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"Feasibility of Relating Recruitment to
Environmental Variables"
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Feasibility of Relating Recruitment to Environmental Variation[1,2]

by

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Abstract

The feasibility of relating recruitment to environmental variation depends upon the development of a model defining this relationship. A recruitment-environment model would need to contain components relating both to the ecosystem "engine" and various sensors or gauges to measure its performance. Trophic transactions are an important component of the ecosystem engine. We describe a gauge capable of measuring the probability of these transactions as they are affected by motion, irradiance, and temperature. The method in principle considerably shortens the causal linkages that need to be examined and thereby materially increases the feasibility of developing a predictive model on trophic energy exchange in the sea and opens the door to studying the special case of the relation of the physical environment to ichthyoplankton mortality.

Introduction

Predicting recruitment is a central problem in fisheries biology. As might be inferred from Shepherd, Pope and Cousens (1984), our capability to predict recruitment is at about the same level as it was thirty years ago when Carruthers, Lawford and Veley (1951) published a paper in which they claimed that they could forecast haddock brood strength, Gulland (1952) suggested these correlations were spurious, and Allen Saville 1959 confirmed this assertion. The work of Carruthers et al., at that time, examined in retrospect, was creative, Gullands observations insightful, and that of Saville a much needed specific follow-up, not often seen today. Despite the fact that our capability to predict recruitment has been relatively static over the past thirty years, we have acquired a considerable amount of information on the problem, particularly its complexity.

However, apparently without regard to the early fishery-specific papers demonstrating, often by hindsight, the difficulty of relating recruitment to the oceanic environment and first lessons in statistics, many authors have succumbed to the temptation of publishing uncritical correlations. To many, though, the admonishment to seek causal rather than correlative relationships is fairly well-known and the point would not warrant additional discussion, except for the fact that 1) the stakes associated with being able to understand the oceanic environment and its affects on the fish stocks are higher than ever and 2) our understanding of the process, or at least our measurement capability has lept forward in recent years, thus suggesting that it is worthwhile to reevaluate our perspective on the entire problem.

With regard to the stakes, concerns for understanding recruitment variability in fisheries have not lessened, but in addition there is a broadening interest in the effects of human activity upon the the atmosphere and the ocean and the combined affect of these upon the habitat of the fish stocks. These broadening interests have a strong economic content relating to a wide variety of issues. For example, should there be a moratorium on fishing a particular stock? Should we build or not build a power plant which we think could have an affect on fish stocks? Should we think that anthropogenically caused atmospheric warming will increase some stocks and decrease others, possibly having a major effect on some of the fishery industries of the world?

In other words, in addition to direct concerns for fishing, there is also concern regarding how man's activities affect the oceanic habitat. In this regard, the population dynamics of fish constitute an important bioassay for anthropogenic effects. The bioassay is particularly important because it provides an opportunity not only to measure the effects of man's activity, but to consider as well the tradeoffs between the costs and benefits of human activity and the costs and benefits associated with anthropogenically induced changes in fish stocks, should these in fact exist.

With regard to our understanding of the process, the dynamics of recruitment variability seems to behave much like the weather and climate (J. Smagorinsky, pers. comm.) in the sense that it is a system characterized by nonlinearities, positive and negative feedbacks, with an over-all negative feedback. The understanding of such a system will require extraordinary theoretical development. This theoretical development is not likely to occur in one giant leap but in a series of small increments explicitly involving empirical observations interspersed with theoretical advance. The "new" opportunities for empirical development are extensive, ranging from CCI-technology to advanced plankton nets, to acoustic imagery of plankton.

This paper explores the factors associated with the feasibility of advancing beyond a more-or-less correlative approach toward a more direct understanding of recruitment variability. The remainder of this paper addresses the problem setting, the constraints to understanding the interaction of the environment and recruitment variability, and considers the feasibility of eliminating the constraints.

Problem Setting

In thinking about the need for empirical and theoretical development it is

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well to examine some examples that deal with causality and to resurrect the old argument of whether a change in stock abundance can be attributed to the environment, or a fishery or both. While in recent years we have often attributed stock declines to fishing, the evidence is not always clear.

