I2
Some Varieties
of Biological
Oceanography

J. H. Steele

12.1 Introduction

The apparent uniformity of the oceans has turned out to be an illusion generated by the original need for widely spaced sampling both horizontally and vertically. We can no longer accept concepts based on relatively smooth gradients in temperature or salinity. In his paper, "Varieties of Oceanographic Experience," Stommel (1963) pointed out the wide range of scales, in space and time, on which variability occurred. Improvements in technology and development of theoretical bases (Rhines, 1977) portray the oceans as a physical system whose structure can be as rugged as that of the terrestrial world (see chapter 11).

The spatial and temporal variability of the organisms that inhabit the oceans has been recognized for decades. Without this variability, commercial fishing would be uneconomical and sport fishing unexciting. Patches of plankton extending for tens of kilometers were reported in the 1930s (Hardy and Gunther, 1935) and mapped in the 1960s (Cushing and Tungate, 1963). There was, however, no detailed knowledge of the possible relation of these biological observations to corresponding physical structure.

In recent years there have been several attempts to integrate the physics and biology, but on two different levels. The development of fluorometric techniques (Lorenzen, 1966) has permitted continuous *in vivo* measurement of phytoplankton pigments. This, combined with continuous measurement of nutrients such as nitrate, allows detailed portrayal of the spatial structure of the first step in the production cycle. When combined with temperature and salinity measurements from a moving ship, they provide the basis (figure 12.1) for attempts to determine the physical factors determining horizontal phytoplankton patchiness—or, alternatively, to ascribe some aspects of this patchiness to biological mechanisms. The basic technique, spectral analysis, was started by Platt (1972) and developed both theoretically and technically (Steele, 1978a).

The other major area of interest in environmental variability relates to the study of fish populations. The expansion, indeed overexpansion, of commercial fisheries leads to fishing on populations with a younger average age. The fisheries, and the populations themselves, become more and more dependent on the yearly recruitment. In nearly all stocks this recruitment has very large year-to-year fluctuations (figure 12.2). The study of these fluctuations has attracted much research and produced many hypotheses. A large proportion of these hypotheses has attempted to relate variable recruitment to changes in the physical environment, either year-to-year differences or longer-term trends (Hill and Dickson, 1978). During this same period, however, it has been realized that individual species cannot be treated separately, and "multispecies man-
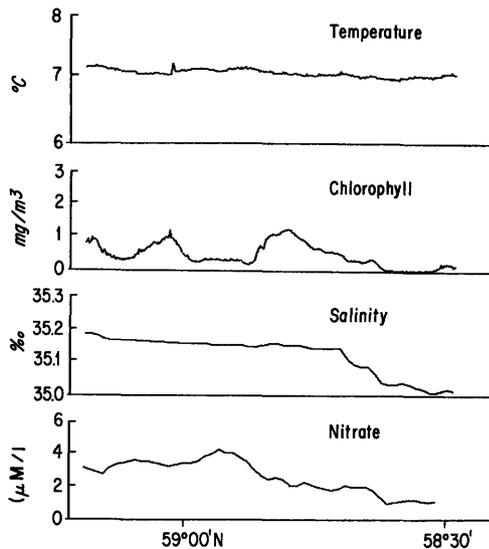
Figure 12.1 Measurements made at 3 m in the northern North Sea during the hours 0000-0500 on 16 May 1976. There are no obvious relations between variations in chlorophyll and nitrate, or between these and the physical parameters temperature and salinity.
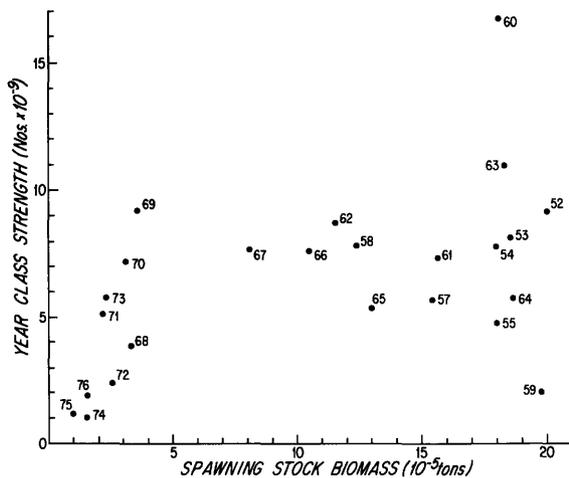

Figure 12.2 Year class strength of North Sea herring as a function of the biomass of the spawning stock. Only in the final years of stock collapse, 1974-1976, do the values of recruitment fall outside the range of previous variability. (Ulltang, in press.)

agement" is now in vogue. This recognizes the interrelation between species, in their food requirements and, potentially, in their recruitment. Thus, again, there is a need to separate the physical and biological factors acting to produce the observed distribution and abundance of fish populations.

