Chapter 2. EFFECTS OF UPPER OCEAN PHYSICAL PROCESSES (TURBULENCE, ADVECTION AND AIR-SEA INTERACTION) ON OCEANIC PRIMARY PRODUCTION

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1. Introduction

What we know of the ocean and, to a large extent, the questions we ask about it are the result of continual evolution of the observational tools available. In physical oceanography, this evolution has led from larger to smaller time and space scales, as bottle sampling evolved to include conductivity-temperature-depth (CTD) and microscale profiles, and as single wire–lowered current meters were replaced by current meter moorings and subsequently joined by drifters and Doppler profilers. Biological oceanography has followed a similar path—net tows defined biogeographical differences in mean biomass and species community structure, while the Hardy plankton recorder began to reveal the variability of populations within such biogeographic regions. The more recent development of continuously recording in situ sensors, as well as the tools of molecular biochemistry, is finally enabling the study of individual phytoplankters within their natural environment.

Because the progression from communities to populations to individuals is also generally the progression from large to small spatial scales, and from long to short

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time scales, a space-time framework has frequently been used to structure discussions of biophysical interactions (e.g., Harris, 1986; Bidigare et al., 1992). However, the occurrence of some important interactions at discordant time-space scales has led us to use instead a structure that is roughly inherent in the historical framework. Thus we first consider those physical processes that contribute to mean biogeography-the differences in average biomass and community structure which easily allow biological oceanographers to distinguish a sample taken from the middle of a subtropical gyre from one taken within one of the subpolar gyres, or between open ocean and coastal samples. We next consider the variance in the phytoplankton system that is produced when variability in the physical environment interacts with physiological rate processes of individual plankters to produce space- and time-variable populations within broad biogeographic communities. Indeed, different ocean regions may be characterized as much by their variance properties as by their mean conditions. We then examine the level of individuals, where physical processes influence the physiological rates themselves. In this review we focus on the mechanisms by which physical processes, both atmospheric and oceanic, act to set the levels and determine the pathways of primary production by marine phytoplankton. The effect on phytoplankton production of zooplankton grazing, arguably of importance comparable to that of physical processes (Banse, 1995), is generally left to other parts of this book.

Lacking the roots and branches of their terrestrial relatives, marine plants depend to a much greater extent on the physical processes that create the upper ocean environments of light, temperature, and nutrients (both macronutrients and micronutrients) needed for plant growth. At all time and space scales, phytoplankton production is strongly affected by the tension between physical processes that act to stabilize or destabilize the surface layer of the ocean. The interplay among such processes determines the fields of upper ocean irradiance and temperature as well as the rates of nutrient resupply to and phytoplankton loss from the euphotic zone.

Upper ocean physical processes are themselves predominantly forced, either directly or indirectly, by the atmosphere. In Section 2 we describe how patterns of atmospheric wind stress structure the delivery rates of essential nutrients, and in doing so determine major differences in mean biomass and community structure between eutrophic and oligotrophic midocean gyres. Geographical differences in incoming solar radiation also contribute to structural differences between communities, as does the annual cycle of upper ocean buoyancy forcing by ocean–atmosphere heat and water transfers. In Section 3 we address those physical processes that generate variance in phytoplankton community characteristics such as biomass and community structure. In Section 4 we consider the effects on individual physiological rate processes of the advective and diffusive processes on the diurnal time scale. Finally, in Section 5 we consider briefly ecological impacts of tidal mixing, an aspect of physical forcing that is not related, either directly or indirectly, to the atmosphere, and that acts most strongly in coastal areas.

2. Physical Processes and Mean Characteristics of Marine Phytoplankton: Communities

Recent color-sensing satellites have graphically reinforced what has long been suspected from shipborne measurements: chlorophyll (an indicator of phytoplankton

biomass) is higher in high latitude and coastal regions than in the central subtropical ocean gyres. In addition, we know that although smaller species of phytoplankton are ubiquitous, the larger species are geographically distinct. The differences in biomass and community species structure at large spatial scales are a product of evolutionary adaptation. Thus, the differences can be said to describe a *mean* state, one in which large changes are unlikely unless a major change were to occur in the underlying physical systems which set the environmental characteristics.

Global distributions of atmospheric momentum, heat, and freshwater fluxes (Peixoto and Oort, 1992) are the major forcing functions for the ocean processes involved in structuring pelagic phytoplankton communities. Atmospheric forcings affect the phytoplankton community in three major ways:

- 1. The mean wind field sets up the large-scale topography of nutriclines and drives the turbulence that accomplishes the flux of nutrients to the surface layers. As well, the wind field is responsible for aeolian transport of essential micronutrients such as iron.
- 2. Upper ocean stability (stratification), resulting as an integration of solar radiation and the atmospheric delivery of heat and fresh water to the ocean surface, strongly affects upper ocean fields of nutrient and light.
- 3. The spatial dependence of atmospheric fluxes of heat across the ocean surface sets up horizontal (primarily latitudinal) gradients in ocean temperature which contribute to differences in productivity and community structure through temperature effects on growth rates.

We now examine the community-scale biological effects of these modes of atmospheric forcing of the upper ocean.

2.1. Macronutrient and Light Environments

Momentum transfers associated with the global patterns of mean winds drive the shallow circulation of the ocean. As illustrated in Fig. 2.1, the curl of the wind stress field in subpolar gyres drives divergent surface layer flows [for a general description, see Gargett (1991)]. Divergences provide not only an advective supply of nutrients to the euphotic zone but also a shallow nutricline that is more strongly affected by surface forces such as storms. In subtropical gyres, the field of wind stress curl instead drives convergent surface layer flows, producing downwelling that moves the nutricline to average depths well below the euphotic zone. Weak vertical mixing (associated with the more equitable weather characteristic of these latitudes) and a relatively deep nutricline combine to produce low rates of nutrient resupply to the euphotic zone.

By thus sculpting the topography of the nutricline on gyre scales and setting rates of turbulent resupply of nutrients, atmospheric wind forcing helps to divide oceans into regions of higher and lower average phytoplankton biomass, termed respectively *eutrophic* (nutrient-rich) and *oligotrophic* (nutrient-poor). In addition to effects on biomass, the nutrient concentration of the upper ocean influences community structure through effects (over evolutionary time scales) on phytoplankton size and morphology. Oligotrophic conditions favor motile organisms, such as flagellates, which can actively search for scarce nutrients, while the strong turbulence that maintains



Fig. 2.1. Schematic of the large-scale physical processes that act to differentiate planktonic communities. Wind-driven upwelling and downwelling in the major ocean gyres sculpts the surface of the nutricline, moving it, respectively, closer to and farther from the sea surface within subpolar and subtropical gyres. These large-scale differences affect rates of resupply of new nutrients, producing euphotic zones that are macronutrient replete in most subpolar gyres but relatively nutrient starved in the vast subtropical gyres. North–south variation in intensity and duration of sunlight is also a major influence on the structure and functioning of phytoplankton communities.

eutrophic conditions at higher latitudes also augments diffusive nutrient transport to levels necessary to support larger, nonmotile organisms such as diatoms.

Another major factor affecting primary production is light. The annual variation in solar radiation, greatest at high latitudes, is believed to limit planktonic communities in subpolar gyres, setting the level of winter phytoplankton and zooplankton populations that are available as "seed" stocks when light returns in the spring. Although the light field is in some sense an external variable, it is now realized that its biological effectiveness is strongly influenced by the stability of the upper ocean (to which, of course, solar radiation also contributes). In eutrophic oceans that have strong nearsurface stability, such as the North Pacific, winter mixing layers cannot penetrate the main pycnocline; phytoplankton thus held relatively near the surface receive enough light to remain viable at levels sufficient to support an overwintering (micro)-zooplankton population. When primary productivity increases with spring light levels, this population is in place, able to remove excess plankton biomass quickly, hence maintain phytoplankton biomass at the low and quasiconstant levels observed (Evans and Parslow, 1985; Miller, 1993). In contrast, in an ocean such as the subpolar North Atlantic, which has much lower near-surface stability, winter mixing extends to much greater depths. Average levels of winter light and consequently, primary productivity are low, supporting less zooplankton in the winter surface layer. In spring, time delays associated with zooplankton growth allow the phytoplankton community to escape grazer control temporarily, resulting in a spring bloom. Thus even in regions where macronutrients are abundant and annual cycles of incoming solar radiation are similar, quite different average biological communities can evolve as a result of different upper ocean stability. If this stability changes as atmospheric heat and freshwater forcing varies under climate change, there is a strong foundation for the expectation that biological community structure will also change, a point to which we return at the end of this section.

