

Chapter 8. PHYSICAL INFLUENCES ON MARINE ECOSYSTEM DYNAMICS

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1. Introduction

Physical processes determine the structure of pelagic ecosystems, directly by their influence on the growth of phytoplankton and indirectly by affecting food web interactions. Consequently, the basic type of ecosystem that occupies any particular region is determined by its physical attributes. Here, we examine geographic variability in the sea and temporal variability in an oceanic gyre in an attempt to identify and dis-

tinguish the influences of direct versus indirect effects of physical processes on the structure of pelagic food webs in the sea.

We begin by reviewing some well-established paradigms in plankton ecology that relate the dominant forms of plankton to turbulence, which often controls the supply of nutrients to the photic zone. Recent information on the microbial loop, nitrogen (N_2) fixation, the effects of iron (Fe) on planktonic processes, and different modes of nutrient delivery to surface layers of the ocean shows that more detailed descriptions of the relationships between physical processes and ecosystem structure need to be developed, based on hypotheses relating physical forcing, temporal variability of nutrient supply, and the characteristic but different responses of large phytoplankton versus the microbial loop.

To develop a better appreciation of physical forcing functions, we describe geographic variability in the processes that control turbulence and vertical components of velocity, hence the availability of light and nutrients to phytoplankton in surface layers of the sea. We show that the well-recognized linkage between turbulent mixing and the availability of nutrients is expressed differently in different regions of the ocean, and also that temporal scales of physical forcing must vary with latitude, not only because of the gradient in seasonality, but also because of the changing value of the Coriolis parameter. We present a case study of temporal variability of physical forcing in an oceanic gyre, along with concomitant changes in ecosystem structure, to demonstrate that enrichment of the photic zone with nutrients need not be accompanied by enhanced turbulence. It is argued that both temporal variability of nutrient input and transient alleviation of light limitation, propagating through food webs, may determine the extent to which chemical energy and materials escape the microbial loop for transfer to higher trophic levels. We conclude by presenting some methods from modeling for assessing the influences of physical processes on pelagic food web interactions.

Our focus is on the development and testing of hypotheses relating variability in pelagic ecosystems to regimes of physical forcing, and our emphasis is on phytoplankton, the base of food webs. Procedures for implementing models of physical–biological coupling are described by Rothschild in Chapter 7, with detailed consideration of the responses of higher trophic levels.

2. Turbulence, Nutrients, and Food Web Structure

2.1. *Established Relationships*

Margalef (1978) elegantly showed how the inputs of external energy, on which advection and turbulence depend, determine in large part the prominent life forms of the phytoplankton in pelagic ecosystems (Fig. 8.1a). The essence of his argument is stated simply: If surface waters are not perturbed by physical forcing such as wind or tides, nutrients will be sequestered by phytoplankton and bacteria, incorporated into the food web, and ultimately stripped from the photic zone by the sinking of particles. Small phytoplankton with high ratios of surface area to volume, hence low sinking rates and advantages in competition for nutrients, will dominate in these stable, nutrient-depleted waters. Turbulence or upwelling brings nutrients to the surface layer, supporting rapid growth of larger cells, which are adapted to compete in a temporally variable, nutrient-rich environment. The special case of high nutrients

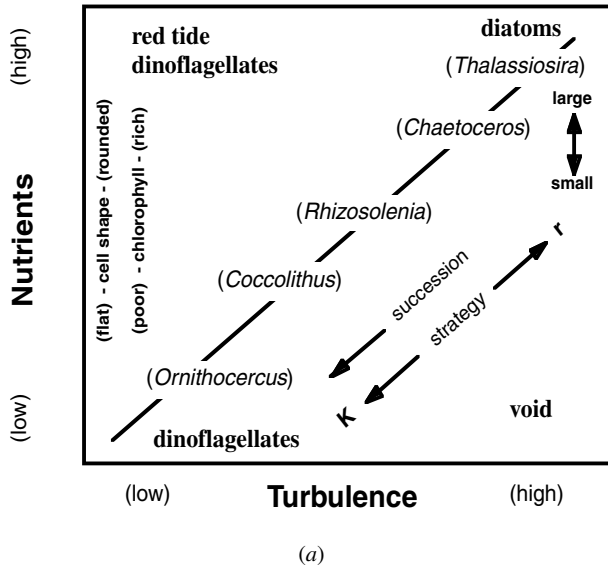
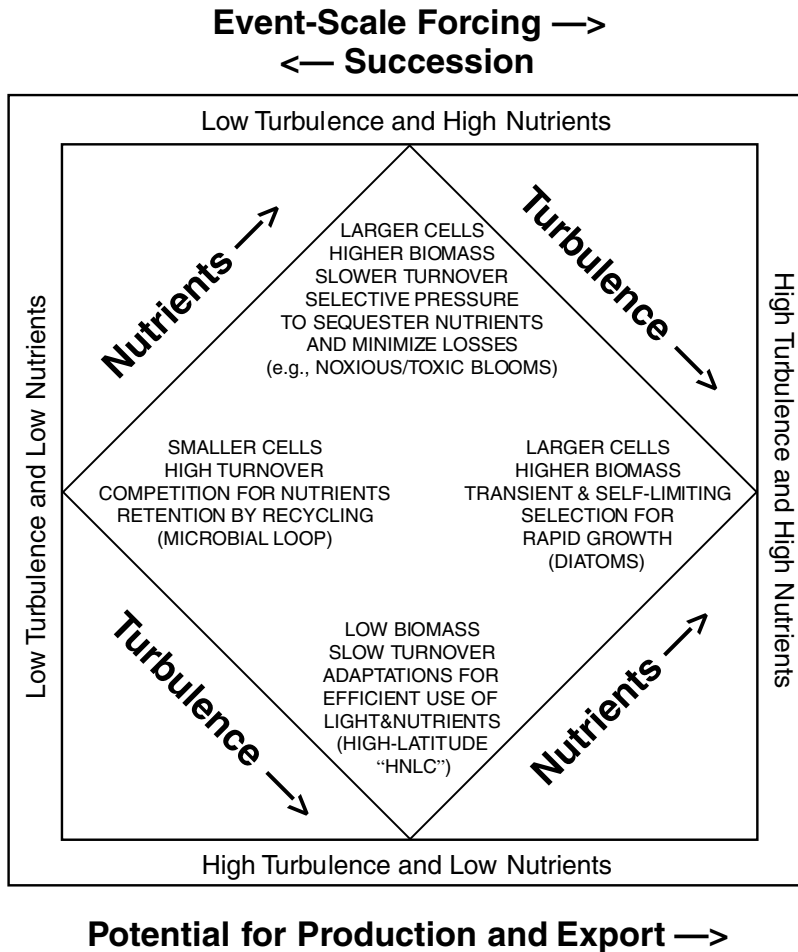


Fig. 8.1. Relationships between turbulence, nutrients, and characteristics of food web structure, based on figures presented by Margalef and colleagues. (a) Emphasis on life forms of phytoplankton. [From Cullen and MacIntyre (1998) after Margalef (1978).] (b) Emphasis on characteristics and adaptations of phytoplankton assemblages and how they relate to food web structure. This general classification of turbulence–nutrient regimes, based on a framework presented by Margalef et al. (1979), is presented to guide our discussion by identifying some trends in pelagic food web structure. Iron-limited, high-latitude waters, conventionally classified as “high-nutrient, low-chlorophyll,” are placed in the high-turbulence, low-nutrient quadrant that Margalef and colleagues classified as a void. The microbial loop is present in all regimes (with much diminished importance in polar waters), but it dominates phytoplankton biomass only in the low-turbulence, low-nutrient regime. Many exceptions to these trends exist (e.g., blooms of the picoplanktonic cyanobacterium *Synechococcus*; Glover et al., 1988). Also, much detail is unexplained, such as the dominance of *Synechococcus* in the North Atlantic but *Prochlorococcus* in the North Pacific (Andersen et al., 1996). Regardless, much can be learned by using classifications like this to explore physical–biological coupling. The classification might be improved by considering the effects of temperature and incorporating irradiance, as influenced by seasonality (see Margalef et al., 1979) and its correlation with latitude.

and low turbulence, which can occur in stratified coastal waters, is associated with specially adapted phytoplankton that can form red tides. Margalef (1978) concludes: “The combination of sedimentation with turbulence or the variance in components of velocity is believed to be the most important factor in the biology of phytoplankton.”

This link between physical forcing and ecosystem structure was established before it was widely appreciated that picoplankton dominated the phytoplankton in oligotrophic waters and that flows of nutrients and chemical energy through phytoplankton could be strongly enhanced by processes such as aeolian deposition of iron, encouragement of N_2 -fixation by increased stratification, and doming of isopycnals associated with mesoscale eddies. So, retaining Margalef’s classification of hydrographic regimes (see also Margalef et al., 1979), adding further consideration of special adaptations to mixing and stratification (Cullen and MacIntyre, 1998), and focusing on implications for food web structure (Fig. 8.1b), we will consider a broader range of relationships between physical processes, nutrient inputs, and ecosystem



(b)

Fig. 8.1. Continued.

structure in our attempt to develop a description of the influences of physical processes on marine ecosystem dynamics.

2.2. *Regimes of Turbulence and Nutrients*

Low Turbulence and Low Nutrients

Understanding of the low-turbulence, low-nutrient situation in the open ocean has been improved substantially, now that the importance of autotrophic picoplankton (Waterbury et al., 1979; Chisholm et al., 1988) and the heterotrophs which they nourish—the microbial loop (Pomeroy, 1974; Azam et al., 1983; Hobbie, 1994; Landry et al., 1997)—is better appreciated. Growth of phytoplankton in stable, low-nutrient waters is largely supported by regenerated nutrients (e.g., Azam et al., 1983; Wheeler and Kokkinakis, 1990), so only a small proportion of primary production is available to

higher trophic levels or for export to the deep sea (Legendre, 1981; Michaels and Silver, 1988; Legendre and Le Fèvre, 1989; Peinert et al., 1989; Kiørboe, 1993). Specific growth rates of large phytoplankton are relatively low, due to nutrient limitation of these cells with lower surface-to-volume ratios (Chisholm, 1992). Some larger phytoplankton persist through special strategies, such as vertical migration (Villareal et al., 1993; Richardson et al., 1996; Cullen and MacIntyre, 1998) and mixotrophy (Sanders, 1991; Maranger et al., 1998). Morphological (Kiørboe, 1993) and chemical (e.g., Miralto et al., 1999) adaptations can increase resistance to grazing (see Smetacek, 1998). However, given the same concentration of biomass per unit volume of seawater, larger cells, due to their relative scarcity compared to small cells, would have reduced specific loss rates to grazing (Kiørboe, 1993) and viral infection (Fuhrman, 1999), independent of any special adaptations. Thus, larger cells can persist in highly stable, low-nutrient pelagic systems, but they do not turn over rapidly, and therefore they cannot support large flows of chemical energy to higher trophic levels.

We conclude that food web structure in low-nutrient regimes is determined primarily by biological interactions but that physical processes, principally stratification, impose the ultimate constraints on the life forms of phytoplankton, the trophic interactions that can persist, and thus on the structure of the pelagic food web.

High-Nutrient and Low-Chlorophyll Waters It should be recognized that so-called high-nutrient, low-chlorophyll waters (Chisholm and Morel, 1991), if they are stratified, as in parts of the equatorial Pacific and north Pacific, actually belong in the low-nutrient, low-turbulence category. Iron limitation strongly influences the species composition of phytoplankton (e.g., Price et al., 1994) and flows of nutrients and energy through the food web, imposing on the system many characteristics of oligotrophic waters, although the concentration of chlorophyll is not as low (Landry et al., 1997).

High Turbulence and Low Nutrients

Iron-limited waters of the Southern Ocean (Martin et al., 1990; Boyd et al., 2000) may belong in the low-nutrient, high-turbulence quadrant of the Margalef diagram, previously considered to be a void (Fig. 8.1*b*). If a paradigm can be developed to describe the high-turbulence, low-nutrient regime, it will probably encompass interactions between light limitation and iron limitation (Maldonado et al., 1999), along with effects of cold temperatures on microbial processes (Pomeroy and Deibel, 1986).