For these two extremes of the food web, phytoplankton and fisheries, there is an extensive literature, which I shall review very briefly. For both, it is apparent that the biological factors limiting our understanding lie in the intermediate components of the food web—the zooplankton, which graze on the plants and which, in turn, are the source of food for the fish populations. But these interactions must be placed in the context of the variability of the physical environment at a wide range of space and time scales.

These problems are applicable to all regions of the sea, but, scientifically and economically, are most acute in areas of the continental shelf. Certain parts of the open ocean, such as the centers of gyres (Eppley, Renger, Venrick, and Mullin, 1973), may be considered relatively uniform horizontally, but the shelf is dominated by changes in all significant physical, chemical, and biological parameters—depth composition of the bottom, temperature, salinity, nutrients, and the quantity and quality of living organisms—at all the possible horizontal scales. Moreover, there is an equally great variability in the vertical structure of the water column, and this variability is conditioned by, and related to, horizontal changes. An example of vertical changes is shown (figure 12.3) in the close correspondence between temperature and fluorescence during passage of an internal wave packet produced by variable bottom topography in Massachusetts Bay. For these reasons, there is an emphasis in this chapter on variability in coastal areas.

12.2 Space and Time Scales of Variation

12.2.1 Physical Variation

As a point of departure, it is necessary to start with certain observed regularities that relate to patterns of horizontal variability. Experiments on dye dispersion by Okubo (1971) and others show a consistent relation between the variance of concentration across a patch and the time from release of the dye. This relation demonstrates the expected dependence of horizontal diffusivity on spatial scale. Using the standard deviation σ derived from this variance, the relation with time t is, approximately,

$$\sigma = t^{1.17}, \tag{12.1}$$

where the units are kilometers and days (Steele, 1978b). This almost linear relation suggests that populations spreading from some initially small area should have a patch "size" in kilometers numerically similar to

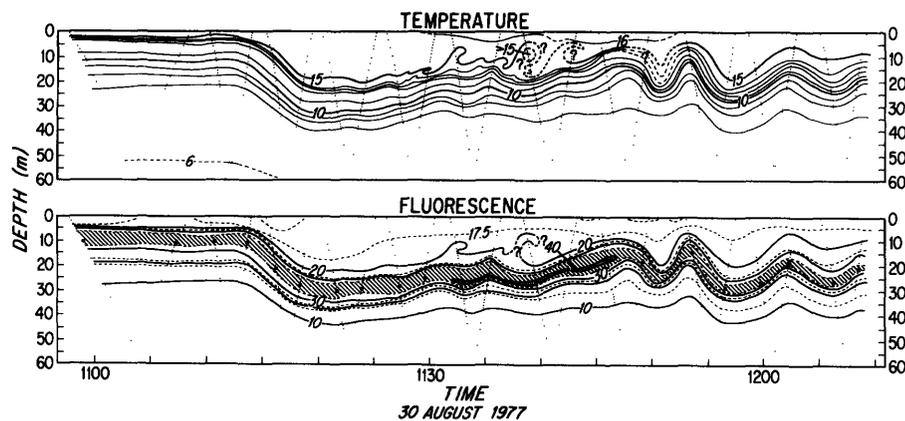Some Varieties of Biological Oceanography

Figure 12.3 The passage of an internal wave packet past a drifting ship in Massachusetts Bay produces rapid changes in vertical structure, shown by the temperature profiles, with a close correspondence of the changes in fluorescence that gives a measure of the concentration of phytoplankton. (Haury et al., 1978.)

their lifetime in days. Yet such a relation cannot be general. Not only will land boundaries limit the extension, but internal vertical features, such as fronts, will alter radically the way in which variance changes with time. The general effect of such boundaries is partly predictable when they have some measure of permanence. But there are also highly unpredictable events, associated with weather, that can alter significantly the temporal variability. These events tend to have their greatest impact on the shelf, particularly near coasts (Csanady, 1976). Thus persistent fronts (Pingree, 1978) and wind-driven motions produce features whose combined time and length scales are very far from the relation derived in equation (12.1).