2.2. Temperature Structuring of Growth Rates

As well as determining upper ocean stability, the strongly latitudinal variation of atmospheric heat and salt forcing of the upper ocean imprints a similar variation on surface-water mass properties, producing the geographically distinct water masses recognized by physical oceanographers. At low latitudes, strong surface heating and an excess of evaporation over precipitation produce warm and salty upper-layer waters. In contrast, subpolar surface waters are forced toward colder and fresher characteristics by strong winter heat losses and excess precipitation. Upper ocean water mass properties change most sharply across the frontal boundaries between the major wind-driven gyres. The temperature change at such large-scale boundaries is of major biological significance given the influence of temperature on phytoplankton growth rates and community structure (Eppley, 1972). Possibly even more important is the strong influence of temperature on rate parameters governing the zooplankton stocks (Huntley and Lopez, 1992), since these arguably exert a crucial influence on phytoplankton production (Banse, 1995).

2.3. Micronutrient Environments

Finally, we consider the role of physical processes in supplying the euphotic zone with micronutrients, in particular with iron (Fe), an essential component of phytoplankton metabolism. Over the last decade, the idea that availability of Fe can limit primary production in high-nutrient, low-chlorophyll (HNLC) regions of the ocean has progressed from controversial hypothesis (Martin, 1990) to a generally accepted canon of open-ocean plankton biology, following the success of an open-ocean Fe-enrichment experiment (Coale et al., 1996). Other less direct evidence for Fe limitation of new production has come from the EqPac synthesis (Landry et al., 1997) in the central equatorial Pacific, as well as from other nutrient-rich oceans (Martin and Fitzwater, 1988; de Baar et al., 1995).

Iron limitation affects community structure by shifting the dominant flora away from larger species that require Fe to reduce NO_3 toward smaller organisms that use NH_4 preferentially as a nitrogen source. Thus in those ecosystems that support the larger phytoplankton species, physical processes are required to resupply the euphotic zone not only with macronutrients, but also with Fe and any other essential micronutrient. Associated with early debate of the iron hypothesis was a conclusion that most iron was delivered to its planktonic consumers by aeolian (atmospheric) transport (Duce and Tindale, 1991). However, it now appears that the physical mechanisms by which phytoplankton are provided with Fe may prove to be more varied, indeed may have to be determined separately for different large-scale systems. At present, candidate mechanisms are (1) the same vertical advective and diffusive processes that resupply macronutrients, (2) aeolian transport, (3) sea ice melting (indirectly, aeolian transport, but with an important storage history), and (4) transport from boundaries.

As seen in Table I, the relative importance of the first two mechanisms differs with oceanic region. New iron in the equatorial Pacific comes predominantly via wind driven vertical upwelling of water from the equatorial undercurrent (Landry et al.,

	Iron Fluxes (nmol Fe m ⁻² per day)			Upwelling Velocity, Wa	Turbulent Diffusivity, <i>K</i> ₁ ,
HNLC Ocean	Upwelling	Diffusion	Aeolian	$(10^{-7} \text{ m s}^{-1})^b$	$(10^{-5} \text{ m}^2 \text{ s}^{-1})^c$
North Pacific Equatorial Pacific Antarctic	26 120 130	1.2 0.2–14 15	150 5–25 15	5 1.23 15	0.7 0.86 3

 TABLE I

 Estimated Magnitudes of Iron Fluxes^a

Source: Equatorial Pacific values: Landry et al. (1997); Antarctic and North Pacific values: de Baar et al. (1995).

 $^a{\rm Associated}$ with the physical processes of vertical advection (upwelling), vertical turbulent diffusion, and aeolian transport.

^bUsed in calculating advective transports.

^cUsed in calculating diffusive transports.

1997), while the subarctic North Pacific was believed to be supplied mainly by direct aeolian transport of terrestrial dust picked up from regions with dry loess-type soils in Asia (Duce and Tindale, 1991) and Alaska (Boyd et al., 1998). However, another possible source of iron to this region may be boundary transport. Under certain conditions, anticyclonic eddies are observed to form along the eastern boundary of the North Pacific and propagate slowly into the interior as discernible entities (Thomson and Gower, 1998; Crawford and Whitney, 1999). It is presently uncertain how much biologically available iron is supplied by this mechanism.

In the Antarctic, iron supply appears to be more complex than the upwelling dominance suggested by Table I. In the Atlantic sector, despite the large advective estimate shown in Table I, de Baar et al. (1995) found only moderate primary productivity in water upwelled in the Antarctic Circumpolar Current. Major spring blooms were found within the iron-rich Polar Frontal Jet, which may have picked up dissolved iron from sediment sources while flowing over and around complex topography downstream of the Drake Passage. A similar wake of high biomass, presumably supported by sediment-derived iron, is observed in flow downstream of the Galapagos Islands platform in the eastern equatorial Pacific (Martin et al., 1994). A land-based supply of iron is also suspected of supporting high levels of productivity near Antarctica. However, Sedwick and Di Tullio (1997) provide convincing evidence for the additional contribution of aeolian input, as stored in the seasonal sea ice cover and released into the upper ocean by melting in synchrony with the return of light in the spring. The storage capacity of ice may thus increase the biological effectiveness of the generally meager aeolian delivery to antarctic latitudes [although Banse and English (1997) suggest that windborne Australian dust may produce sporadic blooms observed in Coastal Zone Color Scanner (CZCS) data from waters east of New Zealand]. Finally, recent SeaWiFs data show consistent enhancement of chlorophyll in waters lying above the deep (>2000 m) Pacific-Antarctic Ridge. Moore et al. (1999) conjecture that increased production is fueled by enhanced vertical transport of micronutrients by geostophic eddies generated as the Antarctic Circumpolar Current flows over the ridge. It seems unclear which (if any) of the mechanisms above is the dominant means of micronutrient delivery to the Southern Ocean.

In this section we have tried to describe in general terms how atmospheric forcing sets upper ocean properties. Physical conditions in the upper ocean are of profound importance in shaping phytoplankton communities, through the biological characteristics of the species that have evolved to exploit various environments of light, nutrients, micronutrients, and temperature. If one accepts that major changes in crucial aspects of the physical environment will inevitably show up at the community level, the challenge is to determine which aspects of the physical environment are dominant in structuring particular ecosystems. Although the dominant processes are certainly not universal (Longhurst, 1995), upper ocean stability is one characteristic of the physical environment that has major effects on the embedded biological systems. Earlier discussion suggested that differences in upper ocean stability are fundamental for understanding major differences between planktonic community structures in the North Atlantic and North Pacific Oceans. Recently, the effect of changing upper ocean stability has been implicated as the root of changes in planktonic ecosystems in both the North Pacific (Venrick et al., 1987; Brodeur and Ware, 1992; Polovina et al., 1995; Roemmich and McGowan, 1995), and the North Atlantic (Taylor, 1995). The importance of upper ocean stability to marine ecosystems essentially involves the biological tension between the supplies of light and nutrient available to fuel primary production. Environments of light and nutrients in the euphotic zone are modulated by upper ocean turbulent processes that are strongly affected by near-surface stratification. Strong vertical stratification severely inhibits the vertical motions associated with turbulence, holding phytoplankton in strong light but decreasing the vertical turbulent fluxes that resupply nutrients to the euphotic zone. In contrast, where water columns are weakly stratified, vertical excursions and fluxes may be large, supplying adequate nutrients but moving phytoplankton to much lower average light levels. The competing influences of water column stability on the light and nutrient requirements for primary production suggest the existence of an optimal "window" of water column stability, as shown schematically in Fig. 2.2, within which productivity is maximized because supplies of both substrates are adequate (Gargett, 1997b).

