:

$$\Delta N = aNe^{-\theta N}. \tag{5}$$

This is the first mathematical deduction of the Ricker formula that we are aware of. It has been pointed out by Ricker himself [4, p. 281] that it works well for cannibalistic species; but heterofore the link was not formally established. (Cannibalism is perhaps not the only mechanism which produces a Ricker-style curve; scramble competition could yield the same result.)

In conclusion, a simple production model (at the stock-recruitment level in this case) has been justified by a calculation that takes place in the realm of structured population models. That occurrence will be characteristic of our approach.

A word of caution: Equation (5) cannot be used in a simple-minded way for continuously spawning stocks.

Equation (4) does not tell us the whole story. There is a consistency condition to be met. Going back to (2), we see that the number of prey eaten by predator per unit of time is

$$c(t) = \int_0^{\epsilon} \gamma(a)n(a,t)\,da. \tag{6}$$

Let us study the limit of (6) when $\epsilon \downarrow 0$ by using (4) and (3) again:

$$\begin{aligned}
c(t) &= \int_0^1 \zeta(\sigma)b(t-\epsilon\sigma)\exp\left(-\int_0^{\sigma}\zeta(\tau)p(t-\epsilon\sigma-\epsilon\tau)\,d\tau\right)d\sigma;\\
\lim_{\epsilon\downarrow 0} c(t) &= b(t)\int_0^1 \zeta(\sigma)\exp\left(-p(t)\int_0^{\sigma}\zeta(\tau)\,d\tau\right)d\sigma\\
&= \frac{b(t)}{p(t)}\exp\left(-p(t)\int_0^{\sigma}\zeta(\tau)\,d\tau\right)\Bigg|_1^0 = \frac{b(t)}{p(t)}(1-e^{-\theta p(t)}).
\end{aligned}$$

Indeed the right hand side equals decline in population density, at time t, per unit of time, due to early predation, divided by the predator density.

The dynamics of a cannibalistic population becomes automatically nonlinear. If the effective number of predators is

$$p(t) = \int_0^{\infty} k(a)n(a,t)\,da$$

where $k(a)$ is the age-specific propensity to cannibalism, we get from (1), instead of the usual linear Volterra integral equation for $b(t)$, the following nonlinear system of Volterra equations:

$$\begin{aligned} b(t) &= \int_0^\infty b(t-a)\beta(a)e^{-\theta p(t-a)} \exp\left(-\int_0^a \nu(a')\,da'\right) da, \\ p(t) &= \int_0^\infty b(t-a)k(a)e^{-\theta p(t-a)} \exp\left(-\int_0^a \nu(a')\,da'\right) da. \end{aligned} \tag{7}$$

In both formulae, $\nu(a)$ represents a "natural" mortality rate that we have to add at the right hand side of (1) and $\beta(a)$ is the "maternity function".

We will not pursue the matter further here because equations (7), being based on age, are not easily amenable to include the positive effects of young consumption on growth and fecundity of adults.

Cannibalism may happen between the juveniles themselves and then the positive effects just mentioned may become very important. This seems to be the case for tuna [9]. We shall deal with this subject below.

3. LENGTH INSTEAD OF AGE

We will be using length-based models or weight-based models, which are almost (but not quite) equivalent. The use of this kind of models, instead of the good old age-structured models borrowed from demography, may surprise some. But fishes are not endothermic animals whose internal environment is so stabilized that ageing and development are mainly determined by inner gauges and clocks. In cold-blooded animals, as in many plants, development is poorly correlated with calendar age and external environmental conditions are all-important. Perhaps more to the point, statistical data on tropical fisheries are given in terms of length; indeed, fishing gear operates with respect to length. There is at present no cheap or reliable way to measure age, indeed this is one of the objectives of the CRSP. The more subtle reason is that, as we shall verify in the next section, length-structured models are more informative that age-structured models.

4. THE VON BERTALANFFY EQUATION REVISITED

According to the philosophy explained in **I**, before we set out to systematically introduce our length (weight) based models, we have to look at the life history of the individuals.