Further, there are questions about the adequacy, in a biological context, of representing horizontal changes by a process of eddy diffusivity. This concept ignores the related vertical features. An alternative (Taylor, 1954; Bowden, 1965; Kullenberg, 1972) derives horizontal dispersion explicitly in terms of vertical processes. A combination of vertical shear and vertical mixing can explain much, but not all, of the horizontal dispersion. Potentially, this can be used to describe temporal changes in rates of dispersion due to variations in wind stress. This picture has considerable advantages in the study of particles, living or inorganic, that move vertically through the water. At this stage in the discussion, the concept of horizontal diffusion has a provisional and heuristic value.

12.2.2 Biological Variation

When we turn to the plant and animal populations, a similar and very simplified portrayal of space and time scales has been used to indicate the main features of variability (P, Z, F) at different trophic levels (figure 12.4) (Steele, 1978b). The life span of individual phytoplankton cells is a few days. Theoretical calculations (Steele, 1975) suggest that there is a critical scale of a few kilometers at which growth rate of a phytoplankton population P can overcome physical dispersion processes to cause biologically induced patchiness. At the other extreme, pelagic fish F such as herring in the North Sea, have an average life span of a few years and an ambit, produced by their annual migrations, on the order of 1000 km. Herbivorous zooplankton Z are the main link between phytoplankton and pelagic fish in the food chain. Copepods, which are the dominant herbivores, have a life span of 20-50 days (Marshall and Orr, 1955), and there is some evidence for patches of copepods on scales of tens of kilometers (Cushing and Tungate, 1963).

The simple linear P-Z-F derivation in figure 12.4 is, once again, a heuristic device to emphasize the scale relations. These connections imply that any ecological interrelations in the food chain necessarily require interactions between different space and time scales. Thus the inherent difficulties, technical as well as conceptual, in modeling or sampling the complete range of physical events in the ocean, apply equally to the modeling and sampling of the related biological processes.

From equation (12.1) and figure 12.4, it appears that there is a rough correspondence between the scales in space and time of physical and biological dispersion. This could imply that the biological system has evolved to take advantage of the regularities associated with the general temporal and spatial character of physical dispersion in the sea. This is too simple since it ignores the actual relations involved. Theories of phytoplankton patchiness have been based on horizontal diffusivity, but pelagic fish migration is usually associated with, and possibly related to, particular features of current systems (Harden Jones, 1968). Also, zooplankton aggregations may depend on the combination of their own vertical migration and the vertical shear in the water column (Hardy and Gunther, 1935; Evans, 1978).
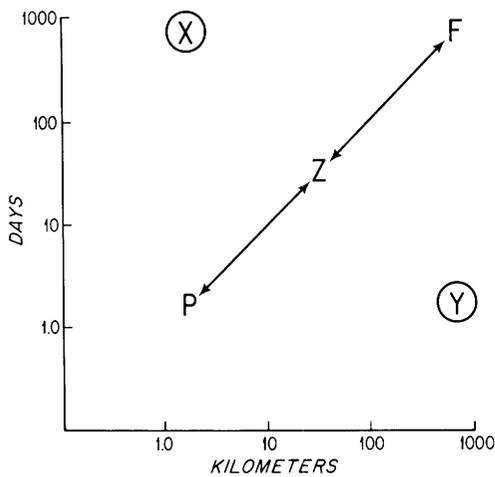
J. H. Steele

Figure 12.4 A heuristic presentation of scale relations for the food web P (phytoplankton), Z (herbivorous zooplankton) and F (pelagic fish). Two physical processes are indicated by (X) predictable fronts with small cross-front dimensions, and (Y) unpredictable weather-induced effects occurring on relatively large scales.

Further, the simple diagonal relation in figure 12.4 ignores the existence of physical features above and below this line. Many observations show that fish are often found at discontinuities such as fronts. The concentrations of phytoplankton at such small-scale features (taking the appropriate scale to be at right angles to the front) can be explained by events at similar small scales (Pingree, 1978). But the fish aggregations require a long-term evolution involving selection of these areas as part of much larger-scale migrations. Thus small-scale features that are persistent or predictable on large time scales (X in figure 12.4) are one biologically significant divergence from the simple pattern.

