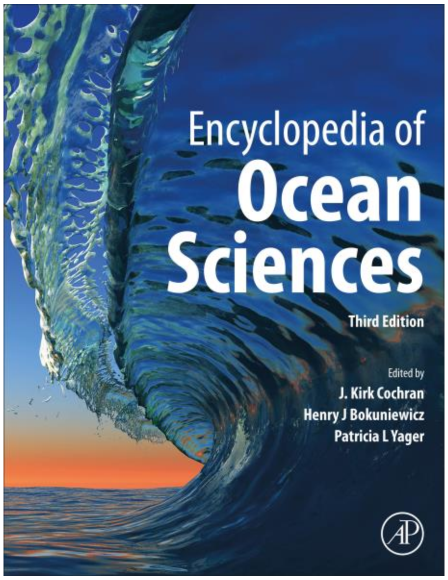

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Models of Plankton Patchiness[☆]

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Introduction

Patchiness is perhaps the most salient characteristic of plankton populations in the ocean. The scale of this heterogeneity spans many orders of magnitude in its spatial extent, ranging from planetary down to microscale (Fig. 1). It has been argued that patchiness plays a fundamental role in the functioning of marine ecosystems, insofar as the mean conditions may not reflect the environment to which organisms are adapted. For example, the fact that some abundant predators cannot thrive on the mean concentration of their prey in the ocean implies that they are somehow capable of exploiting small-scale patches of prey whose concentrations are much larger than the mean. Understanding the nature of this patchiness is thus one of the major challenges of oceanographic ecology.

The patchiness problem is fundamentally one of physical–biological–chemical interactions. This interconnection arises from three basic sources: (1) ocean currents continually redistribute dissolved and suspended constituents by advection; (2) space–time fluctuations in the flows themselves impact biological and chemical processes; and (3) organisms are capable of directed motion through the water. This tripartite linkage poses a difficult challenge to understanding oceanic ecosystems: differentiation between the three sources of variability requires accurate assessment of property distributions in space and time, in addition to detailed knowledge of organismal repertoires and the processes by which ambient conditions control the rates of biological and chemical reactions.

Various methods of observing the ocean tend to lie parallel to the axes of the space/time domain in which these physical–biological–chemical interactions take place (Fig. 2). Given that a purely observational approach to the patchiness problem is not tractable with finite resources, the coupling of models with observations offers an alternative which provides a context for synthesis of sparse data with articulations of fundamental principles assumed to govern functionality of the system. In a sense, models can be used to fill the gaps in the space/time domain shown in Fig. 2, yielding a framework for exploring the controls on spatially and temporally intermittent processes.

The following discussion highlights only a few of the multitude of models which have yielded insight into the dynamics of plankton patchiness. Examples have been chosen to provide a sampling of scales, smaller than the planetary scale shown in Fig. 1A. In addition, this particular collection of examples is intended to furnish some exposure to the diversity of modeling approaches which can be brought to bear on the problem. These approaches range from abstract theoretical models intended to elucidate specific processes, to complex numerical formulations which can be used to actually simulate observed distributions in detail.

Formulation of the Coupled Problem

A general form of the coupled problem can be written as a three-dimensional advection-diffusion-reaction equation for the concentration C_i of any particular organism of interest:

$$\underbrace{\frac{\partial C_i}{\partial t}}_{\text{local rate of change}} + \underbrace{\nabla\cdot(\mathrm{v}C_i)}_{\text{advection}} - \underbrace{\nabla\cdot(K\nabla C_i)}_{\text{diffusion}} = \underbrace{R_i}_{\text{biological sources/sinks}} \tag{1}$$

[☆] *Change History*: September 2018. Author P.J.S. Franks added, title changed to "Models of Plankton Patchiness." DJ McGillicuddy and PJS Franks updated sections, figures, references and throughout the text.

This is an update of D.J. McGillicuddy, Small-Scale Patchiness, Models of, *Encyclopedia of Ocean Sciences* (2nd Edn), edited by John H. Steele, Academic Press, 2001, pp. 474–487.

