Chapter 1. INTRODUCTION—BIOLOGICAL–PHYSICAL INTERACTIONS IN THE SEA: EMERGENT FINDINGS AND NEW DIRECTIONS

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1. Status and Progress in the Study of Interactive Dynamics

The stage is now set for dramatic progress toward a more complete understanding of the interactive dynamics among the physical processes that influence biogeochemical cycles and population dynamics and the attendant feedbacks in these systems. The 1990s were a period of significant progress toward these goals. Substantial research accomplishments helped to reveal causes of variabilities in the abundances of organisms and their rates of production. Questions rooted primarily in the biological and physical aspects of these interactions were refined, and new observing capabilities employing instrumentation, moorings, and satellite sensing systems were implemented.

In the context of climate and global change, some research foci of the past decade were designed to better quantify baseline conditions, as in the case of the carbon cycle. Some intensive field campaigns were sited in regions for which time scales of biological processes from seasonal to multiannual are clearly influenced by physical processes. Some of these campaigns were directed toward regions of the ocean where neither light nor major nutrients seem to limit production, such as the equatorial

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Pacific and the Ross Sea in summer. Still others focused on food web configurations and how physical processes influence these, especially at higher trophic levels.

Satellite and in situ sensors became routine in this era, and they now provide essential temporal continuity and synopticity in key data sets. Renewed interest in sustaining observations at time-series stations have been similarly justified. Moreover, a new generation of models has been developed that can now exploit the wealth of these new data and generate new data requirements and experimental directions. The intellectual underpinning of many linkages among processes and domains has matured. These include marine population dynamics and biogeochemical cycles, the coastal and open ocean, climate and ocean biology, the near surface and deep ocean, and natural and anthropogenic change in properties and processes. Studies in these areas are producing surprises in virtually every domain in which investigations are being focused, surprises in the sense that extant theory would neither have forecasted nor indeed have encompassed observed conditions and relationships. All in all, these endeavors now engage a broad spectrum of ocean scientists in a remarkable era of emergent new understanding of fundamental processes in the sea, especially their variabilities across broad temporal and spatial ranges.

Many examples of such fundamental advances are described in the chapters that follow. We now know much more about physical processes across a wide range of length scales (e.g., small-scale turbulence, submesoscale and mesoscale processes) and time scales (e.g., El Niño–Southern Oscillation, North Atlantic Oscillation, Pacific Decadal Oscillation). In addition, recent findings relating to internal waves and near-surface physical processes help to understand the environment of the mixed layer. Major advances in data processing and computing capabilities can now accommodate sophisticated and complex linkages among ocean theory, data, and models. Moreover, enormous progress has been made in physical aspects of ocean dynamics by engaging the methods of data assimilation. This is timely, since it is now widely accepted that the resource requirements for obtaining accurate regional-scale three- and four-dimensional maps and time series of fields with mesoscale resolution via direct sampling are prohibitive. By melding observations with dynamics, data assimilation provides a feasible basis for obtaining accurate synoptic mesoscale realizations over the space–time scales and domains of interest. These techniques are widely used in meteorology and are increasingly common in studies of physical oceanographic processes. The next step is to apply them broadly to biological state variables. Capabilities such as these offer great promise for improved understanding of biological–physical interactions in the sea.

Future progress requires that new emphasis be placed on interactive processes both within and between the physical and biological domains, at multiple temporal and spatial scales. Because of inherent scale mismatches among different processes, attention must be given to sampling schemes that are specifically designed to obtain compatible data sets.

Most assessments of biological–physical interactions in the sea assume smooth dynamics, whereas the natural world is characterized by episodic event dynamics. This effect can be manifested in the internal dynamics of either the physics or the biology in the form of thresholds and responses that are unstable and give rise to dramatic changes in the state of the system. Moreover, matching, mismatching, and/or competing scales among physical and biological processes will determine the sensitivity of a particular response to the rate of a forcing process. For example, physical processes on an hourly time scale will affect primarily the physiology of plankton. At diurnal scales the effect will be on growth rate. At longer scales it will be on population and community dynamics. Thus, the rate of emergence of a particular physical event as well as its duration can strongly influence the biomass and size distribution of organisms and their community's new and export production.

An illustrative example is provided by oceanic iron enrichment. How would the biological responses differ between a pulsed and a more even rate of delivery? Moreover, the physics that would be associated with a natural delivery of iron, such as upwelling, diffusive flux, or aeolian transport, will also affect biological processes within an oceanic plankton community both directly and indirectly. In addition, in one region the upwelling velocity required to supply a certain level of iron could be multiples of that required in another area. Furthermore, the upper ocean mixing conditions associated with a vigorous upwelling delivery of iron versus aeolian delivery to the surface of a quiescent mixed layer have very different implications for photic zone plankton response to ambient light. Clearly, a planktonic food web response to a natural delivery of iron must be considered as a response to both nutrient enrichment and the physical processes of delivery.

Multiscale interactions can provide important feedbacks up and down the spectrum. Direct, large-scale interactions, such as changes in the global wind field, can influence small-scale interactions, such as among predator and prey species, and can thus affect the species composition and age structure of a food web. Figure 1.1 shows schematically three developmental stages of increasing size with respective predator and prey. The Kolmogorov scale is the size of the smallest turbulent eddy. The Batchelor scale is the smallest scale fluctuation of an advected and diffused property. The critical process here is the encounter rate, which differs depending on whether organisms are small enough to be in a laminar environment or large enough to be in a turbulent environment. Notice that when wind changes, the diagonal that separates the laminar and turbulent interaction shifts. A change in wind field affects not only encounter rates but also entrainment of nutrient-rich water in the euphotic zone. This example shows how different processes on different scales are interrelated: for example, slow formation of entrainment and fast encounter rate.

