Future needs for biological oceanographic studies in the Pacific Ocean

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A personal introduction

My academic career started in agriculture, then I obtained my doctorate in the faculty of medicine, and only after this did I become aware of ecology as a science applied to fisheries. I had learned to gather data on complex problems in agriculture and medicine, analyse the data and form conclusions. When I started to study the biology of the sea in the late 1950s, it was apparent that biological studies were dominated by fisheries science. This science had a different approach to those that I had learned earlier – fisheries science was dominated by a theory on population dynamics in which there was little agreement between the data and the theory. The literature was full of stock/recruitment curves in which the data points seldom, if ever, fell on a line supporting the theoretically assumed relationship. Fisheries scientists were not responsible for collecting these data; they came largely from fish catch and the scatter of points was assumed to reflect inaccuracies in catch data rather than any fault in the ecological theory. At the same time, other branches of ecology had evolved in a largely conceptual sense characterised by a language of terms which were difficult to define precisely, such as biocoenosis, niche and neutralism – some of which also required further definition such as hypervolume niche, realised niche, etc. There was also a heavy use of probability statistics, particularly in fisheries science, which substituted for a lack of real understanding of processes. The whole science seemed to be more an expression of mystical faith than an understanding of Nature.

At that time, biological oceanography was in its infancy and had been largely concerned with measuring plankton abundance and nutrients, with little attempt to couple life in the sea with the ocean environment. It was not until the late 1940s (*e.g.*, Riley 1946) that some dynamic processes were described. These efforts remained largely unnoticed until the early 1970s when some awkward questions were asked by society regarding such practical problems as ocean pollution and declining fish stocks.   These questions required a more pragmatic approach to the science of the sea and, in the case of fisheries, a more scientific approach was called for in order to provide some realistic answers ("The Marine Revolution", Ray 1970).   I believe that this revolution is still underway and that the key to our understanding of life in the sea lies in the accumulation of extensive new data, such as has already changed the course of other biological sciences (*e.g*., agriculture and medicine).   We should also avoid the promulgation of any ecological theories or models (such as the historical dominance of Population Dynamics in fisheries science), if they are not based on factual relationships, which can be further tested from subsequently collected data.

In summary to my introduction, I believe that studies on the biological dynamics of marine life have fallen far behind other branches of applied biology, such as agriculture and medicine. I do not believe that this is due entirely to a lack of financial support, but that we have in the past been heading in a wrong scientific direction. We have a lot of catching up to do.

The holistic approach to ecosystem understanding

The basic model

The need to include environmental or climatic changes in models aimed at ecosystem understanding can be given as shown in Figure 1. In this model we include the forcing functions of climate on the ecosystem and predator control through fish abundance, which is itself controlled by the extent of fisheries at the other end. There are two potential short cuts, which I believe are to be avoided at all cost. The first is to assume that fish abundance can be determined from some

probability relationship directly with climate. There are numerous examples in the literature in which strong correlations have been shown to occur between a physical parameter, such as wind, and a fish population, only to see the correlation collapse after a few years. For example, Drinkwater *et al.* (1996) reviewed a number of papers that related temperature to lobster abundance. They concluded that increased lobster catches could not be related to temperature, in spite of several earlier findings to the contrary. In fact, it seems intuitively correct that no species could have evolved with a heavy dependence on a single environmental factor that is highly variable.
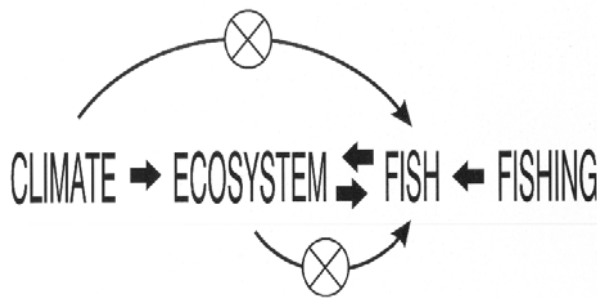

Fig. 1 A general relationship between climate, the ecosystem and fisheries indicating two alternate pathways for study which have been proved largely unacceptable in the past.