High Turbulence and High Nutrients

The classic diagram developed by Margalef (Fig. 8.1*a*) highlights the positive relationship between turbulence and nutrients. It serves very well to describe key aspects of pelagic ecology on coastal shelves and open-ocean regions such as the North Atlantic, where the delivery of nutrients to the surface layer is largely mediated by vertical mixing. Consequently, when considering the open ocean, the strong link between inputs of external energy (i.e., that which influences turbulence and advection) and fluxes of nutrients to the surface layer tends to dominate our view. Physical forcing can increase the co-occurrence of nutrients and light (Yentsch, 1974, 1980; McGillicuddy et al., 1998), leading to the development of a food web with larger cells that transfer a greater proportion of primary productivity to higher trophic lev-

els, including fish (Legendre, 1981; Michaels and Silver, 1988; Legendre and Le Fèvre, 1989; Kiørboe, 1993). In turn, a greater proportion of primary production is exported to the deep sea (e.g., Eppley and Peterson, 1979; Michaels and Silver, 1988).

Low Turbulence and High Nutrients

Red-tide dinoflagellates occupy the low-turbulence, high-nutrient corner of Margalef's diagram (Fig. 8.1a). This regime is associated with external inputs of nutrients to coastal waters. Special adaptations to increase competitiveness or to minimize losses, such as vertical migration (Eppley et al., 1968; Cullen and MacIntyre, 1998), deterrence of grazers (Ives, 1987), and allelopathic inhibition of potential competitors (Maestrini and Granéli, 1991) have been recognized in some bloom-forming flagellates.

The low-turbulence, high-nutrient condition is relevant to much more than dinoflagellate blooms in coastal waters, because stratified surface waters in a broad range of environments can be enriched by processes that are not linked to enhanced turbulence. These enrichment processes need further study. For example, eutrophication has transformed coastal ecosystems, but in many cases the consequences for fisheries (Micheli, 1999) and the occurrence and impacts of harmful algal blooms (e.g., Smayda, 1990) are difficult to establish. Also, it has been shown that significant quantities of macronutrients reach coastal waters through atmospheric deposition (Paerl and Whitall, 1999), and atmospheric deposition is known to be a significant source of iron to open-ocean waters (Donaghay et al., 1991; Duce and Tindale, 1991; Young et al., 1991; Bruland et al., 1994). Fluxes from atmosphere to ocean, chemical transformations, and ecological consequences are difficult to quantify, however. It is nonetheless recognized that enrichment of surface waters with iron can stimulate N_2 fixation (Rueter, 1982; Falkowski, 1997), especially in conjunction with stratification (see Bruland et al., 1994). New nitrogen is thus supplied to surface waters without altering the turbulence regime (Karl et al., 1997). Finally, there is a need to consider the possible responses of pelagic ecosystems to intentional fertilization (Chisholm, 2000), for example, with iron (Coale et al., 1996), phosphorus, iron and trace elements (Schueller, 1999), or nitrogen (Jones and Otaegui, 1997), actions that would increase nutrients significantly without increasing turbulence.

As with the low-turbulence, low-nutrient regime, the physical process of stratification ensures that biological interactions have a strong influence on community structure, while imposing limitations on the types of food webs that can exist. Increased availability of nutrients should relax one of the constraints that favors small cells in stratified, oligotrophic waters, so communities might include significant populations of larger phytoplankton, resistant to grazing (Riegman, 1998; Smetacek, 1998) and adapted to minimize sedimentation. The factors that strongly influence grazing losses of larger cells during physically forced nutrient enrichment of surface layers, for example, the effects of turbulence on encounter rates (Kiørboe, 1993) and the development of temporal and spatial mismatches between sporadically growing microphytoplankton and slower-growing but mobile macrozooplankton grazers (e.g., Legendre, 1981; Cushing, 1989; Kiørboe, 1991), will not strongly influence grazing losses of larger phytoplankton whose growth is stimulated by nutrient enrichment in the absence of physical disruption. In turn, adaptations of large cells, such as motility (e.g., dinoflagellates) and buoyancy regulation (vacuolate diatoms and *Trichodesmium*), can minimize sedimentation of larger phytoplankton.

It follows that to understand controls on food web structure in pelagic surface layers, we should try to understand the consequences of nutrient enrichment, with and without concomitant increases in physical forcing.

2.3. *Physical Processes and the Structure of Food Webs*

Without exploring the influences of physical processes on life histories of consumers (see Chapter 7), we discuss the influence of physical processes on pelagic ecosystem structure through their effects on phytoplankton life forms and thus on the foundations of food webs. The diagram developed by Legendre and Le Fèvre (1989; Fig. 8.2) will guide our discussion. We know that when concentrations of limiting nutrients in the euphotic zone are increased, enhanced growth of larger phytoplankton (1 → 2 in Fig. 8.2) and increased flows of chemical energy and materials to higher trophic levels will follow, resulting in greater losses of organic matter to deeper waters through sinking (Michaels and Silver, 1988; Legendre and Le Fèvre, 1989) and transport associated with vertical migration (Longhurst and Harrison, 1988). It follows that alleviation of light limitation in nutrient-rich water will have a similar effect. Observations show the consequences: In general, the ocean seems to support a relatively constant background of small phytoplankton (e.g., Olson et al., 1990), and enrichment of surface

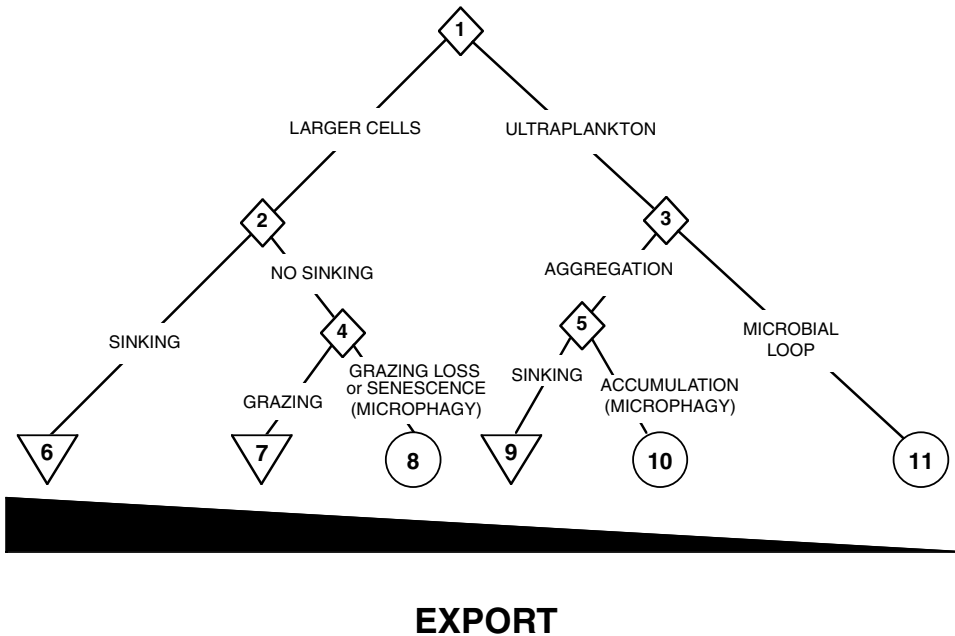


Fig. 8.2. Flows of chemical energy and materials through pelagic food webs. Branch points, indicated by diamonds, were called hydrodynamic singularities by the original authors. Branches to the left indicate a higher probability of export, branches to the right favor regenerated production. The fates of energy and materials are indicated by triangles (export) or circles (accumulation). [Modified from Legendre and Le Fèvre (1989) with modifications at branches 4 and 5 after Cullen (1991), and with inclusion of alternative fates for grazed materials.]

layers with nutrients, generally associated with physical processes (Margalef, 1978; Yentsch, 1980) leads to incremental addition of bigger cells (Malone, 1980; Furuya and Marumo, 1983; Yentsch and Spinrad, 1987; Yentsch and Phinney, 1989; Ciotti et al., 1999).

It can be argued that the lower bounds on concentrations of phytoplankton must be set by density-dependent loss processes (Strom et al., 2000), such as grazing (ibid.) or viral lysis (Fuhrman, 1999). Clearly, the added nutrients permit larger cells to proliferate, unconstrained by the tight grazing control that characterizes the microbial loop (Cullen, 1991; Morel et al., 1991; Banse, 1995; Landry et al., 1997). Increased concentrations of nutrients thus support the development of a different web of grazers and their predators, more closely resembling the classical diatom–copepod–fish paradigm ($1 \rightarrow 2 \rightarrow 4$). Biological response to a pulse of nutrients is self-limiting: As the food web shifts toward larger cells and grazing by mesozooplankton, dissolved nutrients are stripped from the surface layer, and particulate organic material is exported to deeper waters, thereby returning the system to a low-nutrient condition dominated by smaller phytoplankton ($1 \rightarrow 3 \rightarrow 11$). Self-shading by phytoplankton could slow this process but not change its trajectory. If the enhanced supply of nutrients is sustained without significant physical disruption, for example through geostrophic uplift of the nutricline (see Yentsch, 1980), selection should favor an expanded microbial loop and large plankton that accumulate through reduced losses to grazing and sinking ($1 \rightarrow 2 \rightarrow 4 \rightarrow 8$). Therefore, nutrients must be delivered to the photic zone on a time scale shorter than that for complete food web response if elevated concentrations of nutrients and enhanced flows of chemical energy and nutrients to higher trophic levels are to be maintained (see Walsh, 1976; Legendre, 1981; Legendre and Le Fèvre, 1989; Kiørboe, 1993).

2.4. *Physical Processes and Phytoplankton Blooms*

Three mechanisms, each forced differently by physical processes, may initiate population growth of the larger planktonic organisms in the open ocean, always led by the algal cells whose doubling time is many times shorter than that of most of their consumers. Such accumulation of unconsumed autotrophic cells generally does not occur within the smaller, background fraction of the pelagic food web. We follow McCreary et al., (1996) and Banse and English (2000) in classifying these blooms:

1. *Upwelling blooms*, in which Ekman divergence either at a coast or in the open ocean induces upward motion of deep water into the photic zone, more or less continuously for a significant period. In such situations, the upwelled, nutrient-rich water entering the photic zone is strongly illuminated (because accumulating cells are advected away from the upwelling cell) and growth of larger cells may be sustained for the entire period during which upwelling occurs.
2. *Entrainment blooms*, which occur when a stable mixed layer, supporting only the background of small cells, deepens either by the action of increased surface wind stress or of reduced solar heating and consequent negative heat flux across the sea surface. Here, the progressive erosion of the pycnocline entrains deeper, nutrient-rich water into the photic zone and initiates rapid growth of the sparse, large algal cells; in such events, progressive seasonal reduction in

irradiance, or self-shading and shoaling of the photic zone, may terminate the bloom.

3. *Detrainment blooms* are represented by the classical spring bloom of the North Atlantic and, generically, occur when near-surface stratification is induced in a deep mixed layer of nutrient-rich water, thus conserving the increasing numbers of large, overwintering algal cells within the photic zone. The required stratification may be induced by a variety of physical processes: a net heat gain across the sea surface during a season of increasing irradiance, or through near-surface dilution by precipitation, by ice melt, or by river efflux.

Given that the time scale for enhanced flows of chemical energy and materials to higher trophic levels is governed by characteristic growth rates for larger phytoplankton versus the response time of their grazers, temporal variability of upwelling, entrainment, detrainment, and nutrient enrichment from processes such as atmospheric deposition will have a strong influence on ecosystem dynamics. Because relative growth rates of autotrophs and their consumers determine these dynamics, irradiance and temperature could have an important influence on the consequences of particular perturbations.

3. Hypotheses

Recent information on the microbial loop, N_2 fixation, the influence of iron on plankton dynamics, and different modes of nutrient delivery to surface layers of the ocean shows that more comprehensive descriptions of the relationships between physical forcing and ecosystem structure should be developed, based on hypotheses relating physical processes, temporal variability of nutrient supply, and the responses of large phytoplankton versus the microbial loop. The frameworks for these hypotheses have already been established (e.g., Margalef, 1978; Legendre, 1981; Legendre and Le Fèvre, 1989; Moloney and Field, 1991; Moloney et al., 1991; Kiørboe, 1993; Landry et al., 1997; Carr, 1998), and we feel that the major features of these hypotheses are widely accepted.