Despite the usefulness of the optimal window as a simple framework for combining the nutrient and light effects of stability, the actual biological consequences of increased stability will often be more complex-for example, increased average light levels may eventually become inhibiting, turning an apparent advantage of increased stability into a disadvantage. Additional biological complexity is demonstrated by the results of Karl et al. (1995), who found that the 1991-1992 ENSO event in the North Pacific subtropical gyre was associated with an increase in water column stability. Although the straightforward consequence of increased stability would be a decrease in nutrient resupply, hence decreased productivity, measured productivity increased instead. The authors attribute this increase to a shift in species composition. The calmer surface conditions that led to the increased stability favored Trichodesmium sp., a cyanobacterium capable of nitrogen fixation and thus able to relieve the chronic nitrate limitation of the subtropical gyre. Despite such complexities, the subject of ecosystem shifts under varying physical forcing must be pursued, not only because of its importance to marine fisheries but also because of its effects on rates of CO₂ uptake and dimethyl sulfide (DMS) production, which affect the atmospheric burden of greenhouse gases (Denman et al., 1995). Understanding marine ecosystem responses to physical forcing may be essential if we are to predict the contribution of the oceans to Earth's climate in the coming era of global change.



Fig. 2.2. Schematic of an optimal "window" in stability, a physical variable that is the net result of stabilizing and destabilizing forcings of the upper ocean. Stability has both positive and negative effects on primary production. By restricting vertical motions and fluxes associated with turbulent processes, increased stability brings an increase in the average light seen by a phytoplankter (positive) but a decrease in the resupply of needed nutrients (negative); decreased stability reverses these effects. Any such variable is associated with a window at intermediate values within which primary production is maximal.

3. Physical Processes and Variance within Phytoplankton Communities: Populations

While the average distributions of biomass and community structure that define general biogeographic regions of the world's oceans have long been known in broad outline, the existence of significant spatial and temporal variability about these averages has also been recognized in the concept of populations within communities. By *populations* we encompass aggregations of planktonic organisms whose space-time mean properties resemble those of the biogeographic region to which they belong, but whose instantaneous properties of biomass and/or species composition may depart substantially from those mean values. Such departures from the mean (the variance of the biological system, whether viewed in space as horizontal or vertical patchiness or in time as blooms or succession) result from interactions between the vital rates of planktonic organisms and fluctuations in the physical environment which occur on relevant time scales.

Biologically relevant time scales for phytoplankton are inherent in standard saturation curves (see, for example, Fig. 2.4a), which not only determine mean response to light and nutrients but also the ability of an organism to respond to change. The initial slope α of a saturation curve determines how quickly an organism can respond to increase in light (nutrient), while saturation or inhibition thresholds determine how much of any such increase is superfluous or, in the case of light, possibly inhibitory. For significant biological effect, physical modulation of the environment must be maintained over time periods long compared to the doubling time of planktonic species. This does not necessarily imply that the physical process itself acts continuously in time, merely that the effect be frequent enough to be perceived as continuous in terms of the biologically important variables; see the discussion of internal waves in Section 3.2). Because of large species-specific differences in doubling times and saturation–inhibition thresholds, the same change in physical forcing can lead to very different results, depending on the suite of opportunistic organisms present at its initiation.

Some of the major physical processes that affect the upper ocean environment on time scales greater than the one to several days that are characteristic of phytoplankton doubling times are the seasonal cycle of insolation-stability, geostrophic eddies, geostrophic fronts, Rossby waves, equatorial waves, internal tidal waves, and eventscale and coastal wind-driven upwelling. Where these processes are addressed elsewhere in this book, our treatment will be relatively brief, intended just to delineate in a broad sense the dominant means of influence on primary production. With the exception of internal tides, all the processes listed above originate either directly or indirectly in the atmospheric forcing of the ocean emphasized in Section 2. Geostrophic eddies form through instability of currents driven by winds and buoyancy. Atmospheric forcing of upper ocean temperature and salinity causes the annual stability cycle and sets up the horizontal differences in water properties which, coupled to circulation, leads to oceanic fronts. Planetary waves are generated by large-scale variations in wind forcing, while smaller-scale wind variations drive upwelling. Moreover, although we focus here on time scales from several days to a year, the interannual and longer time scales considered in Section 2 will also affect populations, since populations comprise communities.

All of the physical processes listed above cause temporal and spatial fluctuations in the supply of nutrients and light to the euphotic zone. Through processes similar to those outlined in the preceding section, such fluctuations can structure an originally homogeneous community into a range of populations characterized by different biomass levels. However, in addition to effects on biomass, variations in nutrient supply and stability are also responsible for biological succession, a process that creates populations characterized by different community structure as well. Succession is usually associated with the seasonal variation observed in high-latitude subpolar oceans, where the diatoms making up the bulk of the spring bloom decline as a proportion of the population as they use up the previous winter's supply of nitrate and are replaced by populations using a much larger fraction of recycled nutrients. Succession has also classically been assumed to be absent from more constant environments such as the subtropical gyres and thus might be argued to be a community property, addressed more properly in the preceding section. However, if generalized to describe major time change in local species structure, succession is not a process confined to the annual time scale nor to high latitudes, but a general consequence of opportunistic reactions by phytoplankton populations to improved nutrient or light conditions. Variable primary production, fueled by physical processes acting over a wide range of scales, interacts with predation to shape the species composition of populations. In the remainder of this section, we describe some of the physical processes that modulate nutrient or light environments on time scales shorter than annual.

3.1. Geostrophic Eddies

Pycnocline deformations associated with geostrophic balance in cyclonic and anticyclonic geostrophic eddies are mesoscale analogs of the major upwelling and down welling gyres, respectively, considered in Section 2 (Fig. 2.1). In the center of cyclonic eddies, the nutricline may be several tens of meters nearer the ocean surface than it is in surrounding waters. Shoaling of the nutricline may be of sufficient magnitude that the upper part of the nutricline lies within the euphotic zone itself, fueling production directly. Even where it remains below the euphotic zone, the relative shallowness of the nutricline means that turbulent events driven by surface processes, either directly or indirectly through radiated internal waves, can more easily resupply nutrients to the surface layer. Increased surface layer primary production has been documented in a cyclonic eddylike circulation observed in the lee of the Hawaiian Islands (Falkowski et al., 1991). Reporting a trail of enhanced productivity behind this feature, Olaizola et al. (1993) suggest that this circulation is unlike that of the rings which detach from energetic western boundary currents. The term ring will be used here in a more general sense to describe geostrophic eddies of vigor sufficient to trap and transport water masses, reserving the term *eddy* for nonlinear geostrophically balanced fluctuations which do not do so. In a biological sense, the difference between rings and eddies, thus defined, lies in the space-time distribution of nutrient enhancement. A population within the water mass trapped in a ring receives enhanced nutrients for an extended period of time, but the effect is spatially localized within the ring during its lifetime. Eddies that do not trap populations may nonetheless produce upwelling at a particular spatial location over a time scale sufficiently long to produce a transient bloom at this location. However, because this effect propagates with the eddy, the resulting production is a spatially diffuse trail like that observed by Olaizola et al. (1993).

Analogy with oligotrophic gyres would suggest that anticyclonic eddies should, in contrast, be regions of lowered productivity. However, observations demonstrate that the process of decay of such eddies produces interior upwelling which shoals and steepens the nutricline, enhancing production by advection or diffusion of nutrients (Nelson et al., 1989). It thus appears that eddy variability should increase primary productivity in regions where it is limited by macronutrients (McGillicuddy and Robinson, 1997) or in those micronutrient-limited regions where resupply is dominated by the same (vertical) processes effecting upward transport of macronutrients. In contrast, subpolar regions which are instead limited by either light (North Atlantic) and/or airborne micronutrient supply (North Pacific) should be unaffected by eddyinduced vertical nitrate fluxes. There is a suggestion of such gyral asymmetry in results obtained with a simple biological module coupled to an eddy-assimilating numerical model of the North Atlantic (Oschlies and Garçon, 1998). While model eddy kinetic energy was high along the entire path of the Gulf Stream and the North Atlantic Current, primary production was enhanced only along the approximately east-west boundary of the nitrate-starved subtropical gyre, not within the nitratereplete subpolar gyre. Within oligotrophic gyres themselves, eddy-enhanced productivity should bear the imprint of the predominantly longitudinal decrease in eddy kinetic energy from western to eastern sides of ocean basins (Stammer, 1997). However satellite-derived maps of surface primary production (see Fig. 10.4) do not show this expected pattern. Indeed, Falkowski et al. (1991) estimate that eddy pumping of nutrients would enhance primary production in oligotrophic gyres by only 20%, in which case east-west trends should prove nearly impossible to observe in reality, given variation in other factors influencing primary production.