Next consider an example of how smaller-scale processes can provide dominant influences upon larger scale processes. Figure 1.2 demonstrates how large-scale time-averaged new production is mediated by meso- and submesoscale injections of nutrients into the euphotic zone. Nutrients are injected directly by the lifting of isoclines of constant nutrient as mesoscale eddies form and propagate. An equally or possibly more important mechanism is that of the submesoscale event that occurs when two or more mesoscale eddies interact. These intermittent, albeit infrequent events have been shown to have basin-scale implications for primary production in the North Atlantic.

Dynamic processes, whether physical, biogeochemical, or ecological, occur on multiple interactive scales, many of which are bidirectional with powerful feedbacks. These processes occur as a response to both direct forcing and internal dynamics. In the last decade ocean scientists have identified and dynamically described some important and fundamental ocean interactions. However, we do not yet know which are the dominant processes and which are the scales of interaction that give rise to any particular configuration of a marine ecosystem and its environment. This stands as one of the central problems of contemporary interdisciplinary ocean science. Future

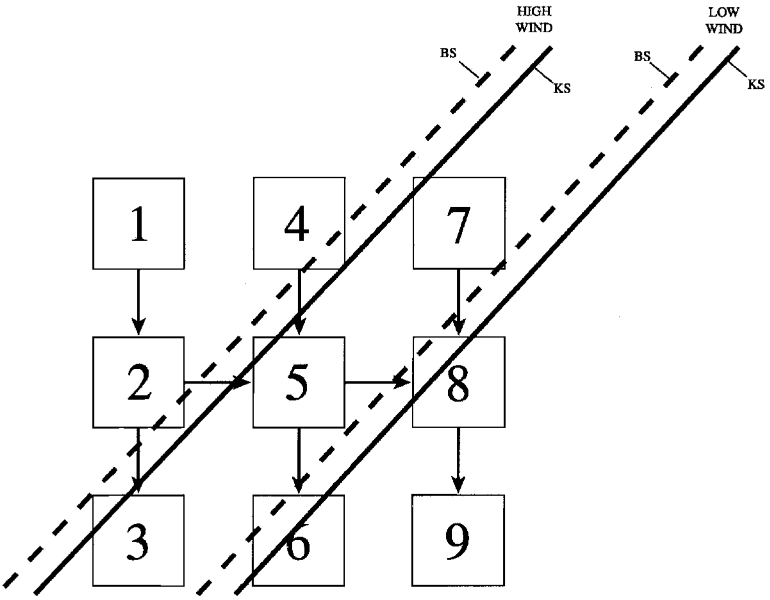

Fig. 1.1. Interaction of hypothetical food chain with high-wind and low-wind scale range. Scale increases both downwards and to the right. Dashed lines indicate the Batchelor Scale (BS), while solid lines indicate the Kolmogorov Scale (KS). There are nine size classes of organisms, and arrows represent schematized pathways of ingestion. The numbers refer to the size of the organism, where 1 denotes the smallest organism and 9 denotes the largest organism. The numbers refer as well to the interparticle distance, where 1 relates to the smallest interparticle distance and 9 to the largest. It can be seen that in the high-wind scenario, the Kolmogorov and Batchelor scales affect smaller organisms more than under the low-wind scenario.

advances will require guidance from ocean observations and experiments along with concomitant theoretical and numerical modeling and data assimilation. We believe that the attainment of better understanding of the subtleties of interactive processes across multiple scales will lead to genuine progress in this problem area.

2. Overview of the Book

Although it is clear that physical factors that vary on scales ranging from small-scale turbulence to basin-scale circulation and from daily cycles of incoming solar irradiation to multiyear climate phenomena have a bearing on the overall topic of this volume, it is not possible in an effort such as this to treat thoroughly either all scales of importance or even most of their interactions. Moreover, since emphasis was placed on areas for which there has been significant progress during the last decade, these chapters obviously cannot reflect full knowledge of the broad topics they encompass.

The problem of understanding the linkages among physical processes and primary production and the transfer of this organic matter through the marine food web involves several kinds of interactions, such as those associated with exposure of phytoplankton cells to nutrients remineralized in the deep sea, those related to the exposure of phytoplankton cells to nutrients regenerated via heterotrophs in near-surface