Temporal variability in the biology is demonstrated at all trophic levels and is probably greatest for populations on the shelf. It is most extreme and has been best documented for the annual variation in recruitment of fish stocks, where the ratio of maximum to minimum can be 10^3. This great variability is generally associated with the short-term but relatively large-scale unpredictability in weather. Normally, the populations or communities can accommodate such unpredictability and may have evolved to utilize it (Steele, 1979). Extreme variations, especially when combined with heavy fishing, can be disastrous. El Niño, off Peru, is the best-known case (Wooster and Guillen, 1974), but fish kills in the New York Bight are another example (Walsh et al., 1978). These events, of short duration but on a larger scale, can be depicted by Y in figure 12.4.

A general portrayal of the types of physical variability occurring in the sea would occupy all the space of figure 12.1. Two locations, X and Y, have been chosen to simplify the discussion because they epitomize the

problems facing an interpretation of biological processes in terms of physical structure. In essence, they provide an alternative caricature of the physical environment. Instead of smoothly changing parameters determined by horizontal diffusion, there is an ocean with relatively uniform areas divided by steplike fronts with some degree of permanence relative to biological processes. Within these large areas having long-term spatial uniformity, there is a temporally fine structure subject to great and unpredictable variability. These simplifications may provide a framework for diagnosing the ecological and technical problems involved in linking the extremes of the food chain.

12.3 Ecological Variations

Because theories or hypotheses cannot handle the whole of the space-time field, the area must be decomposed into conceptually and technically manageable pieces. On occasion this can be done by choosing particular hydrographic features or using special experimental methods. Thus the eddies known as Gulf Stream rings found in the Sargasso Sea, with a diameter of about 100 km, have been used to study the progression in time of the zooplankton populations isolated within the rings (Wiebe et al., 1976). On a smaller scale, large plastic enclosures containing about 100 m^3 can be used to study interactions of phytoplankton, herbivores and invertebrate carnivores for periods of about 100 days (Menzel and Steele, 1978). Both techniques rotate the diagonal of figure 12.4 into a purely time-dependent system.

An alternative approach is to seek out aspects of the ecosystem that may be relatively independent of the spatial variability. In figure 12.4 the components P, Z, F are regarded as single entities, but, in fact, each contains a great diversity of species and, for Z and F, a wide range of age classes for each species. By considering size structure as a first approximation to species diversity or to age composition, it is possible to study the size-frequency distributions within P, Z, or F as a function of their own metabolism and of their size-related intake of food. This approach can be used to construct general theories about size structure (Silvert and Platt, 1978), or to depict possible changes with time in size composition dependent on variations in environmental conditions or predator populations (Steele and Frost, 1977). By considering such "internal" features of the ecosystem, regularities in structure, independent of patchiness, can be predicted and tested.

These experimental or analytic techniques avoid rather than solve the general problems of relating ecological structure and its variance to physical conditions. The inherent difficulties, if not impossibilities, of a full-scale treatment have focused research on par-
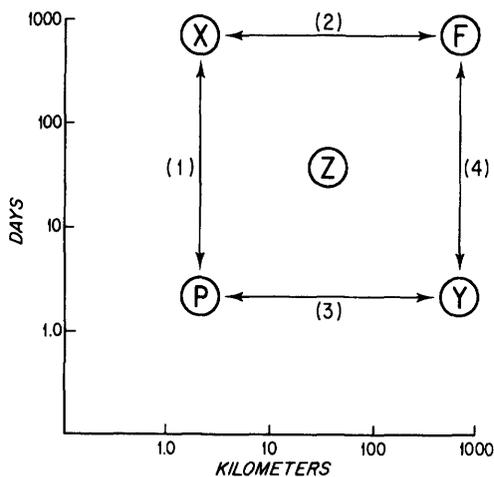
Figure 12.5 An indication of the four main links between physical and biological factors that can be studied within logistical constraints. The details are described in the text.

ticular scales, and these may be categorized by the four components in figure 12.5.

(1) Phytoplankton variability in areas with relative horizontal uniformity has been studied using fluorometers with water intakes at various depths (Fasham and Pugh, 1976). When compared with simultaneous temperature data, both results have wavenumber spectra varying as K^{-n}, with n generally in the range $1 < n < 3$ where K is the wavenumber. Differences in the slopes of the two spectra have been used to deduce effects of biological rather than physical origin. Decreases in n for the chlorophyll spectrum for wavenumbers less than 1 km^{-1} have been taken to indicate the consequences of phytoplankton population growth rates counteracting diffusion processes (Platt and Denman, 1975). Values of n for chlorophyll greater than those for temperature may arise as a result of grazing by the herbivorous copepods (Steele and Henderson, 1979).

