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# Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: Conceptual templates and schematic constructs

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ABSTRACT

The ability to abstract and symbolize ideas and knowledge as simplified schematic constructs is an important element of scientific creativity and communication. Availability of such generalized symbolic constructs may be particularly important when addressing a complex adaptive system such as a marine ecosystem. Various examples have appeared in the climate–fisheries literature, each more or less effectively integrating hypothesized effects of several interacting environmental and/or biological processes in controlling population dynamics of exploited fish species. A selection of these are herein presented and reviewed, including *match–mismatch*, *connectivity*, *school trap*, *loopholes*, *ocean triads*, *stable ocean hypothesis*, several classes of nonlinear feedback loops (e.g., '*P2P*', *school-mix feedback*, *predator pit*), as well as several prominent large-scale integrative climatic index series (*SOI*, *NAO*, *PDO*). The importance of considering the potential for *adaptation* and/or *rapid evolution* is stressed. An argument is offered for the potential utility of such widely recognizable schematic concepts in offering relatively well-understood, fairly well-defined frameworks for comparative identification and elaboration of important mechanistic linkages between climate variability and fishery dynamics, as well as in easing effective communication among scientists from different regions and disciplinary backgrounds. Certain difficulties in the application of the comparative method are discussed. It is suggested that alleviation of such difficulties may be one of the major benefits of international collaborative programs such as GLOBEC and IMBER.

## 1. Introduction

It is clear that climatic variability can have major effects on the population dynamics of exploited fish stocks. The resulting unexplained variability in resource abundance and distribution tends even to obscure the key linkages and dynamical thresholds that determine the consequences of human impacts, notably fishing, on marine populations and ecosystems. In particular, we seem to be continually surprised by the population responses even of the primary exploited population itself. And if surprise remains the rule, i.e., if we cannot predict the outcomes of actions taken, how can we hope to manage the heavy impacts we impose on the systems so as to yield the results that we consider most preferable (or least deplorable)? Nevertheless, after decades of effort, an adequate understanding of the linkages of climate to fish population dynamics continues to largely elude us. We have various assumptions as to the nature of those linkages, and lots of ostensibly predictive models based on those assumptions, but little real predictability and little clear understanding (other than the obvious asymptotic limit to all possible dynamical trajectories, i.e., that if we catch all the fish today, there will be none to catch tomorrow).

Certainly, the conventional paradigm that has dominated fisheries science over the past half-century has clung to some rather arbitrary assumptions that seem to have been largely based on terrestrial, rather than marine, experiences and insights (i.e., perhaps better reflecting the dynamics of one's garden pond than those of an ocean ecosystem). For example, "density-dependence" and "carrying capacity" have been watchwords of the conventional methodologies, even though there is little evidence that the simple processes they imply actually exert major controls on the complex dynamical milieu of an ocean ecosystem; readers that retort "but they must" might wish to reflect as to whether their reaction may be based more on habit and on terrestrial analogies than on real knowledge of marine ecosystem function on scales larger than a human being can personally observe (note that intertidal and restricted shallow demersal situations might, in the context of this particular discussion, be considered more "terrestrial" than "marine"). Thus, for many decades prior to the previous one, the preoccupation of fisheries oceanographers (at least of those involved in resource management science rather than in the much easier task of merely aiding efficiency of exploitation) had been in fitting environmental time series to the deviations of stock assessment data from various simple, notoriously poorly fitting, steady-state, density-dependent stock-recruitment or production models that were assumed to reflect the major underlying dynamics of a marine resource population.

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It must be said that the great framers of modern fishery science, Beverton, Holt, Ricker, and others, working in the middle of the last century when very little knowledge of the real operation of marine ecosystems was available, were very successful in constructing a beautifully ingenious conceptual framework to support management decisions, resolution of conflicts, etc. But it seems that their very success and the "beauty" of their constructions may have eventually impeded scientific progress, with the practice of fishery science often tending to be very much more a methods-oriented activity than a creative intellectual exercise.

In any case, the common practice in past decades of attempting to "explain" deviations from a poorly-fitting standard steady-state density-dependent model by correlating them with one to several (usually highly inter-correlated) environmental time series has to be viewed as having been optimistic, to say the least. Natural ecosystems operate as complex adaptive systems (Levin, 1998, 1999). Accordingly, it should not be surprising that attempts to understand them as simple stationary systems have not worked very well.

But what is the alternative? The available data series are short compared to the relevant time scales of variation. How can we hope to assemble the multiple realizations of the controlling processes in order to confidently identify the basic dynamics? Moreover, if one surrenders the assumption of system stationarity, how can one hope to parameterize any sort of predictive model? This is all true. But reality is reality; it must be faced. If one is confronted with a complex adaptive system, wishing (or pretending) it were otherwise may yield "answers". But these probably will not be the correct, comprehensive, useful answers that are needed.

