Because time, trained intelligence, and society's resources are scarce, biological and fisheries oceanographers must be judicious in choosing scales of investigations in order to understand the resulting variability in pelagic ecosystems. We must decide whether the ecological effects can be predicted best from correlations based on long time series of coarse-grained field data (i.e., data taken on scales large relative to the daily ambit or life span of individuals). We have, actually, rather few such sets of data for anything other than commercial catches and coastal climate, and one can argue that we need many more, for more elements of the food web. In this perspective, study of small-scale processes would be, in effect, irrelevant to predicting large-scale variation, or at best an inefficient way to proceed.

As the alternative approach, we must (a) deduce the implications of large-scale climatic change ("global" or "regional" models) for the physics (and chemistry) at the much smaller scale of individual organisms (micrometers and milliseconds for bacteria, kilometers and hours for fish)—change both in the mean conditions and in their variability; (b) analyze through controlled experiments the changes in physiology and behavior that these will cause ("process submodels"); (c) determine quantitatively all the critical interactions between species under these altered conditions; and then (d) reason back "up the spectrum" to variations in populations and communities by some weighted summation process and some food web paradigm. One problem with such linked models is that each is likely to be an incomplete or imperfect description of nature, even at its own scale, and we might well question the reliability of a prediction arising from concatenated uncertainties.

This dichotomy of approach is not so stark as I have painted it, nor are the choices so mutually exclusive. However, there is no question that our intellectual, technological, and financial resources for environmental research are limited and therefore must be deployed efficiently.

2
DISTRIBUTION AND PRODUCTION IN THE PLANKTONIC FOOD WEB: LARGEST AND SMALLEST SCALES

My purpose in this and the following chapter is to review, by means of examples, some of the distributions in space and time of components of the plankton and their rates of growth, particularly those distributions that can be related to specific scales of physical/chemical processes and that are likely to affect the food webs of larval and juvenile fish. I shall emphasize examples from the open ocean, though many of the strongest correlations between distributions and physical parameters are found in estuaries. As indicated in Chapter 1, the ultimate (but as yet unattained) goal should be to understand how the different scales affect each other, so that impacts of change in the physics and chemistry of the ocean on a large scale can be predicted on several biological scales. Ideally, these would also be the scales of greatest societal concern.

I shall set the stage by a brief description of "conventional" understanding of the large-scale, average distributions of planktonic biomass and production, as a contrast to what follows. I most definitely do not denigrate this understanding, nor do I imply that physical and chemical processes are less well integrated into it than into the studies I have chosen to review in greater detail. However, I shall explore more fully both the implications of some scales of physical and chemical processes that have been suppressed in the conventional descriptions (and, often, by conventional methods of measurement) and the question of whether these scales will be affected by changes in the ocean on larger scales. This summary is background to a consideration of whether variability on the scale of populations and communities is likely to be predictable from a summation of the effects of small-scale, altered processes. Unfortunately, such consideration does not provide a definitive answer.

I shall also review some mathematical models that simulate the effects of physical and chemical properties on biomass and production of plankton. The particular models are examples of a larger body of work; such models are usually unrealistic in their simplicity, but they permit the investigator to explore the consequences of a particular process in a way that even controlled experimentation does not. The best such models lead to conclusions that are both counterintuitive and testable with field data.

Ocean Basin and Regional Scales

The optimal large-scale conditions for rapid growth of phytoplankton in the open ocean occur in middle and low latitudes, where daylength exceeds eight hours all year, in those regions where the surface layers are only weakly stratified vertically. Regions in the higher latitudes can also support rapid growth, but only for the sunlit part of the year. These generalizations reflect the need of phytoplankton for adequate light and a supply of nutrients from waters below the euphotic zone (or, in some circumstances, from horizontal advection). In principle, grazing by zooplankton could keep phytoplanktonic biomass small by removing it as fast as photosynthesis produced it, but in fact the regions of rapid growth (on this large scale) also tend to have greater biomasses of phytoplankton than do less eutrophic regions, so the primary production (biomass-specific productivity times biomass) can be quite high (Table 2.1).

Table 2.1. Geographical variation in standing crop and primary production by phytoplankton

Type of area	Euphotic depth (m)	Chlorophyll (mg m^{-3})	(mg m^{-2})	Phytoplankton biomass (g C m^{-2})	Gross production [mg C (m^{2} day)$^{-1}$]
Strong upwelling[a]	< 30	10–25	100–400	5–20	500–4,000
Weak upwelling, mixing, benthic regeneration[b]	< 80	1–10	20–100	1–5	200–500
Weak mixing[c]	< 100	0.1–1	10–20	0.5–1	50–200
Minimal mixing[d]	< 150	0.05–0.1	5–10	0.25–0.5	10–50

[a] Benguela, Chile–Peru, other eastern boundary currents, some bays (runoff).
[b] Equatorial countercurrents, Gulf Stream, Oyashio Current, most shelves.
[c] Equatorial currents, tropical oceans.
[d] Sargasso Sea and other subtropical central gyres, Mediterranean.

Nitrate (NO_3^-) can be taken to represent all nutrients regenerated from sinking particulate matter by decay and (for N) subsequent oxidation. As a first approximation, it is supplied to the euphotic zone by turbulent diffusion or advection from deeper water. This provides the N for what has come to be called "new" production (which technically could include N in rainfall, etc.). Ammonium (NH_4^+) is regenerated within the euphotic zone as a result of metabolism and excretion by zooplankton and bacteria (Dugdale and Goering 1967). As a result, separate measurement of the uptake of these two forms of N illustrates the role of supply from below in fueling both high biomass-specific and total primary production of eutrophic waters. Figure 2.1 shows the relations between specific growth rate and the ratio of new to total primary production (sometimes called the "f" ratio) and the ratio of regenerated to total primary production as a function of total primary production as carbon.

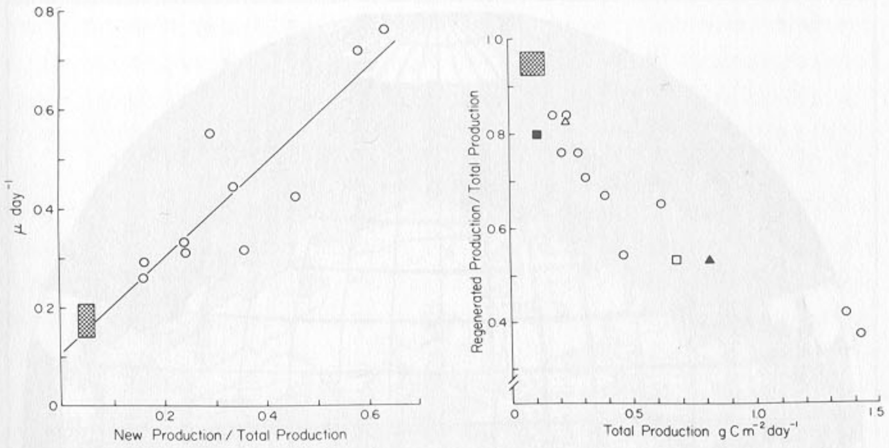

Figure 2.1 *Relations between growth of phytoplankton and source of nutrients.* Left: *biomass-specific growth rates (per day) of natural assemblages of phytoplankton vs. "f" ratio of new to total primary production.* Right: *regenerated (NH_4^+-based) as a fraction of total primary production vs. total primary production as carbon.* Open circles *are individual stations in the Southern California Bight,* shaded rectangle *is several stations in the North Pacific Central Gyre,* solid square *is Caribbean data,* open square *is offshore Monterey Bay,* solid triangle *is eastern tropical Pacific, and* open triangle *is eastern Mediterranean. From Eppley 1981.*

Conversely, at large spatial/temporal scales, nitrogenous biomass that is removed from the euphotic zone, for example, when particles sink or fish are caught, must be replaced by "new" N if primary production and the food web are to continue to function (Eppley and Peterson 1979, Eppley et al. 1983, Horne et al. 1989). Interestingly, this concept is also an important one in considerations of change in global climate because of the so-called Redfield ratio, the intimate linkage between C and N in metabolism. The recycling of carbon within the euphotic zone, its sinking into deeper water, and the degree to which it remains there rather than returning to surface waters all affect how the ocean counteracts or augments anthropogenic changes in atmospheric CO_2 and the resultant "greenhouse" heating.