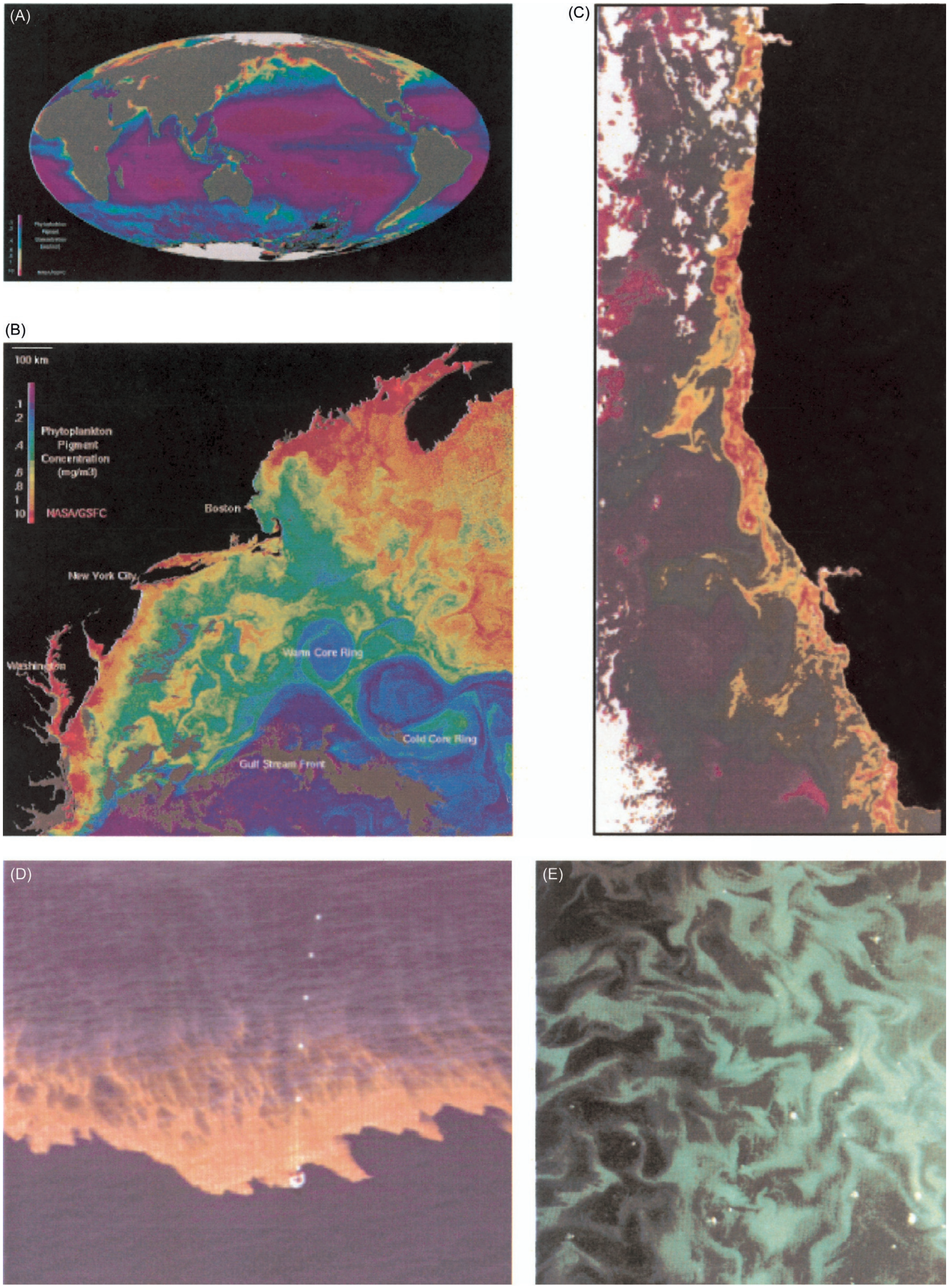

Fig. 1 Scales of plankton patchiness, ranging from global down to 1 cm. (A–C) Satellite-based estimates of surface-layer chlorophyll computed from ocean color measurements. (D) A dense stripe of *Noctiluca scintillans*, 3 km off the coast of La Jolla, California. The boat in the photograph is trailing a line with floats spaced every 20 m. The stripe stretched for at least 20 km parallel to the shore. (E) Surface view of a bloom of *Anabaena flos-aquae* in Malham Tarn, England. The area shown is approximately 1 m^2. (A–C) Images courtesy of the Seawifs Project and Distributed Active Archive Center at the Goddard Space Flight Center, sponsored by NASA. (D) Photograph courtesy of P.J.S Franks. (E) Photograph courtesy of G.E. Fogg.

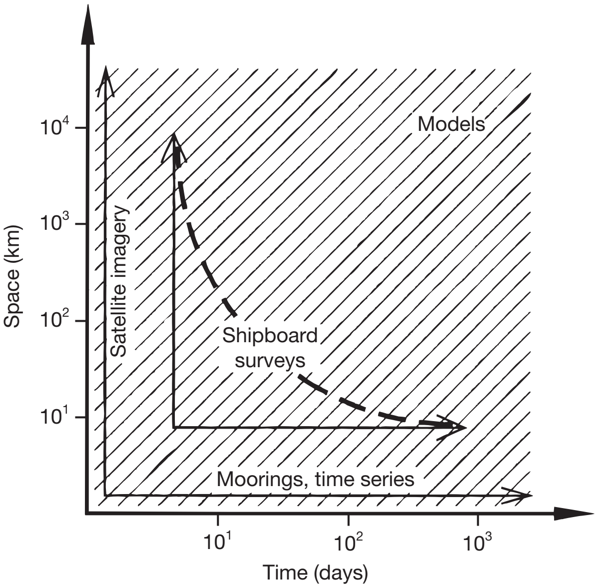

Fig. 2 Space–time diagram of the scales resolvable with current observational capabilities. Measurements tend to fall along the axes; the *dashed line* running between the "shipboard survey" axes reflects the trade-off between spatial coverage and temporal resolution inherent in seagoing operations of that type. Models can be used to examine portions of the space–time continuum (*shaded area*).

where the *v*ector v is the fluid velocity, v_c represents any biologically-induced transport through the water (e.g., sinking, swimming), and K the turbulent diffusivity. In cases where there C is a passive tracer ($v_c = 0$) the advection term is often written simply as $\mathrm{v}\cdot\nabla \mathrm{C_i}$ because the ocean is an essentially incompressible fluid (i.e., $\nabla\cdot v = 0$). The "reaction term" R_i on the right-hand side represents the sources and sinks due to biological activity.

In essence, this model is a quantitative statement of the conservation of mass for a scalar variable in a fluid medium. The advective and diffusive terms simply represent the redistribution of material caused by motion. In the absence of any motion, Eq. (1) reduces to an ordinary differential equation describing the biological and/or chemical dynamics. The reader is referred to the review by Donaghay and Osborn for a detailed derivation of the advection-diffusion-reaction equation, including explicit treatment of the Reynolds decomposition for biological and chemical scalars (see Further Reading).

Any number of advection–diffusion–reaction equations can be posed simultaneously to represent a set of interacting state variables C_i in a coupled model. For example, an ecosystem model including nutrients, phytoplankton, and zooplankton (an "NPZ" model) could be formulated with $C_1 = \mathrm{N}$, $C_2 = \mathrm{P}$ and $C_3 = \mathrm{Z}$. The biological dynamics linking these three together could include nutrient uptake, primary production, grazing, and remineralization. R_i would then represent not only growth and mortality, but also terms which depend on interactions between the several model components.