There is very much less information on the spatial distribution of these herbivores in the appropriate range, $0.01 < K < 10 \text{ km}^{-1}$, because of the technical problems in sampling vertically migrating populations, but some results by Mackas (1977) show even greater variations for near-surface populations at night (figure 12.6) and suggest that there can be negative correlations with chlorophyll at scales with $K < 1 \text{ km}^{-1}$.

(2) There are many cases of high phytoplankton concentrations associated with frontal systems. Detailed studies have been made by Pingree, Holligan, and Head (1977) of the phytoplankton near fronts produced by the relation between tidal energy and shelf depth (Simpson and Hunter, 1974). The observed concentrations of chlorophyll (figure 12.7) are much greater than would be predicted on the basis of the conversion of available nutrient concentrations into plant biomass.

It would seem likely that a particular combination of vertical motions of the water and of the phytoplankton relative to the water is required.

The relation of these concentrations to herbivore grazing is not known, but in other areas, such as the early spring front found at the western edge of the Baltic outflow into the North Sea, above average densities of herbivores occurred which were linked to concentrations of herring (Steele, 1961).

(3) Migrations of pelagic fish and whales in relatively dense aggregations are the normal pattern of behavior. At any time of year, a particular stock is usually found in a restricted part of its overall area of distribution, with the remainder of the area at near-zero densities. Ryther (1969) and Sheldon, Prakash, and Sutcliffe (1972) have shown that as one goes up the trophic ladder there is a decrease in average productivity by a factor of 5 to 10 between adjacent trophic levels. There is a corresponding increase in length of life, however, which results in a near equivalence in average biomass. If one considers the peak concentration of biomass, then the trend is reversed, and, for the particular example of the Antarctic summer (figure 12.8), there is an almost linear relation between appropriate length scale of the organisms and concentration factor (data from Sheldon et al., 1972; Omori, 1978; El-Sayed, 1971).

Figure 12.8 demonstrates that these increases in peak concentration are not purely local events but must depend on concentrating organic matter over large
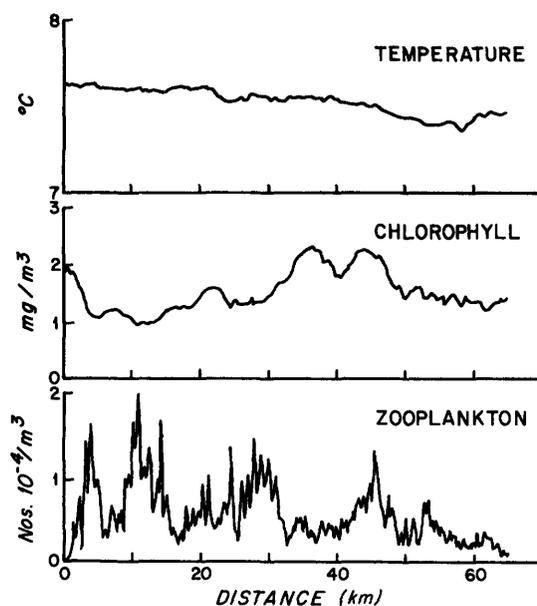

Figure 12.6 Data at 3-m depth on temperature, chlorophyll, and zooplankton numbers collected in the northern North Sea, 19–20 May 1976, between the hours of 2200 and 0400, when the zooplankton are concentrated in the near surface layer. (Mackas, 1977.)
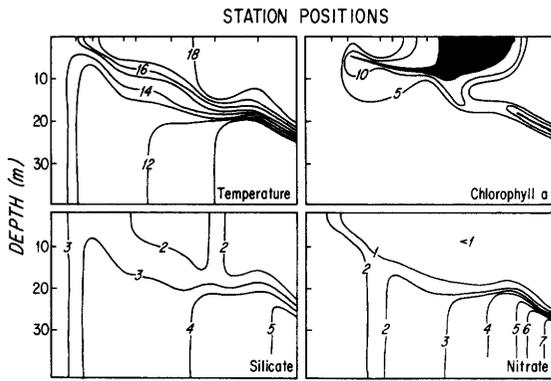
J. H. Steele