The second tempting short cut in the model above, is to consider only how the ecosystem affects fish abundance and to leave out the climate as a more or less random function. An example of how this too does not work is given by Trites *et al.* (1999) who used Ecopath and Ecosim models to account for an almost four-fold increase in pollock biomass and other changes that occurred over two time periods following changes in whaling and fishing in the Bering Sea. The mass-balance models *per se* failed to account for the observed changes, but there was a strong indication that environmental factors affecting primary production and recruitment were more important than predator/prey interactions alone. Thus mass balance ecosystem models that do not include climate variability cannot provide reliable information on trends in marine fish production. 'Quick fix' models that are not based on this fundamental understanding of ocean ecosystems should be avoided.

The problem of scaling results

Biological oceanographers have been studying the oceans on two different scales. One involves very large-scale events over long time periods, such as the identification of regime shifts in fisheries data (*e.g.*, Beamish *et al.* 2000; Klyashtorin 1997). The other involves much more detailed studies of ecosystem relationships which are carried out over relatively small areas (*e.g.*, Robinson and Ware 1994) and, in some cases, inside mesocosms (*e.g.*, Andersen *et al.* 1987). Because of the amount of data on different parameters that are required by the latter studies, they cannot be performed over vast areas. The problem is how to project the small-scale studies into the large scale studies to give us some understanding of how whole ocean systems can change.

This problem can be partly resolved if ecosystem understanding can be focused on a critical period in the life cycle of a fish. For example, Beamish and Mahnken (1999) have described critical size/critical period events in the life of coho salmon. The first event is density-dependent predation when the salmon enter the sea, and the second event is density independent and related to mortality of the young smolts in the fall and winter months depending on how well they fed during the summer. Thus the need to study the whole of the coho salmon ecosystem is narrowed to two critical periods. Another example is found in Kruse and Tyler (1989) who describe several critical periods related to climate in the reproduction of the English sole.