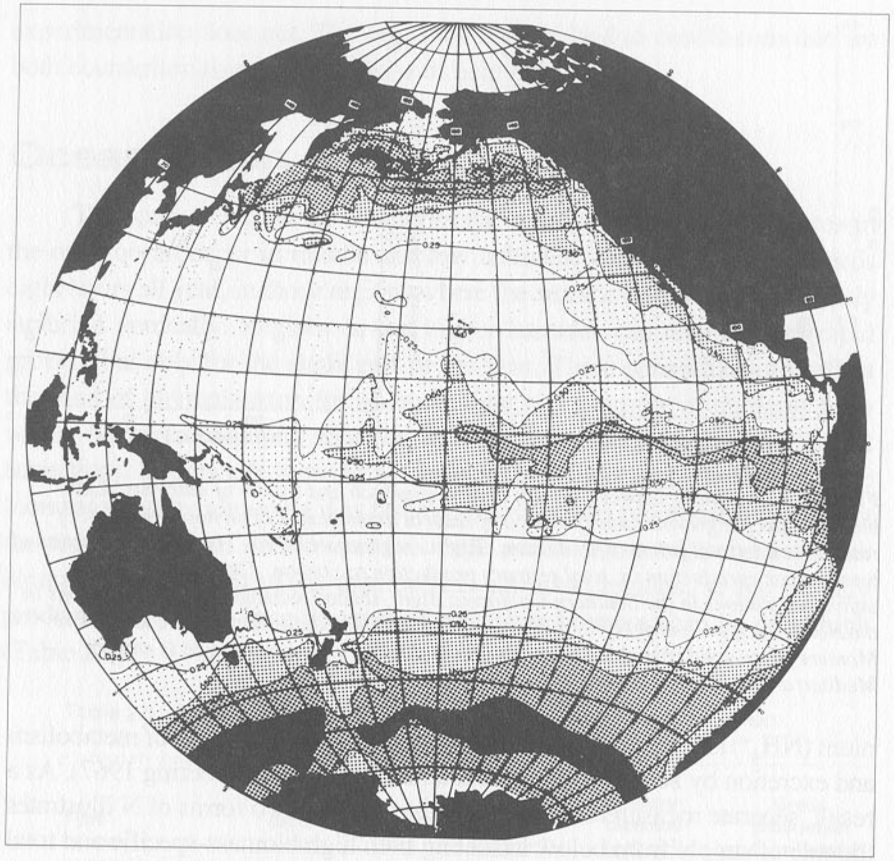

Figure 2.2 Distribution of PO_4^{-3} (µM) at the surface in the Pacific Ocean. Darkest shading indicates values > 2 µM. From Reid 1962.

As illustrated by the maps for the Pacific (Figures 2.2 and 2.3), zooplanktonic biomass in the upper few hundred meters also tends to be positively correlated with nutrients (phosphate; PO_4^{-3} in Reid's maps). These maps were prepared from data collected over several years, different areas being sampled in different years. The large-scale, general patterns are thus semipermanent, though the permanence of smaller features is unknown. In general, the areas that are eutrophic with respect to nutrients and plankton are also regions of the major pelagic fisheries (in terms of tonnage, if not value), though the distribution of fisheries is strongly biased by political, cultural, and economic constraints.

A major perturbation of the ocean climate such as the El Niño provides an illustration of the relation between nutrient supply and planktonic biomasses on large scale. Associated with the major Californian El Niño of 1958–59 were dramatic reductions of zooplanktonic biomass throughout the California Current (Reid 1962, Chelton et al. 1982). Properties of phytoplankton were not measured at that time, but more recent studies show dramatic reductions in phytoplanktonic biomass during the 1982–83 Californian El Niño. This was associated with a reduced incidence of cold, presumably upwelled water near Point Conception and marked a deepening of the nutricline, meaning that a greater portion of the euphotic zone was nutrient depleted (Fiedler 1984, McGowan 1985). Perhaps equally important for subsequent elements of the food web, less extensive sampling suggested that the size composition of the phytoplankton also was different in 1982–83, with very small cyanobacterial cells becoming a much larger component of the biomass and primary production (Putt and Prezelin 1985).

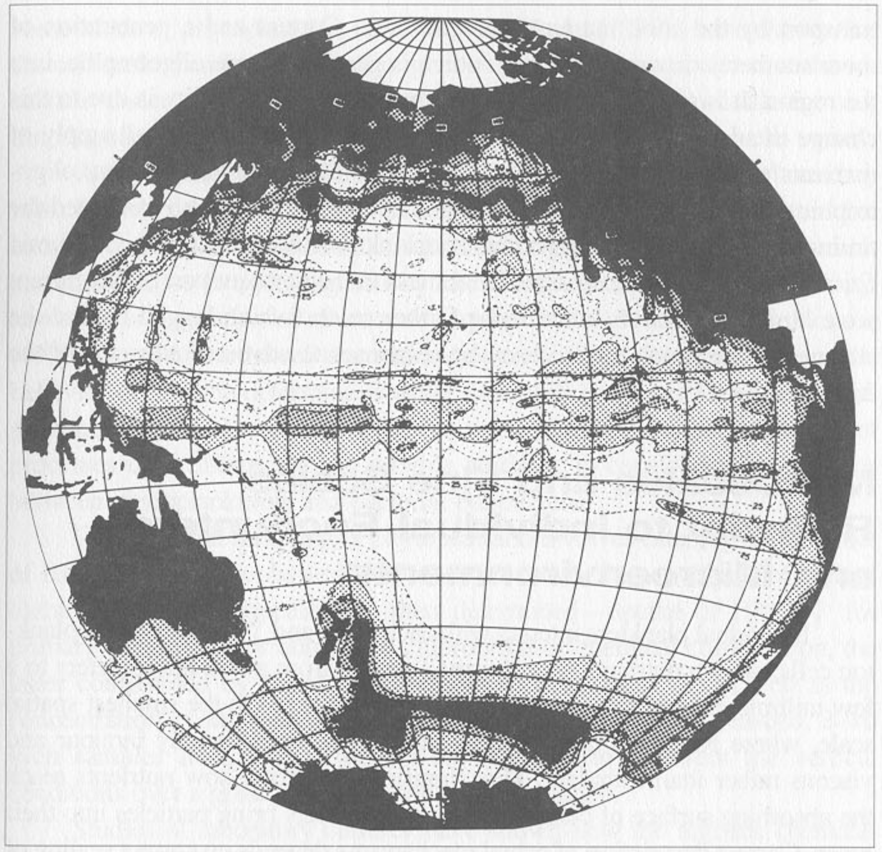

Figure 2.3 Distribution of zooplanktonic biomass [ml $(10^3 m^3)^{-1}$] in the upper 150 m of the Pacific Ocean. Darkest shading indicates values approaching 1 ml m^{-3}. From Reid 1962.

Exact causation is more difficult to establish, however. Evidence from fauna (i.e., "indicator" species) and a rise in sea level (indicative of altered geostrophic flow and thermal expansion) indicate a decrease in southward transport by the cool, nutrient-rich California Current and a penetration of more southerly or westerly water, which is generally more oligotrophic, into the region. It is not clear how much of the reduction in fertility is due to this change in advection, and how much to local reduction in vertical supply of nutrients to the euphotic zone (because of the thicker layer of warm, oligotrophic water at the surface). Roesler and Chelton (1987), who examined the timing of changes in transport and zooplanktonic biomass in the California Current, argued that the changes in biomass in the northern part of the current were largely advective, while those farther south (which lagged behind the changes in transport) were caused by responses to advected nutrients of the food web itself.

Microscales and Fine Scales Relevant to Individual Encounters and Microenvironments

Individual plankters interact with each other and, if they are phytoplankton cells, absorb nutrients on very small scales, from a few micrometers to a few millimeters and for no more than a few seconds. On the smallest spatial scale, where Reynolds numbers are small, flow is essentially laminar and viscous rather than turbulent. This significantly affects how nutrients reach the absorbing surface of cells and how zooplankters bring particles into their grasp. Correct description of actual mechanisms depends on correct scaling of the fluid dynamics. What is uncertain is the degree to which such correct descriptions will help us understand changes (or steady states) in populations and communities.

An individual phytoplankton cell is surrounded by a boundary layer of fluid through which nutrients (or bacteria) must diffuse to reach the outer membrane of the cell. As recognized by Munk and Riley (1952), a cell stationary in the water depletes nutrients in a microzone around it through absorption; sinking (or other motion relative to the water) minimizes this local depauperization. The size and shape of a particular cell affect both the severity of this depletion and the hydrodynamics of sinking. Even when uptake of nutrients is formulated as a saturable process (Gavis 1976), the issue is still a significant one.

Turbulence on the scale of tens of micrometers might then enhance uptake of nutrients (Munk and Riley 1952, Thomas and Gibson 1990a). However, there can be a negative aspect to such turbulence as well, at least for some kinds of phytoplankton. Thomas and Gibson (1990b) have shown that the cell-scale shearing stress that might be expected from turbulence at the sea surface under moderate winds can inhibit the growth of red-tide-forming dinoflagellates by causing loss of the flagellae with which these cells swim.