3.2. Geostrophic Fronts, Internal Tides, and Coastal Upwelling

In contrast to the ubiquitous nature of geostrophic eddies in the ocean, the physical processes considered next tend to be spatially localized. The open ocean fronts considered here range in horizontal linear extent from the hundreds of kilometers of shelf-break fronts or upwelling fronts through the tens of kilometers of shelf-sea fronts (coastal or headland fronts with scales of a few kilometers are considered in Section 5). A *front* is defined generally as a region of large horizontal gradient(s) of water properties (including any or all of temperature, salinity, macronutrients, micronutrients, and density). Depending on the property one chooses to look at, one's definition of *large*, and the observational resolution of available measurements, fronts may be either sparse or, like geostrophic eddies, also ubiquitous. There appears to be almost as much range in the biological effectiveness ascribed to them, despite a general belief that fronts are responsible for significant resupply of nutrients to the euphotic zone.

It is generally accepted that shelf-break fronts in particular are regions of increased primary productivity and of higher than average phytoplankton biomass (Marra et al., 1990), with the increased biomass dominated by diatom species that thrive on new nitrate. Less clear are the physical mechanisms involved here. On the southwestern side of the Atlantic, the shelf-break frontal boundary is frequently distorted by the passage of offshore rings and eddies shed by the nearby Gulf Stream, as well as by the inherent instability of the shelf-break current associated with the front. Thus new nutrients may be supplied by geostrophic upwelling, the upward vertical velocities associated with one phase of the geostrophic adjustment process of time-variable (hence) quasigeostrophic flows.

On the southeastern side of the Atlantic, another explanation of enhanced nutrient supply at and near the shelf break is in terms of internal tidal waves generated by incidence of the barotropic tide on the shelf break (Pingree et al., 1986). Internal tidal waves decay as they propagate shoreward but at least initially may be of sufficient amplitude to produce enhanced nutrient fluxes by the episodic lifting of the nutricline toward the surface during the passage of wave crests. Occurring on the semidiurnal period of the tides, this nutrient pumping is experienced as nearly continuous by the phytoplankton population—hence not only fuels the increase in phytoplankton biomass observed, but guarantees its persistence.

The relative importance of geostrophic upwelling and internal wave pumping to the productivity of shelf-break fronts varies from one shelf region to another [i.e., internal wave pumping has been documented on the western side of basins (Haury et al., 1983), while the effect of eddy-induced geostrophic upwelling has been observed on the eastern side of basins (Mooers and Robinson, 1984)]. With increasing knowledge of the "geography" of geostrophic eddies as well as the relative predictability of internal tidal amplitudes, it may soon be possible to make first-order estimates of which (if either) process dominates nutrient supply in particular shelf-slope fronts.

Moving seaward of the strong shelf-slope fronts, there is still ongoing debate about the biological importance of deep-ocean fronts. During two fluorometer surveys of the Azores Front in the eastern North Atlantic, Fasham et al. (1985) found little evidence for increased phytoplankton biomass associated with the front. In the same region, Kahru et al. (1991) observed the same near constancy of chlorophyll concentration (biomass), but also a dramatic change in size structure, from small nanoflagellates to larger diatoms, in passing from the western (subtropical gyre) side to the eastern side of the front. While the diatom population might have been assumed to be associated with frontal supply of new nutrients, a negative correlation between chlorophyll and diatom concentrations suggested that the diatom population was in the poor physiological condition characteristic of the decay stage of a bloom. The fact that this situation remained constant over the entire two weeks of observations strongly suggests to us that the diatom bloom was actually fueled elsewhere, with the bloom by-products redistributed by the horizontal advection and convergence associated with the frontal jet. Thus the question of remote supply of new nutrients followed by horizontal redistribution, which will be emphasized in Section 5 when discussing the coastal ocean, may also be of importance in deep-sea frontal regions, further complicating the question of their importance to primary production.

Mesoscale fronts are also generated as a part of the process of coastal upwelling, which varies on the time scales associated with wind forcing, from the annual cycle in the large-scale atmospheric circulation to the several days associated with passage of individual pressure systems. Wind-driven upwelling produces highly productive regions, fueled by new nutrients brought to the surface by Ekman divergence along the eastern boundaries of many ocean basins. Cold nutrient-rich water upwelled at the coast warms and stratifies as it moves offshore in a thin surface layer. Regions of coastal upwelling are productive through a succession of two processes, resupply of new nutrients followed by retention of organisms in a stable lighted upper layer, which Legendre (1981) postulated as essential to high levels of new production and which is implicated in many of our previous discussions of the biological impacts of specific physical processes. With finite time lags associated with the development of planktonic biomass, neither surface layer chlorophyll concentrations nor zooplankton distributions are necessarily maximum at the coast. In a classic example, Boyd and Smith (1983) presented distributions of chlorophyll ranging from 1.5 mg of chlorophyll per cubic meter in newly upwelled waters along the coast of Peru to a maximum of 50 mg of chlorophyll per cubic meter approximately 20 km offshore. An advection time scale of approximately 11 days, estimated from solar heating of the surface layer, was consistent with measured phytoplankton doubling times of order one per day.

Despite the consistency of this overall picture of coastal upwelling, repeated surveys with an airborne radiation thermometer showed that these conditions could evolve rapidly (Boyd and Smith, 1983), a result confirmed by the spatially detailed maps of temperature and chlorophyll now routinely provided by satellites. Satellite images also show that instantaneous property fields in upwelling regions are usually strongly distorted by the ambient eddy field and by formation of squirts and jets linked to coastal geometry (Brink and Cowles, 1991), instabilities that can distribute the products of coastal upwelling far offshore. The complexity of biological and physical variables in the frontal zone marking the transition between nearshore upwelling and the offshore ocean has been documented extensively in the Californian upwelling system, as reported in a special volume of the Journal of Geophysical Research: Vol. 96(C8), 1991. Underlying the wealth of detail, however, lies one of the physical mechanisms discussed above in connection with shelf-break fronts: provision of new nutrients to the lighted surface layer through geostrophic upwelling associated with a meandering boundary current and/or transient eddies. Observations in the coastal transition zone also demonstrate that the ephemeral phytoplankton (predominantly diatom) blooms that result in such areas may subsequently be removed from the euphotic zone through downwelling (subduction) (Washburn et al., 1991).

In the same journal volume, Abbott and Barksdale (1991) document large interannual variability in satellite-derived chlorophyll distributions in this area during the period 1981-1983. Because of the enormous importance of upwelling regimes to global ocean production of marine fish stocks, factors underlying this variability must be sought. Inherent in our previous discussion of the relative strengths of physical processes leading to increased versus decreased upper ocean stability is the possibility that variation in local (or far-field) buoyancy forcing may play an essential role in producing interannual variability. Indirect evidence of such a stability effect may be seen in recent observations (Kinkade et al., 1997) of an order-of-magnitude increase in average surface chlorophyll in the Indonesian Seas between monsoon seasons. During the high-production southeast monsoon, high values of surface phytoplankton biomass occur in the eastern seas, correlated with cooler sea surface temperatures, presumably caused by increased upwelling and/or vertical mixing. By the same associations, onset of the northwest monsoon might be expected to move the center of upwelling, mixing, and high productivity to the western seas. This did not occur, probably because large riverine inputs of freshwater to this western region produce a stability cap during the northwest monsoon, preventing upwelling waters from reaching the surface and perhaps also reducing the effectiveness of turbulent mixing.

3.3. Equatorial Waves

Gargett (1991) reviews the oceanic planetary wave modes that govern the response of the ocean to time-variable winds. The Rossby waves of midlatitude oceans generally have longer time scales than those of concern to populations. However, additional modes possible near the equator allow the equatorial ocean to respond to both remote and local wind forcing on much shorter time scales, and apparently provide the major physical forcing of variance in the equatorial ecosystem. Nutrients and micronutrients supplied by wave-induced upward vertical displacement of the equatorial pycnocline (also a ferrocline) have been implicated in the generation of biological variability on a broad range of time scales, from the few to several years of El Niños (Barber et al., 1996), through the 20 to 30 days typical of tropical instability waves, to the 6 to 8 days of equatorially trapped internal gravity waves (Friedrichs and Hofmann, 2001).

