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A historical perspective of biological studies in the ocean

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Abstract

A holistic perspective of the last 150 years of studies in ocean biology reveals two distinct scientific activities. The first involved scientists in many expeditions from the "Challenger" in the 1870s to the Indian Ocean Expedition in the 1960s. These studies ended with what Ray (1970) has called the "Marine Revolution". This was caused by the need for marine biologists to pay much more attention to practical problems of fisheries, pollution, undersea mining and in particular the biology of the 200-mile economic zone which was established by many maritime nations in the 1970s. The new biological science of the oceans moved from largely descriptive ecology into the field of dynamic processes, holistic models, ocean monitoring and networking of different national and international organizations. Further progress in the biological sciences is needed in these areas, particularly in determining the carrying capacity of the seas and oceans and the ecological consequences of removing marine species of fish from the oceans as part of the annual industrial harvest. These problems are only likely to be solved by a consideration of the properties of entire ecosystems, which are often different, to that expected, from the sum of the determinate parts.

Keywords: Ocean ecology, fisheries, marine environment, pollution, holistic models, methodology, historical account.

Une perspective historique des études en océanographie biologique.

Résumé

Une perspective générale des 150 dernières années d'études biologiques des océans révèle deux activités scientifiques distinctes. La première implique les scientifiques dans de nombreuses expéditions depuis celle du « Challenger » dans les années 1870 à l'expédition dans l'océan Indien, dans les années 1960. Ces études se terminent avec ce que Ray (1970) a dénommé « la révolution marine ». Ceci en raison de la nécessité, pour les biologistes marins, de porter davantage d'attention aux questions pratiques des pêches, de la pollution, des ressources minérales sous-marines et, en particulier, à propos de la biologie dans la zone économique des 200 milles, qui a été établie dans les années 1970 par les nations maritimes. La nouvelle science des océans passe alors de l'écologie largement descriptive aux champs des processus dynamiques, des modèles globaux (holistiques), des réseaux océaniques de surveillance de différentes organisations nationales et internationales. D'autres progrès dans ces domaines des sciences biologiques sont nécessaires, en particulier en déterminant la capacité à produire, des mers et des océans, et les conséquences écologiques du prélèvement des espèces marines, poissons, etc. des océans, comme une partie d'une production industrielle annuelle. Ces problèmes sembleraient résolus en prenant en considération les propriétés de l'ensemble de l'écosystème, qui est souvent différent, de ceux prévisibles, de la somme des parties déterminantes.

Mots-clés : Écologie des océans, environnement marin, modèles globaux, méthodologie, perspective historique.

INTRODUCTION

The crises in world resources and widespread pollution are likely to remain at the forefront of human concerns at least well into the 21st century. These concerns were first recognized in what Ray (1970) described as the "Marine Revolution". This revolution began about 25 years ago in terms of new maritime laws (e.g. anti-dumping laws for oil tankers), the establishment of 200-mile economic zones surrounding maritime nations, offshore mineral exploitation and the ever-expanding fishing fleets of the world in competition with each other for diminishing resources. All of these problems and more have added up to a renewed need to understand the biology of the seas before the fish resources are severely depleted or widespread pollution causes hydrospheric damage. The author notes that *"An emphasis must be given to marine ecosystems and to the role of the marine ecologist in the oceanographical debate"*. The question is whether our basis for understanding the oceans' biology is sufficiently flexible to undertake this task, or whether we are rooted in some historical paradigms which may make scientific progress difficult in this field.

Toward the end of the 19th century, Lord Kelvin's (1824-1907) view of physics was that there was little more to be investigated – that there only remained some minor difficulties which, together with determining physical constants to an increasing number of decimal places, generally summarized the future of the science. This narrow view of physics by an outstanding physicist has not been unique in the history of science. Prior to the 1930s, we have only to turn to medicine to learn that before the discovery of antibiotics, enzyme chemistry and physiological function, a lot of medicine was an unscientific art. The medical professional was known to have a "practice" and practice they did on many an unfortunate patient (*i.e.* the "patient" being one who was defined as enduring pain, largely without remedy). In fisheries science today, the lack of advancement is aptly stated by Larkin *et al.* (1984) *"... it must be acknowledged that for some fisheries the costs of research have been high for many years but the fisheries are currently no more rewarding financially than they were twenty years ago"*. This is epitomized also by the reprinting of a fisheries textbook (Beverton and Holt, 1957) in the 1990s after a period of nearly 40 years in which, unlike other sciences, little seems to have happened to add new chapters to our knowledge of how to manage the fish resources of the oceans.