Growth and Diffusion—The "KISS" Model

Some of the earliest models used to investigate plankton patchiness dealt with the competing effects of growth and diffusion. In the early 1950s, models developed independently by Kierstead (KI) and Slobodkin (S) and Skellam (S)—the so-called "KISS" model—were formulated as a one-dimensional diffusion equation with exponential population growth and constant diffusivity:

$$\frac{\partial C}{\partial t} - K\frac{\partial^2 \mathrm{C}}{\partial x^2} = \alpha \mathrm{C} \tag{2}$$

Note that this model is a reduced form of Eq. (1). It is a mathematical statement that the tendency for organisms to accumulate through reproduction is counterbalanced by the tendency of the environment to disperse them through turbulent diffusion. Seeking solutions which vanish at $x = 0$ and $x = \mathrm{L}$ (thereby defining a characteristic patch size of dimension L), with initial concentration $C(x,0) = f(x)$, one can solve for a critical patch size in which growth and dispersal are in perfect balance. For a specified growth rate α and diffusivity K, patches smaller than L will be eliminated by diffusion, while those that are larger will result in blooms. Although highly idealized in its treatment of both physical transport and biological dynamics, this model illuminates a very important aspect of the role of diffusion in plankton patchiness. In addition, it led to a very specific theoretical prediction of the initial conditions required to start a plankton bloom, which Slobodkin subsequently applied to the problem of harmful algal blooms on the west Florida shelf.

Homogeneous Isotropic Turbulence

The physical regime to which the preceding model best applies is one in which the statistics of the turbulence responsible for diffusive transport is spatially uniform (homogeneous) and has no preferred direction (isotropic). Turbulence of this type may occur locally in parts of the ocean in circumstances where active mixing is taking place, such as in a wind-driven surface mixing layer. Such motions might produce plankton distributions such as those shown in Fig. 1E.

The nature of homogeneous isotropic turbulence was characterized by Kolmogoroff in the early 1940s. He suggested that the scale of the largest eddies in the flow was set by the nature of the external forcing. These large eddies transfer energy to smaller eddies down through the inertial subrange in what is known as the turbulent cascade. This cascade continues to the Kolmogoroff microscale, at which viscous forces dissipate the energy into heat. This elegant physical model inspired the following poem attributed to L. F. Richardson:

> Big whorls make little whorls which feed on their velocity;
> little whorls make smaller whorls, and so on to viscosity. . .

Based on dimensional considerations, Kolmogoroff proposed an energy spectrum E of the form

$$E(k) = A\varepsilon^{\frac{2}{3}}k^{-\frac{5}{3}}$$

where k is the wavenumber, ε is the dissipation rate of turbulent kinetic energy, and A is a dimensionless constant. This theoretical prediction was later borne out by measurements, which confirmed the "minus five-thirds" dependence of energy content on wavenumber.

In the early 1970s, Platt published a startling set of measurements which suggested that for scales between 10 and 10^3 m the variance spectrum of chlorophyll in the Gulf of St Lawrence showed the same $-5/3$ slope. On the basis of this similarity to the Kolmogoroff spectrum, he argued that on these scales, phytoplankton were simply passive tracers of the turbulent motions. These findings led to a burgeoning field of spectral modeling and analysis of plankton patchiness. Studies by Denman, Powell, Fasham, and others sought to formulate more unified theories of physical–biological interactions using this general approach. For example, Denman and Platt extended a model for the scalar variance spectrum to include a uniform growth rate. Their theoretical analysis suggested a breakpoint in the spectrum at a critical wavenumber k_c (Fig. 3), which they estimated to be in the order of 1 km^{-1} in the upper ocean. For wavenumbers lower than k_c, phytoplankton growth tends to dominate the effects of turbulent diffusion, resulting in k^{-1} dependence. In the higher wavenumber region, turbulent motions overcome biological effects, leading to spectral slopes of -2 to -3. Efforts to include more biological realism in theories of this type have continued to produce interesting results, although Powell and others have cautioned that spectral characteristics may not be sufficient in and of themselves to resolve the underlying physical–biological interactions controlling plankton patchiness in the ocean.

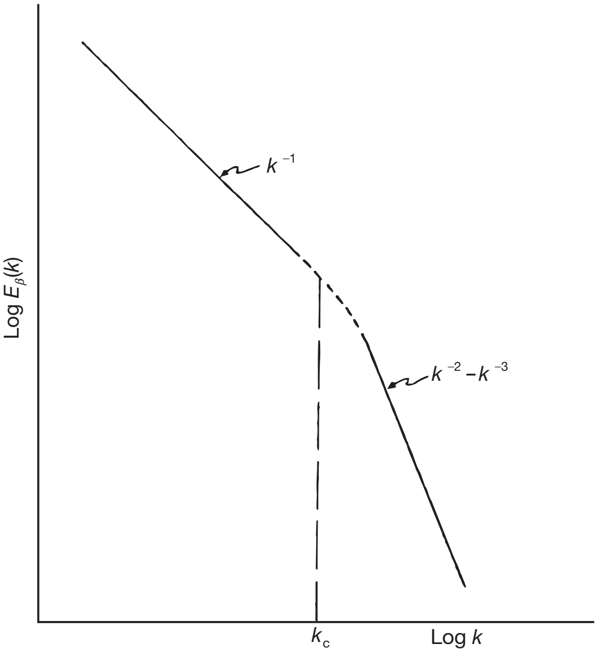

Fig. 3 A theoretical spectrum for the spatial variability of phytoplankton, $E_\beta(k)$, as a function of wavenumber, k, displayed on a log–log plot. To the left of the critical wavenumber k_c, biological processes dominate, resulting in k^{-1} dependence. The high wavenumber region to the right of kc where turbulent motions dominate, has a dependence between k^{-2} and k^{-3}. Reproduced with permission from Denman, K. L. and Platt, T. (1976). The variance spectrum of phytoplankton in a turbulent ocean. *Journal of Marine Research* **34**, 593–601.