1. Food intake. The ingestion of food by an individual fish of length l and weight w ($w = l^3$ in suitable units) at food density x may be taken as

$$f(x)l^2 = f(x)w^{2/3}$$

where

$$f(x) = \frac{\delta x}{\alpha + x}, \qquad \text{so } f(x) \underset{x\to\infty}{\longrightarrow} \delta, \quad f(x) \underset{x\to 0}{\sim} \tfrac{\delta}{\alpha} x.$$

This form for f is Holling's formula [10], which is based on satiation and handling time considerations and is empirically well established. The l^2 dependence above is due to the fact that digestion rate scales with the surface area of the digestive apparatus.

2. Growth. Part of the energy from the ingested food is channelled into maintenance, part is channelled into growth. So we have, assuming isometric growth:

$$\frac{dw}{dt} = \frac{1}{\eta}(f(x)w^{2/3} - \lambda w) \tag{8}$$

where η is an efficiency conversion factor of food units into weight units, and λ is a maintenance parameter. Assuming that the right hand side is positive, we would get

$$\begin{aligned} \frac{dl}{dt} &= \frac{dl}{dw}\frac{dw}{dt} \\ &= \tfrac{1}{3}w^{-2/3}\frac{1}{\eta}(f(x)w^{2/3} - \lambda w) = \frac{1}{3\eta}(f(x) - \lambda l) =: g(l;x) > 0. \end{aligned}$$

Let us call l_b the length at the time of birth, t_0:

$$l(t_0) = l_b.$$

If food conditions remain invariable during the fish lifetime, we get

$$l = L_\infty(x) + (l_b - L_\infty(x))e^{-k(t-t_0)} \tag{9}$$

where $k = \lambda/3\eta$, $L_\infty = f(x)/\lambda$. This is the celebrated von Bertalanffy equation. Note that the maximum length depends on the availability of food.

3. Reproduction. So far we have left reproduction out of account. Reproduction drains a lot of energy from the parents (think of the salmon!) and that has to be reflected somehow in the growth function g.

The usual solution [10] is to say that a constant fraction of the food intake, $(1-\kappa)f(x)w^{2/3}$, with $0 < \kappa < 1$, is channelled into reproduction. This way, we have the same equation (9), where $L_\infty(x) = f(x)/3k\eta$ is replaced by

$$L_\infty(x) = \frac{\kappa f(x)}{3k\eta}. \tag{10}$$

There being no observed change in the feeding rate, nor a noticeable deviation from the law of growth at the onset of the maturity, we will assume that equation (9), with L_∞ given by (10), is valid for the entire lifetime of the fish, under constant environmental conditions. Presumably, the $(1-\kappa)f(x)/3k\eta$ portion of the energy intake serves the building of the reproductive apparatus.

There are some paradoxes involved here, that will be taken up partially in §6. For the time being, our sticking to this particular version of von Bertalanffy's law rewards us with a precisely determined form for the length-specific maternity function $\beta(l;x)$. Let l_m be the length at which the fish mature (we are here considering models in which maturity happens in a "knife-edge" way, rather than fuzzily, a questionable assumption, to be sure). We have

$$\beta(l;x) = \begin{cases} 0 & \text{if } l_b \le l \le l_m \\ \frac{1}{\eta w_b}(1-\kappa)f(x)l^2 & \text{if } l_m \le l \le L_\infty(x). \end{cases} \tag{11}$$

Here w_b is the weight of a newborn and we are supposing that food supply is enough for reproduction to start. Note that Diekmann and Metz [10] write $(\omega w_b)^{-1}(1-\kappa)f(x)l^2$ for the last part of the equation; but there is no good reason for taking $\omega \neq \eta$.

5. THE BASIC MODEL (CONSTANT ENVIRONMENT)

The dynamical equation is:

$$\frac{\partial}{\partial t}n(l,t) + \frac{\partial}{\partial l}(g(l;x)n(l,t)) = -\mu n(l,t). \tag{12}$$

We shall take the mortality rate μ to be constant. It is proven in I that the solution of this equation tends asymptotically to a stationary length distribution, with exponential growth or decay. Let us find this distribution. We insert $n(l,t) = \psi(l)e^{rt}$ in (12) and we find

$$\psi(l) = C(l - L_\infty)^{\frac{\mu+r}{k}-1}$$

that is:

$$\psi(l) = \psi(l_b)\left(\frac{L_\infty - l}{L_\infty - l_b}\right)^{\frac{\mu+r}{k}-1} \tag{13}$$

In this and subsequent formulae it is tempting to take $l_b = 0$, given the fact that length at birth is very small anyway. It will be seen later that this would be a mistake.