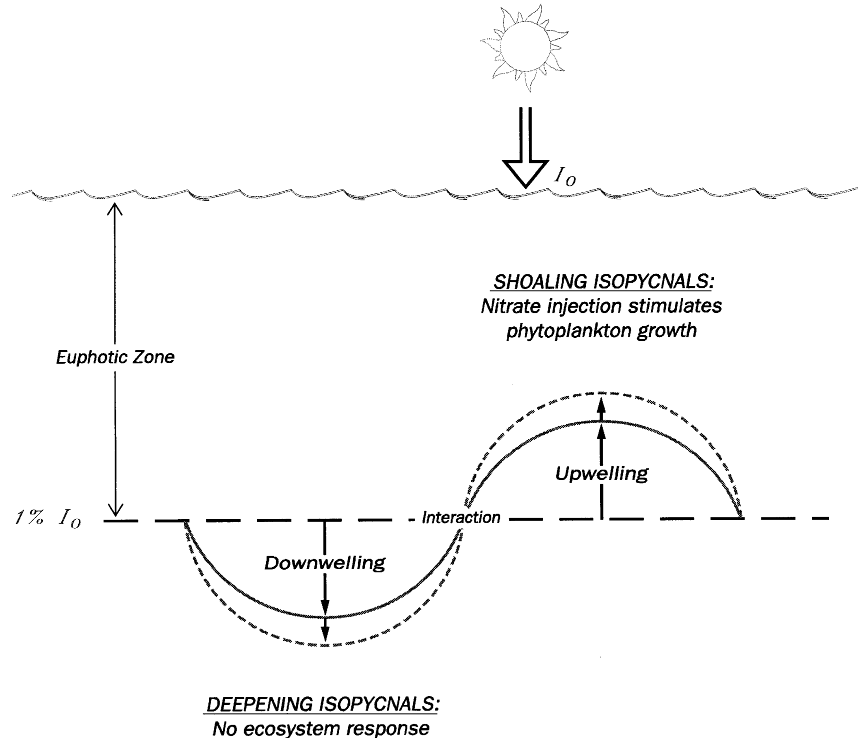

Fig. 1.2. Schematic representation of the eddy upwelling mechanism. The solid line depicts the vertical deflection of an individual isopycnal caused by the presence of two adjacent eddies of opposite sign. The dashed line indicates how the isopycnal might be subsequently perturbed by the interaction of the two eddies. (Reprinted with permission from McGillicuddy et al., 1998, *Nature*, **394,** 263–265, www.nature.com, copyright 1998, Macmillan Magazines Ltd.)

waters, those associated with predator–prey dynamics, and those associated with the exposure of phytoplankton cells to light. All of these processes are subject to temporal and spatial scale considerations that transcend the ranges mentioned above. Moreover, additional complexity is added with the realization that the heterotrophic processes alluded to, for organisms ranging from bacteria to large carnivores, are also under the influence of physical factors.

In Chapter 2, Gargett and Marra concentrate on how physical forcing affects the delivery of nutrients remineralized in the deep sea. Wind forcing plays an important role in affecting the basin-scale horizontal and vertical density structure, which affects the juxtaposition of a phytoplankton cell to nutrient concentrations, light, and temperature. Because minor nutrients are generated by several sources, their delivery to phytoplankton cells is more complicated. Physical processes and their influence on primary production are classified by length and time scales. The authors also consider the effects of upper ocean physical processes—turbulence, advection, and air–sea interaction—on oceanic primary production. They choose particular scale windows to classify the processes: a window related to the mean biogeography, and a window related to variance driven by the interaction between physical variability and physiological rate processes of individual plankters.

From a large-scale point of view, the primary production setting involves atmospheric forcing:

1. The mean wind field sets up the large-scale topography of nutriclines and drives the turbulence, which accompanies the flux of nutrients to the surface layers.
2. Upper ocean stability (stratification), a result of the integration of solar radiation and atmospheric delivery of heat and fresh water to the ocean surface, strongly affects upper ocean fields of nutrients 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.

These structuring factors affect communities in terms of nutrients and light environments, influence growth rates via temperature variability, and help to shape the micronutrient environment.

The issues of physical forcing and organism–organism interaction are encapsulated by Yamazaki, Mackas, and Denman in Chapter 3. They review the physical processes associated with the upper ocean and focus on the seminal discovery of the importance of small-scale turbulent flow on the population dynamics of the plankton. Although the idea of the impact of small-scale turbulent flow began with its influence on the trophic transactions among organisms, Yamazaki et al. discuss influences on other important aspects of population dynamics, such as mating and feeding. The chapter concludes with a discussion of modeling futures, the main point of which involves the evolution of ecological continuum models to Lagrangian models.

To obtain a complete picture of primary production, it is necessary to understand the physics associated with regenerated production, the major component of primary production in the ocean. The authors discuss the physical setting for many aspects of regenerated production, focusing on the smallest scales, which is a relatively new feature of oceanographic research. This is important, because on the smallest scales organism–organism interactions contribute to the population dynamic and ecological variabilities and perturbations, which in turn drive and are affected by events in the meso and basin scales. This chapter is an interesting contrast with Chapter 2 in the sense that it focuses on the relatively new understanding of what might be called small-scale physical processes.

The physical processes of the mixed layer are summarized in the context of bulk models, turbulent closure or K-theory models, and hybrid models. However, these models are generally not implemented on very small scales. To lead into very small scales, the subject of small-scale turbulent flow and the Kolmogorov, Taylor, and Ozmidov scales (defined in this chapter) become important.

A significant point is that turbulence is often conceptualized as if it were a simple diffusion process. This generally provides insights for interpretation of spatially or temporally averaged effects. The implied smoothing of structure with a simple diffusion interpretation may have important effects. Yamazaki et al. postulate that vortex tube structures may play a role in reproductive behavior and predator–prey interactions. Patchiness is discussed in the context of the graininess of the environment. Particularly important aspects are the velocity, temperature, and salinity gradient spectra, as these couple with the generalized mortality rates discussed in Chapter 7.