In recalling these historical facts it is appropriate to ask whether biological studies of the oceans suffer from the same complacency, or whether there are grounds for some optimism in seeing this science progress toward the useful goals of prediction and eventual management of Nature. In this regard we have attempted to track the evolution of biological studies in the ocean, starting with the systematists working in the middle of the 19th century, through to the ambitions of present day ecosystem modelers. In tracking this record (*fig.* 1) we are not writing a history, but only recording the advancement of thoughts about ocean biology as they were developed by various scientists. Thus all reference material [(1)] is only given as an example of a certain quality of work that represents a need to understand biological processes in the ocean. In this sense our review has something in common with Wust's (1964) attempt to classify major deep-sea expeditions and record progression in oceanographic understanding. Taking into account this classification, we have called the first 100 years of biological studies in the oceans the "Era of Expeditions". Starting in about 1970 with the Marine Revolution (Ray, 1970), we have then described the next decades as the "Era of Practical Problems" which is concerned with formulating solutions to many problems of benefit to humanity (*fig.* 1). Finally we shall discuss some aspects of future research in ocean biology.

Early developments in the understanding of the ocean's biology

Studies of the systematics and distribution of marine organisms by naturalists (e.g. Edward Forbes, 1815-1854; *see* also Abe, 1986) were among the earliest scientific contributions to ocean biology. By the latter part of the 19th century, such studies were being conducted on a global scale (e.g. the "Challenger" Expedition, 1872-1876) and large expeditions remained a characteristic approach to ocean biology right up to the 1960s, culminating in the International Indian Ocean Expedition of that decade. By the end of the 19th century, marine biological laboratories and societies had been founded in many countries and continued to proliferate into the 20th century. Publications in marine biology starded with monographs on marine organisms but eventually a synthesis of oceanographic knowledge appeared in "The Oceans" by Sverdrup *et al.* (1942). This latter publication was representative of a state-of-the-science compilation of oceanic physics, chemistry and biology, but it was in fact one of the last publications for many years to take such a holistic view of the ocean environment. By the 1950s, interests in the economics of fisheries removed the study of the abundant top predators of the ocean from the rest of the biological studies; in addition, the physics and chemistry of the oceans tended to be studied in isolation from the biology. For several decades biological oceanography became largely reduced to a study of plankton. However, in spite of the relative isolation of plankton studies from fisheries

(1) Most reference material in this text is taken, by example, from North American, European and Japanese journals.