A phytoplanktonic cell not only takes up nutrients through the boundary layer but also excretes or leaks organic matter into it, organic matter that bacteria can utilize as a metabolic substrate for growth. Whether a bacterium can move close to a leaking cell by chemotaxis and remain in its vicinity, however, is a question of microscale physics (Mitchell et al. 1985). Jackson (1987) showed how the cell size and leakage rate of the phytoplankton and the behavior of bacteria determine whether there will be any effects on bacterial growth. The relevant point for the present discussion is that modeling of processes on a microscale can provide guidance in considering interactions between phytoplanktonic and bacterial populations.

Conventional sampling of phytoplankton involves catching on the order of 10^5–10^6 cells in a volume of 500 ml or so, drawn from a volume of several liters. Their bulk properties are then determined—uptake of $H^{14}CO_3^-$ for primary production, or content of chlorophyll or chemical composition, the latter confounded by nonphytoplanktonic particles present—as well as the concentration of nutrients in the same volume. For practical reasons, 3–10 such samples from various depths are assumed to represent the vertical conditions over a great horizontal and temporal range.

Studies of laboratory cultures have shown how the nutrient chemical concentration in cells and the growth rate increase with the external concentration of nutrients. Yet, phytoplankton sampled in oligotrophic waters with no measurable nutrients often has a chemical composition (and, by inference, a rate of growth) characteristic of plentiful nutrients. McCarthy and Goldman (1979) and Goldman (1984) have suggested that, since uptake is much faster than growth, rapid uptake by individual cells of nutrient micropatches (a few cubic micrometers) might supply sufficient nutrient for growth over a longer period (e.g., 24 hours). Such encounters would have to occur often enough to affect the bulk properties of the phytoplankton, but an instantaneous, large-volume sample cannot capture the process.

Other evidence of rapid phytoplankton growth in oligotrophic waters (Shulenberger and Reid 1981) lends credence to this suggestion. Experimental tests of uptake of NH_4^+ (an excretory product) support the idea, at least in part (e.g., Goldman et al. 1981, Horrigan and McCarthy 1982), and Lehman and Scavia (1982) presented evidence that excretion by individual zooplankters can create such usable micropatches. Jackson (1980) and Currie (1984a,

b) argued that, because of turbulent dissipation and nonlinear responses of uptake, excretory micropatches are unlikely to provide a significant number of cells with an adequate supply of nutrients. However, the idea is still attractive that microscale or small-scale processes are significant but cannot be detected by conventional sampling because of homogenization or statistical undersampling, or both.

In considering the larger issue of patchiness of nutrients, it is worth remembering that variability in nutrient concentrations may play a role in floral diversity as well as in the overall rate of growth of the phytoplanktonic assemblage. Species differ in the kinetics (rate and saturating concentration) of uptake of nutrients, so that temporal variation may permit several "kinetic types" to coexist, even when all are apparently limited by the same element (see, e.g., Grenny et al. 1973, Turpin and Harrison 1979). Floral composition may affect the pathways of primary production, whatever its magnitude, through the food web to juvenile fish and therefore represents, for the fisheries oceanographer, a second facet of the question of nutrient patchiness.

At slightly larger scales, organic aggregates and the physical/chemical microhabitats they create become significant because they are an important exception to the classic view of plankton as organisms suspended individually in a relatively homogeneous environment. They are potentially relevant to the foregoing discussion because they might provide a physical barrier retarding the dissipation of the metabolic byproducts of their microcommunities. By "organic aggregates," I refer to assemblages of heterogeneous organisms and other seston, loosely bound together in a detrital matrix of organic origin. Because the larger aggregates can be individually collected by divers, they have been studied the most. Such aggregates vary in size (several micrometers to several centimeters), shape (sheets, flakes, flocs, fibers, diaphanous webs), texture (mucilaginous, fibrous), and origin (cast exoskeletons, mucous feeding structures, feces, bacterial films, clumps of chain-forming diatoms). The common feature is the relatively long term proximity of the associated organisms and the chemical microhabitat created by their metabolism. Alldredge et al. (1990) showed that aggregates derived from larvacean houses are sufficiently robust to resist disruption by normal turbulent energy dissipation rates.

Phytoplankton blooms are traditionally thought to end by exhaustion of nutrients and grazing by an increasing stock of herbivorous zooplankton. Occasionally, however, residues of blooms are found as flocs of apparently uningested phytoplankton on the seabed, rather than as fecal pellets. Jackson (1990) has argued, from considerations of hydrodynamic events on the microscale, that the transition from a developing bloom of individual phytoplanktonic cells to a postbloom condition of sinking aggregates made up of adhering cells can be quite sudden, even without the increase in sinking rate of individual cells that is known to accompany depletion of nutrients. These diatom flocs, while still abundant in the water column, are the type of aggregate most likely to contribute more than a small fraction to the summation of metabolic processes there (Alldredge and Gotschalk 1990).

The microenvironments of aggregates can be ecologically important if the metabolic byproducts are themselves nutrients for other organisms. For example, Shanks and Trent (1979) and Alldredge and Gotschalk (1990) reported elevated concentrations of NH_4^+ in the immediate vicinity of aggregates, and Gotschalk and Alldredge (1989) demonstrated buildup of NH_4^+ around aggregates enclosed for several days. Primary productivity, however, is not necessarily enhanced (Alldredge and Cox 1982, Prezelin and Alldredge 1983), and the biomass of phytoplankton associated with aggregates (at least macroscopic ones) is usually insignificant relative to the overall biomass in the water column (e.g., Alldredge and Cox 1982, Beers et al. 1986, Alldredge and Gotschalk 1990), although the concentration of phytoplanktonic biomass on aggregates usually exceeds that in the water.

The physical surface of an aggregate, as well as its chemical nature, may make it a site of greatly elevated concentrations of bacteria and heterotrophic protozoans (e.g., Caron et al. 1982). Mitchell and Fuhrman (1989) invoked this possibility to explain fine-scale patchiness of bacteria sampled blindly. Large-scale distributions, such as onshore-offshore gradients, may be different for organisms associated with aggregates than for those free in the water (Caron et al. 1986). Indeed, there may be on microscales a pattern of succession in the microbial community living on aggregates (though not necessarily restricted to them), a pattern that results from processes on larger scale (e.g., plankton blooms) which enhance the formation of the aggregates (Davoll and Silver 1986). Net consumption of O_2 by aggregates, even in the light, suggests that heterotrophic processes exceed photosynthesis (Alldredge and Cohen 1987). However, on a larger scale the concentration of free-living bacteria so far exceeds that of bacteria associated with macroscopic aggregates that the free-living bacteria dominate heterotrophic processes in the water column, even though the rate of heterotrophy per bacterium may be significantly enhanced on the aggregates.

Aggregates significantly affect the concentration and predator–prey interactions of the organisms that occupy them. By aggregating living and dead particles of many sizes and types, they also affect the transport of particulate organic matter from the euphotic zone to greater depths. However, the influence of this group of phenomena on macrozooplankton and larval fish, either directly as food or indirectly, is uncertain. It would be interesting to determine, by analysis of gut contents with appropriate antibodies, the extent to which larval fish benefit from the microbial food web on aggregates by ingesting heterotrophic microflagellates that are too small to be captured individually.

Feeding by herbivorous copepods has been studied both because it is a source of mortality for phytoplankton and because it provides nutrition for a major food of small fish. The process was once viewed as a mechanical filtration, in which water is driven through a filter of setae or the filter is raked through the water, and cells caught on the filter are transferred to the mouth for ingestion. The mechanisms of capture of food particles are now better known, thanks to the studies of Strickler and others (e.g., Strickler 1982, 1984, Paffenhöfer et al. 1982, Price et al. 1983), and to the realization that, because of the fluid dynamics on this scale, such filtration is impractical in viscous media. Many particle-grazing copepods create some sort of flow to bring water and phytoplankton near their mouthparts, but Strickler's films reveal that at least some copepods sense the presence of an individual large cell before contact, and alter the motion of the mouth parts so as to draw the cell towards the mouth. Ancillary evidence suggests that copepods "smell" (i.e., sense chemically at a distance) the approaching cells; Andrews (1983) has modeled how a sphere of scent around a cell is distorted in the feeding current created by the copepod, and Paffenhöfer and Lewis (1990) determined by microcinematography the distances at which copepods react to cells.