Vertical Structure

Perhaps the most ubiquitous aspect of plankton distributions which makes them anisotropic is their vertical structure. Organisms stratify themselves in a multitude of ways, for any number of different purposes (e.g., to exploit a limiting resource, to avoid predation, to facilitate reproduction). For example, consider the subsurface maximum which is characteristic of the chlorophyll distribution in many parts of the world ocean (Fig. 4; see review by Cullen in Further Reading). The deep chlorophyll maximum (DCM) is typically situated below the nutrient-depleted surface layer, where nutrient concentrations begin to increase with depth. Generally this is interpreted to be the result of joint resource limitation: the DCM resides where nutrients are abundant and there is sufficient light for photosynthesis. However, this maximum in chlorophyll does not necessarily imply a maximum in phytoplankton biomass. For example, in the nutrient-impoverished surface waters of the open ocean, much of the phytoplankton standing stock is sustained by nutrients which are rapidly recycled; thus relatively high biomass is maintained by low ambient nutrient concentrations. In such situations, the DCM often turns out to be a pigment maximum, but not a biomass maximum. The mechanism responsible for the DCM in this case is photoadaptation, the process by which phytoplankton alter their pigment content according to the ambient light environment. By manufacturing more chlorophyll per cell, phytoplankton populations in this type of DCM are able to capture photons more effectively in a low-light environment.

Models have been developed that can produce both aspects of the DCM. For example, consider the nutrient, phytoplankton, zooplankton, detritus (NPZD) type of model (Fig. 5) which simulates the flows of nitrogen in a planktonic ecosystem. The various biological transformations (such as nutrient uptake, primary production, grazing, excretion, etc.) are represented mathematically by functional relationships which depend on the model state variables and parameters which must be determined empirically. Doney et al. coupled such a system to a one-dimensional physical model of the upper ocean (Fig. 6). Essentially, the vertical velocity (*w*) and diffusivity fields from the physical model are used to drive a set of four coupled advection-diffusion-reaction equations (one for each ecosystem state variable) which represent a subset of the full three-dimensional Eq. (1):

$$\frac{\partial C_i}{\partial t} + w\frac{\partial C_i}{\partial z} - \frac{\partial}{\partial z}\left(K\frac{\partial C_i}{\partial z}\right) = R_i \tag{3}$$

The R_i terms represent the ecosystem interaction terms schematized in Fig. 5. Using a diagnostic photoadaptive relationship to predict chlorophyll from phytoplankton nitrogen and the ambient light and nutrient fields, such a model captures the overall character of the DCM observed at the Bermuda Atlantic Time-series Study (BATS) site (Fig. 6).

Broad-scale vertical patchiness (on the scale of the seasonal thermocline) such as the DCM is accompanied by much finer structure. The special volume of *Oceanography* on "Thin layers" provides an excellent overview of this subject, documenting small-scale vertical structure in planktonic populations of many different types. One particularly striking example comes from high-resolution fluorescence measurements (Fig. 7A). Such profiles often show strong peaks in very narrow depth intervals, which presumably result from thin layers of phytoplankton.

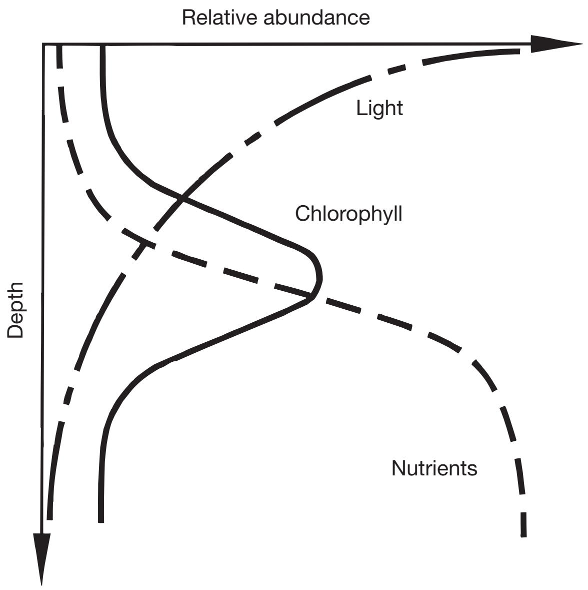

Fig. 4 Schematic representation of the deep chlorophyll maximum in relation to ambient light and nutrient profiles in the euphotic zone (typically 10s–100s of meters in vertical extent).

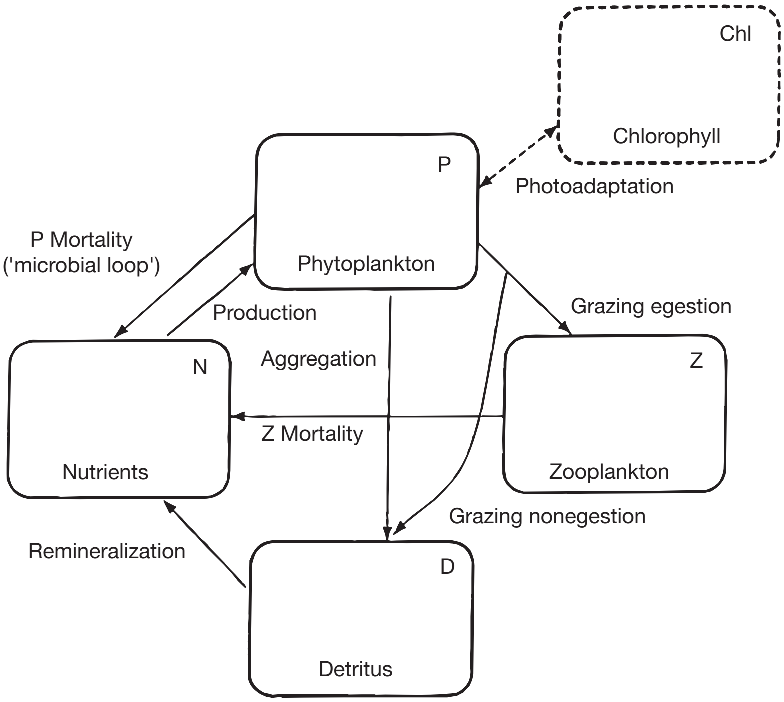

Fig. 5 A four-compartment planktonic ecosystem model showing the pathways for nitrogen flow. Reproduced with permission from Doney, S. C., Glover, D. M., and Najjar, R. G. (1996). A new coupled, one-dimensional biological–physical model for the upper ocean: Applications to the JGOFS Bermuda Atlantic Time-series Study (BATS) site. *Deep-Sea Research II* **43**, 591–624.