- *Hypothesis 1.* In well-lit surface layers, small microbes outcompete larger phytoplankton for limiting nutrients. Consequently, in the absence of temporal variability in nutrient fluxes or in physical forcing, the microbial loop will dominate the flows of chemical energy and nutrients in surface-layer plankton.
- *Hypothesis 2.* Because microbial grazers respond rapidly (both in grazing rate and growth rate) to changes in availability of food, the net population growth rates of picoplankton and ultraplankton are maintained close to zero on the time scale of days. Responses of mesozooplankton to changes in food availability are somewhat slower and require increases in abundance of larger cells; time lags ensure fluctuations in the net growth rates of larger phytoplankton in response to increased nutrient fluxes or alleviation of light limitation. As a result, the biomass of small phytoplankton and the microbial loop represent a relatively constant background in the ocean, and larger phytoplankton account for variability associated with physical forcing and nutrient inputs.
- *Hypothesis 3.* Pulses of nutrients (e.g., from upwelling, vertical mixing, atmospheric deposition) or transient alleviation of light limitation (stratification of

nutrient-rich mixed layers) differentially encourage accumulation of phytoplankton that can attain high rates of cell division and are not immediately susceptible to grazers. The key time scale for enhancing the fluxes of nutrients and chemical energy to larger phytoplankton and higher trophic levels is in the window between generation times of phytoplankton and the response time of herbivorous zooplankton; it corresponds to the event scale (days to weeks) and should be influenced by temperature and irradiance.

- *Hypothesis 4.* Under sustained nutrient enrichment, selection is for phytoplankton that can escape losses to grazing, viral lysis, and sinking. If physical forcing does not change significantly, this leads to adjustments in food web structure until losses of organic material to sedimentation, mixing, and biological transport balance the flux of nutrients into the photic zone. Biomass accumulates and nutrients are sequestered in organic pools: the microbial loop, larger cells and zooplankton, and dissolved organic matter. Partitioning between pools is determined more by biological interactions than by mixing and advection.

Hypotheses like these may be useful in attempts to explain the responses of pelagic ecosystems to variable nutrient enrichment when this enrichment may or may not be linked directly to the input of mechanical energy to the photic zone. Also, they can guide critical examination of the four regimes described in Section 2.2. As a first step toward evaluating the hypotheses, it is instructive to consider relevant aspects of physical forcing in the ocean and the degree to which enrichment of surface layers with nutrients is linked to physical disturbance in different locations and seasons. We begin by exploring geographic variability in modes of physical forcing and the links between physical disruption and nutrient enrichment in different parts of the ocean.

4. Latitudinal and Seasonal Variability in the Dominant Forms of Physical Forcing

4.1. Determination of Ecosystem Structure by Ocean Physics

Ocean basins have individual and complex geometry within which seasonally variant solar radiation and wind stress at the surface induce motion and structure at all temporal and spatial scales. The richness of the consequent physical structure in the water column is expressed biologically in the characteristics of the pelagic ecosystem typical of each region. Here we argue that the forcing of ecosystems by ocean physics differs significantly between individual oceans and at different latitudes. It is these differences that structure the singularities exhibited by the pelagic ecosystem from region to region.

As we have discussed, it is axiomatic that physical motion and the density structure of the water column intimately control the ecology of phytoplankton, primarily through mechanisms that recharge the euphotic zone with inorganic nutrients in a manner determined by the characteristic oceanography of each region. Such processes form a continuum from strongly seasonal regimes, in which nutrients are recharged either by winter mixing or upwelling, to weakly seasonal regimes in which vertical nutrient recharge occurs across a permanent pycnocline. This series is equivalent to the continuum between eutrophic and oligotrophic regimes, or between successional and climax communities or biomes.

The associations of phytoplankton species are structured appropriately and in accordance with hypotheses 1 to 4 above. Although zooplankton, nekton, and fish are progressively more independent of their physical environment, a characteristic pelagic fauna is, nevertheless, associated with each characteristic algal regime. The zooplankton associated with seasonally pulsed phytoplankton growth has low diversity and high biomass in which herbivores dominate; in weakly seasonal regions, where nutrient recycling within the euphotic zone is an important process, the characteristic zooplankton have smaller biomass but greater taxonomic diversity with a more equitable balance between herbivores and predators (Longhurst, 1985).

We infer from such observations that it is the characteristic physical oceanography of each region that primarily determines the functional composition and seasonal biomass of the pelagic ecosystem from plants to predators. This bottom-up control of the ecosystem is mediated by the time-dependent supply of inorganic nutrients to the euphotic zone, which, in turn, constrains the fluxes of energy and materials through the ecosystem, hence the type of food web that can develop. Consequently, top-down modulation of ecosystem structure by herbivory and predation can be considered a subsidiary process, as we have already suggested in our opening remarks. In this, the pelagic biomes resemble terrestrial biomes. A simple combination of geology, latitude, altitude, exposure, and rainfall determines the characteristic flora, with its associated fauna of each terrestrial biome. Although terrestrial herbivores undoubtedly modulate the final expression of forest or tundra, neither elephants nor reindeer determine which vegetation type or biome will develop.

It can be argued that a similarly parsimonious set of factors determines the distribution of pelagic biomes, each with its characteristic flora and fauna. For the open ocean, these factors are simply those required by Sverdrup (1953) to control illumination and the vertical stratification of the water column; they may be reduced to latitude (irradiance), regional winds, cloud cover, and the flux (if any) of low-salinity surface water. From these factors may be deduced sufficient information to predict the seasonality and kind of phytoplankton production and of consumer response. Over continental shelves we must also know water depth and tidal range. Copepods and whales do not determine which groups of plants will flourish; like the phytoplankton, they are themselves expressions of the regional physical oceanographic regime.

4.2. *Latitudinal Variations in Physical Forcing*

Consider, as a special case, some overlooked but direct consequences of latitude for pelagic ecology. The equatorward vanishing of the Coriolis acceleration, which might seem unlikely to have ecological significance, is actually a primary factor in structuring the pelagic ecosystem. The vanishing Coriolis effect requires that the slope of the sea surface associated with a given horizontal velocity should diminish toward the equator. Consequently, wind stress is rapidly translated into horizontal momentum at low latitudes and even sustained monsoon winds (\geq Beaufort Force 7) such as occur in the Arabian Sea in boreal summer fail significantly to deepen the mixed layer; rather, it is the seasonally variant flow of current systems, induced by seasonal changes in the direction and velocity of winds, which modulate mixed layer depths by modifying the geostrophic balance in each region. It is to be noted that such changes in mixed layer depth involve no erosion of the pycnocline and its associated nutricline and hence no recharging of the Ekman layer with nutrients.

The facts explain the rapid reversal of the deep Somali Current at 8 to 10°N by the seasonally reversing monsoon winds (Lighthill, 1969; Philander, 1985), a reversal that could not occur by similar seasonal changes in winds over the Gulf Stream. This seasonal shift has important consequences for algal ecology in the Arabian Sea, permitting a winter bloom in response to the cold, dry northeast monsoon that drives the current southward, deepening the mixed layer landward while shoaling it offshore. Six months later a major summer bloom is induced by coastal divergence along Somalia and Arabia in the now-reversed northward flow of the current (Longhurst, 1998).

In addition to the effect of the equatorward vanishing of the Coriolis acceleration, the mixed layer of low latitudes is peculiarly resistant to wind deepening because of the high stability of the permanent tropical pycnocline, partly due to an excess of precipitation over evaporation, but more generally because the heat balance over tropical oceans involves a mean downward heat flux and hence no tendency to convective overturn of the water column. The resistance to mixing of the subsurface stability maximum within the pycnocline (typically between 50 and 100 m depth) is expressed as the Brunt–Väisälä frequency N , in cycles h^{-1} . In the permanent pycnocline equatorward of about 20° of latitude, N commonly takes values about double those of the summer thermocline at higher latitudes (Emery et al., 1984; Houry et al., 1987). For all these reasons, seasonally strong wind stress in winter at moderate to high latitudes, but not at low latitudes, rapidly deepens the mixed layer by erosion of the summer thermocline (as in the North Atlantic) except where the density structure is reinforced by light, low-salinity surface water (as in the North Pacific).

Here, then, is a very fundamental difference in the induction of nutrient recharge of the mixed layer that is latitude dependent and is associated with factors not classically considered to be ecologically significant. But there are also others that perhaps should be thought about. Satellite imagery has revealed to what extent nutrient recharging of the euphotic layer in mesoscale eddies and Rossby waves is an important component in regional productivity (McGillicuddy et al., 1998). Measurements in situ have also revealed responses of phytoplankton to nutrient pumping (Falkowski et al., 1991). And as Emery and colleagues (1984) have demonstrated, the internal Rossby radius of deformation is the appropriate length scale for such baroclinic phenomena, and is a function of water depth, latitude, and the stability of the water column. Latitude is expressed in the balance between gravitational flattening of a free surface and the Coriolis acceleration to deform it, and stability as the distribution of N in the profile. So it might be expected that the eddy field of the open ocean, and hence fields of chlorophyll and diagnostics of phytoplankton physiological status (Falkowski and Kolber, 1995), will change fundamentally as a function of latitude, although the question does not appear to have been addressed formally.

4.3. *Pelagic Biomes*

From consideration of just a few simple physical processes, outlined above, falls out a first-order classification of the biomes of the marine pelagic environment comparable with the major natural biomes ashore—desert, tundra, steppe, savanna, and forest—and as for the terrestrial biomes, it is also possible to distinguish climax from successional communities of organisms. A recent synthesis of pelagic biomes (Longhurst, 1998), conducted along these lines, concluded that it would be conve-

nient to recognize four primary units of the pelagos: biomes of polar seas, of the regions lying under the westerly wind systems, of the trade wind regions, and of the continental margins and shelves. The manner in which these are thought to be physically forced may be summarized as follows.

1. *Polar biome*—at high latitudes where wind stress is moderate compared with under the westerlies, and where the physical consequences of the freeze–melt cycle of sea ice dominate the very brief light-limited productive season, and having its equatorward limit generally at the Polar Fronts. Here, detrainment blooms may be induced very early in the spring since shallow stratification is a widespread feature and winter mixing is carried only to moderate depths. Consequently, except at retreating ice edges, the bloom may rapidly become constrained by lack of nutrients and enter a brief oligotrophic phase. The pelagic ecosystem, strongly successional, is characterized by low specific diversity at all levels and by the presence of abundant nekton specialized for feeding on the large diatoms characteristically dominating algal biomass in the seasonal bloom.
2. *Westerlies biome*—at midlatitudes, where wind stress is maximal and consequently where winter mixing is carried especially deep prior to the establishment of a shallow thermocline in early spring by positive heat flux across the sea surface. Here, the production cycle is dominated by a spring detrainment bloom which is successional and leads to the establishment of a climax community of pelagic biota, dominated by small cells supported by regenerated nutrients. As the summer advances and the mixed layer deepens, event-scale nutrient entrainment supports blooms of larger cells.
3. *Trades biome*—equatorward of the subtropical convergences between trades and westerlies. Winter mixing is relatively unimportant, so that observed seasonal shoaling or deepening of the mixed layer is dominated by geostrophic response to distant forcing. Here, where seasonality is dampened, the dominant pelagic biota comprise a climax community, the paradigmatic small cell association regenerating nutrients internally by heterotrophy. It is toward this climax that the biota of summer seas in higher latitudes develops. Entrainment of nutrients may occur at the event scale, causing brief blooms or at divergences, as at the equator, when blooms may be of longer duration and a successional community established. It is in this stable biome that the effects of the lunar cycle of nocturnal illuminance is most readily observed to modify the diel migration compartment of many plankton and nekton species.
4. *Coastal biome*—landward of the shelf-break front, where the seasonal production cycle is forced by a great variety of factors: winter mixing, topographic effects, and coastal divergences in lower latitudes dominating. It is only here that the effects of the tides become significant, and this may, especially on wide continental shelves, dominate the algal growth regime. A simple relationship between tidal current and depth establishes where summer stratification may develop over midlatitude shelves (Pingree et al., 1978); fronts at the edges of tidally mixed regions may carry a summer-long chlorophyll enhancement, attributed to entrainment at the advancing stratified side of the front as the lunar month advances. The coastal biome is the most susceptible to further logical subdivision to represent different modes of physical forcing. It is

also the hardest to define, because incursions of oceanic water over the shelf, as occur routinely in most areas, carry with them 'wrecked' or expatriated populations of organisms from the oceanic biomes.