So how might our science move itself forward? The great evolutionary ecologist, Ernst Mayr (1982), has called the experimental method and the comparative method the "two great methods of science". The comparative method offers an alternative to the experimental method in situations in which the ability to impose experimental controls may be lacking, which is almost always the case when addressing ecosystem mechanisms at the level of large populations of mobile marine organisms.

But the comparative method, when applied inter-regionally, generally requires dialog between scientists who may not be accustomed to being in active conversation with one another. This often produces unexpected difficulties. What may seem perfectly clear to the person speaking, and would be perfectly clear to the people with whom he or she may be accustomed to converse, can very often be received as something quite different by a listener accustomed to conversing with a different group. And when this happens, the speaker may have no clue that his or her message is being misapprehended. In such cases, the ability to encapsulate ideas and conceptual frameworks in easily-communicated mutually-understood terms may be a first step to effective communication. If, moreover, these conceptual concepts should offer useful frameworks for arraying available fragments of information in ways that may reveal informative patterns, so much the better. If, in addition, they point to objective ways (i.e., not derived from the data itself, a procedure that inevitably depletes the empirical degrees of freedom available for drawing inference) to reformulate and/or combine available data series in ways that may focus more sharply on particular processes and mechanisms to be investigated or tested, even better still.

## 2. Integrative constructs of current interest

Several such schematic constructs, which may more or less effectively encapsulate a specific notion of a way in which various processes and mechanisms may interact to control fish stock dynamics, have been fixtures in fisheries–environmental research efforts for some time. Others are more recent. A selected group of some of the more prominent examples are briefly presented and reviewed in the following paragraphs. Index time series of some of the environmental or climatic factors that may be components of one or more of them have in the past been employed in attempts to "explain" variability in fish recruitment and in population size and/or distribution, either by correlating them directly with the variations themselves or with deviations from a density-dependent stock-recruitment curve, surplus production model, etc. These attempts have produced some limited insights. A potential advantage in reformulating such studies in terms of coherent integrative constructs of the type reviewed below (as opposed to "shotgun" correlation searches) may be in the ability to generalize findings for a particular population or geographic area in terms of more universal patterns of evident correspondence among similar (or dissimilar) species groups, similar (or dissimilar) geographic, oceanographic or climatic settings. Thus they may provide a structure for progressively "honing in" on the identity of dominant processes and mechanisms (in general, rather than in particular) and on the reasons for their dominance.

### 2.1. Match–mismatch hypothesis

Cushing (1971, 1975, 1990) popularized the idea that year class success in relatively high-latitude systems, because of the short growing seasons for phytoplankton production, may be crucially dependent on the timing of spawning with respect to the timing of availability of sufficient concentrations of larval food particles (e.g., copepod nauplii), with years with a good "match" yielding good reproductive success and strong year classes, and years of substantial mismatch resulting in poor reproductive success and weak year classes. Because of the very important effect of temperature on rates of biological development, interannual temperature variations are important elements of this way of thinking about population variation. Likewise, because the establishment of water column stability tends to determine the onset of the spring phytoplankton bloom in sub-polar systems, incidence of late winter or early spring storms may also be extremely important to annual recruitment strength.

Cushing mainly focused his attention on North Atlantic herring, but the idea obviously may be applicable to a number of different types of species of higher latitudes. For example, Bertram et al. (2001) showed that in the subarctic Pacific, early spring warming can result in early arousal from diapause in *Neocalanus cristatus*. When the plankton grow and return to depth in diapause early, they are not available to the important planktivorous bird, Cassin's auklet, and as a consequence there is reproductive failure in the auklet. Durant et al. (2007) provide an updated general review of the match–mismatch hypothesis and its involved mechanisms with respect to a number of species types, including terrestrial ones.

### 2.2. Connectivity and the "member–vagrant" terminology

Sinclair (1988) presented a detailed treatment of the role of local retention of early life stages by physical ocean structural features in maintaining marine populations. He referred to the individuals retained as "members" and those lost to the local population as "vagrants". Sinclair's essay has done much to call attention to the essential linkages of ocean hydrodynamics to marine population dynamics, particularly to the fact that it is only the "member" portion of the surviving offspring that is important to year-to-year population variation and to the essential question of degree of "openness" or "closedness" of a local population segment.

Because many marine species use separate locations for spawning, larval development, juvenile feeding, and adult feeding, successful connections between spatially segregated locations are necessary to "close" the life-cycle and successfully produce subsequent generations. Fishing pressure and/or climate (e.g., by altering ocean flow patterns) could potentially affect any of these critical linkages. Such