Traditionally, experiments to determine the rates of grazing and ingestion by copepods have been conducted in closed containers that are either unstirred or stirred at some arbitrary rate to keep the particles of food in suspension. Rothschild and Osborn (1988) have correctly pointed out that these conditions may be quite artificial relative to natural turbulence, and they demonstrate mathematically that turbulence may increase the rate at which copepods contact cells by 20% or even 50%, relative to the rate in stagnant water. This may be important when the cells are too rare to saturate the mechanism of capture and ingestion. Simulation of the motions of swimming predators and prey in a turbulent environment also demonstrated that contacts increase, especially if the radius within which the predator can detect and capture the prey is fairly large (Yamazaki et al. 1991). Examination of the rate of ingestion by cod larvae of copepod nauplii at various concentrations under conditions of different wind-induced turbulence has shown up to a twofold increase in feeding caused by turbulence in this predator–prey situation (Sundby and Fossum 1990; see also Chapter 4).

Much attention has been paid to ingestion as a function of concentration of food and to the small-scale patchiness of food (see, e.g., Mullin and Brooks 1976). Small-scale turbulence can be quite patchy in time and space (e.g., Yamazaki and Osborn 1988), and Rothschild and Osborn's results suggest that one should consider this patchiness as well.

However, turbulence and patches of plankton are antithetical. If patches of anomalously dense concentrations are important places for feeding, as indicated by the model constructed by Davis et al. (1991), planktivores can be well nourished either when absence of turbulence permits small-scale patchiness or when turbulence is sufficient to enhance markedly the rate of encounter between an individual predator and its prey. Intermediate levels (or scales) of turbulence may be the least advantageous for the predators.

It is also possible that change in the large-scale physical circulation of the mixed layer is accompanied by changes in the distribution and intensity of small-scale turbulence, and therefore affects the grazing of copepods. However, I doubt that this change, even if extreme, would outweigh the concurrent changes experienced by the food web of the copepods, such as altered advection and altered supply of nutrients mixing into the euphotic zone from deep waters.

Small-scale Vertical Distributions

Some of the earliest investigations in pelagic ecology concerned the vertical distributions of plankton and how, for many species of zooplankton, these distributions change dielly, seasonally, and ontogenetically on scales of tens to hundreds of meters. While there are still valid questions concerning the proximate and ultimate (i.e., evolutionary) causes and consequences of such distributions, I am here concerned with vertical distributions on smaller scales, such as those within the euphotic zone.

Even in situations in which physical and chemical properties are uniformly distributed with depth in the upper few tens of meters, forming the so-called mixed layer above the thermocline, plankton may be patchy (i.e., nonrandom) in distribution. In some cases, the horizontal extent of such features is great enough to consider them layers, but information is generally insufficient to establish this because even data taken continuously in the vertical are generally from stations that are widely separated horizontally. Underway acoustic data frequently show quasi-continuous layers of micronekton, but they are usually far below the thermocline, at least by day, and are made up of large, mobile organisms. However, a sound-scattering layer extending across the North Pacific at depths shallower than 100 m day and night, dominated by the copepod *Calanus (Neocalanus) cristatus*, was reported by Barraclough et al. (1969).

The question of vertical patchiness of larval fish food is of concern because larvae reared in the laboratory often require concentrations of food which considerably exceed the average concentrations in surface waters. Success in early larval life might therefore depend on feeding in patches of anomalously high concentrations of food—either that, or the rearing experiments have been misleading. (By "anomalous patches," I mean that regions with high concentrations are more frequent than would result from a random distribution of abundances about the mean.) Whether such patches exist in the mixed layer, how long they persist, and whether they are associated with physical features that might increase the probability of larval occurrence, are therefore significant issues. I shall return in Chapter 4 to the importance of patches and layers of anomalously high concentrations of plankton for first-feeding larval anchovy; here I review a few other examples and their implications for larval fish generally.

Owen, in a recent study (1989), has observed patchy distributions of plankton within vertical distances of 2 m, which is essentially on the fine scale. The coefficients of variation (standard deviation/mean) on this scale for various types of plankton often exceeded those on the scale of 1–10 m, while nutrients and temperature were more variable on the larger scale (but still much less so than the plankton). Particular types were often patchier than were measures of total biomass such as chlorophyll or total particles.

On this scale, then, the composition of potential prey for larval fish was more variable than the biomass, but in fact the types thought to represent larval food were less patchy than the potential competitors or predators on the larvae. The physical stability of the water column may have influenced patchiness, since vertical profiles tended to be least patchy at wind speeds greater than 10 m $\sec^{-1}$, in the "mixed" layer rather than in the thermocline, and in shallow areas rather than over deep water. How much of the observed patchiness might be due to the association of particular organisms with relatively rare organic aggregates is not known.

Patchiness was greater diurnally than nocturnally in Owen's study. Although the mechanism was not established, this finding is consistent with nocturnal cooling and overturn of surface waters; and since larval fish are daytime feeders, perhaps it is fortunate that this is the case. Certainly the implication of Owen's study is that the distributions of prey and predators on the scale that a larval fish might traverse in a few hours can be quite variable. It is unfortunate that larval fish were too scarce to be sampled on this scale as well. It is also unfortunate that the horizontal dimension characteristic of the patches was not established, since this affects their potential permanence and the likelihood that a larval fish, once finding a patch, could feed there for many hours.

A striking example of small-scale patches or layers, though based on only a single station and time, is reported by Bjornsen and Nielsen (1991). Within a vertical range of 2 m around a sharp pycnocline, a larval fish could have encountered very high concentrations of a toxic dinoflagellate, *Gymnodinium aureolum*, and few edible protozoans, or significantly more abundant oligotrichous and tintinnid ciliates above and below the layer of maximal *Gymnodinium*.

Rearing of copepods in the laboratory has led to a conundrum analogous to that arising from larval fish rearing: the mean concentrations of phytoplankton do not seem to be sufficient for survival and growth. The problem is complicated by the fact that we do not really know how to measure the food supply of a naupliar copepod in nature. Is it total chlorophyll, total particulate organic carbon, total living carbon (as estimated from, say, ATP), or some particular size category or biochemical subset of one of these?

Because gradients in phytoplanktonic biomass (i.e., change in biomass per unit distance) are much stronger vertically than horizontally (e.g., Mullin 1986), much attention has been paid to whether zooplankters occur and feed in layers (or vertical patchiness) of anomalously high concentrations of food. Mullin and Brooks (1972, 1976) reported examples from the Southern California Bight in which the abundance or biomass of the copepod *Calanus pacificus* was positively correlated with biomass of phytoplankton (though with great variability; see Figure 2.4), due primarily to vertical distributions on the scale of meters to a few decameters. Although the mean concentration of phytoplankton was insufficient for growth at many stations, distributions of "malnutrition and surfeit" during the two periods studied could be calculated from the specific vertical distributions and laboratory data on feeding and respiration. Cox et al. (1983) calculated similar distributions for two portions of the Bight, one richer than the other, from similar data taken in another year (Figure 2.5).

These relations result from sampling, at different times and locations, of the vertical distributions of a copepod species and its presumed food (or, at least, a property, chlorophyll, presumed to be correlated with food). The

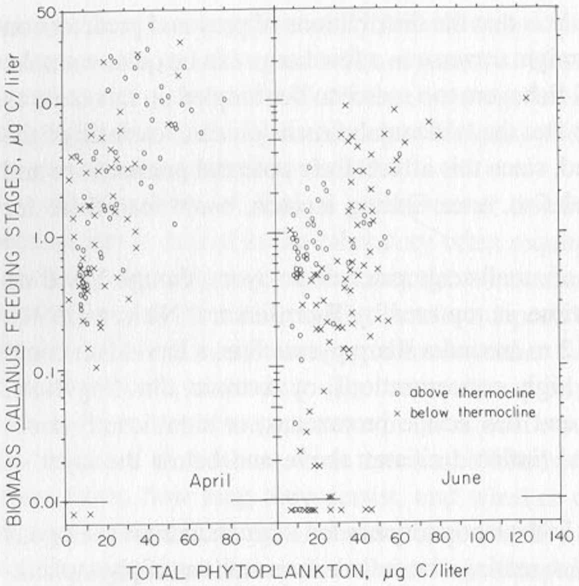

Figure 2.4 Biomass of Calanus pacificus *and phytoplankton at various stations and depths in the upper 50 m of the Southern California Bight on two occasions. See Figure 2.5 for metabolic implications of distributions. From Mullin and Brooks 1976.*