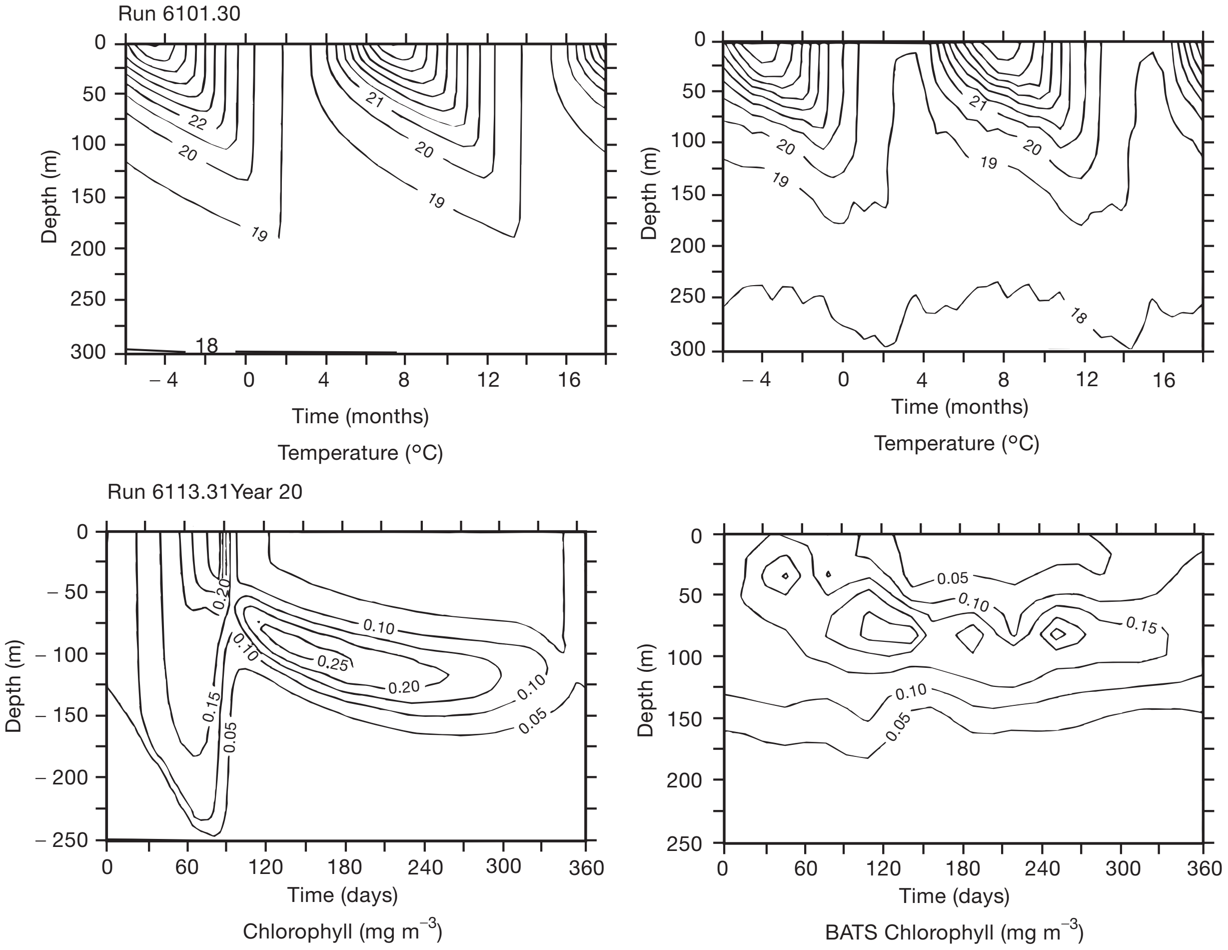

Fig. 6 Simulated (left) and observed (right) seasonal cycles of temperature and chlorophyll at the BATS site. Reproduced with permission from Doney, S. C., Glover, D. M., and Najjar, R. G. (1996). A new coupled, one-dimensional biological–physical model for the upper ocean: Applications to the JGOFS Bermuda Atlantic Time-series Study (BATS) site. *Deep-Sea Research II* **43**, 591–624.

The earliest model of such thin layers was supplied by J.B. Derenbach and his colleagues, in which they showed that such layers could form by phytoplankton sinking and slowing down at micro-pycnoclines. From Eq. (1), assuming steady state, no horizontal gradients, no diffusion, and no reaction terms, we can integrate vertically to show

$$C(z) = \frac{constant}{w_s(z)} \tag{4}$$

where $w_s(z)$ is the sinking speed as a function of depth. Eq. (4) shows that the local concentration will increase where the sinking speed decreases, giving the potential to form a thin layer at a small density gradient as the sinking particles decelerate and subsequently accelerate.