In addition, the near-equatorial ocean is a region of strong meridional circulation caused by divergence of water upwelled at the equator, as well as strong zonal circulations associated with off-equatorial trade winds. Instabilities of these zonal currents, whether viewed as wavelike instabilities (Legeckis, 1977) or as finite-amplitude vortices (Flament et al., 1996), produce zones of strong convergence and divergence which move slowly along the front between the South Equatorial Current and the North Equatorial Countercurrent. Biological production fueled by equatorially upwelled nutrients and exported from the equator in the mean meridional divergence can be collected in the convergences, sometimes with dramatic effects on localized biomass (Yoder et al., 1994).

4. Effects of Physical Processes on the Physiological Response of Individuals

In the past, most marine observations have addressed primary production at the level of the mean (communities) and its variance (populations), as discussed in preceding sections. However, with recent development of new measurement techniques, it is now possible to address physiological variability at the scale of the individuals that make up populations. Sophisticated fluorescence methods (Falkowski and Kolber, 1995) and high temporal resolution of photosynthetic rates (Jassby, 1978; Marra, 1978) place increased focus on the local physical environment of individuals and its high-frequency variability, which we define as variability with time scales comparable to those of cell processes, from seconds to a few days. Physical processes with such time scales are numerous: convective or stress-driven turbulence within and below the surface mixing layer, Langmuir circulations, internal gravity waves in the pycnocline, and high-frequency variation in solar irradiance.

4.1. Physical Processes with Time Scales of Seconds to Hours

Considering first the surface mixing layer, ordinary turbulent eddies and Langmuir circulations produce similar effects on passive tracers, which for now we assume includes most individual phytoplankton organisms. First, tracers are advected by motions with characteristic velocity $q \propto \langle e \rangle^{1/2}$, where $\langle \cdot \rangle$ denotes averaging of turbulent kinetic energy e over a characteristic length scale Λ . Denman and Gargett (1983) discuss how such Eulerian scale estimates are used to predict the associated Lagrangian displacements of phytoplankton. The magnitudes of q and Λ depend on the particular physical process spawning the large eddies. Convection driven by surface heat loss J_0 (W m⁻²) through a mixed layer of depth D is associated with $q \propto (DJ_0)^{1/3}$ and $\Lambda \propto D$ (Caughey and Palmer, 1979). For those eddies driven by wind stress at the surface, $q \propto U$ and $\Lambda \propto z$, where U is the wind speed at 10-m height above the surface and z is the distance to the free surface. [Note, however, that observations in the presence of breaking waves show near-surface turbulent dissipation, which is larger than that predicted by stress-driven boundary layer scaling (Gargett, 1989; Craig and Banner, 1994), implying large-eddy energy in excess of the value of q given above. Understanding the relationship of this excess to some readily observable parameter such as sea state is an area of ongoing research.] Langmuir circulations, helical vortices aligned roughly in the direction of the wind, are also characterized by $\Lambda \propto D$, but the only prediction for the associated value of q (Li and Garrett, 1993) involves not only wind speed U, but less readily observable parameters such as Stokes drift, set by the surface wave field, and mixed layer eddy viscosity, set by the turbulent field. In considering advection, it is not yet clear whether Langmuir eddies must be treated as distinctive entities or can be considered merely as part of the wind-driven large-eddy field, as suggested by Denman and Gargett (1983).

In addition to large-eddy advection, the smallest scales of turbulence act to diffuse passive tracers, inexorably separating originally neighboring entities, whether chemical molecules, phytoplankton, or particles, and ultimately smoothing out spatial gradients. As a consequence, turbulent diffusion (or its absence) in the upper ocean strongly affects the small-scale spatial distribution of planktonic organisms, either horizontal patchiness (Owen, 1989) or vertical layering (Desiderio et al., 1993), as well as the processes of (dis)aggregation and loss/retention of the marine snow particles which appear to be an important part of the upper ocean food web (Alldredge and Silver, 1988). It is in the realm of diffusion that there may be significant differences between shear-driven turbulent eddies and Langmuir cells. While vertical property gradients are eliminated within the depth D engulfed by Langmuir cells within a very short time (about 1 h) after the onset of the circulations (Li and Garrett, 1997), it would take shear-driven turbulence longer to homogenize the same depth range. Gargett and Moum (1995) suggest that turbulence driven predominantly by energy input directly to the vertical velocity component (such as Langmuir circulations and free convection) may mix more effectively than stress-driven turbulence driven by energy input first to the horizontal velocity component. Because of the importance of upper layer mixing to the light and nutrient environments of phytoplankton, their small-scale spatial distributions, and their net rates of loss/retention in the mixed layer, further progress on this question of turbulent mixing efficiency is essential.

In situations where the depth of the surface mixed layer is less than that of the euphotic zone, advective (but not diffusive) effects similar to those discussed above may arise from vertical displacements associated with internal gravity waves traveling in the pycnocline. The period of significant fluctuations is the local buoyancy period $T_b = 2\pi (BVF)^{-1}$, where $BVF = (-g\rho_0^{-1} d\rho/dz)^{1/2}$ is the Brunt–Väisälä frequency, because only internal waves with periods near T_b have substantial vertical velocities (LeBlond and Mysak, 1978). Buoyancy periods range from values of order 5 minutes in cases of strong coastal stratification to about 50 minutes for stabilities more typical of the permanent thermocline. Since this range is comparable to that of typical large eddies in these environments (Denman and Gargett, 1983), internal wave displacements may have comparable effects.

4.2. Physical Processes with Time Scales of Hours to Days

On time scales longer than those of individual turbulent eddies, the interplay between stabilizing and destabilizing physical forcing of the surface layer modulates the properties of near-surface turbulence at diurnal and longer time scales. Over the past decade, the diurnal cycle of turbulent mixing in the ocean has been extensively observed (Moum et al., 1989; Brainerd and Gregg, 1993) and modeled (Price et al., 1986; Large et al., 1994). Of all the observations, the neutrally buoyant float measurements of D'Asaro and Dairiki, shown in Fig. 2.3, are the most graphic demonstration of this cycle, interpreted biologically by identifying a float as a phytoplankton particle (except that unlike truly passive phytoplankters, none of the floats end up within the stable diurnal thermocline during daylight hours: This is because the "neutrally buoyant" floats are actually ballasted to be very slightly positively buoyant, as a safety measure (D'Asaro et al., 1996). In the observational conditions of light to moderate winds, heat loss from the ocean surface was sufficient to drive penetrative convective motions starting soon after sunset and growing in amplitude and period overnight. Shortly after sunrise, surface heat gain and the depth-distributed heat gain due to solar radiation rapidly formed a shallow diurnal thermocline and restricted the vertical excursions of the floats (turbulent eddies, advected phytoplankton). After sunset, the cycle begins again.

The upper layer turbulence shown so graphically in Fig. 2.3 will evolve with changes in any of the physical processes which act either to stabilize the surface layer (surface heat gain, surface freshwater flux, solar insolation) or to destabilize it (surface heat loss and/or evaporation, wind stress). Because on all time scales the stratification of the upper ocean is the result of a delicate balance between these opposing sets of forces, it too will evolve in concert with changes in turbulence levels. In the present example (Fig. 2.3), the presence of stronger wind mixing and/or



Fig. 2.3. Displacements of an ensemble of acoustically tracked neutrally buoyant floats in a convectively forced surface layer. A composite track (heavy line) can be interpreted as the time history of a single phytoplankter during one diurnal cycle. These measurements confirm the dramatic influence of the diurnal cycle of surface heat loss/gain on the vertical scale of turbulent eddies that advect the nonmotile component of the phytoplankton in the strongly surface-intensified light field of the upper ocean. (Modified with permission from E. D'Asaro and G. Dairiki, University of Washington.)

the formation of Langmuir cells could lead to a deeper diurnal thermocline, or even prevent its formation altogether.

4.3. Biological Responses to High-Frequency Physical Variability

The physical variability described above must lead to biological variability, as ecologically opportunistic organisms find physiological means of contending with considerable uncertainty in the supplies of necessary substrates, particularly light and nutrients. Such physiological responses and adaptations must allow them to survive periods of poor growth conditions, yet increase rapidly when conditions improve.