There are many aspects of the relation between small-scale physics and specific biological issues. These include selective pressures, feeding, predator avoidance, aggregation, and reproductive interaction. Many of these issues are involved in population dynamic equations. Those that relate to environmental grain and patchiness in the context of feeding are particularly relevant. The chapter concludes with a discussion of modeling, focusing especially on the relation between the Lagrangian approach and a conventional continuum approach. The Lagrangian approach seems to be almost a necessity at small scales, particularly if there is an interest in the probability distributions of organism behavior.

In Chapter 4, Flierl and McGillicuddy discuss physical processes occurring at physical scales intermediate to the more familiar small and large scales. Mesoscale and submesoscale motions (eddies) range over space scales from tens to hundreds of kilometers and time scales from days to years and are generally ubiquitous and energetically dominant. Mesoscale structures evolve on longer, slower scales with intermittent, strong synoptical–dynamical events occurring interactively on faster, smaller submesoscales. Phenomena include planetary waves, jets, eddies, coherent vortices, and stratified, nearly geostrophic turbulence, which interact with each other, with topography, and with the coupled ocean–atmosphere planetary boundary layer system. Biological dynamics, embedded in this physical environment, represents a complex food web involving interactions among many populations of age- and stage-structures species, which in the absence of physical interactions, can exhibit multiple stable and unstable equilibria, temporal and spatial variabilities, and chaotic behavior.

Eddies transport plankton and nutrients both horizontally and vertically, and the resultant space–time variabilities of the environment stimulate and suppress biological processes and modulate biological rates. In addition to local effects, mesoscale biophysical interactions can mediate between small- and large-scale biological processes that statistically can have important global influences, as exemplified by the discussion of new production in the North Atlantic presented above. A useful and illuminating series of idealized biogeophysical fluid dynamical examples are presented for basic wave instability, coherent isolated vortex, and eddy-interaction processes. The interactions among basic processes and with boundaries require vigorous biogeophysical fluid dynamical research. Additionally, the authors argue the importance of numerical models for testing hypotheses concerning complex real ocean interactive phenomena. They stress the importance of investigating sensitivities to both model formulations and parameters in order to establish robustness of results since small changes in the biological models can significantly modify the response induced by eddy motions. This type of research is essential and promising but challenging and only in its infancy.

In Chapter 5, Olson focuses on fronts, the physical demarcations that constitute boundaries between different water masses. Although the existence of oceanic fronts has been known for centuries and fronts have been both exploited empirically for fisheries and studied extensively, a most fundamental scientific question remains to be answered. Do fronts provide the major focus of life in the sea, or are they merely regions of intense aggregation of biomass over all trophic levels, which thereby attract scientific attention? Many types of fronts occur throughout the deep and coastal seas, and frontal biophysical interactions are diverse and considered to be the most complicated that occur in the ocean. Physical processes of frontogenesis include horizontal advections that increase concentration gradients associated with shearing flows and convergence; wind-driven and topographic upwellings; and diabatic mixing (e.g., tidal), which eliminates stratification on one side of a front. Along the frontal length, scales range from 10^2 to 10^3 km, meander wavelengths range from 1 to 10^2 km, and passively advected material can remain in the fronts from days to months.

Although biological processes involved in frontal dynamics vary by location and trophic level, a unifying principle is the extreme sensitivity of the ocean ecosystem to vertical motion at all trophic levels. Altered light and nutrient levels affect productivity and reproduction, and aggregations and flow induce taxis and kinesis. Biological scales and rates associated with these processes vary by orders of magnitude from the lowest to the highest trophic levels. Detailed process discussions are presented for phytoplankton, zooplankton, and nekton. As noted above, relative time scales can dramatically control responses, and here the ratios of concentration rate, given by the horizontal velocity gradients of the shears or convergence, to population growth rates can be crucial. Specific research issues are discussed which can help address the major questions of the role of fronts in the overall productivity of the oceans and in the population dynamics of organisms trapped and stressed in fronts or exploiting fronts for foraging, migration, and reproduction. Present measurements of rates, biomass, and turbulence are representative rather than definitive. Compatible, coordinated physical and biological measurements and synoptic time series are necessary, which as discussed above, are now feasible.

The biological production cycle in the sea begins for the most part with primary production: the photosynthetic, chlorophyll-mediated autotrophic production of carbohydrates, lipids, and protein within phytoplankton cells via the photosynthetic process. Heterotrophic producers consume the biomass elaborated via primary production, mostly via the direct grazing of phytoplankton cells or uptake of exuded or degraded organic material. The pace of the photosynthetic process depends on many factors: especially light, nutrients, and ambient temperature. There are three types of nutrients that are important: major nutrients remineralized in the deep sea and transported or captured in the photic zone, minor nutrients either associated with the major nutrients or delivered to the surface of the ocean by aeolian activity, and nutrients that are largely regenerated via excretion by heterotrophs. Even though the primary production process is often initiated by an injection of the major nutrients [except in high-nutrient, low-chlorophyll (HNLC) regions], phytoplankton depend to a large degree on the availability of regenerated nutrients.

Physical processes in the upper ocean that influence biological processes and ultimately determine distributions of biological properties have broad temporal and spatial ranges. These span a continuum from turbulent processes to seasonal and interannual cycles in atmosphere–ocean dynamics. Moreover, many of these processes are amplified and perhaps are most critically manifested as events. The rate of progression of a physical process will determine how this process affects the physiological rates, growth rates, and population dynamics of marine organisms.