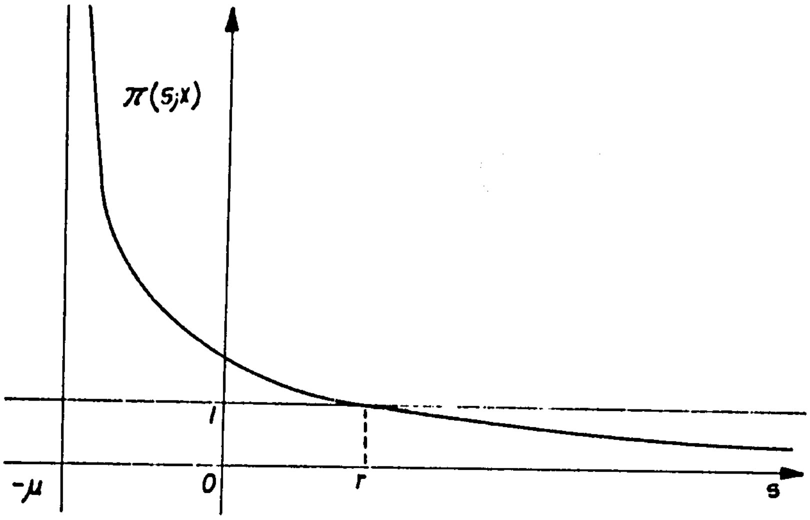

Figure 1. Graph of $\pi(s;x)$

To get r, still unknown, we use the boundary condition:

$$b(t;x) = g(l_b;x)n(l_b,t), \qquad \text{where}$$
$$b(t;x) := \int_{l_m}^{L_\infty(x)} \beta(l;x)n(l,t)\,dl.$$

Inserting $n(l,t) = \psi(l)e^{rt}$ in the appropriate places again, we obtain

$$\pi(r,x) := \frac{3(1-\kappa)f(x)}{\lambda w_b(L_\infty(x)-l_b)^{(\mu+r)/k}} \int_{l_m}^{L_\infty(x)} l^2(L_\infty(x)-l)^{\frac{\mu+r}{k}-1}\,dl = 1. \tag{14}$$

This is to say, r solves the "characteristic equation" $\pi(s,x) = 1$ with the functional form of π given by the expression above. This function may be given a more explicit form by integrating (14):

$$\begin{aligned}\pi(s,x) = {}& \frac{3k(1-\kappa)f(x)}{\lambda w_b}\Bigg(\frac{L_\infty^2(x)}{\mu+s}A^{\frac{\mu+s}{k}} \\ & - \frac{2L_\infty(x)(L_\infty(x)-l_b)}{\mu+k+s}A^{\frac{\mu+k+s}{k}} + \frac{(L_\infty(x)-l_b)^2}{\mu+2k+s}A^{\frac{\mu+2k+s}{k}}\Bigg)\end{aligned} \tag{15}$$

where

$$A = \frac{L_\infty - l_m}{L_\infty - l_b}.$$

The result is valid if $s > -\mu$. Moreover, $\pi(s;x)$ is a strictly decreasing and convex function of s, and $\lim_{s\to\infty}\pi(s;x) = 0$. Then the equation $\pi(s;x) = 1$ has a unique simple solution, which furthermore may be approximated easily by Newton's method. Have a look at Figure 1.

We have:

$$r \gtreqless 0 \iff \pi(0;x) \gtreqless 1 \tag{16}$$

That will be readily interpreted in biological terms. Let y be defined by $L_\infty(y) = l_m$. Then clearly $\lim_{x\to y} \pi(s;x) = 0$ if $s > -\mu$ and then $r \to -\mu$. Thus there is a critical food density defined by $\pi(0;x_c) = 1$, such that $-\mu < r < 0$ if $x < x_c$ and $0 < r < r_m$ if $x < x_c$, where r_m is the solution of $\pi(s;+\infty) = 1$.