Determining the physiological mechanisms that respond to environmental forces varying over the time period of vegetative cell growth is a difficult problem, both from the standpoint of quantifying the environmental variability discussed above and from the standpoint of understanding cellular physiology. Nevertheless, it seems clear that the variability of upper ocean processes can substantially modify physiological processes associated with both nutrient uptake and light harvesting.

Turbulence in particular may play an essential role in nutrient supply to individual cells, despite the fact that on the scale of individual phytoplankters, the fluid environment is one of low Reynolds number (Pedley, 1995), in which molecular rather than turbulent diffusion of chemical species through cell walls should dominate crucial processes of nutrient supply and waste removal. The thickness of the diffusive bound-

ary layer around a cell, which determines the time scale of chemical species transfer from the fluid to the cell boundary, is a sensitive function not only of cell size and nutrient concentration in the ambient fluid, but also of *relative* fluid motion. Holding the first two factors constant, nutrient flux can be increased by processes—swimming or sinking motion of the cells, or shear in the surrounding fluid—which thin some portion of the boundary layer about the cell. Karp-Boss et al. (1996) used established engineering solutions for flow around simple shapes to suggest that nutrient flux enhancement is dominated by self-induced cell motion for small organisms but by turbulent shears for larger organisms such as chain-forming diatoms and filamentous bacteria. Through such size-dependent effects on nutrient supply at the level of individual cells, the average level of turbulence in the upper ocean environment may play a major role in determining the species structure of planktonic ecosystems.

Of all the factors affecting phytoplankton growth, irradiance probably exhibits the greatest natural variability. The problems associated with irradiance variation may be appreciated by considering the measurement of phytoplankton photosynthesis at sea, a technique that typically involves incubating a series of samples for several hours or more, at fixed positions in the water column, then assaying for the determinants of photosynthesis. Although the objective is to obtain a value for the daily rate of primary production for a locale in the ocean, this can clearly provide only an approximation to the actual photosynthetic processes occurring, because the time period of incubations is long with respect to changes in phytoplankton physiology, upper ocean physical processes, and local meteorology (Franks and Marra, 1994; Kamykowski et al., 1994). If the goal is to understand how phytoplankton make their living in a variable environment, both that environment and phytoplankton physiology itself must be observed with appropriate temporal resolution.

The daily transit of the sun is the first-order change in irradiance over the time scale of phytoplankton growth. In many cases it causes an entrainment of the growth cycle to the 24-h diel cycle, in which cell cycle events are synchronized to day- or nighttime periods (Chisholm, 1981). Cellular metabolism is also naturally tied to the solar cycle, in some cases separating processes that are light dependent (e.g., carbo-hydrate production) and those that are non-light-dependent into appropriate times of the day. In terms of bulk water column properties, particle concentration (or size) increases during the day, while at night, loss processes exceed those of growth, leading to overall declines. The cycles of cell division of particular populations, however, may differ markedly from the changes in the properties of the cells (e.g., their chlorophyll content) over the solar day (Vaulot et al., 1995; Durand and Olson, 1996). Thus some parameters may show cycles at variance with the solar cycle.

At higher frequencies, irradiance variation will be generated by physical processes associated with vertical velocities that are much greater than both the swimming speeds of phytoplankton and their known sinking speeds under quiescent conditions (Smayda, 1970). Such vertical motions transport phytoplankton as essentially passive particles through an irradiance field that decays exponentially (and changes its color) as a function of depth. Especially nearer the ocean surface, even small vertical displacements will mean short-period variations in the intensity and spectrum of the light which are substantially greater than the diurnal variation at a fixed depth (Gallegos and Platt, 1982). Thus, phytoplankton potentially experience a highly variable light environment over the time scales of their vegetative growth, from minutes or hours to a few days.

Awareness of the effects of irradiance variability on phytoplankton photosynthesis

is not new, going back at least to the early 1970s (see, e.g., Harris, 1986). The earlier work will not be reviewed here, but is summarized by Gallegos and Platt (1985) and Ferris and Christian (1991). Taken together, the previous studies have produced equivocal or inconclusive results, and there are at least two reasons for this. First, at any given time we are largely ignorant of the kinds of mixing and stirring that are occurring in the environment, hence of the actual irradiance variability experienced by phytoplankton. This, of course, makes it difficult to design experiments that simulate mixed layer stirring and mixing processes, either in the laboratory or at sea. Second, we don't understand the physiological response to irradiance variability all that well. The response may be complex and involve not only carbon fixation but also chloroplast orientation (Kiefer, 1973), light-energy distribution to the photosystems, pigment variations (Demmig-Adams, 1990), and fluorescence (Demers et al., 1991). In addition, the response may not be expressed solely in terms of short-term photosynthesis, but rather, along other metabolic pathways, such as respiratory processes (e.g., photorespiration) or buoyancy modification. Finally, we might expect that there will be species differences in the response to variable light regimes (Marra, 1980), with different organisms adapted to different mixing regimes, since it is mixing that regulates the supply of substrates, including light.

Despite these complexities, responses to short-term irradiance variability have been established in the laboratory, and when these are parameterized in plankton ecosystem models, there is an effect on overall production (e.g., Denman and Marra, 1986; Patterson, 1991; Franks and Marra, 1994). Two recent observational studies also provide indirect support for the importance of the response. The first is a comparison of the flux of total CO₂ in the mixed layer with carbon assimilation, measured in situ with the ¹⁴C technique at fixed depths to the depth of 1% irradiance penetration (Chipman et al., 1993). This study showed reasonable agreement between carbon assimilation in the incubations and the changes in TCO₂ in the water integrated over the mixed layer. The interesting aspect is that early in the observational period, the mixed layer was about twice as deep as the depth of 1% surface irradiance (Ho and Marra, 1994), the nominal productive layer, but the agreement between incubated and in situ estimates of primary production was maintained throughout. Thus, the phytoplankton were apparently able to compensate for mixing that periodically took them out of the productive layer by enhancing their photosynthetic rate while resident in lighted depths. The second study is an analysis of the spring diatom increase in Lake Windermere (Neale et al., 1991). Production calculated from laboratory measurements of light-saturated rates of photosynthesis appreciably underestimated the actual diatom increases observed in the lake. A model based on the mean irradiance in the mixed layer, however, agreed very well, and the authors concluded that exposure to high irradiances for short periods would lead to higher light-saturated rates of photosynthesis than the rates measured over longer periods or under conditions of constant irradiance in the laboratory.

The photosynthesis—irradiance response (P versus E) curve has proven a useful theoretical tool for considering the nature of photosynthesis in phytoplankton. Although there are practical problems with its measurement (e.g., the requirement for an incubation, during which the response itself may change; detection of small signals at low irradiances; and the spectral quality of the light source), the P versus E curve nevertheless encapsulates the overall photosynthetic response, and its characteristics can reveal aspects of the physiological condition of the phytoplankton.



Fig. 2.4. (a) A standard P (productivity) versus E (illumination) curve (heavy line) is characterized by two parameters: photosynthetic efficiency α and light-saturated maximal productivity P_{max} , which occurs for $E > E_0$. Different phytoplankton species may have different values of either (or both) parameter: the dashed (thin) curve has higher P_{max} (α) than the standard, but the same α (P_{max}). The range from 0 to E_d is that associated with a time-variable field of illumination E(t), shown schematically in (b). (c) For phytoplankton characterized by the standard P versus E curve, photosynthetic response to E(t) becomes constant (heavy curve) once E(t) exceeds E_0 . Species with higher P_{max} (dashed curve) or higher α (light curve) can achieve overall photosynthesis which is greater than that of the standard (shaded area).

A generic *P* versus *E* curve (heavy line in Fig. 2.4*a*) has negative curvature, so that the physiological effect of irradiance variability above a certain level (E_0) is smoothed out rather than amplified. This standard *P* versus *E* curve can be described by an equation with two parameters:

$$P = P_{\max} \tanh(\alpha E / P_{\max}) \tag{1}$$

Here P_{max} is the maximal, or light-saturated, rate of photosynthesis (see Fig. 2.4*a*). The initial slope α represents the photosynthetic efficiency of the organism, since it is the linear increase in the rate of photosynthesis with increasing irradiance. Empirically, both P_{max} and α have been found to be variable. However, we use equation 1 as a basis for discussion, since it has been found to represent the general photosynthetic response (Jassby and Platt, 1976), with the exception of very high irradiances where photosynthesis may become photoinhibited, a subject to which we return later.