In Chapter 6, McCarthy calls attention to the role of transient physical processes that give rise to such events as strong wind mixing, upwelling, and internal waves and discusses how they are responsible for adjustments in chemical and biological properties and processes. Historically, biological responses to changes in nutrient milieu were studied by isolating a single factor, the addition of a specific nutrient, for example, without considering as well the concomitant response to an altered physical condition, such as in turbulence.

Application of new analytical approaches during the last two decades resulted in the discovery of an entirely new group of phytoplankton, the *Prochlorococcus*, which is now considered to be the most abundant genus of marine phytoplankton. The ubiquitous presence of this miniscule phytoplankter in tropical and subtropical waters, and the possibility that its abundance had in earlier times been mistaken for that of heterotrophic bacteria, causes us to rethink seriously the organization of marine food webs and the regulation of both primary production and biomass levels in the sea. The additional possibility that *Prochlorococcus* has unusual capabilities with respect to nitrogenous nutrition raises a host of profound questions regarding both the forces that drive primary production in the sea and the fate of this production.

Quantification of the abundances of phytoplankton with high precision and repeat sample frequencies now allows entirely new interpretations of biological responses on event scales, the role of diatoms in new production, the interactive roles of nitrate and iron, and the physical processes that deliver these nutrients to the photic zone. Further application and refinement of these approaches is certain to lead to improved understanding of the partitioning of biological production among new and regenerated components, and ultimately to regulation of the biological pump. Especially relevant are interactions among the temporal and spatial scales of processes responsible for the delivery of nitrogen and iron to, and their recycling within, the photic zone.

In Chapter 7, Rothschild discusses the population-dynamic tools that might be applied to understanding how individual populations of phytoplankton and heterotrophs interact with an ecosystem. Attempting to explain many examples of ecosystem variability requires a focus on the complexities of the way that multiscale physical processes affect the dynamics of the populations that comprise the ecosystem. The basic idea is that to understand population-dynamic variability, it is necessary to understand ecosystem variability. However, to understand ecosystem variability, it is necessary to understand the diversity, scope, and multiscale nature of physical variability. This requires the development of a taxonomy of models that is space-scale specific with regard to both scale windows and the interactions among scale windows. To understand the dynamics of populations and ecosystems involves a need to shift from population and ecosystem kinematics to population and ecosystem dynamics, a shift that can only be achieved via a thermodynamic or at least a thermodynamiclike approach.

In framing the population-dynamic approach, it is important to consider the age structure of the population. This can be as true for bacteria and phytoplankton as it is for zooplankton. The classic analysis of age structure proceeds from the life table that generally treats age, stage, or size as a discrete property. Other models are introduced that treat age as continuous. All of these models are amenable to studying the probable effects of physical forcing via perturbation of the parameters. For example, a small change in temperature might speed up or slow down mortality. The subtle issue related to these perturbations is that space can usually be partitioned according to the dynamic behavior of the system. Therefore, it is relatively easy to explore how a perturbation affects the dynamic behavior of a population and its sensitivity to being either stable or unstable, or smooth or oscillatory, in its approach to a characteristic steady state. Through the theory of population dynamics as developed in the field of fisheries, it is possible to integrate in a single model the effects of the physical environment on both growth and mortality so that the effects of these changes in population equilibrium standing stock can be analyzed. Although most models involve parameters that represent growth, mortality, and reproduction, the theory for estimating these parameters from observations is not well developed in the plankton literature. Methodologies are reported for parameter estimation as well as population simulation.

In Chapter 8, Cullen, Franks, Karl, and Longhurst discuss physical influences on marine ecosystem dynamics, focusing primarily on the phenomenology of new production, setting aside issues of regenerated production and secondary production. As a point of departure, they consider Margelef's idea that the ecosystem could be classified in terms of the ambient level of turbulence and nutrient supply and proceed to a classification according to regimes of turbulence and nutrients: low turbulence and low nutrients, high-nutrient and low-chlorophyll waters, high turbulence and low nutrients, low turbulence and high nutrients, and high turbulence and high nutrients. Upwelling blooms—entrainment blooms and detrainment blooms—could further characterize these regimes.

The classification described above led to four hypotheses:

1. In well-lighted surface layers, small microbes outcompete larger phytoplankton for limiting nutrients.
2. Microbial grazers respond rapidly (both in grazing rate and growth) 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.
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 acceleration of phytoplankton that can attain high rates of cell division and are not immediately susceptible to grazers.
4. Under sustained nutrient enrichment, selection is for phytoplankton that can escape losses to grazing, viral lysis, and sinking. The physical forcing that might be associated with testing these hypotheses varies among the various biomes of the ocean: the pelagic, polar, westerly, trades, and coastal biomes.

In considering the various hypotheses and biomes, it is necessary to take into account what might be called the special-case behavior of biotic response, such as event-scale eddies that induce ephemeral blooms, which, in turn, induce swarms of zooplankton. A body of observations of events is building, which raises the interesting question as to whether these events are signals or noise. This question is addressed in the context of multiscale windows in scale space.

The aggregate effect of the small- and intermediate-scale biological and physical processes in concert with large-scale ocean circulation processes gives rise to vertical and horizontal gradients in the distribution of chemical and biological properties in the sea. In Chapter 9, Gruber and Sarmiento discuss how comparative analyses of distributions of various constituents reveal subtleties in the manner in which biogeochemical processes sequester and release specific elements. Some of these patterns are explained by the differential roles of different combined forms of the same element, such as particulate dissolved, organic versus inorganic, or different oxidation states. Some forms are the substrates and others the products of biological processes in the near-surface ocean, although the opposite reactions may dominate in the deep ocean. Moreover, the relative time constants for biogeochemical processes and those for physical processes that redistribute vertically and horizontally the biogeochemical constituents (diffusion, advection, thermohaline and wind-driven processes, and gravitational settling) interact to yield varied temporal and spatial patterns in these biogeochemical constituents.