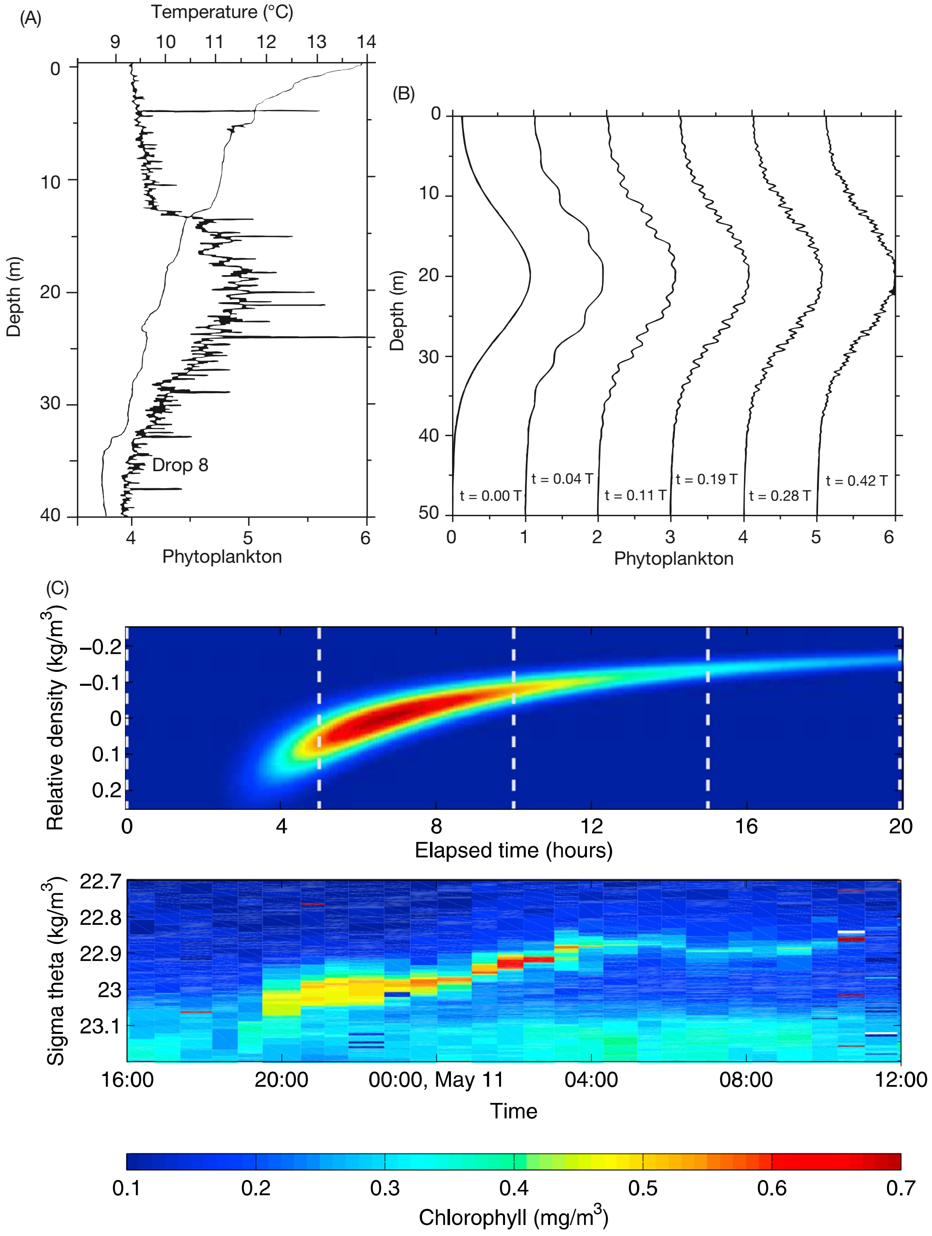

Fig. 7 (A) Observations of thin layer structure in a high-resolution profile of fluorescence (*thick line*, arbitrary units). The thin line shows the corresponding temperature structure. (B) Simulated vertical profiles of phytoplankton concentration (arbitrary units) at six sequential times. Each profile is offset from the previous by 1 phytoplankton unit. The times are given as fractions of the period of the near-inertial wave used to drive the model. (C) An example of a thin layer of phytoplankton (lower panel) observed in the Philippine Sea, and an application of a shear model to explain the patch structure (top panel). (A) Data courtesy of Dr. T. Cowles. (B) Reproduced with permission from Franks, P. J. S. (1995). Thin layers of phytoplankton: A model of formation by near-inertial wave shear. *Deep-Sea Research I* **42**, 75–91. (C) Reproduced with permission from Hodges, B.A. and Fratantoni, D. M. (2009) A thin layer of phytoplankton observed in the Philippine Sea with a synthetic moored array of autonomous gliders. *Journal of Geophysical Research* **114**, C10020, doi: https://doi.org/10.1029/2009JC005317.

Another mechanism for thin layer formation was identified by P.J.S. Franks, in which he used a model to show that vertical shear can tilt existing *horizontal* gradients of phytoplankton to create ever-thinning *vertical* layers (Fig. 7B). The shear could be supplied by near-inertial internal waves, or other flows that are common and energetic in the ocean. These shears slide the top and bottom of a horizontal patch relative to one another, thereby forming a vertical layer that thins as it continues to be sheared. This theory was developed further by D.A. Birch and his collaborators, and was used to explain the formation of a thin layer observed using undersea gliders in the Philippine Sea by B.A. Hodges and D.M. Fratantoni (Fig. 7C).

Mesoscale and Submesoscale Processes

Just as the atmosphere has weather patterns that profoundly affect the plants and animals that live on the surface of the earth, the ocean also has its own set of environmental fluctuations which exert fundamental control over the organisms living within it. The currents, fronts, and eddies that comprise the oceanic mesoscale, sometimes referred to as the "internal weather of the sea," are highly energetic features of ocean circulation. Driven both directly and indirectly by wind and buoyancy forcing, their characteristic scales range from tens to hundreds of kilometers with durations of weeks to months. Their space scales are thus smaller and timescales longer than their counterparts in atmospheric weather, but the dynamics of the two systems are in many ways analogous. Impacts of these motions on surface ocean chlorophyll distributions are clearly visible in satellite imagery (Fig. 1B).

Mesoscale and submesoscale phenomenologies accommodate a diverse set of physical–biological interactions which influence the distribution and variability of plankton populations in the sea. These complex yet highly organized flows continually deform and rearrange the hydrographic structure of the near-surface region in which plankton reside. In the most general terms, the impact of these motions on the biota is twofold: not only do they stir organism distributions, they can also modulate the rates of biological processes. Common manifestations of the latter are associated with vertical transports which can affect the availability of both nutrients and light to phytoplankton, and thereby the rate of primary production. The dynamics of mesoscale and submesoscale flows are replete with mechanisms that can produce vertical motions.