For an ecological interpretation of the response at the level of individual cells, we consider the photosynthetic response to variation of irradiance over the range zero to E_d shown on the *E*-axis of Fig. 2.4*a*. A schematic time-dependent E(t) is shown in Fig. 2.4*b*. In Fig. 2.4*c* the heavy curve shows the photosynthetic response to E(t) for a phytoplankter characterized by the generic *P* versus *E* curve: *P* first increases in direct proportion to the increase in light intensity, but levels off for values of $E > E_0$. For the same light variation, a cell can increase its level of photosynthetic production

over that of the generic cell by increasing either α or P_{max} . (At least to first order, these choices can be treated as independent, since the two parameters are thought to characterize quite different physiological systems, with α dependent primarily on the pigment suite absorption properties of the cells, P_{max} on enzyme kinetics.) The higher the efficiency of photosynthesis α , the lower the irradiance at which phytoplankton achieve their maximum growth rate, as illustrated by the high- α curve of Fig. 2.4*a*. The higher the value of P_{max} , the wider the range of irradiance that is "tracked" by photosynthesis. The associated photosynthetic response curves shown in Fig. 2.4c illustrate that both strategies can achieve higher overall photosynthesis than the generic case, albeit by different means. Which of the two physiological responses is invoked to maximize photosynthesis is probably determined by the time period of typical environmental light fluctuations (purposefully left unspecified in Fig. 2.4b). Because the suite of photosynthetic pigments that determine α cannot be changed quickly, adaptation to fast light variation is probably achieved through changes in the physiologically fast enzyme kinetics that determine P_{max} . Thus organisms in strongly mixed (fast) systems may achieve optimal productivity by changing P_{max} , while in strongly stratified systems, where primary variability occurs on the slow time scale of diurnal solar transit, varying α may be the more effective strategy.

The analysis above has avoided the question of photoinhibition, largely for simplicity, but also because we feel that the general significance of photoinhibition is an open question. Although photoinhibition no doubt occurs at very high irradiances (Neale, 1987), it is typically measured under experimental conditions (constant depths, or irradiances) which may actually be experienced only infrequently by phytoplankton in situ.

As another example of interaction between physical and physiological processes, we note that some species of phytoplankton apparently have physiological means of increasing their buoyancy in order to remain longer in the upper lighted regions of the sea. For example, diatoms have the ability to alter their intracellular ionic composition (Anderson and Sweeney, 1977) to exclude potassium ions in favor of lighter sodium ions. Similarly, metabolism may be shifted toward fat production to maintain position in the upper layers. Although the degree to which such strategies are necessary will presumably depend on the suite of physical processes active (or not) in the euphotic zone, we have not located any literature relevant to this potential influence of physical processes on the physiology of individuals.

The diurnal cycle of near-surface stability and mixing layer depth and its modulation on seasonal time scales have significant implications for biological communities, as discussed in Section 2. At the level of individuals, Woods and Onken (1982) used a Lagrangian ensemble biological model, embedded in a one-dimensional model of the upper ocean, to demonstrate how irradiance variations associated with diurnal cycling of upper layer turbulence (such as that seen in Fig. 2.3) can structure the depth distribution and energy uptake of a group of multiplying cells. Such Lagrangian models also document how the diurnal cycle affects the rate of loss of organic material from the upper ocean. As the mixed layer deepens during the night, phytoplankton and inanimate particles produced in a shallow mixed layer during one day are mixed downward at rates far larger than their still-water settling rates. Some of this material will be isolated at depth by formation of the diurnal thermocline on the following day. Settling in a zone of diminished mixing, the largest phytoplankton "particles" may escape reincorporation into a mixing layer the following night (particularly when the diurnal thermocline is shallowing in springtime), being thus moved below optimal growth environments by the diurnal variation in mixing layer depth. Gardner et al. (1995) coined the term *mixed layer pump* for the enhanced particle exchange between upper and deep ocean which is driven by variation of mixing layer depth on all time scales.

5. Primary Production in Tidally Dominated Regimes

As bottom depth decreases toward land, physical processes of the upper ocean are no longer necessarily dominated by atmospheric forcing. Instead, processes associated with tidal flows become increasingly important and often dominant. In this section we consider briefly the biologically significant differences between tidally dominated coastal regimes and the pelagic regimes considered up to this point.

From a large-scale viewpoint, the periods and sea-level variations associated with the barotropic tides are the most predictable of oceanographic variables. Even on smaller scales, extensive networks of tide gauges provide predictions of tidal velocities that are much more accurate than predictions of mean velocities resulting from wind and buoyancy forcing. However, the major biological effects of tidal currents result from the light and nutrient effects of instabilities in which barotropic tidal energy is converted into internal waves (of tidal or shorter period) or into turbulence. These conversions are strongly modulated by the large variability characteristic of near-surface stability in the coastal ocean, as forced by variations in cooling/heating, evaporation/precipitation, ice formation/melting, and freshwater runoff from land. Unfortunately, such buoyancy effects are related to atmospheric forcing, hence are much less predictable than tidal velocities. Because of these indirect connections to the atmosphere, the biological consequences of tidally dominated regimes cannot, after all, be considered as significantly more predictable than those dominated directly by atmospheric forcing.

Instabilities of coastal tidal flows leading to internal waves or to turbulence tend to be strongly localized in space. The internal tides mentioned in an earlier section are generated most strongly in regions where the barotropic tidal wave has a significant velocity component normal to local topography (Baines, 1982). Generation of higher-frequency nonlinear internal wave packets and/or turbulence is usually associated with major changes in either topography (i.e., depth) or morphology (i.e., horizontal structure such as headlands, abrupt change in tidal channel direction or width, the merging of multiple tidal channels, etc.). Packets of nonlinear internal waves with periods of a few to tens of minutes are generated by stratified tidal flow over steep topography (Farmer and Smith, 1980; Haury et al., 1983) and break, generating turbulence, as they travel shoreward (Gargett, 1980). Many tidal flow instabilities directly generate turbulence, which frequently interacts with stratifying forces of surface heating and/or freshwater input to form small-scale fronts of various types. In shallow seas, shelf-sea fronts (Simpson and Hunter, 1974) separate tidally well-mixed and stratified waters. In regions of complex topography, headland fronts are associated with sharp changes in orientation of tidal flow, and convergent fronts are caused by near-normal intersection of two tidal streams (Farmer et al., 1994; Gargett and Moum, 1995; Gargett, 1999).

All of the processes above result in localized physical structures characterized by large rates of nutrient resupply to the euphotic zone, large fluctuations in light levels, and accelerated loss of phytoplankton and particles from the euphotic zone. The extremely high productivity of most near-coastal regions suggests that the role of tidal mixing mechanisms in supplying new nutrients outweighs the potentially negative effects on primary production associated with lowered average light levels and increased particle losses. Part of this effectiveness results from the strength of tidal flows compared with offshore mean currents, which makes them more likely to become unstable and generate turbulence. However, major tidal instabilities are usually spatially sparse, occupying only a small percentage of coastal ocean volume. In addition, the associated vertical mixing varies in strength with all the fundamental tidal harmonics and so may be considered sparse in the temporal domain as well. How, then, do localized but intense nutrient transport events support a spatially diffuse increase in primary productivity? The answer to this question resides in dispersal of the effects of localized mixing events by the strong horizontal flows associated with both barotropic (depth-independent) tidal flow in shallow waters and baroclinic (vertically sheared) exchange flows driven by the strong buoyancy forcing typical of nearcoastal waters. Horizontal dispersion associated with reversing tidal flows diffuses the localized effects of individual mixing events over scales of several kilometers within a few to several days (Csanady, 1990). Thus before being utilized completely, nutrients supplied to the euphotic zone in a small area over a short time may support primary production throughout such a zone of influence. As an example, modeled phytoplankton production on Georges Bank (Franks and Chen, 1996) is supported by nutrients mixed upward during the flood-to-ebb transition of a strong tidal front on the northern edge of the bank, then advected onto the bank during ebb tide. Even larger zones of influence are associated with the mean exchange flows of strongly estuarine regimes. In the example shown in Fig. 2.5, Crawford (1991) estimated various nutrient supply rates to the highly productive outer shelf region off southern Vancouver Island (British Columbia), and concluded that the dominant contribution was advection from the surface layer exiting the Strait of Juan de Fuca. Nutrients are mixed into this layer predominantly in tidal fronts and hydraulic jumps generated in the complex of channels bordering the southern Strait of Georgia, roughly 150 km upstream in the estuarine flow.