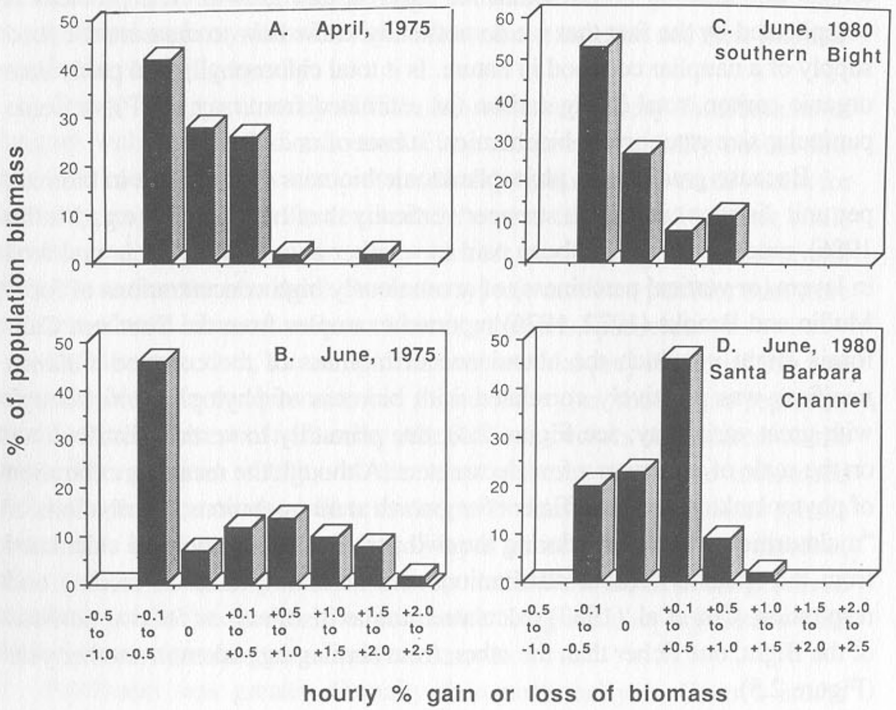

Figure 2.5 Distributions of fractions of the biomass of the Calanus pacificus *population in the Southern California Bight experiencing different percentages of hourly losses or gains of biomass at four times or locations, calculated from ingestion, assimilation, and respiration at several stations and depths. For correlations with* A *and* B, *see Figure 2.4. Modified from Mullin and Brooks 1976, and Cox et al. 1983.*

questions yet to be answered concern the roles of behavior of the copepods, the imbalances between reproduction and grazing on phytoplankton, and turbulence in restructuring the vertical distributions at one location. Mullin et al. (1985) studied vertical distributions before and after a local storm, and found surprisingly little disruption. (This observation will be discussed more fully in Chapter 4.)

While it is tempting to invoke the use by zooplankton of patches or layers of food as the "solution" to the apparent insufficiency of average concentrations to sustain growth, the range of natural situations, even within one geographical area (the Southern California Bight), is much more complex. First, the variability shown in Figure 2.4 means either that the relation between phytoplanktonic carbon and quality of food is quite variable (on this issue, see Mullin and Brooks 1976, with regard to cell size, and Napp et al. 1988a, concerning biochemical composition) or that the copepods are not very efficient at finding the best places to feed. Second, there is at least one example in which *Calanus* and other zooplankters seemed almost to avoid a dense layer of food (Fiedler 1982). Third, Napp et al. (1988b) found no relation between the vertical distribution of many species and that of phytoplanktonic biomass. Finally, Dagg and Wyman (1983) and Mullin et al. (1985) were unable to show that there was a relation between the vertical distribution of chlorophyll and the depths at which copepods fed most intensively (as reflected by plant pigments in their guts).

Vertical Motions and Their Effects on Primary Production

Because of the vertical attenuation of light in the sea (which as a first approximation is an exponential decay) and the reservoir of oxidized nutrients represented by deep water, the scale of a few meters to a few tens of meters below the surface is crucial for the physiology of phytoplankton. In stable situations, cells photoadapt; that is, cells living near the surface have less chlorophyll than those living near the base of the euphotic zone, and different kinetic responses to light. The nitrogenous nutrient used by phytoplankton near the surface is likely to be ammonium excreted by heterotrophs, while deeper-living cells often use nitrate (depending on the penetration of light relative to the depth of the nutricline, where nitrate begins to increase with depth). Finally, there may be distinct communities of species at different depths, particularly if the euphotic zone extends below the thermocline (e.g., Venrick 1988).

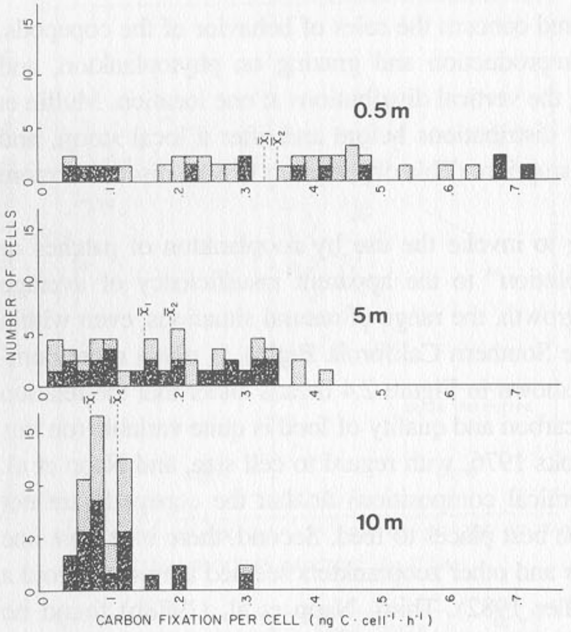

Figure 2.6 *Primary productivity of individual cells of* Ceratium tripos *at three depths. Shadings denote two water samples. Mean productivity per cell of each sample is given. From Boulding and Platt 1986.*

All this means that both conceptual and simulation models of the euphotic zone as a vertically stratified column are well developed (e.g., Jamart et al. 1977). In general, these models consider the phytoplankton at any depth to be physiologically homogeneous (i.e., to respond similarly, having had similar previous exposure to nutrients and light), and to move vertically only by sinking (or, in the special case of some dinoflagellates, by swimming vertically). Most measurements of primary production at sea are based on this conceptual model.

Nevertheless, there is good evidence that the individual cells at a given depth and time do differ in physiological properties. Micro-autoradiography of samples incubated with ^{14}C has shown that species within less than a liter of water differ in their photosynthetic rates (e.g., Maguire and Neill 1971, Knoechel and Kalff 1976a, b). Even within a species, photosynthetic uptake may differ considerably (Figure 2.6). The possible sources of this variability are the sizes and ages of the cells, their environmental histories (they may have been brought together from different depths by physical mixing), and their genetic makeups.

Denman and Gargett (1983), in reviewing the processes resulting in vertical motions in surface waters, evaluated each in terms of characteristic time and space scales, relative to the time course of adaptation of photosynthesis. Turbulent mixing and internal waves were the most important motions

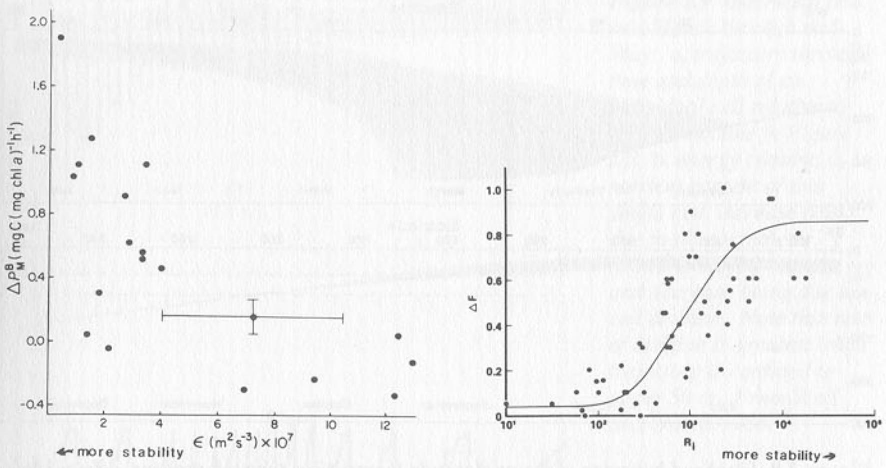

Figure 2.7 *From two studies, differences in photosynthetic responses between surface-living and deep-living phytoplankton, plotted against rate of mixing.* Left: *difference between maximal photosynthetic rates of surface and deep samples as a function of turbulent dissipation rate (higher values mean more mixing). From Lewis et al. 1984.* Right: *difference between relative inhibition by* DCMU *of photosynthesis of samples from deep water (where the effect tends to be greatest) and inhibition at the surface (higher values mean greater difference between depths) as a function of the Richardson number (lower values mean more mixing). From Harris 1984.*

in terms of their effect on primary production.