A more general presentation of this idea is given by Bax *et al.* (1999) who describe "leverage points" as points in time and space within an ecosystem where particular components are most vulnerable to change. This is illustrated in Figure 2 where various critical points are identified in an ecosystem model. These are identified in order to suggest to managers of fisheries resources where the ecosystem becomes highly dependent on a particular process. For example, the quantity of phytoplankton sinking out of the water column versus that which remains suspended, is a point that divides the primary production between the pelagic and benthic ecosystems. Or in another example, both the precautionary approach to
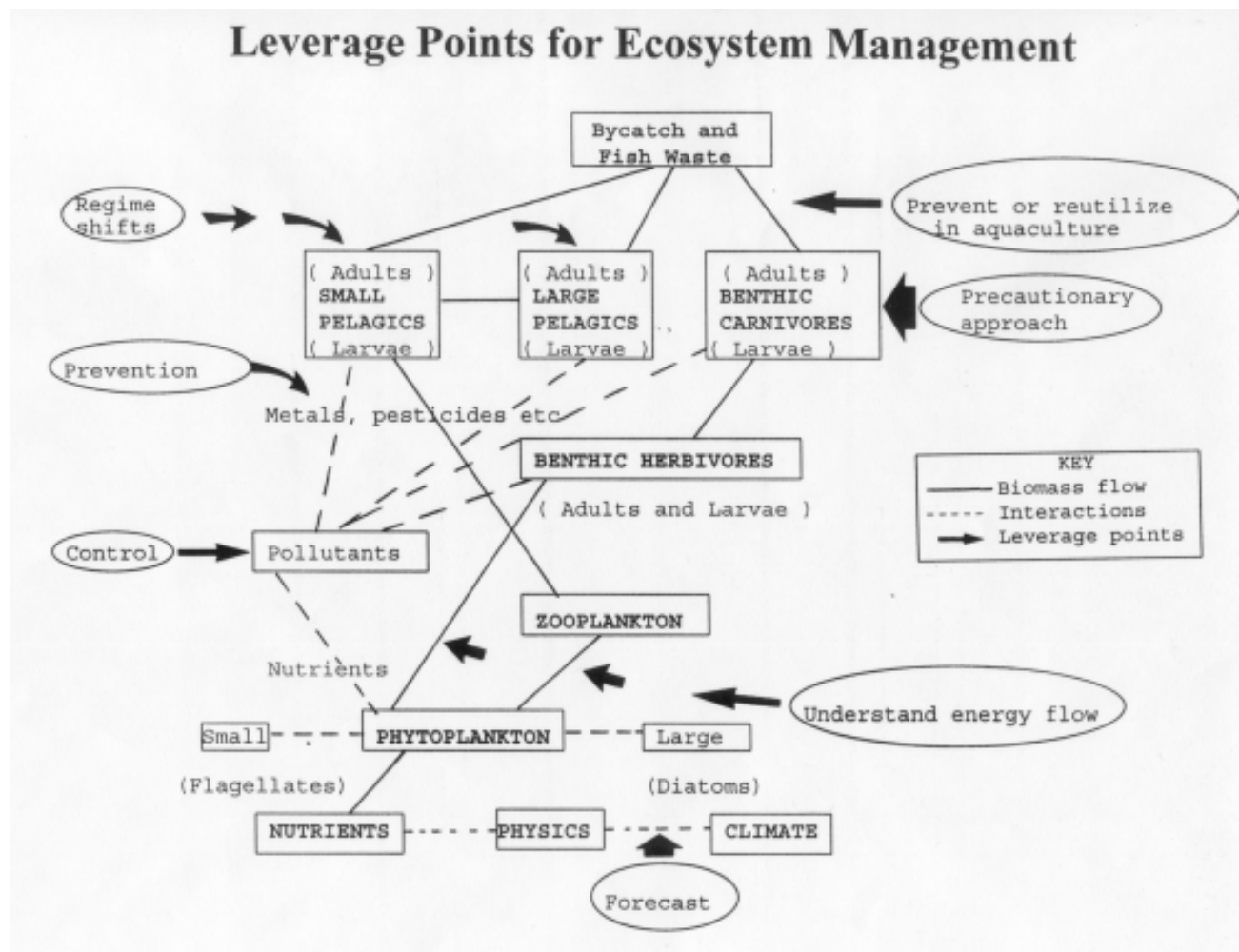
Fig. 2 A marine ecosystem model indicating "leverage points" of particular importance to management (adapted from Bax *et al.* 1999).

catching fish and the occurrence of regime shifts are critical points in predator control of the ecosystem. The role of bycatch in the ecosystem is generally ignored and should be included along with plans to utilize this high quality protein, such as in aquaculture. Pollution is another "leverage point", especially the eutrophication of coastal waters, which now appears to be widespread. By identifying these points, the problem of applying detailed small-scale data to large ecosystems may become more tractable.

Gathering new kinds of data over large areas and long time scales

Recently, the idea of "operational oceanography" has been defined as the application of science to provide timely, accurate, value-added oceanographic products and services that affect decisions of clients. This is a very broad definition and it is made in order to include a wide range of user agencies. However, among these, operational oceanography is mandated to include real-time information on changes in ocean environments and primary productivity, with forecasts of their impact on ocean ecosystems. The purpose of this desideratum is to better manage and protect the fisheries resources of the ocean (Bancroft, personal communication). Thus gathering of biological data needs to be part of operational oceanography if we are to supply data for forecasting ecosystem change. This will require new methods and new programs.

Although methodology seems a mundane part of science, in fact about half of the Nobel prizes awarded annually have been essentially for gaining scientific insight using a new method. Methods form the basis of data collection, and accumulated data are our only source of understanding ecosystems. I do not want to dwell on the past, but I want to look at some of the newer techniques that are becoming available to study the vast expanse of the oceans. We need new and original ways of gathering data at minimum expense. While I cannot review techniques, which are yet to be invented, it serves my purpose in drawing attention to the value of methodology, to briefly review some of the new techniques that have recently impacted biological oceanography. For example:

- New ways of taking multiple samples of plankton, nutrients and the physical characteristics of water masses are essential. Such equipment replaces the traditional plankton net and bottle casts, and can be towed off commercial vessels; programs have to be developed for the North Pacific (*e.g*., using Batfish and BIONESS samplers).