Paradoxically, the sparse nature of tidal mixing is also essential to the high levels of productivity that are frequently characteristic of coastal oceans with strong tides. Provided that significant coastal mixing sites are sufficiently sparse in space and time, nutrients pumped up to the surface during passage through a single intense mixing zone subsequently reside within a strongly stratified layer, producing favorable nutrient and light conditions over a period of time comparable to that of vegetative growth. With increased space–time density of mixing sites, the negative effects of strong mixing could predominate.

While other biologically significant differences between coastal and open ocean euphotic zones may exist, that is, if the vertical scale of advection in the light field becomes limited by the distance to the bottom (Perry and Dilke, 1986) rather than by large-eddy scales, or if the turbulence associated with particular types of tidal instability proves more efficient than offshore processes at mixing (Gargett and Moum, 1995), the potentially dominant importance of nonlocal nutrient supply is perhaps the major difference between coastal oceans, strongly forced by buoyancy and tides, and the more weakly forced and horizontally homogeneous deep-sea environment considered in most of this chapter.



Fig. 2.5. Due to the strength of horizontal advective flows, biological effects of turbulence in the coastal ocean may be highly nonlocal, as illustrated in this example from the coastal waters of southern British Columbia, Canada. (*a*) Juan de Fuca Strait is characterized by strong estuarine surface outflow. The shaded area shows the highly productive outer shelf region off Vancouver Island, while dots indicate sites of strong localized mixing that have been identified inside Vancouver Island. (From Gargett, 1994, 1999.) (*b*) Estimates of contributions to the outer shelf nutrient supply in summer indicate that local tidal (t) and wind-driven (w) mixing are insignificant relative to supply by advection in the outflowing surface waters of Juan de Fuca Strait. Nutrients carried by this outflow are supplied by strong mixing at sites [see (*a*)] that are spatially far removed from the shelf itself. The frequent importance of such nonlocal balances is a characteristic that distinguishes coastal from pelagic ecosystems. (Adapted with permission from Crawford, 1991.)

6. Conclusions

The conclusions we have reached through the process of writing this chapter are presented in the form of some outstanding questions that must be addressed if fundamental connections between physics and biology are to be clarified and, in particular, quantified.

ANN GARGETT AND JOHN MARRA

6.1. Essential Questions in Physical Oceanography

Despite advances, there are many outstanding questions arising from our lack of knowledge of turbulent mixing processes in the upper ocean. In particular, mixing in the stratified region at and below the base of an active surface mixed layer is parameterized in an ad hoc manner in biological models but is crucial to their results (through effects on resupplying nutrients, maintaining nutriclines, determining losses of organic matter, etc.). Related is the general question of mixing efficiency in stratified regions: Is it constant as generally assumed by observational physical oceanographers, or does it depend (in some inverse sense) on stratification, as various modelers have been forced to assume (e.g., Simpson and Bowers, 1981)? Does salt fingering play a role in maintaining the levels of primary production in oligotrophic gyres (Hamilton et al., 1989)? Does differential diffusion (Gargett, 1988; Merryfield et al., 1998) operate in the ocean? If so, are there biological consequences? Because turbulent mixing affects phytoplankton directly at the individual level and indirectly at population and community levels, these questions affect all time and space scales of primary production.

We have argued that stability is a physical characteristic of the upper ocean with fundamental importance to primary production. Consequently, we suggest that buoyancy frequency (or period) should be routinely reported as part of marine observations of biological distributions or processes. Moreover, because salinity dominates stratification of the winter euphotic zone in the highly productive subpolar gyres, progress in physical-biological interactions at decadal temporal and basin spatial scales requires surface salinity measurements on time-space scales comparable to present satellite surface temperature products. Even low-resolution satellite estimates of salinity would be of enormous value to studies of decadal change in the high latitude and coastal ecosystems which are among the most productive on the globe.

Further clarification of the physical transfer processes between the "edges" and the interior of the sea are necessary to address questions of biological importance at community scales, particularly the role of boundaries in resupply of micronutrients.

6.2. Essential Questions in Biological Oceanography

The evolution toward biochemical and/or optical means of classifying plankton organisms is probably irreversible: such variables can and increasingly will be made remotely and rapidly, enabling description of planktonic assemblages with the same time and space resolution presently available for many physical variables. Increased resolution has led to profound changes in our view of physical processes, and may be expected to similarly change that of biological processes. The challenge will be to connect these "new" descriptions of organisms with the "old" detailed taxonomic descriptions, to ensure that what has already been learned about individuals, populations, and communities is not lost in the transition.

Major questions are arising with respect to use of satellite measurement of primary production (chlorophyll a). The question of the relation of surface chlorophyll a to the euphotic zone average remains a thorny one, while various authors have recently drawn attention to observations (Karl et al., 1995) or simulations (Denman et al., 1998) in which primary productivity increased significantly without translating into a satellite-observable increase in standing stock. Apparently, such increased productivity can be transferred instead to higher trophic levels, with major effects at the level of human exploitation, making it essential to devise means of combining information (satellite fields, in situ measurements, numerical models) to reveal such variation in productivity in the absence of biomass signals.

6.3. Combined Questions

Perhaps the most difficult question for the combined physical-biological ocean community relates to what causes change in primary and secondary productivity on interannual to decadal time scales. As formulated by Steele and Henderson (1993): "Can ecological changes be simply related to physical trends; or are the changes so modified by the biological dynamics that simple physical consequences will not be observable?" Their subsequent model investigation of the effects of variation in winter mixed laver depth on annual primary production at a Sargasso Sea site suggested that there is indeed a direct effect. Modeled annual production increased with increase in winter NO₃ level (deeper winter mixed layers). However, the connection is confounded to a degree by biological interactions, in that interannual variation in production was proportionally much smaller than that expected on the basis of winter NO₃. In a very different regime, McClain et al. (1996) found no decadal trends in primary or secondary production calculated from a one-dimensional biological-physical model, forced with meteorological and oceanographic variables observed at Ocean Weather Station P from 1951 to 1980. Since this period includes the 1976 North Pacific regime shift, which has been correlated with substantial modification of productivity at all levels of the northeast Pacific oceanic ecosystem (Beamish, 1995), the result suggests that either the significant biological changes are not strongly associated with change in the deep-sea environment (but perhaps, rather, the coastal fringes; Gargett, 1997b), and/or that some connection between physical processes and biological production is missing from the model as formulated. Probable locations of missing links were suggested by further results of Steele and Henderson (1993), who demonstrated that very large differences in overall production and in its partitioning between new and recycled nutrient use could result from reasonable changes in poorly known parameters describing the zooplankton community modeled. These results are not artifacts of the simplicity of a one-dimensional physical model, as similar results have recently emerged from a two-dimensional model of an estuarine ecosystem (Li et al., 2000). Thus, Gargett et al. (2001) suggest that change in physical environment may produce the largest ecosystem effects in an indirect manner, by modifying crucial biological rate functions, in particular those associated with zooplankton. It will clearly be some time before the question posed by Steele and Henderson is answered.

6.4. Concluding Remarks

A strong focus of this review has been the extent to which progress in understanding both physical and biogeochemical processes in the ocean has been associated with progress in observational tools. Over the last decade, the march of technology has moved marine biology toward marine biochemistry, with major advances in understanding the chemical foundation for primary production. Over the same period, physical oceanographers have been forging new tools for measuring turbulent transports of key chemical species. The direction of both developments suggests that in the future it may be possible to make the connections between physics and individualbased phytoplankton biology at the most fundamental level, through the transport and uptake of a common "currency," that of chemical species. The remaining (and even larger!) challenge will be to scale up such results to the population and community levels. At all of these levels, we believe that future progress in elucidating the controls exerted by physical processes on primary production will continue to come, as it has in the past, through advances in measurement techniques.

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