Obviously, no ocean basin develops a symmetric circulation in which the distribution of these biomes is ideally expressed. The alignment of coastlines and the distribution of shoal water, together with the dimensions of the basin itself, determine how each biome will be expressed in individual oceans and seas.

The manner in which the planktonic biota occupy these biomes forms the corpus of pelagic ecology, not reviewed in depth here. The biota of the tropical seas of the trades biome are widely assumed to represent the stable climax community of the pelagos, having internal dynamics much more complex than in the unstable, simpler, successional communities of the polar and westerlies biomes, where life cycles of the primary herbivores may not be completed within a single season and where steady-state is never achieved.

We feel that there is significant utility in combining explicit recognition of distinct pelagic biomes with the consideration of specific hypotheses relating ecosystem structure to temporal variability in nutrient input with and without physical forcing. Such a framework will promote the development of conceptual, descriptive, and predictive models that describe patterns of ecosystem structure and variability within and between biomes.

4.4. *Case Study of Biotic Response*

We note a special case to illustrate the diversity of biological responses that can complicate the development of general hypotheses. This example is particularly relevant to our discussion of subtropical gyres which follows. One of the revelations of satellite remote sensing has been the manner in which the open ocean is populated with event-scale eddies, capable of inducing ephemeral algal blooms in their passage (see above); at low latitudes, the response of algal cells is very rapid. Almost equally rapid may be the response of large gelatinous herbivores, dominated by tunicates and having life-history traits specialized to exploit event-scale blooms in an opportunistic manner: They are normally present in low concentrations but have "rapid growth, short generation time and explosive population increase" according to Allredge and Madin (1982). The induction of an ephemeral bloom may cause the rapid development of swarm concentrations of tunicates, especially salps, capable of clearing 40 to 100% of their resident water volume daily in Gulf Stream frontal eddies (Deibel, 1985). These organisms efficiently filter a wide range of cells from diatoms to bacteria, have higher growth rates than have been recorded for any other metazoan (linear growth of $10\% \text{ h}^{-1}$ and weight doubling in 24 h), their generation times may be as short as 48 h, and asexual reproduction among thaliaceans results in extraordinary high fecundity. Here is an entire community of organisms whose way of life is finely tuned to exploit a specific kind of oceanographic event; their role in exploiting event-scale blooms in the oceanic eddy field, and other outbursts of larger cells, such as those induced by aeolian deposition of nutrients or intentional fertilization of the ocean, awaits investigation.

5. Temporal Variability of Physical Forcing in the North Pacific Subtropical Gyre

5.1. Resolving Temporal Variability

The preceding discussion, based on extensive review and analysis of oceanographic observations (Longhurst, 1995, 1998), addressed geographic patterns in physical forcing with an emphasis on seasonal variability in ecosystem structure. Significant sources of shorter-term variability were identified. However, broad generalizations about physical–biological coupling on these scales are difficult to develop because chronic undersampling is a fact of life in oceanography (Platt et al., 1989) and still constrains the interpretation of available field data. Even though we are rapidly developing the capabilities to resolve short-term variability (Dickey, 1991) and to acquire synoptic descriptions of ecosystem processes from remote sensing (Platt et al., 1991; Lewis, 1992), our present conceptual models are determined largely by data collected during traditional oceanographic expeditions, so both high-frequency (hours to days) physical forcing events and low-frequency (decades to centuries) climate-driven variations are poorly sampled and, therefore, poorly understood. This situation is changing rapidly. Systems for continuous and synoptic observation of the ocean are being developed and deployed, and essential long-term sampling is being conducted at some sites [e.g., the Bermuda Atlantic Time-series Study (BATS; Michaels and Knap, 1996), the Hawaii Ocean Time-series (HOT; Karl and Lukas, 1996), and COLD (Coupled Ocean-ice Linkages and Dynamics), a component of the Antarctic Long Term Ecological Research (LTER) program (Smith et al., 1995)]. We now have the opportunity to address key questions that could not be studied effectively with traditional oceanographic sampling. Selected results from the HOT program are presented here as examples of potentially important but as yet poorly documented coupling between physical and biological processes.

5.2. North Pacific Subtropical Gyre Ecosystem

The North Pacific Subtropical Gyre (NPSG), which at the ocean's surface extends from approximately 15°N to 35°N latitude and 135°E to 135°W is perhaps the largest ecosystem on our planet (see Karl, 1999). Homologous anticyclonic gyres are found in the South Pacific Ocean, the Indian Ocean, and in both hemispheres of the Atlantic Ocean. These subtropical gyres occupy nearly 40% of Earth's surface, but they continue to remain poorly described relative to the more accessible neritic and coastal zones. Once thought to be a homogeneous, static habitat, there is increasing evidence that the NPSG exhibits substantial physical, chemical, and biological variability on a variety of time and space scales. Surface circulation (above 50 m) is driven by wind and maintained by mass distribution. The geostrophic nature of the major clockwise (anticyclonic) circulation assures wind-driven convergence of surface waters in the NPSG (Reid et al., 1978). This convergence serves to isolate these relatively large gyre ecosystems and to restrict exchanges with adjacent current systems (Fig. 8.3), maintaining chronically nutrient-impoverished surface waters. Because the system is isolated and concentrations of nutrients are very low, it is an excellent candidate for studies of temporal variability in physical forcing, nutrient supply, and ecosystem structure.

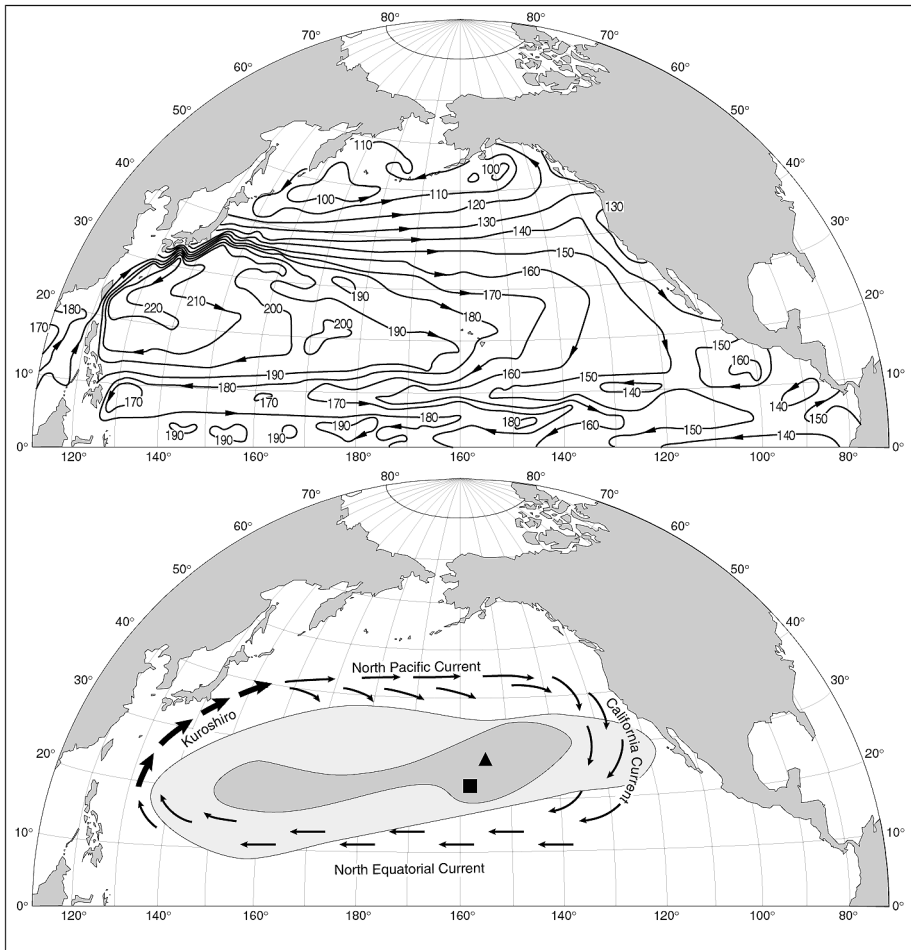


Fig. 8.3. Features of the North Pacific Ocean relevant to the ecology of the North Pacific Subtropical Gyre. The top panel shows dynamic topography of the sea surface (dyn-cm relative to 1000 dbar; redrawn from Wyrski, 1975). Arrows show direction of geostrophic flow. The bottom panel shows the major circulation features which define the approximate boundaries of the gyre and the estimated range of central Pacific Ocean mesozooplankton, based on an analysis of fidelity of mesozooplankton species (redrawn from McGowan, 1974). The darker area is the core of the fauna (100% fidelity) and the lighter area shows 60% fidelity. Stations ALOHA (filled square) and CLIMAX (filled triangle) are both in the core area. (From Karl, 1999.)

5.3. Sources of Variability

To understand relationships between physical forcing and biotic variability in the NPSG, it is necessary to describe variability in the fluxes of nutrients. Unfortunately, pathways for the flow of nutrients in and out of the upper euphotic zone of the NPSG are not well constrained. Potential sources for input include (1) supply from below by a variety of eddy diffusion and mixing processes; (2) air-sea transport (including wet and dry deposition and, for nitrogen, gas exchange); (3) in situ production of bioavailable N via the process of microbiological N_2 fixation; (4) horizontal advective

tion and mixing, usually along isopycnal surfaces, from regions of elevated nutrient concentrations; and (5) transport across isopycnal surfaces independent from water motions. The latter process could include both vertical migrations of plants and animals and passive flux of buoyant, inanimate particles (e.g., Grimalt et al., 1990). Principal pathways for N and P export from the euphotic zone include (1) gravitational settling of particulate matter and adsorbed dissolved matter, (2) downward mixing, and (3) active transport by plant and animal migrations. The quantitative balance among these otherwise unrelated ecosystem processes will determine the standing crops and rates of primary and secondary production in the surface layer; in turn, community structure will vary to reflect, and in part to determine, these balances. Resolving the feedbacks between nutrient supply mechanisms, food web structure, and export processes is therefore central to understanding the relationships between physical forcing and ecosystem dynamics in this oligotrophic gyre ecosystem. We begin by considering supply mechanisms.

Supply of Nutrients from Below

Turbulent diffusion of nutrients to the surface layer of oligotrophic gyres was classically considered to be a slow, continuous process, but estimates of vertical diffusion rates in the open ocean (Lewis et al., 1986; Ledwell et al., 1993) have failed to reconcile estimates of supply and demand. Similarly, based on an analysis of the calculated steady-state nutrient fluxes versus measured nutrient demand, Hayward (1987, 1991) concluded that episodic mixing events must occur in the NPSG in order to achieve a mass balance. Stochastic events of major ecological significance therefore occur; they may be short-lived and are undoubtedly undersampled by present ship-based observation programs (Platt et al., 1989). Even the approximately monthly sampling schedule adopted in the HOT program is too infrequent to resolve important but intermittent nutrient injections (see Cullen et al., 1983; Holligan et al., 1985; Dickey et al., 1998).

How are nutrients transported vertically to the surface layer of the NPSG? There are at least four different physical mechanisms: (1) internal waves and tides, (2) cyclonic mesoscale eddies, (3) wind-driven Ekman pumping, and (4) atmospheric storms. *Internal waves* are ubiquitous in deep-ocean environments (Garrett and Munk, 1972), and it appears that the high vertical shear of low-frequency internal waves contributes to occasional pulses of vertical mixing (Gregg et al., 1986; Sherman and Pinkel, 1991). McGowan and Hayward (1978) were first to document a relationship between episodic mixing and rates of plankton productivity; these events were sufficient to double the local rate of primary production.