Some of the first investigations of these effects focused on mesoscale jets. Their internal mechanics are such that changes in curvature give rise to horizontal divergences which lead to very intense vertical velocities along the flanks of the meander systems. J. D. Woods was one of the first to suggest that these submesoscale upwellings and downwellings would have a strong impact on upper ocean plankton distributions (see his article contained in the volume edited by Rothschild; see Further Reading). Subsequent modeling studies have investigated these effects by incorporating planktonic ecosystems of the type shown in Fig. 5 into three-dimensional dynamical models of meandering jets (Fig. 8). The models show strong correlations between vertical velocities that drive nutrient fluxes into the euphotic zone, and enhanced phytoplankton (chlorophyll) concentrations. These vertical velocities are driven by both mesoscale meanders that penetrate hundreds of meters below the surface (large red-blue features in the bottom panel of the box in Fig. 8), and submesoscale meanders that only penetrate to the depth of the surface mixed layer (narrow red-blue tendrils in the top panel of the box in Fig. 8). The predominantly mesoscale variability of the phytoplankton suggests that the mesoscale motions are the dominant nutrient-flux and horizontal-stirring mechanisms in this model.

What are the implications of mesoscale and submesoscale patchiness? Do these fluctuations average out to zero, or are they important in determining the mean characteristics of the system? How do they affect plankton diversity and higher trophic levels including top predators? These questions are examined in reviews by Lévy et al. and McGillicuddy (see Further Reading).

Behavior

The mechanisms for generating plankton patchiness described thus far consist of some combination of fluid transport and physiological response to the physical, biological, and chemical environment. The fact that many planktonic organisms have behavior (interpreted narrowly here as the capability for directed motion through the water) facilitates a diverse array of processes for creating heterogeneity in their distributions. Such processes pose particularly difficult challenges for modeling, in that their effects are most observable at the level of the population, whereas their dynamics are governed by interactions which occur amongst individuals. The latter aspect makes modeling patchiness of this type particularly amenable to individual-based models, in contrast to the concentration-based model described by Eq. (1). For example, many species of marine plankton are known to form dense aggregations, sometimes referred to as swarms. Okubo suggested an individual-based model for the maintenance of a swarm of the form:

$$\frac{d^2x}{dt^2} = -k\frac{dx}{dt} - \omega^2 x - \phi(x) + A(t) \tag{5}$$

where x represents the position of an individual. This model assumes a frictional force on the organism which is proportional to its velocity (with frictional coefficient k), a random force $A(t)$ which is white noise of zero mean and variance B, and attractive forces. Acceleration resulting from the attractive forces is split between periodic (frequency ω) and static ($\phi(x)$) components. The key aspect of the attractive forces is that they depend on the distance from the center of the patch. A Fokker-Planck equation can be used to derive a probability density function:

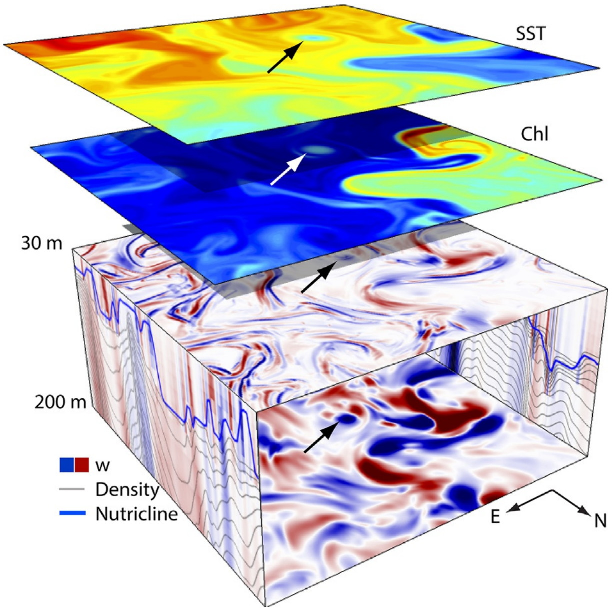

Fig. 8 Results from a submesoscale-resolving physical-biological model. The top surface is sea-surface temperature (SST), showing a meandering mesoscale front, and a cyclonic eddy (*arrow*). The next panel down is the modeled surface chlorophyll (Chl, phytoplankton) concentration. The chlorophyll concentrations trace the meandering front, and there is a slight enhancement in the mesoscale eddy (*arrow*). In the box at the bottom, the *red-blue* colors show downward-upward vertical velocities, respectively, on surfaces at 30 m and 200 m depth. The sides of the box show the vertical structure of the vertical velocities (*red-blue* color), some isopycnals (*gray lines*), and the nutricline (*solid blue line*). Deformations of the nutricline are mostly driven by the mesoscale vertical velocities, rather than the smaller-scale submesoscale velocities. The biological variability is more strongly tied to the mesoscale physical forcings than the submesoscale forcings, due to the deeper penetration of mesoscale vertical velocities into the deep nutrient pool. Model output courtesy of M. Lévy.

$$p(x) = p_0 \exp\left(-\frac{\omega^2}{2B}x^2 - \int \frac{\phi(x)}{b}dx\right) \tag{6}$$

where p_0 is the density at the center of the swarm. Thus, the macroscopic properties of the system can be related to the specific set of rules governing individual behavior. Okubo has shown that observed characteristics of insect swarms compare well with theoretical predictions from this model, both in terms of the organism velocity autocorrelation and the frequency distribution of their speeds. Analogous comparisons with plankton have proven elusive owing to the extreme difficulty in making such measurements in marine systems.

The foregoing example illustrates how swarms can arise out of purely behavioral motion. Yet another class of patchiness stems from the joint effects of behavior and fluid transport. The paper by Flierl et al. is an excellent reference on this general topic (see Further Reading). One of the simplest examples of this kind of process arises in a population which is capable of maintaining its depth (either through swimming or buoyancy effects) in the presence of convergent flow. With no biological sources or sinks, Eq. (1) becomes:

$$\frac{\partial C}{\partial t} + v \cdot \nabla_H C + C \nabla_H \cdot v - \nabla \cdot (K \nabla C_i) = 0 \tag{7}$$