STATION POSITIONS

Figure 12.7 Vertical sections through a front in the English Channel of temperature (°C), chlorophyll a (mg m^{-3}), silicate and nitrate (μM l^1), illustrating the very high concentrations of phytoplankton that can occur in conjunction with particular physical conditions. (Pingree et al., 1977.)
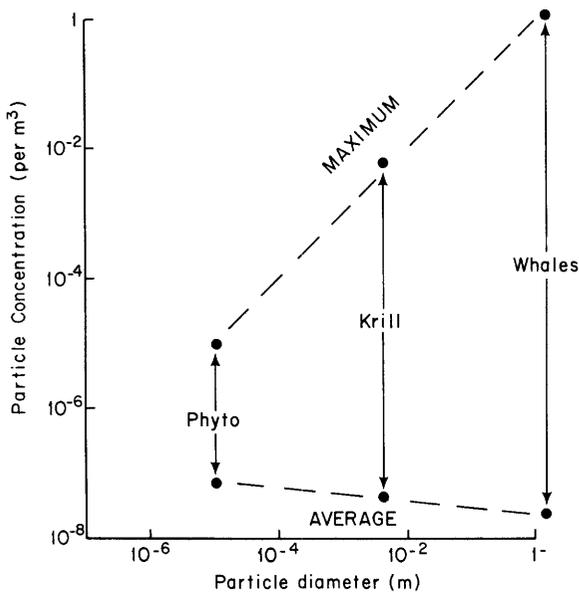

Figure 12.8 The range of concentrations between average and maximum for three trophic levels in the upper layers of the Antarctic in summer. The units are "wet weight" as a fraction of each m^3, or tons per ton, which is an appropriate unit for commercial harvesting.

space and time scales. It is unlikely that any predator—copepods, herring, whales, or fishermen—could operate effectively at the average concentrations. They live off the variance rather than the mean. Thus migrations, or concentrations, of fish at fronts must be partly, but not completely, associated with feeding—and with feeding on herbivores rather than on phytoplankton concentrated at these fronts.

(4) Year-to-year variations in fish-stock recruitment are usually associated with unpredictable environmental fluctuations. In some extreme cases it is possible that they may be linked directly with physical factors, but usually the causal relation is assumed to exist in terms of food availability. For certain species, such as the anchovy, this link can be with phytoplankton populations and, in turn, variations may be related to dependence of the concentration of particular phytoplankton species on thermocline structure (Lasker, 1978). A stable regime in the upper layer is needed to concentrate the food of larval anchovy. Turbulent conditions destroy these aggregations and dilute concentrations of food organisms below feeding thresholds.

Many larval fish, however, feed on copepods, with the preferred size of food increasing from the nauplii to the adults as the larvae grow. But it is not clear that recruitment to the main population is completely determined at these early stages, and the changes in life style around metamorphosis may be critical in terms of corresponding changes in feeding habits (Steele, 1979). Again, there are problems of scale. Spawning stocks, and so initial larval populations, may be confined to a few relatively small areas of the order of 10^2 km^2. These populations disperse as they mature, occupying 10^4-10^5 km^2 around metamorphosis, while the adult populations often move over areas of 10^6 km^2 or greater. Again, the timing of critical events in the life cycle will be related to particular scales, and so postulation of the critical processes is needed to plan the logistics of field programs.

12.4 Discussion

This grouping of ecological studies into four compartments, and their relation to physical features, takes no account of the great body of recent work devoted to the population dynamics of particular species. But these, in turn, often neglect the physical dimensions of the populations. I have chosen to emphasize field and theoretical work that, for logistical and conceptual reasons, has concentrated on horizontal or vertical components in the space-time frame. This approach also emphasizes the division of ecological studies into two almost separate classes; the one based on phytoplankton dynamics, and the other concerned with fish populations. The artificial division of our research ef-

Some Varieties of Biological Oceanography

fort into basic and applied plays some part in this separation, but it is also imposed by the inherent problems in linking events at the different space and time scales. The difficulties are analogous to those in linking studies of the energetics of waves with those of ocean currents. The need to create these links is as great in the ecological as in the physical case. There are other analogies since the linkages will depend on mesoscale events and on the way in which energy and structure are transferred up and down the space–time scales. There are also direct causal connections between the physical processes and the biological changes. In terms of the biological and physical interaction, the diagonal of figure 12.4 divides the space into two regions. In the lower region the variability is dominant and essentially unpredictable in terms of the occurrence of particular events at specified locations. The analyses of data are in terms of statistical criteria, and the simulation of patterns is based on stochastic models. In the area above the diagonal, patterns are generally predictable and theories can be expected to be deterministic.