Mesoscale eddies have been observed in the NPSG for more than two decades (Bernstein and White, 1974); however, until recently it had been difficult to determine their influence on biogeochemical processes. How nutrient-rich water is brought closer to the surface by rotary motion, centrally in cyclonic eddies and peripherally in anticyclonic features, has been understood for many years. In cyclonic eddies, a dome is induced in the pycnocline below the depression of the sea surface (Ring Group, 1981), while in anticyclonic eddies, the process is more complex: In the high-velocity region encircling the eddy, elevation of the pycnocline is associated with a strongly baroclinic structure (Yentsch, 1974). Vortex contraction may strengthen the upwelling of nutrients, especially on the anticyclonic side of the transient jets (Woods, 1988). The evolution of eddies certainly induces intense vertical motion leading to nutrient enhance-

ment (McGillicuddy et al., 1998), with indications of increased primary production (Falkowski et al., 1991). Eddies thus force differential responses of phytoplankton to seasonal forcing by wind and irradiance, as compared to the surrounding ocean.

Recent studies have documented that the NPSG contains a vigorous field of mesoscale variability, including discrete eddies, near-inertial motions, and internal tides (Venrick, 1990). These physical processes can enhance nutrient fluxes into the surface ocean and cause a stimulation of primary production. Furthermore, variable horizontal currents with time scales of 1 to 30 days and space scales of 1 to 200 km, which are nearly tenfold greater than expected, imply vertical circulation rates that are two orders of magnitude greater than the mean for this region (Niiler and Hall, 1988). These conditions have implications for nutrient resupply and for metabolic activities of plankton populations.

Ekman pumping resulting from sea-surface divergence driven by local winds can cause mesoscale eddylike upwelling. Letelier et al. (2000) documented a strong upwelling event at Station ALOHA in March–April 1997 that displaced the nutricline upward by 120 m. The observed upwelling was a manifestation of the combined effects of wind-induced divergence of the surface waters and the simultaneous passage of a large cyclonic eddy through the HOT program study area. These otherwise unrelated physical processes had significant biogeochemical consequences, including a threefold increase in chlorophyll *a* in the near surface (0 to 25 m), a twofold increase in diatom abundance and a change in the chlorophyll fluorescence efficiency. All of these changes were undoubtedly coupled to the increased supply of nutrients caused by the local upwelling event. Despite these occasional observations of stochastic mixing processes in the NPSG, it has been impossible to obtain nutrient budget closure due to the intermittent nature of these processes.

Atmospheric storms play a major role in the establishment of the seasonal variability in nutrient dynamics of the gyre. Each winter, extratropical cyclones track across the North Pacific from west to east, approximately every five to seven days (Karl and Lukas, 1996). The cold fronts associated with these midlatitude storms produce very strong northerly and northeasterly winds and impulsively force the upper ocean. This results in a deepening of the mixed layer and a cooling associated with both enhanced evaporation and entrainment of cooler waters from below, resulting in an enhanced nutrient flux to the euphotic zone. Both the atmospheric storm tracks and their intensities have large interannual and interdecadal variability in part due to the frequency and intensity of basin-scale climate features such as the El Niño–Southern Oscillation (ENSO). Consequently, the annual extent of gyre nitrification by this mechanism is also time variable.

Aeolian Transport

The net flux of major (N, P) nutrients to the surface of the NPSG by the combined effects of wet and dry atmospheric deposition is thought to be small relative to other potential sources. For fixed (bioavailable) nitrogen, the atmosphere supplies, at most, 10 to 15% of the total N required to balance the export of particulate matter (Duce, 1986; Karl et al., 1992), and probably much less. It is conceivable that N deposition may become more important with the increased burden of N in the atmosphere from fossil fuel burning and global fertilizer use (see, e.g., Paerl and Whitall, 1999), but at the present time, this delivery pathway appears to be negligible for the NPSG. In the case of P, the atmosphere appears to be even less important than for N because the

N/P ratio of both wet and dry atmospheric fallout is one to two orders of magnitude enriched in N, relative to the requirements for the growth of plankton (Duce, 1986).

Compared to the relatively minor role of atmospheric deposition for the flux of macronutrients to the euphotic zone, wet and dry deposition of some trace nutrients, especially Fe, appears to be a major delivery pathway. Iron is an obligate cofactor for the nitrogenase enzyme system, and there is rapidly accumulating evidence that Fe availability may be a key parameter in the control of N_2 fixation rates in the upper ocean (see Rueter, 1982; Falkowski, 1997). Most of the Fe that is present in the atmosphere over the NPSG is derived from Asian deserts (Duce and Tindale, 1991). There are large seasonal and interannual changes in dust (e.g., Fe) delivery to the NPSG (Donaghay et al., 1991), and this is largely dependent on climate variability. Human activities that affect the extent of these desertified regions ashore (e.g., reforestation, urbanization) can be expected to alter Fe fluxes and, hence, open ocean productivity and nutrient dynamics. On millennial time scales, these same processes have probably affected marine productivity and carbon sequestration, as global-scale glacial cycles have altered the continental landscapes, especially the extent of arid habitats (Martin, 1992).

Nitrogen Fixation: A Consequence of Stratification

In addition to the traditional view of enhanced turbulence leading to enhanced nutrient flux, it now appears probable that the NPSG gains nutrients, at least nitrogen, when turbulent mixing is at a minimum. Each summer, as stratification intensifies, there is selection for N_2 -fixing organisms and a pulse of N_2 -supported new production. Near the end of the summer, a second pulse of nutrients that appears to be derived from death and autolysis of near-surface plankton fuels another rapid bloom of eukaryotic algae and subsequent export pulse of particulate matter (Karl et al., 1996).

Isopycnal Transport

We often view the ocean in a vertical reference frame when in fact the horizontal scales dominate (e.g., the NPSG is >1000 km across but <5 km deep). Consequently one must consider principally horizontal transport along isopycnal surfaces as a major potential source of nutrients for plankton in the gyre. For example, the low-salinity North Pacific Intermediate Water (NPIW), located in the gyre near the depth of nutrient maxima (about 500 to 700 m), outcrops seasonally in the high-nutrient region of the Pacific, north of 45°N (Reid, 1965). Variations in water mass formation could alter the flux of nutrients into the gyre along this isopycnal surface. Similarly, the relatively shallow (about 150 m) high-salinity water located near the base of the NPSG euphotic zone forms in an area of excess evaporation near the subtropical front at 25 to 30°N, then flows south along isopycnal surfaces (Tsuchiya, 1968). Nutrient mass transport along the approximately $24.5\sigma_\theta$ surface could help resupply the gyre. Quantitative information on water mass distributions and movements are critically important for nutrient budget reconciliation in the NPSG. In this regard, the recently completed World Ocean Circulation Experiment (WOCE), including comprehensive North Pacific Ocean water mass transient tracer measurements (Freons, ^{14}C), should provide an invaluable data set for these flux estimations.

Transport across Isopycnal Surfaces Independent of Water Motions

There are at least two mechanisms whereby nutrients can be transported across isopycnal surfaces in the absence of water motions: vertical migrations of plankton and

the vertical upward flux of buoyant, inanimate particles. Active transport of nutrients by vertically migrating zooplankton has been invoked as a mechanism for net downward flux of C, N, and P from the euphotic zone (Longhurst and Harrison, 1989). Also, certain phytoplankton species can migrate vertically from the lighted, nutrient-deficient surface ocean to depths where sufficient nutrients are present (Cullen and MacIntyre, 1998). Karl et al. (1992) hypothesized that the N_2 -fixing cyanobacterium, *Trichodesmium*, uses regulation of buoyancy to capture and transport phosphorus (P) from the top of the nutricline. This P-harvesting mechanism would effectively separate the N and P cycles in the upper ocean (Karl and Tien, 1997). A similar mechanism has been described for the transport of nitrate by vertically migrating diatom (*Rhizosolenia*) mats. In a series of carefully conducted field experiments, Villareal et al. (1993, 1999) documented the potential importance of this process for the N cycle in the oligotrophic North Pacific. They estimated that this mechanism can account for $\geq 50\%$ of the new N required to sustain the measured export production in this habitat (see also Richardson et al., 1996, 1998).

The other potential mechanism for vertical displacements of nutrients, especially P, is from the upward flux of low-density organic matter (e.g., phospholipid-rich particles). Investigations in the North Pacific Ocean have previously documented the existence and quantitative significance of this upward flux mechanism (Simoneit et al., 1986; Smith et al., 1989). These low-density materials are produced during selective decomposition of organic material (Yayanos and Nevenzal, 1978) and represent a selective reflux of specific elements and as such may alter the otherwise coupled nutrient cycles.

5.4. Seasonal Pattern of Nutrient Supply and the Biotic Response

The NPSG is chronically nutrient depleted; dissolved nitrate concentrations, for example, rarely exceed 10 nM in the surface (0 to 100 m) waters. According to a view based on conventional sampling, upward eddy diffusion of nutrients stored below the euphotic zone is balanced by nutrient export via sinking particulate matter, and because replenishment of the surface layer is very slow, the standing stocks of available nutrients are scavenged to nearly undetectable levels. This model predicts a more or less uniform export flux throughout the year.

The conventional steady-state view ignores the potential for seasonal or stochastic events that could alter the primary pathway of nutrient recharge (e.g., McGowan and Hayward, 1978; Platt et al., 1989). Data from the HOT program have documented a complex temporal pattern of particle export that suggests two major events per annum; one in late winter and a second in late summer (Karl et al., 1996). Based on the nitrogen isotopic abundance of sinking particles collected in a bottom-moored sediment trap deployed at Station ALOHA, Karl et al. (1997) have suggested that the two events are derived from fundamentally different ecological processes. The winter pulse (with a mean $\delta^{15}N = 4.83$) is hypothesized to be largely supported by nitrate ($\delta^{15}N = 6.5$) supplied by a seasonal period of enhanced upwelling of nutrients from below. The required major (e.g., C, P, Si) and trace (e.g., Fe) elements are delivered to the photic zone in the proper stoichiometry to sustain biological activity. In contrast, the later summer pulse (with a mean $\delta^{15}N = 1.53$) appears to be largely supported by nitrogen supplied by bacterial N_2 fixation ($\delta^{15}N = 0$), supporting new production that is biogeochemically and ecologically much different from that supported by upwelled

nutrients. The process of N_2 fixation decouples export of C, N, and P from new nutrient import. Phosphate is stripped from the photic zone, leading to changes in the elemental stoichiometry of ocean-surface particulate and dissolved organic matter and selection for groups of microorganisms suited to the new nutrient regime (Karl et al., 1997). Temporal variations in the inventories and stoichiometries of both the dissolved inorganic and the dissolved organic matter pools have broad implications for microbial population adaptation and community succession. However, there is no explicit model to explain the relationships between nitrogen supplies to the photic zone, stoichiometries of particulate and dissolved pools, and changes in microbial community structure.

5.5. *Developing Interpretation*

In the oligotrophic NPSG, the response of the plankton community to aperiodic nutrient injections will depend on the frequency and duration of the pulse (Robarts et al., 1998); short-term events result in altered physiology of the microbial assemblage, perhaps reflecting the microbial loop's limited capacity to assimilate enhanced fluxes of nutrients (see Glover et al., 1988), whereas long-duration events lead to changes in the species composition with growth of larger cells. Most eddy-induced nutrient injection events are long relative to the generation time of the microorganisms (weeks to months versus hours to days), so community compositional changes are possible. Typically, there is a selection for phytoplankton with high growth rates and low removal by grazers or viral lysis. Although the microbial food web continues to be active, it is "overprinted" by the growth of eukaryotic algae that respond more quickly and, perhaps, efficiently to the allochthonous supply of nutrients. This temporal selection for the classical diatom–copepod–fish food chain is a critical feature of physical–biological coupling.