The benefits of approaches such as these derive from the relative constancy of elemental ratios of phytoplankton (the Redfield ratio). Phytoplankton with significant mineral components (e.g., calcite plates that cover coccolithophorids or siliceous frustules that encase diatoms) provide discernible links between large-scale global patterns of distribution for carbon and silicon and the smallest-scale physical and biological processes that allow organisms in these two groups to flourish at specific times in specific places.

With assumptions regarding limited variability in the so-called soft-tissue component of phytoplankton and the redistribution of these materials, Gruber and Sarmiento discuss the usefulness of quasiconservative tracers, which are unaffected by the production and remineralization of biological materials. This approach has power in that compared with true conservative tracers, resulting inconsistencies can reveal details in circulation. Moreover, they can signal prominent exchanges across boundaries that may otherwise be difficult to detect by direct means. An especially significant example of this relates to inconsistencies in the distribution of nitrogen that can best be explained by largely unmeasured rates of nitrogen fixation and denitrification.

Substantial progress in modeling large-scale physical and biogeochemical processes has improved understanding of how basic processes such as the exchange of carbon dioxide between the surface ocean and the atmosphere is now regulated. This knowledge can be tested against the record of past changes and, most significantly, can be used to refine understanding as to how altered climate in the future will affect, and in turn, be affected by, the workings of the marine carbon cycle.

Although the basic phenomena by which absorption of solar radiation by land surfaces and the sea propel the circulation of the atmosphere and the ocean and energize photosynthetic processes are well known, details of interaction among these processes are responsible for temporal and spatial variability in ocean circulation and biological production. In Chapter 10, Dickey and Falkowski review how new generations of sampling systems—moored, underway with ships, and remotely sensed from space—together with models, have revealed scales of interaction among these physical and biological processes that were previously underappreciated. Improved analyses now also allow for assessment of the phytoplankton species assemblage and its physiological state.

Prior-generation shipboard samplings of regions characterized by seasonal blooms or strong interannual cycles, such as ENSO, gave very incomplete pictures of the progression of restratification and destratification processes. The former, in particular, may be far more uneven than is often assumed, and hence, small precursors of major bloom events have been missed. Similarly, the effects of physical processes that shoal or depress isopycnal surfaces in the photic zone have begun to be observed adequately only in some regions of the sea.

The authors call attention to a new emphasis on the biological feedback to light absorption in the sea via modification of inherent optical properties. The vertical pattern in absorption of solar radiation—the penetrative component of solar radiation—can be strongly influenced by both the vertical distribution of plankton and the dominant species present. This feedback, on mixing layer stratification, for example, has been underestimated in upper ocean energy budgets. A particularly interesting example of the role of species groups is evident in the case of coccolithophorids. The very strong scattering that is caused by the calcite coccoliths results in significant warming within the domain of a coccolithophorid bloom. Many aspects of these problems are amenable to approach via studies that optimize the complementarity of multiple sampling approaches that capture local, and perhaps transient, detail and modeling efforts that can link these events to a greater understanding of the solar irradiance component of climate forcing.

In Chapter 11, Griffiths, Fielding, and Roe discuss biological–physical–acoustical interactions, especially the use of active sonar to observe physical–biological interactions remotely via interpretation of the acoustic backscatter from individual animals and groups of animals. The focus is on zooplankton. Although for the biological oceanographer acoustics is now an essential tool capable of providing an important range of data beyond the capability of conventional net systems, much further research and development are needed to realize fully the potential of this powerful approach. Both acoustic backscatter theory and acoustic instrumentation and system developments are involved. The greatest promise lies in the use of multifrequency systems in conjunction with concurrent environmental sensors. Animals of interest may be fluidlike, may have hard elastic shells, or may have gas inclusions, and the animals' orientations and behaviors are important. Sonic processes involve interactions of sound in the water, within the shells, and inside the animals. Two major problem areas are the forward problem (i.e., the prediction of acoustic backscatter levels based on knowledge of the animal populations) and the inverse problem (i.e., the identification of animal classes present and their abundance from knowledge of the acoustic backscatter at several frequencies). Scientific applications are illustrated from experiments in the Gulf of Oman, the Almería–Oran front in the Alboran Sea, and an internal bore in the Strait of Gibraltar which involves the problem of discrimination of the backscattering from turbulence and animals. A practical problem that must be solved before this technique can be widely utilized relates to the development and manufacture of a reliable, efficient, relatively small, simple, inexpensive system.

In Chapter 12, Robinson and Lermusiaux discuss the process of data assimilation whereby the general dynamics of a model are combined or melded with a set of observations. All dynamical models are to some extent approximate, and all data sets are finite and to some extent limited by error bounds. The purpose of data assimilation is to provide estimates of nature, which are better estimates than can be obtained by using only the observational data or the dynamical model. There are a number of specific approaches to data assimilation, which are suitable for the estimation of the state of nature, including natural parameters, and also for the evaluation of the dynamical approximations.