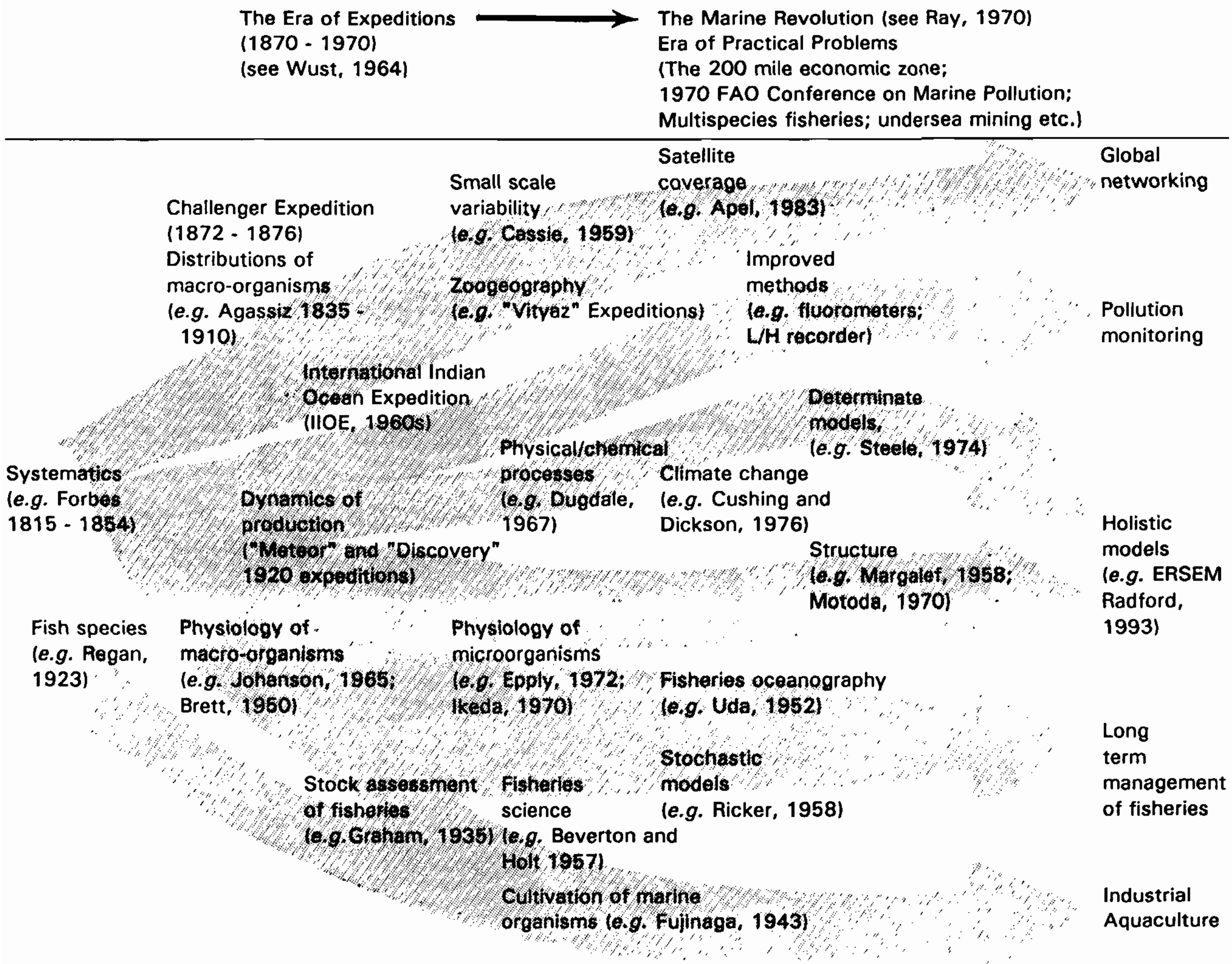

Figure 1. – A schematic history of biological studies in the ocean. The history of biological studies in the ocean is seen in this diagram as being at first exploratory (The Era of the Expeditions 1870-1970–*see* Wurst's reviews, 1964) and secondly an era of practical problem solving which was brought about in the 1970s (the Marine Revolution) by the declaration of 200-mile economic zones, marine pollution (FAO Conference, Rome 1970) and the expansion of world fishing fleets and areas, including problems in aquaculture. During the first of these eras, scientists concentrated on systematics, zoogeography, dynamic processes (including nutrient/phytoplankton and higher trophic relationships) and in fisheries, on the physiology of organisms and on a stochastic approach to fisheries management. In the second era, socio/economic pressures dominated in requiring biologists to give some practical answers. The response of the scientists was an improvement in methodology, the evolution of trophodynamic models, the inclusion of climate in forecasting, the development of fisheries oceanography and the initiation of regional and global monitoring programs (Note: All names associated with developments are given by example only). *ERSEM*: European Regional Seas Ecosystem Model, *L/H;* Longhurst/Hardy.

and other oceanographic disciplines, there were several scientists in the 1940-50s who attempted an integrated approach to phytoplankton dynamics using the first mathematical models (e.g. Riley, 1946) to relate biological production to the physics and chemistry of the sea.

While environmental studies of the ocean became fragmented in the first half of the 20th century, the study of fish physiology progressed as a separate science and yielded a massive amount of information from a few prolific authors (e.g. Johansen, 1965; Brett and McConnel, 1950). Physiological studies were also made on molluscs (e.g. Walne, 1972) and crustaceans (e.g. Fujinaga, 1943), and these together with the studies of fish, were to form the backbone of industrial aquaculture projects. Although many aquaculture projects are still under development, aquaculture already accounted for about 10% of the world harvest of fish and shellfish in 1988 (Rhodes, 1989). Another important result of the work of the physiologists was in determining organism tolerance to various forms of pollutants and to set the LD_{50} standards on which much of marine pollution control is founded (e.g. Trama, 1954).

Progress through methodological advancement

In the history of granting agencies, it is generally considered that persons working on improved techniques are technicians, and that research scientists should concern themselves with philosophical questions about Nature.

Consequently in the distribution of funds, technique development generally has to be disguised within some loftier research proposal if it is to obtain funding. In retrospect, however, it is often the improved technique that has led the way to scientific advancement. In biological oceanography, numerous examples exist of new data sets obtained from new techniques paving the way for an increased understanding of the environment.