- New and better ways of counting and sizing plankton are also needed using more sophisticated instruments, which may sometimes be borrowed from medical science (*e.g*., the flow cytometer).

- Satellite sensing is a wonderful way of covering vast areas of ocean, and the chlorophyll maps which are now available give real-time pictures of events that were not available until only a few years ago. It would be helpful if the size of the phytoplankton could also be measured from space through some light-scattering device.

- The Argo program for examining the physical structure of the world's oceans with profiling CTDs is another advancement of great benefit to biological oceanographers.

- DNA analysis can be used by oceanographers in many ways; for example, in the correct identification of species and the tracing of discrete fish stocks.

- Automated oceanographic buoys need to be employed extensively throughout the oceans to continually monitor many biological, chemical and physical parameters.

These are but a few examples of new methods that will give biologists better time/space data coverage of the oceans. I would like to add in conclusion to this section, that many of these data can only be collected through international co-operation. This is where organisations, such as the North Pacific Marine Science Organization (PICES), can play a vital role in ocean exploration.

Models

There are many different models that can be applied to marine ecosystems depending on whether one is modelling the dispersion of a pollutant, species migrations, food chains, food webs, including or excluding physical forcing functions, and so on. Steele's (1962) pioneering work on trophodynamics, Ryther's (1969) food chain examination of fish production, and Odum's (1967) biological circuitry models were among the first ecosystem models. Much larger models that include physical forcing of the ecosystem, such as the European Regional Seas Model (ERSEM – Baretta *et al.* 1995), have developed over the years together with more complex models dealing primarily with trophic interactions (*e.g*., Ecopath, Polovina 1984). What is the optimal size of an ecosystem model? When the question being asked is very specific, such as in the case of carbon dioxide flux, then the model can be relatively simple (*e.g*., Woods and Barkmann 1993). Or in the case of fisheries, in order to keep models manageable, they should be written to deal with specific parts of the ecosystem, such as that described by Robinson and Ware (1994) for an upwelling system and four species of fish. Complex models are not necessarily better than simple models.

For the estimation of "carrying capacity" and for some aspects of climate change, models based on size relationships (*e.g*., Sheldon *et al.* 1982) may be sufficient to give useful predictions for regional forecasts. Such models have the advantage of being largely independent of species identification which is especially helpful for the plankton community, while at the other end of the spectrum, fish catch can be analysed in terms of the size of fish required (*i.e*., a large biomass of small fish or a smaller biomass of large fish).

In addition to the concepts above, genetic change may also need to be added to some models (see Grant and Waples 2000). This becomes especially important when one considers that a fishery is often inadvertently selecting for particular genetic characteristics (*e.g*., size).

Biological coefficients

In formulating equations for trophodynamic studies, it is necessary to research the values used for biological coefficients in various relationships. This includes determining and revising different forcing, physiological and phasing functions as defined in Lalli and Parsons (1999). Many of these values are fairly well known for the phytoplankton community such as the parameters of the P *vs* I curve. However, for higher trophic levels there is a need to research many relationships. For example, how turbulence and mixing interacts with the plankton and fish community is not fully known.

As another example, I believe that one very important number to study is ecological efficiency. In a paper by Pauly and Christensen (1995, Fig. 2), the authors chose a number for the transfer efficiency by surveying the literature for the most commonly used value. Since most of these values were not determined independently, a great deal of copying of a 10% value had occurred (probably based on a paper by Slobodkin, 1961), and this value was then assumed to be the most probably correct value for the authors to use in their discussion. As Baumann (1995) pointed out, choosing the most popular value of 10 % is not justification of its validity. The transfer efficiency derives its name from the useful concept of how much energy or biomass is transferred between trophic levels. It is really better thought of as the ecological efficiency (E), which is defined the same way. (However, some authors have used the term "transfer efficiency" to indicate the ratio of primary to secondary production, which is really only an indicator of the ecological efficiency; for small differences in these terms, see Parsons *et al.* (1988).