For example, Jakobsson (1985) presented time-series data on fishing mortality and stock abundance for a number of herring stocks. Figure 1 shows his time-series graph for the Icelandic summer spawning herring and Figure 2 shows his time series graph for the Norwegian spring spawning herring. The time series for the Icelandic summer spawning herring shows that the stock increased under fairly constant fishing mortality until about 1960. As fishing mortality increases, the stock begins to decline. Later, as fishing mortality decreases, the stock increases again. In other words, fluctuations in Icelandic summer-spawning herring stock abundance appear to be closely coupled with fishing intensity. The Norwegian spring-spawning herring, however, provides a contrasting example (Figure 2). This stock began its decline before any great intensification of fishing effort and has not recovered even though fish mortality has declined. In other words, the fluctuations in the Norwegian spring-spawning herring do not seem to be closely coupled to fishing mortality.

As a third example, consider the famous decline of the Peruvian anchoveta which is often attributed to El Nino or ENSO as it is now called. In effect the major collapse of the anchoveta may have been related to the particularly great abundance of the anchoveta just before the collapse, a statement not intending to discount ENSO influence or the subsequent interaction of fishing, but rather emphasizing the possibility of an extraordinary effect of ENSO and fishing because the population was at a high level of abundance.

For example, the Report of the Consultative Group on the State of the Stocks of Anchoveta and Other Pelagic Species (Lima, July 1977) noted that through the late 1960's the spawning-stock size was maintained at a level of about 15 million tons and a high recruitment was in evidence. However, the spawning in September of 1971 resulted in weak recruitment. This was noticed in early 1972. Indeed, the recruitment from this year-class appeared to be one-eighth of the recruitment in the late 1960's.

The El Nino of 1972 caused, as is typical, warmer waters in early 1972. This caused the fish to be more concentrated in the cooler waters close to the shore. This made the nominal unit of fishing effort more effective and the combination of the poor recruitment and intense fishing caused the spawning stock in September of 1972 to decline to about 2 million tons.

After 1972, catches were somewhat less than the moderate recruitment and the spawning stock averaged about 4 million tons up until 1975. In 1975, the recruitment conditions apparently improved and the spawning stock increased in early 1976 to about 10-12 million tons.

This optimistic note was dashed, however, when the El Nino and its warmer water reappeared off the Peruvian coast in 1976. Again, the fish concentrated off the coast, but feeding conditions were apparently unfavorable since the normal diatom/zooplankton mix was replaced by dinoflagellates in unusual abundance. The fishes growth was reduced; they were lean and had a low fat content. The September 1976 spawning from these fish was "disastrously low, not more than half a million tons, or well below one-tenth of that of the late 1960's .... additional evidence of the unusual characteristics of the anchoveta

stocks was that in September 1976 the length of first maturity was 8-9 cm, a few centimeters lower than normal."

The decline of the anchoveta in association with the two El Ninos is particularly interesting-because the response of the fish to conditions was evidently different. In 1972 the fish were especially large, but the proportion of mature females during spawning time was particularly low. The fact that these fish may not have spawned is evidenced by the failure of their fat content to decline (see Report of the Fourth Session of the Panel of Experts on Stock Assessment on Peruvian Anchoveta) as is typical for clupeoid fish at spawning time (see, e.g. Perkins and Dahlberg, 1971). In addition, the number of eggs was greatly reduced. The conditions in 1977 appeared to be somewhat different in that the stock size was at a low level, growth was poor, and dinoflagellates dominated the plankton. The low fat content suggested that the fish were in spawning condition, but the apparently low nutritional level may have affected the spawning capability. There is no evidence to indicate at this point whether the poor recruitment was related to spawning or events during the egg and larval stage.

The scenario is that the 1972 and the 1976 collapses were associated with different phenomena. In 1972 it appears that egg production was constrained while in 1976 it appears that feeding conditions for larvae were inadequate. There was no question that fishing was substantial and there is no question that there were environmental perturbations. If these kinds of effects cannot be separated, then it is difficult to make predictions.

There are, of course, questions of why the stock did not recover—possibly high fishing mortality, genetic changes in the stock, or an "environment" that became or continued to be unfavorable. No one knows.