The invention of the continuous plankton recorder (Hardy, 1936) gave us vastly improved data (e.g. Colebrook *et al.,* 1961) on the time and space distributions of plankton in the sea, compared with data from various earlier versions of the towed net. Steemann Nielsen's (1952) use of radioactive carbon made it possible to measure photosynthesis of plankton. Automated nutrient analyses (e.g. Armstrong *et al.,* 1967) increased the output of data on nutrients in seawater by an order of magnitude. Scuba diving observations, manned submersibles and remotely controlled camera systems have enabled scientists to see for the first time the delicate and complex world of nekton and plankton *in situ* (e.g. Harbison *et al.,* 1978) and the deep water benthic communities (e.g. Hessler and Lonsdale, 1991). In the 1980s, satellite oceanography added an enormous visual dimension to our understanding of global distributions of plankton in relation to water type (e.g. Apel, 1983). In addition, acoustical surveys have advanced to the point of providing estimates of the biomass of pelagic fish (e.g. Simard *et al.,* 1993). In nearly all these methods, one has also to acknowledge the tremendous benefit of computer science to oceanographers; this has affected every aspect of the science from data gathering to improved techniques.

This list of advancements in techniques is almost endless and it is safe to assume that the pattern of new techniques leading to discoveries will continue in the future, even though research funds are seldom centered on the techniques themselves. However, the downside of methodology has been a lack of appreciation for some new techniques coupled with a lack of standardization of any one technique for use by international teams of scientists. The first of these problems can only be dealt with by funding agencies encouraging the use of new techniques, whereas the second requires international collaboration such as was achieved in the design of a standard plankton net (UNESCO, 1968), as well as the preparation of updated versions of oceanographic methods (e.g. Omori and Ikeda, 1984).

The pressures of fisheries and pollution

Any science which does not have a socio/political background of support is not likely to receive sustained funding from the public. In the case of marine biological studies of the ocean, it can be said that the very earliest studies were driven more by curiosity than economics. However, large-scale funding through government did not become an assured fact of life until there were one or more problem areas that required data on marine biology. Two such problem areas were fisheries and pollution; in particular, it was the territorial need to understand these two subjects within the 200-mile economic zones, which initiated both the redirection and release of new funds for biological oceanographic research. New funds particularly became available in the early 1970s through the formation of many environmental companies, which represented a substantial new investment in the practical problems of ocean science.

Many fisheries organizations and laboratories were founded in the latter part of the 1800s. In addition to their role in trying to account for declining fish stocks, most of these organizations initiated some fundamental studies on the biology of the seas, particularly with respect to planktonic organisms and benthos. Some of the earliest fisheries scientists considered that environmental effects on fish were important in determining year class strength (e.g. Hjort, 1926). These initial studies waned in importance, however, with the publication of a series of books (e.g. Beverton and Holt, 1957) advocating the management of fisheries through an understanding of stock/recruitment, independent from environmental studies on the life history of fish. However, the lack of long term success in application of fisheries science to management has led to a growing dissatisfaction of governments with the absence of a predictive fisheries science. To quote from a Food and Agriculture Organization (FAO, 1980) report on this subject, *"Major changes in the conditions affecting fisheries development and in the perceptions of fisheries problems have occurred since the early 1970s... These changes have led to a wide-spread frustration and dissatisfaction with the performance of fisheries management and policy and to a sence of crisis".*

A further account of fisheries management is given by Smith (1994) in which he concludes that many committees have been set up to study fisheries problems but that these have invariably been unsuccessful in reaching conclusions. He attributes this to economic and political interference, as well as to the inadequate scale of research programs in fisheries. This has led some scientists to return to the position that multispecies fisheries are part of the total ecosystem of the sea and that the abundance of fish is governed by the environment, as well as by the harvest. This point of view was first re-established by Japanese scientists (e.g. Uda, 1952) who founded the Fisheries Oceanography Society of Japan in 1944. More recently many ecological papers have appeared on the early life history of fish. Further enhancement to biological understanding of the oceans has come through journals dedicated to an understanding of marine ecology (e.g. "Marine Ecology: Progress Series", Publ. Inter Research, Germany). More recently, there is an important role for multidisciplinary resource orientated journals (e.g. *"Aquatic Living Resources"*, Gauthier-Villars, France).