There is an alternative way of solving (12), by introducing the growth curve (9). Note that the age of the fish is given by

$$a(l) = \frac{1}{k} \ln\left(\frac{L_\infty - l_b}{L_\infty - l}\right) \tag{17}$$

Changing the variables in (14), we are led to

$$1 = \frac{3(1-\kappa)f(x)}{w_b\lambda} \int_{a_m}^{\infty} l^2(a) e^{-(\mu+r)a}\, da, \tag{18}$$

where a_m is the age of maturity. It is clear now that the right hand side of the equation is essentially a birth rate: $\pi(0;x)$ is the number of offspring that a newborn individual is expected to bear.

It is also possible to interpret the characteristic equation (14) *in terms of sustainable yields*: if the harvesting rate equals precisely the natural rate of growth, the population size should remain constant. Then $\pi(s;x)$ is the expected number of offspring per individual if we harvest the population at the rate s.

6. ALDENBERG'S PARADOX AND PRODUCTION RATE

There is a paradox noticed by Aldenberg [11] implicit in models that use a continuous growth curve. The sudden appearance of neonates should be accompanied by a negative jump in mean individual weight of the parent cohort: every reproduction is a fission. What we did, tacitly, with our early assumption, was to assume that reproduction proceeded by all individuals in the population contributing continuously infinitesimal shares to a common pool, from which, by some miracle, neonates were produced.

The question is important for production theory, because it is easy to see that classical (Allen's and Ricker's) production models, which do not take into account the foregoing, tend to overestimate production.

Let us write now the "correct" equation, replacing length by weight as the independent variable:

$$\frac{\partial n}{\partial t} + \frac{\partial(gn)}{\partial w} = -\mu n - \beta n + \beta(w + w_b)n(w + w_b). \tag{19}$$

This should be compared to equation (12).

If we are not willing to forsake equation (12), we have to look for a way out of the paradox.

One possibility is to derive a limiting form of equation (19) when $w_b \to 0$. By a Taylor development we readily arrive at equation (12), with g replaced by $g - \tilde{\beta}$, which we define as $\tilde{\beta}(w) = \lim_{w_b \to 0} \beta(w) w_b$. This is most reasonable: the energy substracted from growth is chanelled into reproduction. As we took this into account when we wrote down our growth curve, we might think that we are on safe ground. However, it is clear that in the limit $w_b \to 0$, the number of neonates becomes infinite. This is one of the reasons that prevented us from putting $w_b = 0$ in §4 (another reason will be apparent in §7). This "population explosion" could be countered by an infinite mortality, but this is too artificial.

More to the point is the following result: the rate of production in the models governed by (19) is the same as that in the models governed by (12), provided that g is adequately corrected.

PROOF: Multiplying equation (12) by w and integrating, we get

$$-\int_{w_b}^{w_\infty} w \frac{\partial(gn)}{\partial w}\, dw = \int_{w_b}^{w_\infty} w \frac{\partial n}{\partial t}\, dw + \int_{w_b}^{w_\infty} w \mu n\, dw = \frac{dB}{dt} + E.$$

Here $B(t) = \int_{w_b}^{w_\infty} w n(w,t)\, dw$ is the population biomass and the term E stands for the rate of biomass elimination through mortality. We conclude that the rate of net biomass production is

$$P = \int_{w_b}^{w_\infty} w \frac{\partial(gn)}{\partial w}\, dw. \tag{20}$$

(Now it is a simple exercise to calculate the rate of production of biomass per unit stock, assuming stationary distribution of weight, using $g(w)$ given by (8) and also formula (13). The measured "snapshot" of number over weight distribution should serve for estimating the parameters in these formulae).

Let us continue the proof. Integrating by parts, we get

$$P = w_b g(w_b) n(w_b, t) + \int_{w_b}^{w_\infty} g n\, dw \tag{21}$$

which distinguishes clearly the formation of reproductive material from the individual's growth.