As noted above, differentiation in the kinetics of primary production can arise in a stable water column in cells growing in different microenvironments, from some combination of species differences and physiological adaptations. There ought, therefore, to be measurable effects of the relation between the speed of physiological differentiation and the rate of mixing. Figure 2.7 shows the results of two studies in which a measure of the difference in photosynthetic responses between surface- and deep-living phytoplankton is plotted against a measure of the rate of mixing. Although the relations look superficially different because different properties are plotted, in fact both graphs show that at high rates of mixing the responses are similar, and at low rates there are differences between the two populations—or, more correctly, between the communities, since the specific composition may have differed vertically, also.

It would be interesting to use micro-audiography or the technique of Boulding and Platt (1986) to learn the degree of physiological differentiation within single depths in these studies. One would expect that, as turbulent mixing increases to some intermediate range, within-depth heterogeneity increases and between-depth differentiation diminishes, as cells with different histories (and/or of different species) are increasingly brought together

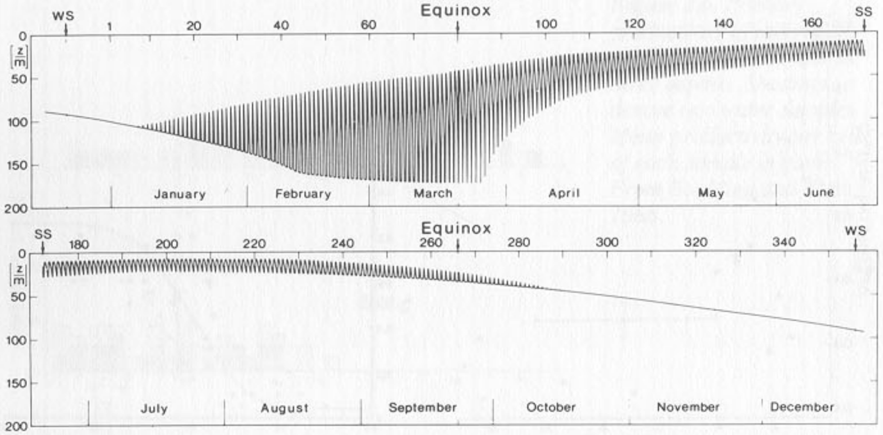

Figure 2.8 Idealized behavior of the midlatitude thermocline through seasons, affected by diurnal heating and nocturnal cooling. From Wolf and Woods 1988.

(Falkowski and Wirick 1981). Gallegos and Platt (1982) designed an interesting incubator to mimic this, but they were unable to demonstrate ecologically significant effects.

A special form of vertical motion which is seasonal in occurrence but diel in period results from the diurnal heating and nocturnal cooling at the surface, which creates a diel deepening and shoaling of the thermocline (Figure 2.8 is an idealized view). Wolf and Woods (1988) have used a Lagrangian ensemble model to simulate the temporal sequence of the bulk property, biomass of chlorophyll. The model explicitly retains information on individual cells with different histories that can co-occur at one depth and time due to random mixing above the thermocline. In principle, at least, such a model should be more realistic than those that treat all the cells in any layer at one time as physiologically homogeneous. In this context, the term "thermocline" may be misleading. What is important is the diel variation in the penetration depth of mixing, which may differ from the depth of the thermocline as a biologist would define it.

In the Wolf and Woods model, if a cell is left behind in the deep, stable layer in the morning as the thermocline shoals, the cell sinks and may or may not be overtaken and re-entrained into the mixing layer as the thermocline deepens in the evening (Figure 2.9). The photic history and nutrient uptake of each cell depend on its location in the water column, and a given cell (or its daughter cells) can vary between nutrient limitation and light limitation over time. Uptake by cells depletes the nutrient pool, and there is no regeneration in the model.

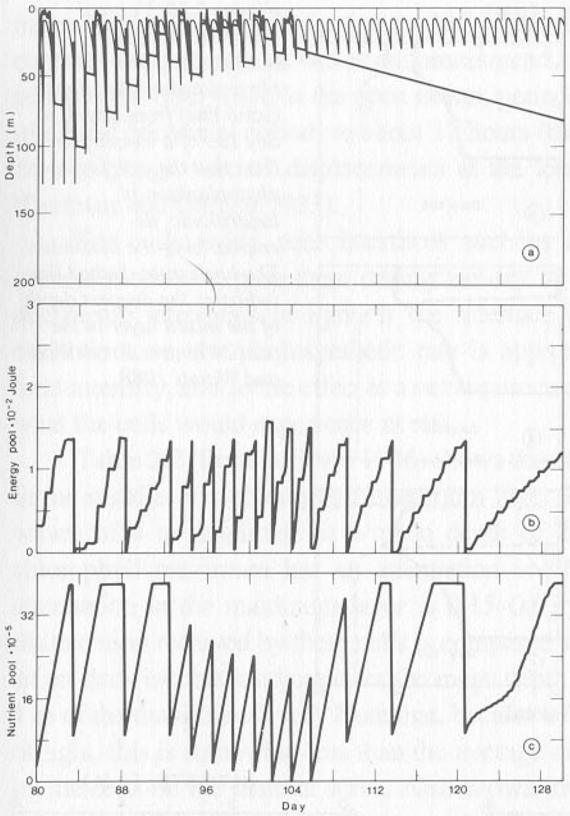

Figure 2.9 Individual cell, mid-March through mid-May: a, *trajectory through time and depth of an individual cell relative to the thermocline in Figure 2.8;* b, *energy content;* c, *nutrient content of this single cell, increase being due to photosynthesis (daytime only) or uptake and decrease being due to cell division. Note that rate of division is greatest when trajectory is confined to upper 50 m. From Wolf and Woods 1988.*

When the vertical distributions of nutrients and chlorophyll are determined as a function of time, a realistic formation and deepening of the nutricline and chlorophyll maximum layer results (Figure 2.10). In fact, this is not too different from the outcome of the simpler model of Jamart et al. (1977), in which variation in sinking rate as a function of nutrient uptake was a significant element; but the Lagrangian model might be more realistic in mechanism and, therefore, a better tool with which to examine the effects of perturbations. Even a single day of deep mixing, such as might be caused by a storm, can alter the vertical distributions significantly (Figure 2.11), and one can imagine a local storm thus creating horizontal patchiness in its wake. Less severe wind conditions, such that Langmuir cells become the dominant agent of mixing, should also be considered.

The first step in assessing the generality of this model is to obtain more data sets demonstrating the circumstances resulting in a diel variance in the thermocline idealized in Figure 2.8. An informative further test would be to conduct an analysis of variance in floral composition and in physiological

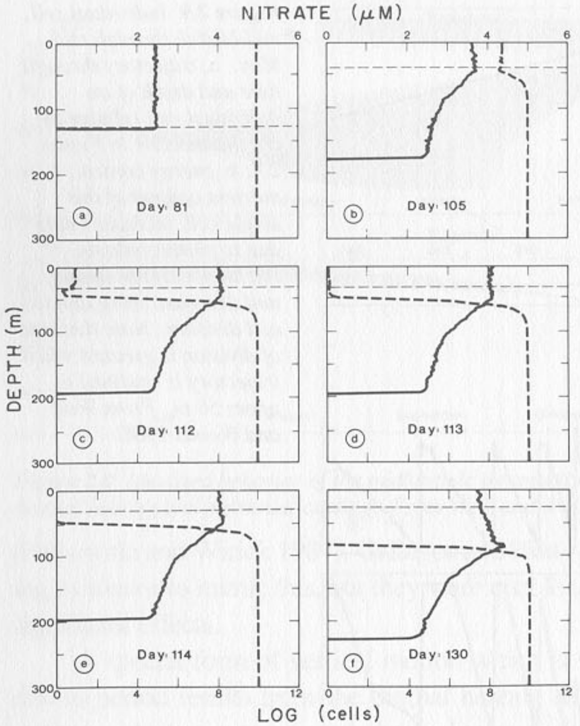

Figure 2.10 Vertical distributions of NO_3^- (dashed line) *and phytoplankton abundance* (solid line) *from day 81 to day 130 of a simulation. Note that the axis for phytoplankton is logarithmic, de-emphasizing the maximum. The horizontal dashed line indicates the deepest depth of the mixed layer in the past 24 hours. From Wolf and Woods 1988.*