The driving force for pollution research in marine biology appears to have arisen later than that for fisheries. Two events that attracted the attention of the public and eventually of politicians, were the occurrence of mercury poisoning derived from fish in Minamata Bay, Japan (1953/1958), and the sinking of the "Torrey Canyon" (1967) from which about 117,000 tons of crude oil escaped into the English Channel. In 1970, FAO organized a world conference on marine pollution to draw attention to the many potential and real forms of oceanic and coastal pollution. A new incentive, combining both the management of fisheries and national studies on pollution, was then provided by the establishment of 200-mile economic zones in the offshore waters of many maritime nations. The USA declaration of such a zone occurred in 1970, but it was preceded and followed by other maritime nations. Within these zones, intensive pollution studies of the biota (e.g. the Mussel Watch Program started in the 1970s) and biological studies of the most productive fisheries ecosystems (e.g. Symposium of Upwelling Ecosystems, Kiel, 1975) started to produce results which gave us a better descriptive view of how marine biological systems function *in toto*.

Today it is generally recognized that anthropogenic effects on the oceans are not confined to the addition of pollutants. The effect of fishing itself, in removing top predators from the ocean, has had an impact on ocean ecology that far exceeds any form of local marine pollution. This is apparent in the restructuring of the Antarctic ecosystem following the decimation of blue whales (Laws, 1985); in the Black Sea where only 5 commercial species of fish are harvested today compared with 26 at the turn of the century (Zaitsev, 1992); and in the Bering Sea, where the removal of 5 million tons of pollock per year is causing changes in the populations of marine mammals and birds (Springer, 1992). While these and other examples have been largely incidental in the context of scientific reporting, the situation is in fact such that there has been practically no scientific investigation of the impact of removing large numbers of fish from marine ecosystems. This should become an area of particular concern in future biological studies of the ocean.

Effects toward a predictive science

In order to achieve any form of predictive capacity in science, it is necessary to establish a criterion against which change can be measured. The simplest criterion for change is some measurable departure from an average state and if this can be shown to occur within some probability statistic (usually $p = 0.05$), any advance knowledge of such a change will amount to a prediction. In biological studies of the ocean, such predictive changes have been used extensively in pollution studies where, if a predetermined level of a toxic substance (LD_{50} response) is exceeded in the environment, the prediction is that there will be extensive fish mortality. Many pollutant assays are based on some biological function in addition to the LD_{50} response, but all of these generally require probability statistics in order to validate the prediction in any environment.

In studies on oceanic ecology, a different approach has been generally adopted in which prediction is based on the combined effect of a number of forcing functions in bringing about a change in a parameter. While the verification (ground truth) of this deterministic approach may also initially require a statistical analysis of ecological data, once the model has been validated, it is assumed to apply (within the limits of the initial assumptions) as an empirical relationship upon which prediction can be based. An early example of such a model was given by Sverdrup (1953) in his mathematical formulation of the critical depth hypothesis for determining the timing of the spring phytoplankton bloom in temperate latitudes. A more recent example is Pingree's (1978) analysis of the biological importance of frontal zones. Phytoplankton physiology also has been formulated in terms of empirical relationships of concentration-dependent nutrient uptake and photosynthetic response to light intensity. Among zooplankton and fish, similar relationships are found for the uptake of food, growth and metabolism (e.g. Dugdale, 1967; Ikeda, 1977; Palaheimo and Dickie, 1966).

Holistic models, integrating some of these empirical relationships, may be quite simple (e.g. Ryther's 1969 model for the determination of fish production from primary production) or they may have greater degrees of complexity depending on the purpose of the model (e.g. Steele's 1974 simulation of planktonic ecosystems). Such models usually contain forcing functions (e.g. light and nutrients), physiological function (e.g. the response of phytoplankton to light), and phasing functions that modify the relationship between other variables (e.g. the extinction coefficient acting on the amount of light). While a holistic model may partly be constructed from the empirical relationships described in the paragraph above, it may also have a physical oceanographic component. The most sophisticated of these models today is probably the European Regional Seas Ecosystem Model (ERSEM) which dynamically simulates the large-scale cycling of carbon, oxygen and macronutrients over the seasonal cycle of the North Sea. Physical transport is included by driving the model with the output of physical circulation and dispersion models (Radford, 1993). The model can essentially be used for a variety of purposes including estimates of fish production, effects of eutrophication, a carbon budget and the effect of climate change. Similar models have been described by others for specific purposes (e.g. Woods and Barkmann, 1993, The Plankton Multiplier Model for determining the effect of climate change on the carbon dioxide budget). In responding to any of these uses, such models generate scenarios of possible change; as discussed below, however, although these models are determinate in function, they are not wholly predictive in output. Prediction can only be given in terms of the probability of the most likely scenario.