The flow from diatoms to copepods to fish in response to pulses of nutrients is not guaranteed. As mentioned in Section 4.4, pelagic tunicates can take over the food web response, and pulses of diatom production can end in mass sedimentation (Peinert et al., 1989). Figure 8.2 illustrates how these different fates are linked to hydrodynamic forcing (Legendre and Le Fèvre, 1989). The governing processes are not well understood in the NPSG, but some modeling is relevant (see also Section 6). Wiegert and Penas-Lado (1995) compared the effects of upwelled pulses of nutrients to a constant supply of an equivalent annual flux. In their simulation model of an open-ocean pelagic community, nutrient pulsing produced a rich dynamical behavior and complex trophic structure that was not present under constant nutrient supply. The winter NPSG habitat appears to be an excellent case study of a nutrient-pulsed ecosystem. If the production of large phytoplankton cells is sustained, there will be an adjustment in the food web structure and a more rapid and efficient transfer of carbon and energy to higher trophic levels and enhanced particulate export to the deep sea. If the nutrient pulse is short-lived or intermittent, the grazer community does not become established and the phytoplankton cells are lost via sedimentation (see Fig. 8.2). Both grazing and sinking remove nutrients and the system reverts to the microbial loop and net sedimentation decreases significantly. This interpretation is consistent with the observed winter pulse in exported particulate matter and with the ^{15}N data suggesting that nitrate is the primary source of new N.

This and other evidence not summarized here clearly document the importance of episodic inputs and export in the NPSG, and the complexities of modeling an ecosystem where pulses of nutrients can come directly from physical forcing or indirectly after a lull in forcing, and high-export cell aggregation and low-export microbial loop processes can occur simultaneously.

5.6. *Decade-Scale Physical–Biological Coupling*

The influence of climate variability, which occurs on decade-to-century time scales and must strongly affect physical forcing, is not well understood. Because of their large thermal inertia, the oceans are expected to play a major role in climate variations on time scales of decades to centuries (Deser et al., 1996). Although there are several case studies documenting impacts of climatic variability on structure and function of selected marine ecosystems, especially fisheries (Mysak, 1986; Polovina et al., 1994; Mantua et al., 1997; McGowan et al., 1998), few data are available to provide a quantitative description of how physical forcing influences pelagic ecosystem structure.

There is accumulating evidence that the NPSG habitat can change over interannual to decadal time periods. For example, Levitus and Antonov (1995) documented relatively large changes in the upper-ocean temperature (up to 0.5°C) over periods as short as three years. It has also been shown that major and sometimes abrupt “regime shifts” can result from changes in the position of atmospheric (e.g., Aleutian Low) or oceanic (e.g., West Wind Drift) features (McGowan et al., 1998), and it is even possible for the boundaries of the NPSG to shift accordingly. These habitat changes can have profound effects on physical–biological coupling and on rates of plankton metabolism.

A major and abrupt shift in the North Pacific climate system occurred during 1976–1977, appearing as an intensification and eastward shift of the Aleutian low-pressure system during winter (Trenberth, 1990). These anomalous conditions persisted for at least a decade before a return to the “normal” state (i.e., the long-term climatology). For regions north of the subtropical gyre, there were a series of cold pulses, corresponding to enhanced westerly winds, that appeared to originate at the surface and propagated downward to approximately 400 m (Deser et al., 1996). The general surface cooling was manifest as vertical anomalies of the 15°C isotherm in winter (Deser et al., 1996). It is conceivable that these anomalies might propagate southward with time along isopycnal surfaces and could eventually influence the nutrient balance of the subtropical gyre. The position of the 15°C isotherm in the gyre exhibits significant interannual and decadal variability with a range greater than 40 m in the mean annual depth (Polovina et al., 1994). During the period 1975–1985, the 15°C isotherm was deeper (>250 m) than at the beginning of the HOT program (230 m). These gyre-scale shifts in the position of the main thermocline could help explain the higher rates of primary productivity that have been reported in the subtropical gyre since approximately 1982, compared to measurements made in the 1970s (Karl and Lukas, 1996).

Changes in the Aleutian low-pressure system also influence both Ekman heat transport and wind-driven ocean circulation. Estimation of the annual mean Sverdrup transport at 30°N 130°E, where the gyre circulation is maximal, indicates an intensification of the rate of gyre circulation of approximately 20% for the period 1976–1985,

compared to 1966–1975 (Yasuda and Hanawa, 1997). This result is consistent with reports of similar increases in the transport of the Kuroshio Current (Qiu and Joyce, 1992). The current velocity and volume transport of the Kuroshio are coupled to the intensity of the North Equatorial Current, which in turn is influenced by the strength of the trade winds (Yamagata et al., 1985). Therefore, an intensification of the subtropical high pressure would lead to a coupled intensification of subtropical North Pacific circulation (Sawada and Handa, 1998). The spinning up of the subtropical gyre would affect the rate of general downwelling in the anticyclonic gyre and, hence, alter the position and nutrient gradients of the permanent nutricline. On even longer, millennial time scales, there is evidence that the strength of the North Pacific subtropical circulation has varied significantly and has, on average, continuously weakened over the past 7000 years (Sawada and Handa, 1998).

In 1987, Venrick et al. (1987) reported that the average euphotic zone (0 to 200 m) chlorophyll *a* concentration in the oligotrophic North Pacific Ocean during summer (May–October) had nearly doubled from 1968 to 1985. Their data set was collected in an area referred to as the Climax region (26.5 to 31.0°N and 150.5 to 158.0°W). The sampling frequency was insufficient to determine whether the chlorophyll *a* increase had been continuous over time or whether there had been a step-function increase between 1973 and 1980 (Venrick et al., 1987). The authors hypothesized that decade-scale changes in the open-ocean habitat, caused by large-scale atmosphere–ocean interactions, had resulted in significant long-term changes in the carrying capacity of the ecosystem. Data from the ongoing HOT program, which also includes occasional sampling near Climax, extend the record of euphotic zone chlorophyll *a* concentrations for nearly another decade. The combined Climax–ALOHA data set shows that the mean euphotic zone chlorophyll *a* concentration from the period October 1988 to December 1997 (HOT program results) is also significantly greater than the average, pre-1976 Climax program chlorophyll *a* concentration. Other ecosystem changes are also evident (Fig. 8.4) and are thought to be manifestations of climate-related variations in the stability of the gyre (Karl, 1999).

The Aleutian low-pressure system alternation and the extratropical effects of ENSO cycles are not solitary phenomena but may simply be examples of a recurring pattern of interdecadal climate variability referred to as the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997). These large-scale atmosphere–ocean interactions can have profound effects on community structure and productivity, primarily through direct interactions with nutrient supply (Fig. 8.4). Several independent lines of evidence have suggested that there have been major biogeochemical changes in the NPSG, including a shift from a N-controlled to a P-controlled habitat. The evidence includes a diverse set of both direct and indirect observations, ranging from an intensification of rates of N₂ fixation (Karl et al., 1997) to the excessive production of photosynthetically derived dissolved organic matter (Karl et al., 1998) and the kinetics of phosphate uptake and regeneration (Björkman et al., 2000). There also appears to have been a fundamental shift in microbial community structure with a selection for prokaryotic populations over the past several decades (Karl et al., 2001). These data and other observations (Karl et al., 1995; Karl and Tien, 1997; Hebel and Karl, 2001) on the mesopelagic zone dynamics of N and P pools are consistent with this general hypothesis of the alternation of N versus P control of NPSG ecosystem processes. The consequences for ecosystem structure from microbes to higher trophic levels are not completely understood.

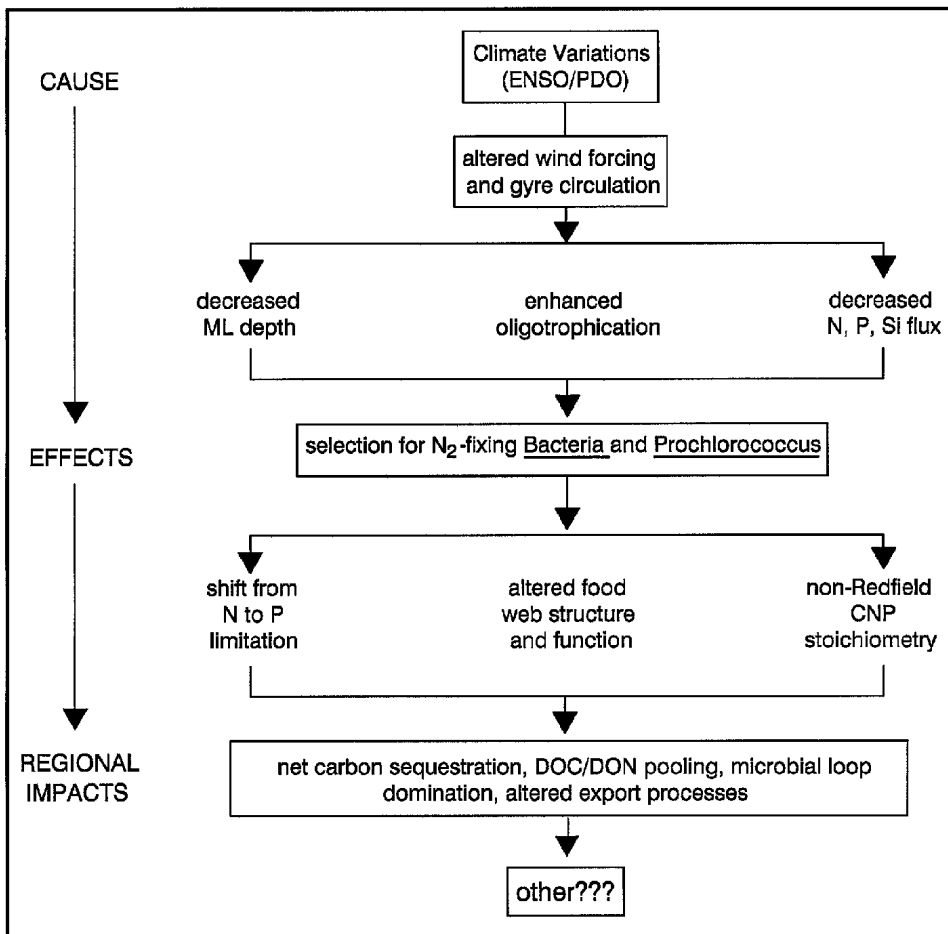


Fig. 8.4. Hypothetical view of the effects of climate variability on ecosystem structure in the NPSG. It is proposed that changes in stratification of the surface ocean have selected for N_2 -fixing bacteria and *Prochlorococcus*. (From Karl, 1999; see also Karl et al., 2001.)

5.7. Making Sense of Temporal Variability

The preceding discussion of recent discoveries in the NPSG demonstrates clearly that the classical view of an ecologically stable oceanic desert, supplied by a trickle of nutrients mixed from deeper waters, does not represent the ecosystem, which retains some strongly consistent ecological features (Venrick, 1999) while responding on a large range of time scales to hydrodynamically forced, atmospherically derived, and biologically mediated pulses of nutrients, with and without enhanced turbulence in the photic zone. This profound shift in perspective (Jumars, 1999) should serve to focus future research on physical forcing and ecosystem dynamics in pelagic systems. The path to progress would include continued and improved sampling designed to characterize more effectively the processes that deliver nutrients to the photic zone and the biological responses to those nutrients, including taxonomic shifts, with the

appropriate physical measurements for context. Modeling can be designed to focus on nutrient dynamics and food web responses, with a special emphasis on time scales and different types of physical forcing, as described below.