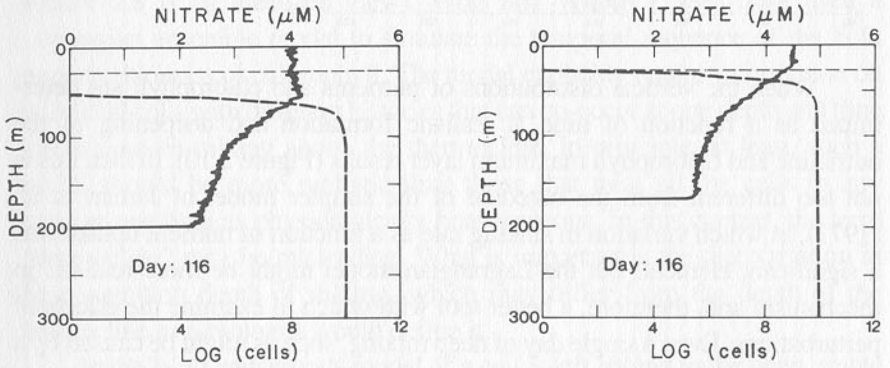

Figure 2.11 Vertical distributions of NO_3^- (dashed curved line) *and phytoplankton (log scale,* solid line): left, *without upwelling; right, effect of upwelling event. Compare with Figure 2.10. From Wolf and Woods 1988.*

states of phytoplankton as a function of season, using methods such as the example by Boulding and Platt (1986) to see whether the variance at a particular depth was indeed greatest, and the floral assemblage most vertically similar, during the season of diel oscillation of the thermocline.

Stratification of the water column reduces turbulent mixing but promotes sharp density interfaces on which internal waves can propagate. On continental shelves, such waves are pronounced at the 12.4-hour period of the semidiurnal tide, while in the open ocean, periods range from a few minutes (the local buoyancy period) to about 17 hours (the local inertial period), with crest-to-trough vertical displacements at the longer periods of up to 30 m (Denman and Gargett 1983).

For cells living near interfaces such as a sharp thermocline, these vertical motions expose them during the day to exponentially increasing or decreasing intensities of light. If the interface is in the lower half of the euphotic zone, the photosynthetic rate is approximately linearly related to light intensity, and so the effect is a net augumentation of photosynthesis over what the cells would experience at rest.

Table 2.2 (from LeFevre 1986) shows the effect on illumination of cells in the middle of a chlorophyll maximum layer 2 m thick riding on internal waves of 4 m amplitude at a mean depth of 25 m. The water above the chlorophyll maximum has an attenuation coefficient of 0.1 m^{-1}, and the attenuation in the maximum layer is 0.15–0.6 m^{-1}. The fraction of surface illumination received by these cells is compared with that received by cells in an on-deck incubator adjusted for the mean depth (24 m of surface water plus 1 m of the maximum layer). Note that, because of the exponential attenuation of light, this is somewhat less than the average of the intensities experienced by the cells on the internal wave. Also shown in the table are the intensities experienced by cells in a bottle suspended in the sea at 25 m on a taut line, where the cells actually experience greater illumination when the trough of the wave passes because this moves the turbid maximum layer below the bottle.

Table 2.2. Ambient light, as percentage of surface value, experienced by cells in the middle of a chlorophyll maximum layer 2 m thick centered at 25 m, compared with ideal on-deck and *in situ* incubations.

Chlorophyll maximum attenuation coefficient	State of internal wave	Illumination (percent)		
		In nature	Deck incubator	Suspended *in situ*
0.15 m^{-1}	crest	11.6	7.8	7.4
	trough	5.2		8.2
0.4 m^{-1}	crest	9.1	6.1	4.5
	trough	4.1		8.2
0.6 m^{-1}	crest	7.4	5.0	3.0
	trough	3.3		8.2

Lande and Yentsch (1988) argued that the maximal increase in primary production should occur when the internal waves coincide with the base of the euphotic zone in eutrophic areas. In the upper part of the water column, light intensities may be great enough to inhibit photosynthesis, and internal waves propagating along a shallow thermocline in oligotrophic seas might actually decrease primary production slightly (Holloway and Denman 1989).

Internal wave packets propagate away from the shelf over deep water, as well as onto the shelf. Holligan et al. (1985) studied a situation in which a deep chlorophyll maximum layer was moved between 0.03% and 6% of surface illumination by packets consisting of 2–6 large (50–80 m) waves with a wavelength of 1–1.5 km. Some evidence indicated that mixing due to overturning of such waves could enrich the surface layer with nutrients during fortnightly spring tides.

Other vertical motions, such as Langmuir circulation, can alter the light intensity experienced over a few minutes (Marra 1980, Marra and Heineman 1982, Denman and Gargett 1983), as can the passage of clouds, and the focusing and defocusing of light by surface waves can do so in seconds (Savidge 1980, Falkowski 1984, Walsh and Legendre 1988). The issues are the depth of penetration of the effect (the spatial scale), the depth or physiological condition of the phytoplankton that makes them most responsive (Abbott et al. 1982), and the speed of change relative to the time scales of physiological change in the phytoplankton. These motions are potentially related to climatic variation through their dependence on local winds, while climatically caused changes in the density structure of the euphotic zone would be more likely to alter internal waves over continental shelves.

The issues reviewed in this section have obvious importance for the estimation of primary production and for the understanding of vertical distribution of phytoplanktonic biomass. They also illustrate the importance of scales in relations between physical processes, supplies of nutrients, and physiology of phytoplankton. Implications for the rest of the food web are less clear. In particular, it is not clear how the spatial and temporal distributions of species of phytoplankton are affected. To the extent that the functioning of the food web depends on the constituent species rather than just on biomass and primary production, the effect that vertical motions on these scales have on community composition needs further study. This observation is analogous to one I made earlier in this chapter concerning the possible role of patchiness of nutrients.

Other Effects of Internal Waves on Plankton

In addition to the physiological effects that internal waves can have on photosynthesis because of the fluctuation they cause in light intensities, internal waves can also cause phytoplankters to aggregate into horizontal patches or strips that dielly move vertically across the density interface on which the waves propagate. Under some conditions of illumination and supply of nutrients, large-celled dinoflagellates form persistently subsurface layers (described later, in Chapter 4, as a feeding ground for larval anchovy). Under other conditions, the same complex of species, when sufficiently abundant, form visible "red tides" at the surface in midday, swimming downward in the evening and upward in the morning.

Kamykowski (1979 and references therein, 1981) has modeled this effect. Figure 2.12, from his work, shows how cells, initially dispersed evenly in an onshore–offshore direction, become aggregated into bands that progress

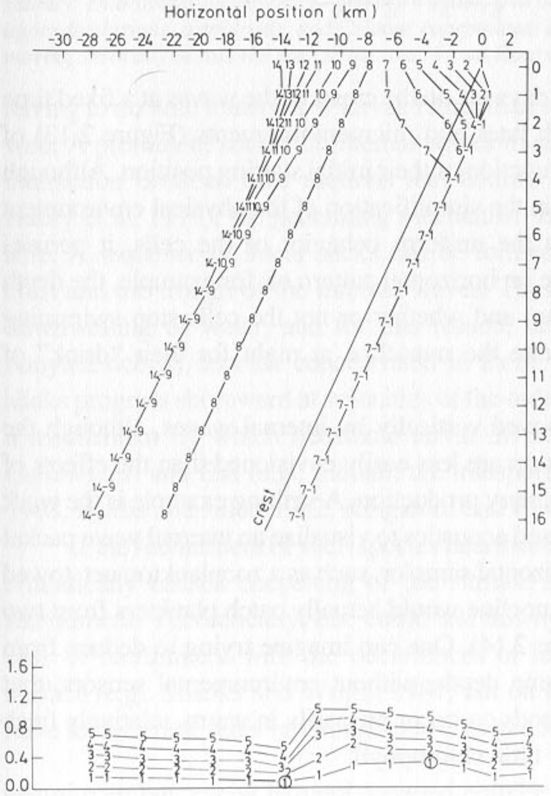

Figure 2.12 Aggregating and physiological effects of internal waves on migrating dinoflagellates. Upper: *offshore position of dinoflagellates on successive days in a semidiurnal internal wave. Cells, initially at positions 1–14, migrate vertically to 1 m below the thermocline each night. If thermocline is too deep for cells to reach, no such pattern is formed. Horizontal position 0 is arbitrary; negative distance increases offshore. Diagonal line shows locations of internal wave crest on successive sunsets.* Lower: *relative growth over 5 days (numbers 1–5) of cells starting at the various positions in the upper map (e.g., circles on day 1 refer to starting positions 4 and 8). Extinction coefficient k is 0.144 m⁻¹ in layer above thermocline, 0.040 m⁻¹ below it. From Kamykowski 1979.*