The chaotic nature of Nature

The movement of the atmosphere around the earth is a relatively simple system compared with the interacting totality of all the biological species and processes which make up Nature. Yet it has been known for some time that models of climate based on a series of complicated equations cannot be used for any longterm predictions of the weather. This is so because there tends to be more than one solution to such predictions. Collectively, these solutions can be used to produce scenarios of possible events as well as some probability concerning which of these scenarios are the most likely occur. Nature, being infinitely more complex than climate, falls into the same problem of being driven by determinate forces, but at the same time it has a direction that is stochastic. Such systems are generally described as being chaotic.

In chaotic systems there are two kinds of variables, the dynamic which change with time, and the static which do not change during the period of the observation. An example in biological oceanography might be the changes in phytoplankton and zooplankton over time (the dynamic variables) with the total quantity of nutrients available, as well as the equation linking nutrients to phytoplankton growth (the static variables). Example of phase diagrams (*fig.* 2) can then be plotted of phytoplankton and zooplankton changing in time. Such a diagram generally has a elliptical shape, but small random changes within the system, even under purely experimental (*i.e.* controlled) conditions, will not allow an observer to trace exactly the same ellipse of phytoplankton vs. zooplankton each time the grazing cycle is repeated. In the theory of chaos, the region traced by this variable phase diagram is known as the attractor. The attractor can have different shapes as illustrated in *figure* 2 (top). The addition of other trophic levels to the model gives the attractor

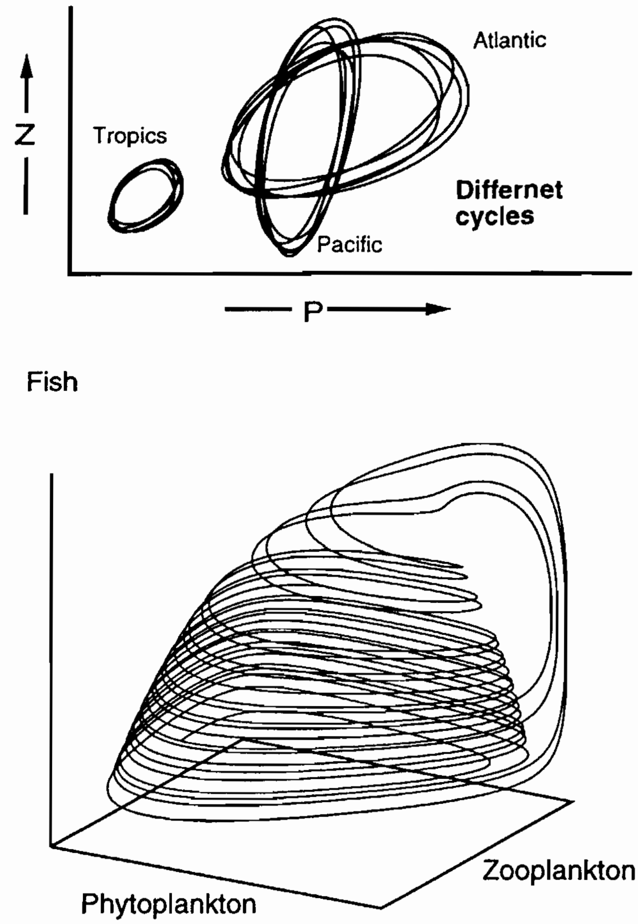

Figure 2. – Chaotic attractors in different oceans (top); a chaotic attractor involving three trophic levels (bottom, redrawn from Hastings and Powell, 1991).

additional phase-space in which the dynamic variables can be found (Hastings and Powell, 1991 – *fig.* 2, bottom). In this last illustration, the role of a top predator in stabilizing the fluctuations in the plankton community can be seen by the much lower variations in zooplankton and phytoplankton at the top of the figure, when the fish biomass is at a maximum. Small changes in initial conditions of such systems can lead towards stable attractors (*i.e.* a state of equilibrium) or they may lead to catastrophic transitions resulting in strange attractors (e.g. Doveri *et al.,* 1993).