Data assimilation has recently entered oceanography and is just now beginning to be applied to interactive biological–physical processes of the sea. There is a considerable potential for data assimilation to contribute to further understanding, modeling, and predicting of such processes. Already by the immediate application of existing approaches, state and parameters can be estimated, processes can be inferred, dynamical hypothesis tested, and fundamental oceanographic biochemical models developed and validated.

However, the complexity and scope of the interdisciplinary problem requires substantial computational resources and adequate data sets and will probably necessitate dedicated assimilation algorithms and new model developments. Care must be exercised in estimating and controlling errors, in choosing and optimizing the assimilation criterion or cost function, in performing sensitivity analyses, and in ensuring the compatibility of data and dynamics. Such research is essential for the development and operation of interdisciplinary observing and prediction systems, including, importantly, the control of loss of predictability associated with the highly nonlinear biophysical dynamics. Robinson and Lermusiaux present a broad range of biophysical phenomena and scales for which data assimilation is useful and discuss important research issues associated with the current state of models, data sets, assimilation methodologies, error characterizations, and the evaluation of observing and prediction systems.

A series of case studies and a comprehensive overview of progress and results to date illustrate these general research ideas and issues. The case studies provide examples of interdisciplinary data assimilation research and are reviewed in detail. Topics include models and data compatibility, issues involving the consistencies of model structure and complexity with available data, the control of biophysical assimilation shocks, the inference of realistic biophysical dynamical processes, and real-time biophysical forecasting. The authors provide a comprehensive summary of results to date and discuss the prospectus for future progress in parameter estimation, field estimation, model identification and improvement, data acquisition and utilization, and error estimation and system evaluation. Data assimilation is a challenging modern scientific methodology for the objective and quantitative fusion of data and dynamics. In modeling and predicting interdisciplinary interactions in the sea, the possibilities for discoveries and formulation of scientific concepts and theories abound over a rich spectrum of needs.

The prediction of marine ecosystem structures and functions depends on a thorough understanding of the physical and biological processes governing the abundance, distribution, and productivity of the organisms on a wide range of time and space scales. In Chapter 13, Hofmann and Friedrichs define predictive models as being models that are forced with observations to produce simulated distributions that are then compared with observations from a specific time and location. An assessment of the predictive capability of some existing marine ecosystem models is provided and several issues and directions for the development of predictive ecosystem models are discussed. The authors do not try to be exhaustive but rather to illustrate some modeling approaches that have been used for coupled ecosystem—circulation predictions as defined. The adequacy of predictions from a particular model is assessed in terms of the ability of the simulated distributions to reproduce the patterns and variances found in the observations.

Five examples are chosen to illustrate the predictive capabilities of coupled ecosystem–circulation models over a range of complexities: a spring bloom, a study of plankton response to climate variations, a simulation of the seasonal cycle in phytoplankton, carbon cycling in the Sargasso sea, and the dynamics of larval fish. The authors summarize the current status; discuss issues related to data, circulation models, ecosystem models and data assimilation; and provide several research directions for the future development of predictive models. In particular, the coupled models reviewed did not adequately represent event-scale processes and also did not use time-and space-invariant conversion coefficients. Important suggested improvements are the inclusion of food quality, micronutrients, and irradiance measurements directly, and a stronger basis in ecology and physiology. Future research on interdisciplinary multiscale observational networks, neural network modeling, and top predator modeling is recommended.

In the last few decades, knowledge of interactions among physical and biological processes in the deep sea has also grown dramatically. In Chapter 14, Vinogradov and Vinogradov describe how deep-ocean observations, especially visual and video records obtained by means of manned and robotic submersibles, have profoundly influenced perspectives on the relationships between distributions of organisms and gradients in physical and chemical properties. In addition, it is now possible to assess how communications among predators and prey and the regulation of reproductive and colonization processes have been tuned evolutionarily to scales of the physical processes of dispersion and advection.

The authors discuss how deep benthic community composition and structure can be strongly influenced by physical processes in the boundary layer, especially the resuspension of fine sediments that are the nutritional substrate of many species of benthic organisms. A particularly dramatic example of physical and biological interactions in the deep sea is the formation and maintenance of communities that thrive in association with deep-sea hydrothermal vents. Detailed sampling has allowed estimation of the effects of the vent communities and dispersion processes on the surrounding benthic ecosystem and the degree to which this is influenced by the species that dominate different vent communities.

In Chapter 15, Schrag and McCarthy end the book by raising questions regarding the effects of projected climate change on biological–physical interactions in the sea over the next several decades. The record of the past helps to put these changes in perspective. Based on proxy data for the northern hemisphere, the rate of warming during the twentieth century is now thought to be the largest of any century in the last 1000 years. Even more telling are the projected rates of warming for the twenty-first century, which are now estimated to be 2 to 10 times the rate of the twentieth century.

Some ocean regions will be affected more dramatically than others. Extrapolations of the last few decades of observations of arctic sea ice areal extent and thickness project a significantly altered habitat for arctic marine ecosystems only a few decades into the future. The arctic region was probably last completely ice free 40 to 50 million years ago, during the Eocene epoch, when atmospheric CO_2 concentrations were 4 to 10 times today's levels. It is known from the Vostok antarctic ice cores that CO_2 concentrations as high as current levels are unprecedented in the past 420,000 years. Moreover, it is likely that the equivalent of today's values have not occurred since the Eocene.

Certain key features in the configuration of continents during the Eocene could have contributed to the very different organization of Earth's climate during that period. A better understanding of feedbacks, especially positive feedbacks, that could have contributed to the reduced meridional temperature gradient in the Eocene would help in refining projections for future climate.