6. Modeling Physical Forcing and Food Web Response

6.1. Governing Equations

Another approach to testing our hypotheses is to use models of the dominant dynamics: the motions of the water and their consequent transports of mass (e.g., advection and diffusion), the responses of organisms to their local environment (e.g., nutrient uptake or response to irradiance), and interactions among organisms (e.g., grazing, viral infection). Models coupling biological and physical dynamics are all versions of the flux divergence:

$$\begin{aligned} \frac{\partial C}{\partial t} + \frac{\partial}{\partial x} Cu(x, y, z, t) + \frac{\partial}{\partial y} Cv(x, y, z, t) + \frac{\partial}{\partial z} Cw(x, y, z, t) \\ = \text{biological dynamics} \end{aligned} \quad (1)$$

This equation states that the local rate of change of concentration of an organism C is driven by motion of existing gradients (left-hand terms) and local growth and death (right-hand terms). The physical motions—velocities u , v , and w —can be both space- and time-dependent and include motions due to swimming, sinking, or floating of the organisms. Often, the small-scale motions (those motions that are unresolved at the scale being studied) are lumped into diffusion terms:

$$\begin{aligned} \frac{\partial C}{\partial t} + \frac{\partial}{\partial x} Cu + \frac{\partial}{\partial y} Cv + \frac{\partial}{\partial z} Cw \\ = \kappa_h \left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2} \right) + \kappa_v \frac{\partial^2 C}{\partial z^2} + \text{biological dynamics} \end{aligned} \quad (2)$$

where κ_h and κ_v are the horizontal and vertical eddy diffusion coefficients (units: length² time⁻¹ and assumed constant in space). The difficulty in applying these equations is obtaining values for u , v , w , κ_h , κ_v , and the biological dynamics. Generally, simplifications are made to make the equations more tractable or to restrict them to a set of motions that is well understood and well constrained (e.g., idealized internal waves or Langmuir circulation).

Models are ideal tools to explore the consequences for ecosystem structure of changes in physical forcing—how the relative abundances of various ecosystem components and the strength and variability of their linkages respond to changes in the physical environment. When such interactions are being modeled, a set of coupled equations will be necessary, including one equation for each component of the ecosystem (the state variables). The coupling between the equations is usually found in the biological dynamics components: for example, nutrient uptake (coupling the nutrient pools and phytoplankton) and grazing (coupling heterotrophs with autotrophs and other heterotrophs). Since the earliest ecosystem models of Gordon A. Riley (e.g.,

Riley, 1946, 1947), a huge number of models has arisen, distinguished largely by the detail of their physical and biological components. Here we examine a few recent models to show how they have been used to explore physical–biological coupling involving nutrient pulses in the ocean and to suggest promising directions for future research.

6.2. *Physical Forcing and Biological Dynamics*

Physical processes manifest themselves in two distinct ways in the biological models. The equations above show that the proximate effect of physical forcing is in advecting or diffusing the state variable in time and space. This can have two quite different impacts on the state variable. The first arises through the interaction of the behavior of the state variable (e.g., swimming, sinking, or floating) with the physical dynamics. Regardless of the biological interactions, motion of the plankton relative to the water gives the potential for significant variations in concentration through accumulation and dispersion, as well as the potential for enhanced horizontal transport (Kamykowski, 1995; Donaghay and Osborn, 1997). Striking examples of this are the bands of phytoplankton associated with internal waves, Langmuir circulation, and other organized flows (e.g., Franks, 1997; Lennert-Cody and Franks, 1999). Patchiness induced by the interaction of water motions and planktonic behavior can have potentially profound effects on local ecosystems. Enhanced concentrations of plankton can affect a population, regardless of interactions with other species, by affecting processes such as sexual reproduction, aggregation, and flocculation. Sinking, which can be accelerated through aggregation, leads to reduced concentrations of phytoplankton in the euphotic zone (Lochte et al., 1993) and can have profound effects on biological couplings among species.

The secondary impacts, due directly to physical aggregation and dispersion, are altered biological interactions forced by changed concentrations of biological variables. If the interactions between state variables were linear, this would be a trivial issue. However, if there is one truism in ecosystem modeling, it is that interactions between state variables are nonlinear. In the simplest models, nutrient uptake by phytoplankton is usually modeled as some version of Michaelis–Menten kinetics, first introduced to phytoplankton ecology by Dugdale (1967):

$$V = \frac{V_m N}{k_s + N} \quad (3)$$

Here V is the uptake rate of the nutrient N , V_m the maximal uptake rate, and k_s the half-saturation constant. It is clear that changing concentrations of N will lead to changes in the uptake rate of nutrients by phytoplankton, with consequent (although not necessarily immediate) effects on their growth rates. The same can be said of the grazing rate of heterotrophs on autotrophs and other heterotrophs, and almost every other biological linkage. Thus, any process affecting the local concentration of a property will have nonlinear ramifications for the structure and dynamics of an ecosystem.

The left-hand-side terms of the flux divergence equation give the local changes in concentration of a state variable driven by spatial movement of that gradient. The model of McGillicuddy et al. (1998) gives a simple illustration of how the mesoscale

vertical motion of a gradient—the nutricline—can have profound effects on the planktonic ecosystem. Their detailed physical model gives the three-dimensional time variation in isopycnal depth driven by an evolving and interacting eddy field in the open ocean. The biological model is conceptual: If an isopycnal enters the euphotic zone, the nutrients on that isopycnal are assumed to turn quickly (days) into phytoplankton. The slow rates of remineralization on a descending isopycnal leave the phytoplankton and nutrient concentrations unchanged. This rectified biological transport leads to a high degree of patchiness of phytoplankton biomass, injection of new nutrients into the euphotic zone, and overall enhanced production compared to a model with no eddies. Thus, the model predicts fluctuations in the relative biomasses of components within an ecosystem, leading to changes in ecosystem structure and trophic fluxes.

More detailed models of biological dynamics have incorporated the concept of the microbial loop (Pomeroy, 1974; Azam et al., 1983). Rather than the simple, linear trophic cascade of earlier models, the concept of the microbial loop incorporated the complex recycling dynamics of the smallest phytoplankton: bacteria and small eukaryotic auto- and heterotrophs. The incorporation of these pathways increased the number of routes by which photosynthetically derived chemical energy could reach the highest trophic levels—large zooplankton and fish.

6.3. *Temporal Variability and Ecosystem Dynamics*

To explore the effects of the advection and diffusion of nutrients into a detailed ecosystem model, we consider the models of Moloney and colleagues (Moloney and Field, 1991; Moloney et al., 1991), which are generally consistent with the principles described in Section 2. Moloney and colleagues modeled the planktonic ecosystem based on allometric relationships; physiological parameters were based on the size of the organism. Three autotrophic and four heterotrophic compartments ranged in size from 0.2 to 2000 μm . The smallest autotrophs were the most efficient at taking up nutrients and would always outcompete the larger phytoplankton if left ungrazed. Similarly, the smallest grazers had the highest mass-specific ingestion rates and growth rates. Each heterotrophic size class could graze on the auto- and heterotrophs in the next-smaller size class. Nutrients were supplied in organic and inorganic pools, including nitrate and ammonium. Organisms and detritus could sink at a speed determined by their size.

Moloney et al. (1991) forced this model in three different ways: a weak diffusion of nitrate ($0.1 \text{ mg-at m}^{-3} \text{ day}^{-1}$: oceanic case), a pulse of nitrate ($10 \text{ mg-at m}^{-3} \text{ day}^{-1}$) supplemented by background diffusion ($0.6 \text{ mg-at m}^{-3} \text{ day}^{-1}$, Agulhas Bank case), and a large pulse of nitrate ($25 \text{ mg-at m}^{-3} \text{ day}^{-1}$) with no diffusion (Benguela upwelling case). The models were restricted to short (15 to 30 days) runs due to their lack of large heterotrophs. The three cases represent points along a continuum of physical perturbation through nutrient input. How did such forcings affect the ecosystem structure and dynamics of this model?

While Moloney et al. (1991) showed the time-dependent evolution of the various biotic components, the more revealing analysis for our purposes was the tracing of carbon fluxes through the food web (Fig. 8.5). In the oceanic simulation, the primary production was largely confined to the smallest autotrophs (58.5%), which were grazed by the smallest heterotrophs. Almost none of the primary production reached

the largest heterotrophs. In contrast, in the Benguela simulation with a large initial nutrient pulse, the largest autotrophs accounted for 8.5% of the primary production, and 1.9% of total primary production reached the largest heterotrophs. In the Agulhas and Benguela cases, the smallest auto- and heterotrophic size classes were still well represented, contributing a smaller *fraction* of the production.

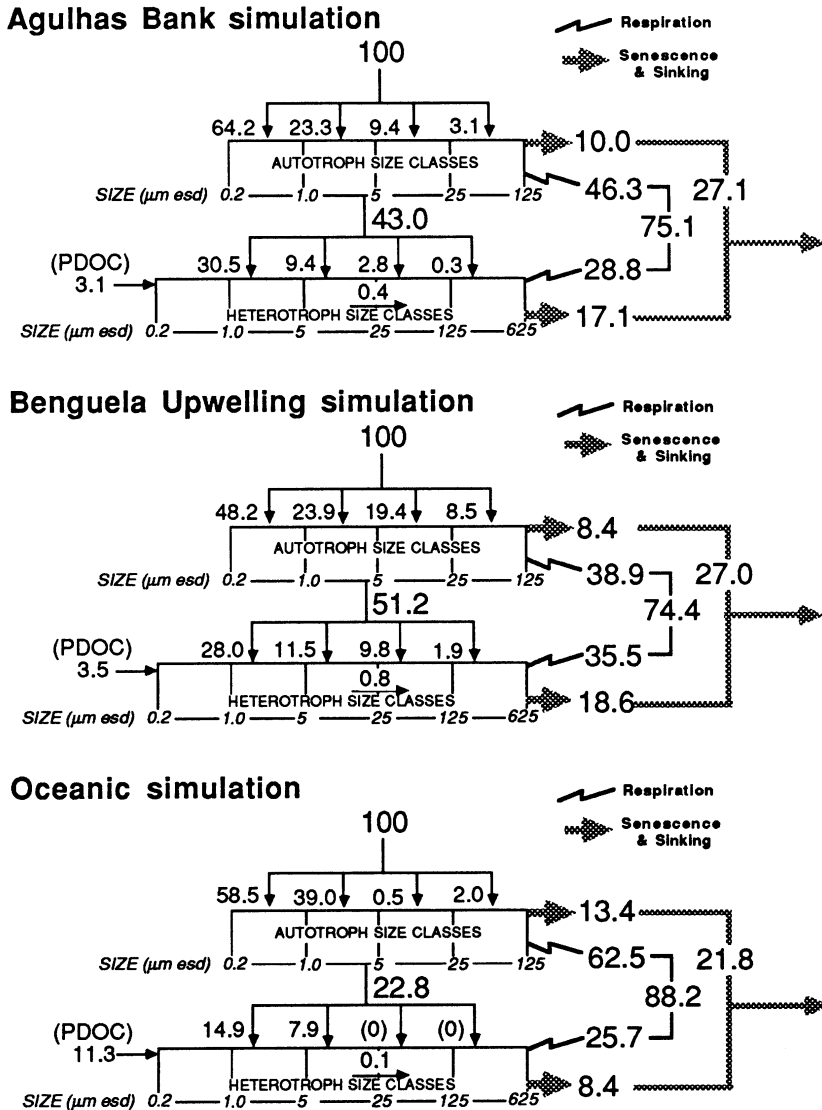


Fig. 8.5. Summaries of the flows of carbon through simulated plankton communities in the model of Moloney et al. (1991). The flows have been standardized to 100 units of carbon fixed by phytoplankton, less excreted dissolved organic C. The simulations for the Agulhas Bank and southeast Atlantic oceanic region were averaged over 30 days; the Benguela upwelling simulation was averaged over 15 days. (From Moloney et al., 1991.)

The model dynamics were consistent with hypotheses 1 and 2 (Section 3) and were summarized by Moloney et al. (1991) in relation to the strength of physical forcing, size of plankton, and length of food chain (Fig. 8.6). In every case, the longest food chain was present. In this chain, primary production by the 0.2- to 2- μm autotrophs was transferred to the largest heterotrophs through a variety of pathways, the shortest being a series of transfers to increasingly large heterotrophs. With increasing physical perturbation (i.e., nutrient pulse), shorter food chains involving larger auto- and heterotrophs developed. At the highest levels of physical perturbation, large phytoplankton could be grazed directly by the largest heterotrophs (e.g., anchovies eating diatoms), leading to an efficient transfer of a relatively high fraction of primary production to the largest size classes. A comparison of Fig. 8.6 with Fig. 8.2 shows that the model of Moloney and colleagues represents key elements of the scheme presented by Legendre and Le Fèvre (1989), but it is not sufficiently detailed to describe explicitly fates such as aggregation and senescence.