In sum, the interrelationships between the effects of fishing and the environment continue to be inextricably entwined. There are instances where stock fluctuations are closely coupled with fishing intensity, but there continues to be examples where the picture is not clear and we are concerned as to whether these examples reflect natural changes, changes which owe to fishing, but not directly coupled with fishing mortality, or changes which owe to some other non-fishing anthropogenic factor.

Constraints to Understanding

It thus appears that the critical issue of separating fishing from the environment are still with us, and while the difficulties of this problem are ultimately associated with the complexity of the population dynamics process, it is clear that a major constraint to our understanding of the recruitment process involves an uneven treatment of the problem.

To show this we have prepared a flow chart (Figure 3) of the population-dynamics process in a fish population and show that only parts of this process are covered by the conventional production model, stock-and-recruitment, and yield-per-recruit theory (Rothschild, In Press). Lacking theoretical coverage, are the events intermediary between stock and recruitment; the partitioning between somatic and reproductive biomass; and, most relevant to our discussion here, the relation between the environment and any of the elements in the population dynamic process.

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In thinking about filling these large theoretical gaps, several approaches come to mind, and of these, it seems apparent that an understanding of the dynamics of fish stocks might be best furthered at this time, not by directly studying the fish, but by better identifying the environment that affects fish-stock variability.

There have been several approaches to "identify" the oceanic environment and we might contemplate the use of these as a theoretical substrate for fish-stock population dynamics. It appears that most of these approaches fit into two categories. The first involves box models which partition the ecosystem into various boxes enabling the study of the standing stock in any box, and the flow among boxes (e.g. Fasham 1985). The second involves characterizing the biota in terms of the size spectrum of individuals that comprise the biota (e.g. Platt 1985).

While both approaches lend considerable insights into the dynamics of the organisms of the sea, both have recognized difficulties. The major difficulty with the box models is that the ecosystem partitioning is idiosyncratic. In other words, since there are no particular rules for constructing boxes, different individuals, depending upon their background, knowledge, etc. are likely to develop different partitionings or sets of boxes for the same ecosystem leading to very different interpretations of how the same ecosystem works. The major difficulty with the size spectrum approach is that it is difficult to separate the factors that affect the change in size particularly growth and reproduction. This might not be a problem if, for example, the relation between stock-and-recruitment in fish and in the other organisms could be accounted for by simple mathematical relationships that could be incorporated in size spectrum or box models, a feat that seems unlikely.

A much deeper issue though is the distinction between what we might call the ecosystem engine and the gauges that measure its performance. The ecosystem engine is the way the ecosystem works; it allocates ecosystem biomass in space and time. An important part of this allocation is the periodic initialization of biomass through the reproductive processes of the populations that comprise the ecosystem. Any model that attempts to represent the engine then, must include the density-dependent and density-independent reproductive processes, the stock-and-recruitment processes of the populations, as important components. Once the engine is described we can think of various gauges or sensors to measure its performance. While the dividing line is sometimes blurred, it appears that both the box model and the size spectrum notion relate more to gauges that can be used to measure engine performance than to the engine itself.

In thinking about the problem, we know that in any region of the sea there is a biota and its associated environment. We can easily imagine characterizing and circumscribing the complex of biota and environment as an ecosystem. It is much more difficult to imagine how the ecosystem engine works. The fact that we can describe the appearance of the engine does not mean that we understand how it works. Even if we do not understand how an engine works, we can attach to it various sensors or gauges to obtain some idea of its performance. For example, we could develop sensors or gauges to measure the flow of energy or materials among components or groups of components, or we could develop other sensors or gauges to monitor the size of components in the system and to examine their metabolism. The question remains, however, as to

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whether these gauges are measuring the right variable in the right way. Answering this question depends upon the structure of the engine and the purpose for monitoring its performance.

The discussion suggests that a predictive capability requires a description of the engine and the gauges appropriate to the predictive process. I have considered the population-dynamics engine elsewhere (Rothschild, In press) and am concerned here with giving an example of a gauging system that reduces the length of the long and often complex dendritic causal chain between the physical environment and recruitment success (at least with regard to that component of recruitment success that relates to egg and larval mortality) and thereby increases the feasibility of developing a stock-recruitment-environmental model which is a prerequisite for year-class strength prediction. My discussion of this type of gauge uses fish larvae as an example. However, it will be obvious that it can be used to monitor all trophic interactions that involve particulate prey, whether the prey are living or dead.