The ecological efficiency is equal to the multiple of the growth efficiency (K) and the ecotrophic efficiency (E_c), and it has been pointed out

(Parsons *et al.* 1988) that, for many aquatic organisms, growth efficiencies are of the order of 30% and the amount of lower trophic levels consumed annually (E_c) is at least 80%. Thus one would expect ecological efficiencies in the sea to be closer to 20% than the popular figure of 10%. Recent discussion of the high ecotrophic efficiency in aquatic habitats is given by Cyr and Pace (1993), and there are a number of independent estimates of ecological efficiencies (*e.g*., Sheldon *et al*. 1977; Iverson 1990; Gaedke and Straile 1994; Parsons and Chen 1994), all of which generally indicate values >15%. A more detailed account of this discussion is given in Parsons and Lalli (1988), and I suggest that this is an example of the kind of physiological value that is widely used, but poorly known, and which therefore requires some fundamental research.

The need to accurately know the various biological coefficients that are used in models is an on-going problem that requires maximum cooperation between the experimental physiologist and the field oceanographer.

Ecosystem structure

It is apparent that a large amount of marine biomass is being excluded from ecosystem studies, either because there are no data on some parts of the food chain, or because traditional focus has always been towards commercially exploitable predators. Thus there are few studies leading to ecosystems models, which include the jellyfish of the sea, non-commercial fishes and migratory mesopelagic fishes. Further quantification is needed of the bacterial loop (*e.g*., Azam *et al.* 1991). In particular, the recycling of photosynthetic products (see Kirchman 2000, for review) now appears to be very important in some environments where the whole ecosystem may depend on the recycling. With anywhere from 10^5 to 10^9 bacteria per ml of seawater, it almost appears that their previously neglected role in holding the food chain of the sea together might be crudely analogous to the missing dark matter in the universe. Bacterial cycles will also require more information on the role of zooflagellates (*e.g*., Fenchel 1982). In addition, the dynamics of viral response to an algal bloom (*e.g*., Yager *et al.* 2001) needs to be understood under different

oceanic conditions. The pelagic/benthic boundary layer (*e.g.*, Smith *et al.* 2001) forms another area for which much more understanding is required, particularly in connection with the large fisheries in the continental seas. The inclusion of more biology in our concept of ecosystem structure appears to me to be essential for the future.

Another problem in studying ecosystem structure is to keep in mind that more than one set of environmental factors can give the same result. An example of this is in the physiological dynamics of phytoplankton blooms (Parsons and Takahashi 1973). It can be shown, for example, that phytoplankton ecology may be dominated by flagellates under conditions of deep mixed water columns and low light, and also under conditions of stable water columns with low nutrients, and under conditions of eutrophication when silicate may limit diatom growth. There is often, therefore, no single explanation for ecological phenomena; cause and effect may be proportioned to a number of causative agents.

The relationship between plankton distributions and small-scale physical disturbance has recently thrown some light on how animals manage to graze particulate matter when it is so sparsely distributed. While the concentration of prey items has been easily measured, it now appears that the aggregation of prey (*i.e.*, patchy distrubtion) is just as important a number as the concentration. The effects of small-scale turbulence summarised by Seuront (2001) are (1) to increase the rate of the nutrient flux around non-motile phytoplankton cells, (2) to decrease the physical coagulation of phytoplankton cells, and (3) to increase predator/prey encounter rates. Processes involved with aggregation and physical turbulence need to be studied further (*e.g.*, Incze *et al.* 2001).

Conclusion

In conclusion, I have tried to emphasise that biological oceanography, including the fish of the sea, is still a young science. We need to collect much more data using new techniques, and we need to learn how to better integrate our results into dynamic models. My talk has emphasised the ecosystem approach as being a focal point of biological oceanographic studies, but this is not intended to distract from studies on species or communities, which I would tend to describe under the different heading of marine biology. In the field pertaining directly to fisheries science, there is no 'quick fix' via inadequate biological models. Fisheries science as part of biological oceanographic studies will only advance if it engages in fundamental studies on ocean ecosystems.

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