Most extant macroorganisms living poleward of the subtropics evolved with an innate capacity to expand and contract their ranges of distribution in response to the 100,000-year glacial periodicity of the Pleistocene. For many of these species the climate that is now unfolding represents uncharted territory. Widespread extinctions of particular groups of organisms, such as occurred with the deep benthic foraminifera during the Eocene, may be unavoidable in the future. Among shallow-water marine organisms, the coral and their associated communities may be most vulnerable to climate change in the near future. Many of these species now thrive in environments that are very close to their upper thermal limits.

In the 1990s there emerged considerable new knowledge of past climate conditions and understanding of the factors that contributed to such climate change. It is suggested that eras of past climate can serve as useful analogs for future climate, especially in anticipating the impact of distributions and abundances of organisms and feedbacks via biogeochemical cycles.

3. Concluding Remarks

Research directions in ocean science have always had a strong interdisciplinary character; the writings of K. Brandt, H. B. Bigelow, and H. W. Harvey early in the twentieth century are a good reminder of this. However, until the last few decades, most major advances in understanding ocean processes largely reflected more traditional disciplinary perspectives. This book calls attention to emerging areas of new understanding in biological–physical interactions that illustrate the power of a convergence of the approaches of these two disciplines.

A long-standing goal in ocean science is to understand the major sources of variability in biological production and its fate, and to account for how production has changed in the past and how it is likely to change in the future. In addition to being fundamentally interesting, this research has profound implications for important societal questions relating to the management of living marine resources and global climate change. Many examples of new understanding relating to this broad research agenda are discussed in this book. However, successful pursuit of this science clearly requires a new level of sophisticated understanding of the manner by which biological processes are influenced by physical processes ranging across scales from those of the immediate and instantaneous environment of the individual organism to those of geostrophic and multidecadal proportions and beyond. In addition, time-averaged changes for some processes miss important or obscure event-scale linkages of physical and biological processes. The frequency and duration of periodic nutrient injections to the photic zone, for example, can yield markedly different responses in planktonic food webs with significantly different implications for rates of new and export production.

An increasing awareness and understanding of the multiscale characterization of physical, biological, and interactive processes is evident throughout much of the research discussed in this book. Crucial research is being carried out over extended scale ranges, new scale windows, and multiscale interactions. This will involve advanced concepts, and some insights may be afforded from complex system science. Historically, oceanographers naturally began researching most readily accessible scales in the context of a global ocean and its seasonal variability. Very small space-scale processes have been important in the evolutionary history of living marine organisms and now require additional research emphasis, particularly because of the recent discovery of an entirely new group of very small phytoplankton (*Prochlorococcus*), which is now considered to be the most abundant phytoplankton. Moreover, the multiscale interactions of small-scale processes (e.g., Fig. 1.1) amplify the importance of such research. Research on the energetic mesoscale interactive processes is in its infancy and portends significant large-scale implications. When taking a research question to larger length and time scales, interactive aspects of the problem are likely to be apparent and unavoidable. Event-scale considerations also bring clearly into focus multiple interactions that might otherwise be avoided when using time-averaged properties and processes on any spatial scale. Long time series of past climate data are a promising potential source of information on biological–physical interactions over a range of oceanic conditions.

Although many methodological advances in the last decade have allowed for more accurate and convenient detection of specific properties and measurement of specific processes, others have specifically facilitated investigation of interactive processes. Satellite and moored instruments and the combination of these plus complementary intensive shipboard investigations have demonstrated the power of multiscale and multiplatform sensing systems in ocean research. Furthermore, dynamical models have evolved to a point where they can now effectively incorporate near-real-time data from these sensing systems. During the past decade the melding of dynamics and observations via data assimilation techniques has emerged as a powerful new approach to the problems that are the focus of this volume of *The Sea*.

We (Robinson et al., 1999) have suggested a systems approach as an efficient and cost-effective strategy for addressing problems such as these. It will require the nurturing of effective application of understanding and new sensing capabilities in a context that embraces a hierarchy of complex coupled physical–biogeochemical–ecosystem dynamical processes spanning relevant length and time scales. Moreover, models will be required that can assimilate nested scales of compatible biological and physical data sets, and include quantitative sampling theoretic methods embedded within observational system simulation experiments. The inclusion of event dynamics in these models will require new theoretical constructs to describe length and time scales of these interactions. This approach could yield a quantum leap in our understanding of biological–physical interactions in the sea.

The success we believe likely to unfold with new efforts at the interface of biology and physics has to some degree been foreshadowed by the successes of chemists and biologists who nurtured the convergence of certain research foci during the last decade. It had become clear that some processes long thought to be explained adequately on the basis of inanimate chemical reactions could not truly be understood without consideration of key biological processes. Similarly, the relevation of detail in the chemical diversity of key nutrients, especially trace elements, and their interactions with other elements and organic compounds provided entire new vistas of understanding into the regulation of biological production in the sea. Importantly, the success of this new research focus on biogeochemical cycles was built in part on new and novel linkages among and across length and time scales of chemical and biological interactions.

Our hope is that a future edition of a book such as this will describe how comprehension of multiscale biological–physical–chemical interdisciplinary linkages has become commonplace in addressing research questions, many of them of long-standing importance, in ocean science. Moreover, as novel understanding is gained on these research questions, a new generation of realistic and feasible research directions must inevitably arise to challenge and stimulate oceanographers.

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