For phytoplankton, it might be possible to regard the overall population distributions and production as a superposition of these two components. For fish populations, however, a more complete integration is needed. Particular species must have evolved to be able to absorb the initial variability displayed in the recruitment data. Communities of closely related species may depend on this variability to retain their diversity (Steele, 1979). Within the same life cycle, however, utilization of major and persistent physical features determines the detailed patterns of movement. Thus changes in the physical environment at a wide range of scales could alter the patterns of fish production, and there is evidence for large-scale (Hill and Dickson, 1978) as well as possible small-scale effects (Lasker, 1978).

In these conjectures, as can be seen from figure 12.5, the missing element is the role of the intermediate stages in the food chain, typified by the herbivorous zooplankton Z. Each of the four connections in figure 12.5 omits the ecological involvement of the zooplankton. For example: (i) the possible role of grazing on scales of patchiness has been described; (ii) the very high densities of phytoplankton at fronts imply a loss of grazing control on these populations; (iii) migrating fish stocks may feed on plankton during their progress along fronts or have feeding areas as their destination; (iv) lastly, the critical factor for larval survival is believed to be the density of copepods of the appropriate size (Jones and Hall, 1973). Thus the links in figure 12.5 should all pass through, or include, Z.

We have some knowledge of the general distribution of certain species such as the *Calanus* spp. in the North Atlantic (Colebrook, 1972) and the North Pacific

(McGowan, 1971). For the smaller species such as *Pseudocalanus* spp. or *Oithona* spp. our knowledge is more fragmentary. But we lack information on the smaller-scale structure, so that the position of Z in figures 12.1 and 12.2 is really a convenient interpolation. Further, we do not have methods for measuring the growth rate of individuals in their natural environment, so our estimates of secondary production are informal guesses. These guesses, however, would suggest the need to study events in areas of 100 km² for periods of 100 days, and it is apparent from the logistics for such studies that they are not easily carried out.

For these reasons there is a desire to parameterize the effects of the herbivores on the higher or lower trophic levels that may be more amenable to study. Such parameterizations depend upon the assumption that interactions are predominantly in one direction, permitting assumptions about closure terms or forcing functions in theoretical presentations. The flow of energy in the ecosystem is upward from the source in photosynthesis to final dissipation at the highest trophic levels, with 80–90% losses at each trophic step. This would appear to define a unidirectional system with the forcing functions located in the physical processes that control the supply of light and nutrients. But, although it is not apparent in the simple diagrams used here, any set of equations depicting the system, or even one link, are essentially nonlinear and there are significant feedbacks. Thus, in nutrient-limited environments, the nutrients excreted by the herbivores can account for two-thirds or more of the nutrients taken up by the phytoplankton. Further, in studies of phytoplankton patch structure, a parameterization of grazing as a reduction in net growth rate of the phytoplankton gives different spectral distributions (Fasham, 1978) from those obtained using simple interactive relations (Steele and Henderson, 1977).

Also, it can be shown theoretically (Steele and Frost, 1977) that in models that represent the internal features of each component in terms of size structure, changes in the predation on the herbivore alters not only the herbivore but also the size structure of the phytoplankton. These *downward* changes can be demonstrated experimentally using large enclosures (Gamble, Davies, and Steele, 1977). This flow of energy upward and of structural changes downward affects our interpretation of perturbations in the fisheries. It seems improbable that functions such as deterministic stock-recruitment relations can adequately describe the interactions with lower trophic levels. Nor will simple stochastic inputs, related to variance of recruitment to individual stocks, be sufficient since these ignore the interrelations of stocks due to total energy limitations.

There are direct causal connections between the difficulties in describing the total spectrum of physical processes and the similar problems in describing the

J. H. Steele

whole food web. There are also analogies between the procedures for approximating the dynamics at particular scales and the parameterizations needed to model portions of the food web. The transfer of energy and structure between scales is a common feature. The nonlinear coupling of variance at different scales is possibly a more significant problem in the biology since at the largest scales, the commercial fisheries, variance in space and time dominates the economics as well as the ecology.