Having characterized one of the simplest biological oceanographic relationships as having the properties of a chaotic system, it must be asked what can be salvaged as being useful for prediction and understanding from such a system? The system may not become more predictable through reductionism; it is the property of the system, as a whole, that is causing the problem in making any kind of prediction. The need in science is for holistic principles which will describe collective activity. Some additional properties of chaotic systems may help in our understanding of what is important in this respect.

Firstly, while chaotic systems do not maximize certainty, they do eliminate considerable uncertainty. The determinate factors driving the system only allow for the system to operate within the chaotic attractor, which eliminates uncertainty of possible results outside this region. For example, in the zooplankton/phytoplankton relationship above, the attractor for tropical systems is quite different to that for temperate systems (*fig.* 2). Secondly, chaotic systems are flexible and can be forced to follow one of many behavior patterns through perturbations. Essentially this is the case in aquaculture where such control is exerted on the predator/prey relationship that there is usually only one cycle of events. Thirdly, the behavior of the dynamic variables within the attractor, tell us something about how the system may operate, independently of environmental change. In *figure* 2 for example, it is only when the top predator (fish) increases in abundance that control is exerted on the two lower trophic levels (phytoplankton and zooplankton). As the fish population declines, large variations start to occur in the two plankton populations such that it is quite possible to generate a bloom of phytoplankton without the addition of more nutrients. This is a revealing result since the occurrence of phytoplankton blooms is generally only interpreted as being a bottom-up causative effect due to eutrophication.

In the natural ecology of the oceans, the fixed parameters and small differences in residual populations can both contribute to long-term changes in populations of marine organisms. The fixed parameters are largely determinate (e.g. solar radiation, the total amount of nitrate available) and fluctuations in these parameters over time (e.g. with season) can be used to make some predictions of natural events. However, the output from such predictions becomes stochastic over longer time periods because as each cycle repeats itself, the small changes in initial populations (such as the overwintering survival of predators) causes subsequent changes to occur in the output which may become magnified over time. Eventually this can lead to a displacement of the equilibrium point of a relatively stable attractor and to the birth of a new system which might be described as a catastrophic change. An example of such a change is described by Steele and Hendersen (1981), who showed that a shift in a relatively stable phase diagram of zooplankton and phytoplankton could be caused by introducing different concentrations of (overwintering) ctenophores. Doveri *et al.* (1993) give another example in which the annual fisheries harvest can be destablized by introducing a small change in the initial fish population.

Thus for a number of reasons, the holistic approach of ecosystem modelling is valid for predictions of short term scenarios as well as for providing insight into the causes of longer-term trends. As long as the initial conditions are reasonably well known and the time or distance scale of the prediction is small, so as not to allow many random events to influence the model, then predictions of such events as the spring phytoplankton bloom or the occurrence of biological fronts become valid (providing also, of course, that assumptions made in the equations are correct). For the purpose of management, however, where there may be a requirement for long term predictions of fisheries or risk analyses, there is always going to be the same uncertainty as is found in much simpler systems, such as in atmospheric forecasting.

The future of the science

An increased understanding of what determines Nature as we see it today can be achieved following four basic lines of research as suggested by Malone (1976). These are: to understand the flow of energy through Nature; to understand the recycling of biologically important elements within the biosphere; to understand the life cycles of plants and animals; and to understand the accumulation of information within the system in terms of its biodiversity. The difficult problem lies in how these four lines of research should be pursued.

While the long-term future may not be predictable as discussed above, the uncertainty of some events may be reduced by a much greater understanding of the present. In order to achieve this understanding it is not simply sufficient to add more and more observational data published in entirely descriptive papers. It is necessary to discover new concepts, either through observations of unique phenomena (the intuitive recognition of a new principle without reference to established dogma), or to ask yes/no questions (hypothesis testing) which reveal greater insight into how Nature works. It is unfortunate that, almost by definition, funding agencies have to favour the latter approach in that they always require a research proposal based on existing science. Further, in this latter approach, Dayton (1979) has cautioned against proposing hypotheses of Nature that cannot be answered, however great the data bank. An example from above might .be not to ask the question, "Is zooplankton abundance in the sea related to the abundance of phytoplankton?" It is impossible to give a yes/no answer to such a question because it is largely the productivity of the phytoplankton, and not abundance, that drives zooplankton production; abundance is only a residual effect of predator/prey relations (Fleming, 1939). Dayton (1979) suggests (borrowed from Robert Pirsig, 1974) that the answer to the question above should be the Japanese term *"mu"*, meaning "no thing". There are indications that, in the past, some scientific investigations in biological studies of the sea have been based on unanswerable *(mu)* questions. A chaotic response, for example, is essentially a *mu* answer to a yes/no question such as, how well do the data fit model predictions? The question being asked may be too small for Nature's response. The model may actually describe the attractor rather than predicting in any factual way how the model results will "match" the data.