The gauge generalizes the idea of a search-tube (Blaxter and Staines, 1971). The search-tube relates to the volume swept clear by the perceptive range of a fish larvae searching for food. The notion is generalized by defining four search volumes.

D_0 volume: The D_0 volume is the track taken by a fish larvae through the water. If the track is considered as being in one dimension then it has no volume. But if the track is in fractal dimension (Mandelbrot 1977) or in the dimension swept clear by the larval corpus, a volume exists. In actuality, we are more concerned by the path and whether it is straight or convoluted in the presence or absence of food, for example (see Hunter and Thomas, 1974).

D_1 volume. This is the volume specified by Blaxter and Staines and consists of the perceived volume swept clear by the fish larvae. However, this volume is only useful for considering prey that do not move because if prey have a particular velocity more will be contacted as their velocity increases. In otherwords, as the fish larvae moves through its D_1 volume, it may contact more or less prey depending on the velocity of the prey.

D_2 volume. If we consider that prey have a velocity then we need to construct a D_2 occupancy volume, which has a diameter which is a function of not only the perceptive capabilities of the predator, but of the relative velocity of both, a well known theory of search strategy (e.g. Koopman 1956). The difficulty with the D_2 volume is that it still does not account for the dynamics of the sea.

D_3 volume. The D_3 volume is intended to take account of the dynamics of the sea because it considers the perceptive fields, the velocity of the prey, as affected by the physics of the sea. For example, small-scale turbulence and shear affect the relative velocity of prey and predator; differences in irradiance as a function of the intensity of light striking the sea surface, turbidity, and depth all effect the perceived area swept clear as well; and finally, temperature affects the D_3 space in terms of, for example, its affect upon the length of the D_0 dimension.

Without going into much detail, we can see that we have been able to develop some ideas that a) express the intimate relation between physical variables and the oceanic environment creating a research climate to examine

the essence of the relationships rather than relying on lengthy and convoluted causal chains such as the relation between some function of windspeed, for example, and recruitment, b) provide a mechanism for thinking about the population dynamics of particles in the sense that intersection of D_3 spaces of organisms is a prerequisite for density-dependent intra-specific interactions, as well as interspecific interactions, and we can easily see, for example, the effects of increases in turbulent kinetic energy, changes in irradiance, and temperature on the intersection of D_3 occupancy volumes, c) provide a framework for a quite general description of oceanic biota which is compatible with the size spectrum and other notions of biovariability in the sea. In fact, the spectra that are most interesting are those of D_3 volumes since they show how variability in the physical properties of the sea affect all trophic transactions.

Feasibility of Eliminating Constraints

It seems then, that the benefits that would accrue from a better understanding of the interrelation of climate and fish-stock recruitment could be substantial. It further appears that the correlative approach has reached its maximum performance. If we are to push beyond the correlative approach we will have to build, as a point of departure, the kinds of models that relate climate and the fish stocks to the ecosystem engine and develop the most efficient gauges or sensors which can be used as independent variables in the predictor process. It seems that we have the methodology in hand to extend our predictive capability by considering the effects of the physical environment on trophic transactions in the sea. The factors that effect mortality of larval fish are, of course, a special case of this more general problem.