We turn now to Aldenberg's equation. The rate of production is now

$$P = -\int_{w_b}^{w_\infty} w \frac{\partial(gn)}{\partial w}\, dw - \int_{w_b}^{w_\infty} w \beta n\, dw$$
$$+ \int_{w_b}^{w_\infty} w \beta(w + w_b) n(w + w_b, t)\, dw.$$

As $\beta = 0$ for $w \leq 2w_b$, the second term on the right can be written as $-\int_{2w_b}^{w_\infty} w\beta n\,dw$, whereas the third term is $\int_{2w_b}^{w_\infty}(w - w_b)\beta(w)n(w,t)\,dw$, so they add up to $-w_b\int_{2w_b}^{w_\infty}\beta n\,dw$.

We get, finally:

$$P = w_b g(w_b)n(w_b,t) + \int_{w_b}^{w_\infty}(g - w_b\beta)n\,dw \tag{22}$$

which is (21), provided that we redefine g suitably. We conclude that, from the practical point of view, equation (12) is safe to stick to. ∎

7. INTERACTIONS

There follows a list of problems that could be readily handled with the tools developed so far.

Of course, the hypothesis of constant environment is not fulfilled in practice. We are interested precisely in harvesting populations which keep dynamical equilibria with their surroundings. Part of our purpose is to look for these equilibria for different realistic assumptions about recruitment, development and reproduction processes.

a. *Competition for food resources.* We intend to attack equation (12) coupled to the equation for the resource:

$$\frac{dx}{dt} = k(x) - f(x)\int l^2 n(l,t)\,dl.$$

Here we expect that $k(x) > 0$ for $0 < x < x_e$ and $k(x) < 0$ for $x > x_e$: we may suppose that $k(x) = \alpha - \beta x$ at least in the vicinity of x_e.

Here time-scale arguments must be employed to simplify the problem: it is reasonable to assume that the relaxation time of the resource is much shorter than that of the population under study, so we can treat the (slow) population variables as constants on the time-scale of the (fast) resource variables and the resource variables as being permanently in equilibrium in the scale of the population variables.

b. For different harvesting rates, we obtain different equilibria in (a). We calculate then the production rate (20), in order to deduce sustainable yields.

c. *Intrajuvenile cannibalism.* Let us suppose that the coincidence between the vulnerable and cannibalistic classes is exact. We sketch a simple model based on age. Reasoning as in §2, we have:

$$n(0+,t) = b(t)e^{-\theta p(t)}$$

where $p(t)$ is defined as $\int_0^\epsilon \gamma(a)n(a,t)\,da$ before going to the limit.

Now we have a consistency condition:

$$p(t) = \frac{b(t)}{\theta p(t)}(1 - e^{\theta p(t)})$$

which may be solved to give p in terms of b. Then we write the renewal equation:

$$\begin{aligned} b &= \int_0^\infty \beta(a)n(a)\,da = \int_0^\infty \beta(a)n(0+)e^{-\nu a}\,da \\ &= \int_0^\infty \beta(a)be^{-\theta p(b)}e^{-\nu a}\,da \end{aligned} \tag{23}$$

which, interestingly enough, turns out to be nonlinear. We can examine the dynamical properties of (23) and then attack the same problem with length based models, where one may follow the energy budgets, in order to compare results. We think that a justification for the use of the logistic model might emerge from this.

It is interesting to note that competition for safe places in the early life stage turns out to be mathematically equivalent.

d. There is evidently an energetic tradeoff between birth weight and birth rate. From evolutionary considerations, the precise relation should be obtained by maximizing r (with respect to w_b). The resulting relationship could be tested empirically and eventually lead to elimination of some parameters of the model (now we see again that putting $w_b = 0$ is not really such a good idea). From evolutionary considerations also, the negative correlation between L_∞ and k alluded to in [**12**] may find an illuminating explanation.

e. One might try to apply Laplace transform methods to Aldenberg's equation, looking for asymptotically stationary solutions.

f. A richer model can be developed, introducing storage of reserves as a second dependent variable, and allowing for stochastic variation of the environment.

We also note that the formalism lends itself to the study of chemical stresses caused by pollution.

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