Another problem area in biological oceanographic models is the subject of biodiversity. Most models reduce the biodiversity of a system in order to simplify the mathematical approach. In doing this they are eliminating an important property that needs to be understood; they may also be inadvertently affecting the outcome of the model through over-simplification of the input.

Returning to *figure* 1, the future of holistic models appears to be, therefore, in creating scenarios of change, including the possibilities of catastrophic change. On a much shorter time scale, real-time forecasting will improve from better satellite imaging as well as from the use of highly specific models. These efforts will be assisted through global and regional networking of scientists, which is already underway in such programs as JGOFS. In these studies, long-term data sets are required (such as the Continuous Plankton Recorder programme) and the initiation of such studies is important in spite of the general lack of enthusiasm for "routine" data collecting among scientists. Such programs should be the function of agencies rather than of individual researchers.

New methodologies are required to improve the gathering of data over protracted periods and vast areas of ocean. A summary of some improvements in this area has been given by Herman (1993) who discusses the use of advanced platforms (e.g. an undulating towed vehicle such as "Batfish") in combination with new continuous recording methods using fluorescence and electronic particle counters. The actual platforms and techniques to be used in sampling the ocean must be tied to the time/space scales of biological events, as illustrated in *figure* 6 from Esaias (1980).

Molecular biology and genetic engineering are going to play an important role in marine biology, both from the point of view of understanding fundamental processes and in the increasingly important role of aquaculture in our society. In addition, new techniques for diagnosing pollutant stress can be expected to be developed from this more sophisticated biological methodology.

The fossil record should continue to provide insight into evolutionary ecology (e.g. Newell, 1978). Data on the hindcasting of events are also needed using the paleo-oceanographic record, or more recent time series data collected from any biological system that records climate (e.g. tree rings in coastal environments). While correlations between historical fisheries data and climate change have not been proved useful in a predictive sense, such data have indicated that various forcing functions of climate may have influenced fisheries over a period of time, only to be replaced later by some other factors. Thus such correlations are essentially investigative science and they should be followed up with testable hypotheses using a multiplicative approach of bottom-up and top-down control of marine ecosystems.

Finally it is necessary (with some urgency) to reorganize the scientific management of fisheries to include environmental factors and the multispecies competition between the teleosts and jellies of the sea. The latter group of organisms pre-date the age of fishes by around 200 million years and they remain to-day as competitors for the same plankton resources that are consumed by many of the commercial species of fish. Avian and Sandrin (1988) have documented one of the few studies in which jellyfish were shown to increase with increasing pressure of fish catch. The effect of commercially removing large amounts of fish from the sea must also be examined in a holistic approach to marine ecology. Among all the scientific disciplines, it is doubtful whether any could have met with less management success than fisheries science, which may be partly due to the science but is also a function of political and economic interference as described by Smith (1993). From the intensively managed stocks of the North Sea to the anchovy of Peru, from the cod stocks of Newfoundland to the demise of 20 commercial species of fish from the Black Sea, the story, for whatever reason, is the same; fisheries have been persistently mismanaged in the absence of any strong predictive science that could be used to determine the carrying capacity of the seas and oceans of the world.

The study of site-specific marine ecosystems, such as estuaries, mangroves, coral reefs, intertidal shorelines and deep vent communities, should continue to be organized through a high degree of networking in order to reduce the cost of developing generic understanding of the unique ecologies of these systems. These communities are often the most heavily impacted by anthropogenic pollutants, and the long-term effects and management of such communities can only come from good cooperative science. The diagnosis of the difference between long term (climatic) change and pollution stress is particularly important in such studies.

CONCLUSION

In conclusion, the history of biological studies of the ocean can be divided into two periods: the first was characterized by many expeditions of discovery; the second by attempts to solve practical problems. Progress in biological studies has been achieved through developments in methodology, physiological investigations, ecosystem modelling, pollution monitoring, aquaculture and global networking of scientific effort. These efforts have met with some success. However, the lack of progress in the application of fisheries science to management may require that a more diagnostic approach be developed using oceanographic information for the understanding multispecies ecosystems and the carrying capacity of the oceans. Long-term data sets, new concepts, new methods and increased international co-operation are all required for the future of the science.

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