To test hypothesis 3 (Section 3), about key time scales for nutrient pulses to enhance flows of chemical energy to higher trophic levels, it is helpful to explore a model's response to frequency, duration, and intensity of nutrient pulses. Carr (1998) forced two modified versions of Moloney's model with upwelling pulses simulating strong (20 m day⁻¹) and weak (10 m day⁻¹) upwelling. Upwelling events were of four-day duration, at a variety of periods (4 to 120 days). The two biological models differed in their resolution of the size structure of the plankton. The first model included one autotroph and one heterotroph category (A1H1), while the second incorporated three autotrophs and four heterotrophs (A3H4). Although the model did not include spatial dependence, the upwelled water was assumed to have a set planktonic and nutrient composition, with low plankton and high dissolved nutrient values. The upwelled water thus diluted the euphotic zone water and its developing planktonic community. At periods of 10 to 20 days between upwelling events, the A1H1 model developed high phytoplankton biomass. At this frequency the upwelling time scale allowed enhanced phytoplankton growth but only limited zooplankton growth due to their slower response time. In the A3H4 model the peak autotrophic and net phytoplankton biomass was achieved at upwelling periods of 10 to 30 days, depending on upwelling strength. The largest phytoplankton never accounted for more than half the autotroph biomass and always <20% of the carbon fixation. The pico- and nanophytoplankton were able to grow quickly enough between pulses to draw down the ambient nitrate in all but the shortest-period events. The picoplankton always accounted for the bulk of the carbon fixation. Grazing was a more important loss term in the A3H4 model than the A1H1 formulation. This was a result of the slow growth rates of the herbivores in the A1H1 model—they were unable to respond to relatively rapid fluctuations in their environment. The smaller, faster-growing herbivores in the more complicated model cropped 30 to 60% of the fixed carbon; grazing was found to vary more with the character of the physical disturbance than with the autotrophic biomass. In general, the simple formulation was more sensitive to physical forcing than the complex formulation, a result of the smallest size classes of the complex model being somewhat independent of the physical perturbations.

Carr's (1998) model was not designed to be used directly to test our hypothesis 3, since it did not include a fast-growing autotroph that was immune to microbial grazing. The largest phytoplankton had growth rates about one-tenth of the smallest picoplankton and were never observed to dominate the biomass or carbon fixa-

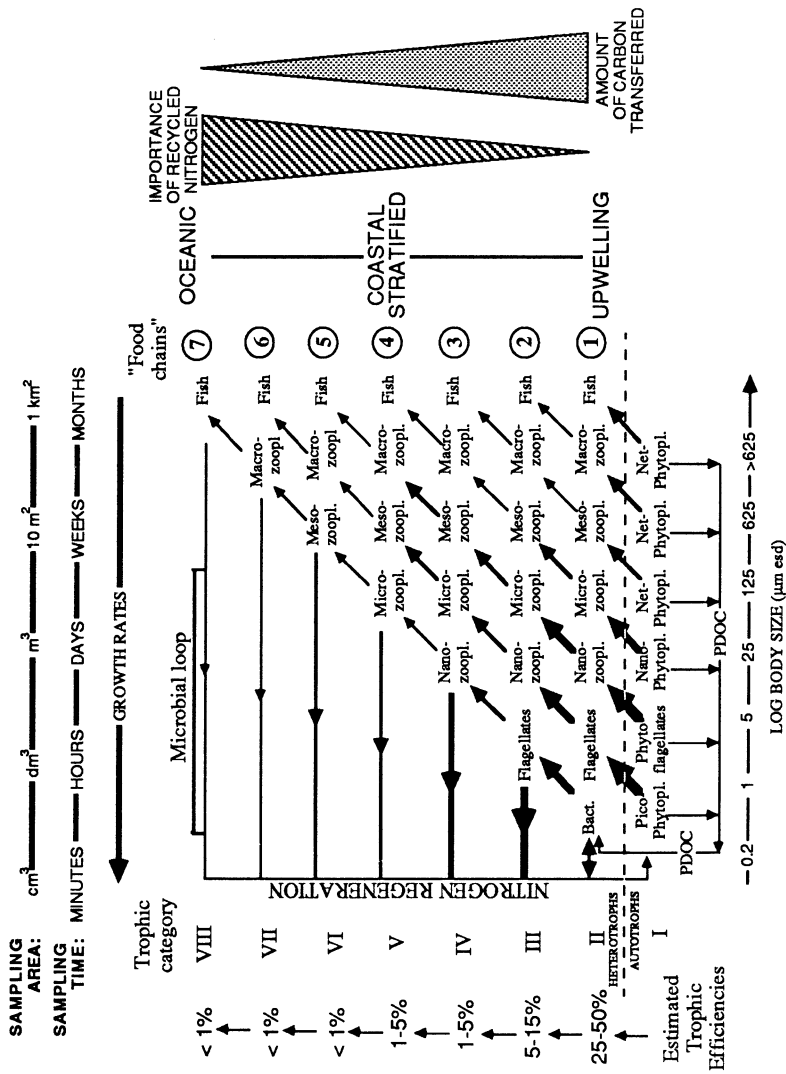


Fig. 8.6 Flows of C and N in the size-based plankton food web. [Modified after Azam et al. (1983) as presented and simulated by Moloney et al. (1991).]

tion rates. Carr suggests the incorporation of a fast-growing chain-forming diatom to fill this niche, as done by Painting et al. (1992). On the other hand, with reference to hypothesis 3, the richness of the response time scales becomes apparent in Carr's (1998) study. The interactions of autotrophs and herbivores with different response time scales under externally imposed fluctuations led to consistent changes in ecosystem structure and function. As Carr notes, however, models such as these are extremely sensitive to initial and boundary conditions. Thus, these results should not be extrapolated beyond the scope of the parameter and state-variable ranges employed by Carr.

Despite its complexity, the models of Moloney and colleagues (Moloney and Field, 1991; Moloney et al., 1991) have some serious limitations that preclude their immediate incorporation into, for example, basin-scale physical models. First, they lack the slow-growing large zooplankton components, which limits their application to time scales shorter than the growth response time scale of these organisms (i.e., scales less than a month). Also, they are not designed to model the opportunistic responses of salps (Section 4.4) or behaviorally mediated aggregation of zooplankton. The models are only nitrogen limited, so the influences of additional limiting nutrients such as iron are not addressed, and they also have some inaccuracies in their formulation of nitrogen utilization in the microbial loop (Ducklow, 1994). Further, they lack a detailed photosynthetic model of primary production. These problems can be addressed by researchers interested in those particular questions; progress will depend on complementary advances in sampling to provide parameterization and validation.

6.4. *Challenges for Future Modeling Efforts*

So where does this leave us in terms of physical–ecosystem models? Curiously, the tendency has been to couple very detailed physical models to relatively simple biological models (e.g., Sarmiento et al., 1993; Franks and Chen, 1996) and to force the most detailed biological models with the simplest physics (e.g., Moloney et al., 1991; Carr, 1998). The reasons for this are twofold. First, the detailed biological models are very nonlinear and have a tendency to show strong predator–prey oscillations, the frequency and amplitude of which vary with the autotrophic growth rate (i.e., depth). When these models are coupled to physical models with a wide spectrum of physical dynamics, the spatial and temporal patterns of biological variables often become uninterpretable. The biological data we collect do not tend to show predator–prey oscillations of such magnitude or frequency. This problem arises in part because we are modeling populations but applying the results to entire ecosystems. Populations within a trophic level may show large oscillations in biomass, while the trophic level as a whole tends to have a relatively constant biomass. With a sufficient number of populations oscillating out of phase, the aggregate trophic biomass (as we tend to measure it) may remain reasonably constant. Armstrong (1999) has addressed this issue in an evaluation of the grazing pressure as a source of oscillations. He showed that food webs containing multiple autotrophs each being grazed by a particular herbivore were inherently unstable. However, by substituting a general herbivore that grazed autotrophs in relation to their abundance (including grazing preferences by the herbivore), the oscillations were damped. This is not to say that there was a single herbivore in the ecosystem. Rather, the aggregate response of all herbivores behaved according to the model. Such a model can reproduce arbitrary size spectra

of phytoplankton populations, including those discussed above, and may help lead to enhanced understanding of planktonic ecosystems and their response to physical forcings.

The second reason that only the simplest models have been coupled to detailed physical models is that the data do not currently exist to thoroughly initialize and test detailed biological models. Most of the small heterotrophic organisms are delicate protists that we have almost no ability to collect, study, or even identify. Until we can carefully initialize and test such models, they remain heuristic tools to help us expand our view of potential physical–biological couplings in the ocean.

7. Concluding Remarks

This review is neither comprehensive nor catholic in its discussion of physical forcing and pelagic ecosystem dynamics (see, e.g., Verity and Smetacek, 1996; see also Chapter 7). Nonetheless, we feel that it illustrates many points that may guide advances in oceanography, as old paradigms succumb to better resolved descriptions of how biological systems respond to physical forcing (Jumars, 1999).

Before expounding on the improved understanding that will come from incorporating new information into conceptual and numerical descriptions of ecological systems, it is important for us to emphasize that the literature abounds with insightful contributions that are as useful now as when they were written. Authors of the classic works recognized key links between turbulence, nutrients, time scales of disturbance, and food web structure. Also, they were able to describe the dominant features of seasonal succession as functions of well-understood physical factors and simplified descriptions of food web response. Newer information on complexity of the microbial web, different modes for delivery of nutrients to the surface layer, and decadal-scale changes in ecosystem structure is reassuringly compatible with established frameworks for interpreting changes in ecosystem structure; similar lines of reasoning can be used to examine these patterns and processes, although different conclusions may be reached. For example, the idea of a slow, continuous supply of nutrients to surface waters of oligotrophic gyres supporting a stable, climax community of plankton no longer holds. Vastly different types of perturbations have been observed, with fundamentally different responses (Section 5.5). Still, aspects of the NPSG ecosystem are similar year to year, showing changes on the decadal time scale. Established paradigms about nutrient pulses and food web response will probably form the basis of new descriptions of these oligotrophic ecosystems—the difference will be that recently discovered processes will be integrated into a model of the system, consistent with a theoretical framework of biotic response to physical forcing and variable supplies of nutrients.

Here, we have tried to present and justify such a framework. The microbial loop constitutes a biological background that tends to dominate the flows of chemical energy and nutrients in surface-layer plankton. Chemical energy flows to higher trophic levels and is exported to the deep sea primarily through bigger cells, the growth of which is stimulated by elevated concentrations of limiting nutrients in well-lit waters. *Trichodesmium* is an exception: It grows better in stratified water and acts as a supplier of N (and through migration, P) to surface plankton when these nutrients are released from the cells (Section 5.4). The principal determinant of flow to higher trophic levels may be the time scale of nutrient pulses. Small or short pulses

may be accommodated by the microbial loop, and sustained inputs may encourage the development of food webs that sequester nutrients and energy in forms that are resistant to grazing. The latter response would represent an undesired outcome to intentional long-term fertilization of surface waters with nutrients such as iron and phosphorus. Clearly, more must be learned about ecosystem response to pulses of nutrients before the consequences of intentional fertilization can be predicted.

To understand how physical forcing determines pelagic ecosystem structure, we need to know more about the relationship between physical forcing and biotic responses over a range of time scales under different conditions, such as ranges of temperature and light. This is done through improved observations, including continuous measurements from moorings and during transects, time series such as HOT and BATS, and synoptic assessments and comparisons of different biomes from satellites. We know that time scales of pulses are important, so we must study them further. Sampling and analysis could be targeted to examine latitudinal variation in the scales of eddies and in the effects of wind forcing, coupled with improved observations of biotic response (including assessment of phytoplankton from space, continuous, in situ measurements of fluorescence response as a diagnostic of phytoplankton physiological state, and optical and acoustic surveys of zooplankton population distributions, including those of pelagic tunicates). Concurrently, models of trophic response to pulsed nutrients should be developed further.

The topic of physical forcing and pelagic ecosystem dynamics is as intimidating as it is intriguing and important. Relevant data are becoming available from a wide variety of sources, while capabilities for new observations and models are advancing rapidly. To make progress in this era of information overload, we need to retain a knowledge of the literature while developing models that can be parameterized and validated by long-term continuous and synoptic observations of the ocean.

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