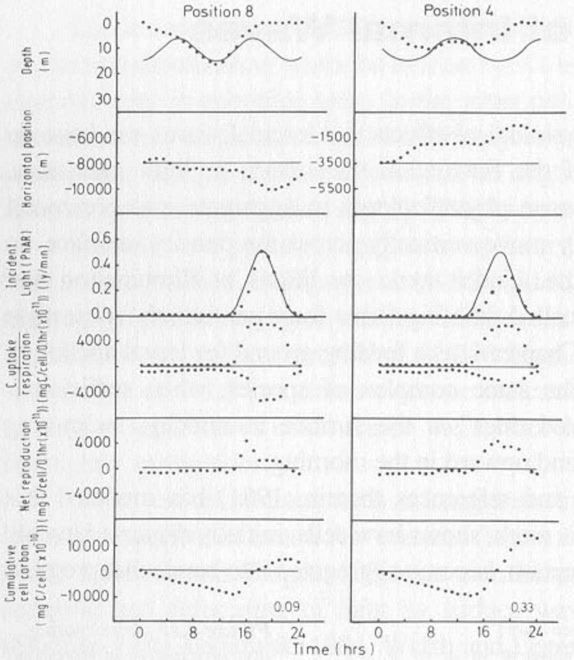

***Figure 2.13** History of cells for 24 hours, starting at positions 8 and 4 in Figure 2.12. Migration* (dotted line) *is plotted relative to thermocline* (solid line); *horizontal position* (dotted line) *relative to start* (solid line); *light experienced* (dotted line) *relative to surface light* (solid line); *and uptake, respiration, and instantaneous ("net reproduction") and integrated net accumulation of carbon. From Kamykowski 1979.*

slowly offshore over several days (as do the crests of the waves at a fixed time of day), and how the growth rates and microenvironments (Figure 2.13) of cells vary through time as a function of their initial starting position. Although the model is idealized, both in the simplification of the physical environment (e.g., no turbulence) and in the uniform behavior of the cells, it permits exploration of the importance on horizontal pattern of, for example, the depth of the thermocline (nutricline) and whether or not the cells stop swimming downward once they penetrate the nutricline at night for their "drink" of nutrients.

Zooplankton is also moved vertically by internal waves, although the effects on secondary production are less easily envisioned than the effects of the changing light field on primary production. A striking example is the work of Haury et al. (1979), who used acoustics to visualize an internal wave packet in Massachusetts Bay. A horizontal sampler, such as a zooplankton net, towed at the mean depth of the pycnocline would actually catch plankters from two distinct environments (Figure 2.14). One can imagine trying to deduce from an integrative tow at the same depth, without environmental sensors, that appendicularians and amphipods co-occur primarily in warm, relatively fresh surface water with relatively little chlorophyll.

There is an interesting relation between internal waves and recruitment

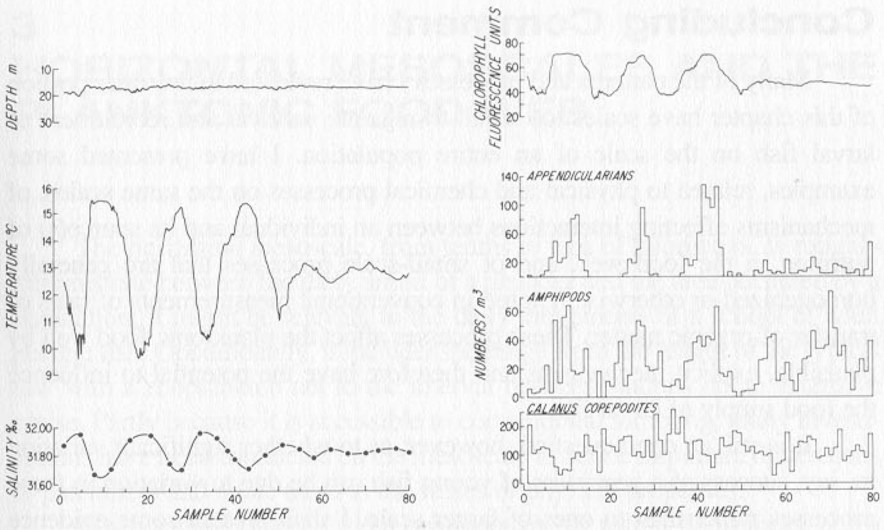

***Figure 2.14** Data from a multiple-sampling net with environmental recorders towed horizontally for 980 m through an internal wave packet: depth of tow; temperature; salinity; chlorophyll fluorescence (arbitrary units); and abundances of zooplanktonic appendicularians, amphipods, and* Calanus *copepodites. Oscillations reflect properties moving vertically across the path of the tow. From Haury et al. 1979.*

having to do with transport of larvae rather than with the dynamics of the food web. A prominent source of internal waves in stratified, shallow water is the interaction between tidal motions and bottom topography of a shelf (e.g., Haury et al. 1979); the generating mechanism is therefore relatively predictable. A sequence of linear slicks can be formed on the surface between the crest and the trough of the internal waves. These slicks are regions of weak downwelling of water, and for this reason, neustonic animals (as well as buoyant debris) become concentrated in them. Under some conditions, the slicks progress shoreward at velocities of the order of 50 cm sec^{-1}, and provide a mechanism by which neustonic larval invertebrates (e.g., the blue crab, *Callinectes)* and fish (e.g., filefish) are transported shoreward (Shanks 1983, 1988, Zeldis and Jillett 1982, Kingsford and Choat 1986).

If the recruitment of such species nearshore depends on this mechanism, climatically caused deepening of the surface layer might alter patterns of recruitment. Theoretically, one could test this hypothesis by correlating success of recruitment with the occurrences of internal waves that affect the surface (e.g., Shanks and Wright 1987, but on larger scales), but one would have to eliminate other environmental changes to demonstrate true causation.

Concluding Comment

Many of the patterns and processes I have reviewed in the latter portion of this chapter have scales too small to regulate survival and recruitment of larval fish on the scale of an entire population. I have presented some examples, related to physical and chemical processes on the same scales, of mechanisms affecting interactions between an individual and its source(s) of nutrition in the food web, and of small-scale processes that are generally homogenized or otherwise ignored in conventional measurements of rates of transfer of organic matter. These processes affect the planktonic food web by plausible, explicit mechanisms and therefore have the potential to influence the food supply of larval fish.

It is still an open question, however, as to whether significant variation in, say, success of a year class of young fish can be due to variation in these processes rather than to ones of larger scale. I shall present some evidence bearing on this question in Chapter 4, but first, in the next chapter, I turn to the mesoscale.

3

HORIZONTAL MESOSCALES AND THE PLANKTONIC FOOD WEB

The horizontal mesoscale, from tenths to tens of kilometers, is roughly intermediate between the daily ambit of a plankter and the area occupied by a population; it might be relevant to the daily movements of a school of adult pelagic fish. Operationally, it includes the range from the length of the typical tow with a zooplankton net to the interval between stations on an extensive cruise. Partly because it is accessible to conventional sampling, many investigations have been conducted on the mesoscale to define important dimensions of patchiness and relate them to the scales of physical properties.

When samples can be taken continuously, as with a fluorometer and a thermistor measuring, respectively, the fluorescence of chlorophyll in intact phytoplankters and temperature, the data can be expressed as a power spectrum, which is basically a double log plot of variance against spatial scale. The slopes of such spectra can indicate the scales at which patchiness of chlorophyll probably has a physical cause (slope similar to that of temperature, close to –5/3) and scales at which there is probably some other, presumably biological, cause. Cross-spectral coherence (i.e., significant covariation of known phase relation at particular scales) can distinguish scales at which chlorophyll varies directly with temperature from those at which it varies inversely (Denman 1976, Denman et al. 1977, Horwood 1978, Platt 1978). The brevity of this description permits only an indication of the conceptual attractiveness of this approach and conceals many difficulties in interpretation (e.g., Star and Cullen 1981).

The examples I have chosen to review here concern horizontal relations between phytoplankton and zooplankton, either as biomass or as species, together with the implications for secondary production. This issue is similar to that concerning the concordance of vertical distributions, and the implications for nutrition, discussed in Chapter 2. Continuous sampling, usually with electronic sensors, has played a major role in facilitating description of these relations (though data themselves are often sampled or averaged into finite intervals). Mackas and Boyd (1979) combined data from an electronic particle counter to estimate numbers and sizes of zooplankters near the surface along a ship's track in the North Sea and a fluorometer and thermistor to show that the zooplankton was more variable (i.e., patchier) than phytoplankton or temperature, especially on scales of 1–5 km. Cross-spectra between phytoplankton