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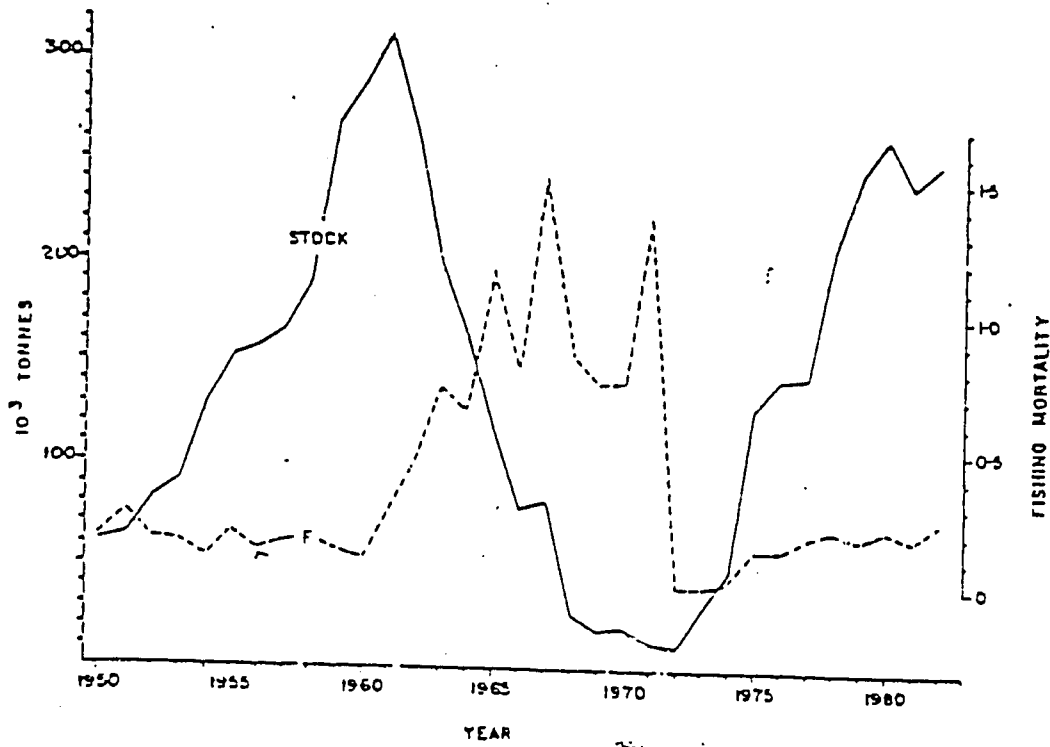
Figure 1. "Spawning stock biomass (Icelandic summer spawners) and fishing mortality rate (F) for 3-yr and older herring, 1950-82." From Figure 16, Jakobsson, J., 1985. Biological, Social, and Economic Aspects of Herring Fisheries Management. Can. J. Fish. Aquat. Sci., 42:207-221.
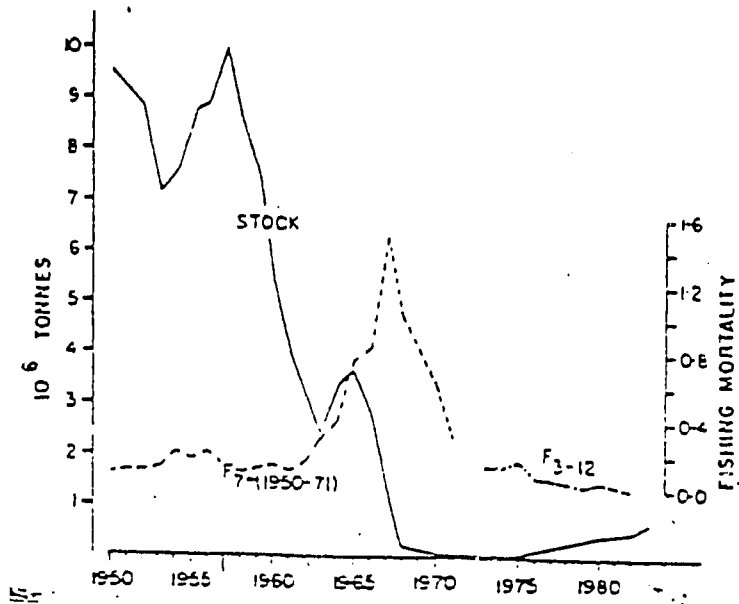
Figure 2. "Spawning stock biomass, 1950-82 (Norwegian spring
spawners), and fishing mortality (F) for 7-yr and
older herring (1950-70) and fishing mortality (F)
for 3- to 12-yr old herring in 1973-82. From
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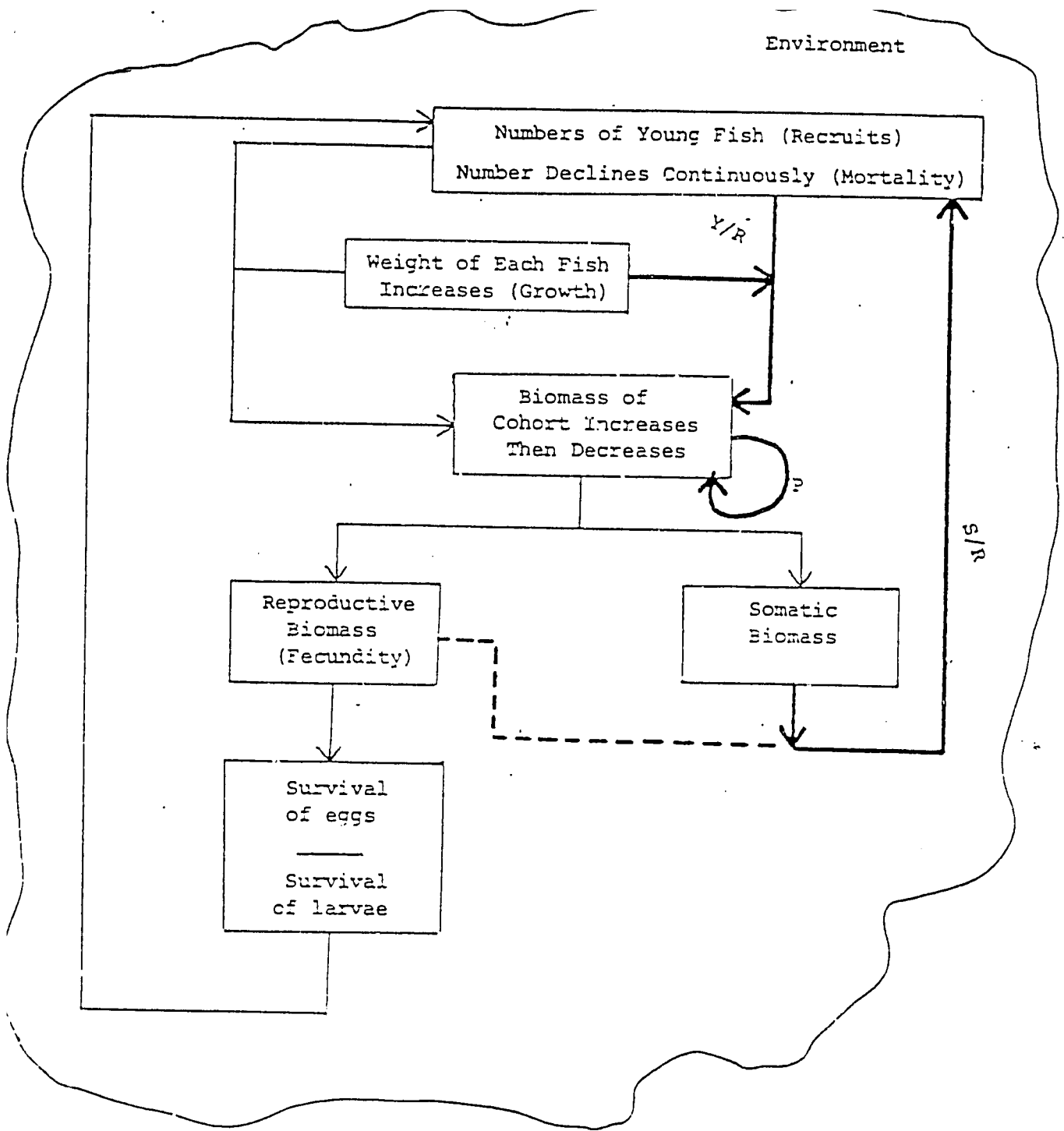Management. Can. J. Fish. Aquat. Sci., 42:207-221.

Figure 3. The mechanics of transfer among life-history stages are represented by light lines. The theories that attempt to account for these transfers are the yield-per-recruit theory (Y/R); the production theory (P); and the stock and recruitment theory (S/R). These are represented by heavy lines. The dashed line connecting reproductive biomass and somatic biomass reflects that stock-and-recruitment relations are presented as functions of either reproductive biomass (which is consonant with the available theory) or as functions of somatic biomass (in actuality, somatic biomass plus some usually unknown quantity of reproductive biomass).