where ∇_H is the vector derivative in the horizontal direction only. Because vertical fluid motion is exactly compensated by organism behavior (recall that the vector v represents the sum of physical and biological velocities), two advective contributions arise from the term $\nabla \cdot (vC)$ in Eq. (1): the common form with the horizontal velocity operating on spatial gradients in concentration, plus a source/sink term created by the divergence in total velocity (fluid + organism). The latter term provides a mechanism for accumulation of depth-keeping organisms in areas of fluid convergence. It has been suggested that this process is important in a variety of different oceanic contexts. In the mid-1980s, Olson and Backus argued it could result in a 100-fold increase in the local abundance of a mesopelagic fish *Benthosema glaciale* in a warm core ring. Franks and his then-student C.E. Lennert-Cody modeled a conceptually similar process, using a version of Eq. (7) to show that depth-keeping organisms would accumulate over the troughs of internal waves as they propagated horizontally, forming bands (e.g., Fig. 1D). Almost 15 years later this hypothesis was finally tested by J.S. Jaffe and colleagues by deploying a swarm of robotic, depth-keeping plankton mimics in an internal wave field. As predicted, the swarm became more concentrated over the internal wave troughs, and dispersed over the wave crests (Fig. 9). This predictable patch formation mechanism may be important for the organisms in encountering mates, or reducing predation risk.

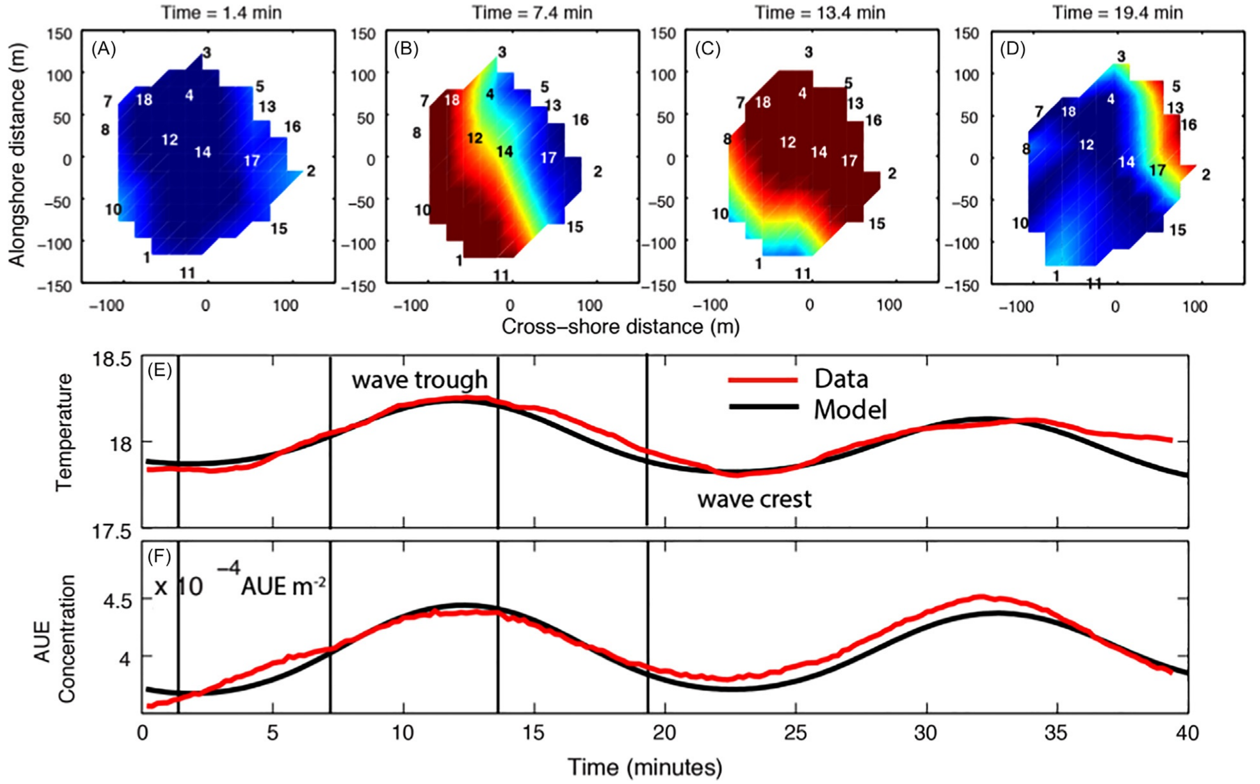

Fig. 9 Accumulation of depth-keeping plankton mimics in the troughs of an internal wave. (A–D) the cross-shore/alongshore locations of 16 mini Autonomous Underwater Explorers (m-AUEs) depth-keeping at 10 m (each number is a different m-AUE), and temperature anomaly recorded by the m-AUEs (color). Warm temperatures (*red* colors) indicate a wave trough, cold temperatures (*blue* colors) indicate a wave crest. Each panel indicates a different time and phase of the wave. A wave trough is propagating from the lower left to the upper right. (E–F) The average temperature anomaly in the m-AUE swarm (*red line* in E) and the concentration of m-AUEs (*red line* in F) given by the data. The *black lines* are model predictions based on equations of depth-keeping organisms in linear internal waves; the internal wave was parameterized using data from the field experiment. The data confirm the model, showing that depth-keeping organisms accumulate over the troughs of internal waves due to the convergences created by the wave currents. Data replotted from Jaffe, J.S., Franks, P.J.S. et al. (2017). A swarm of autonomous miniature underwater robot drifters for exploring submesoscale ocean dynamics. *Nature Communications*. **8**, 14189 doi: https://doi.org/10.1038/ncomms14189.

Conclusions

The interaction of planktonic population dynamics with oceanic circulation can create tremendously complex patterns in the distribution of organisms. Even an ocean at rest could accommodate significant inhomogeneity through geographic variations in environmental variables, time-dependent forcing, and organism behavior. Fluid motions tend to amalgamate all of these effects in addition to introducing yet another source of variability: space–time fluctuations in the flows themselves which impact biological processes. Understanding the mechanisms responsible for observed variations in plankton distributions is thus an extremely difficult task.

Coupled physical–biological models offer a framework for dissection of these manifold contributions to structure in planktonic populations. Such models take many forms in the variety of approaches which have been used to study plankton patchiness. In theoretical investigations, the basic dynamics of idealized systems are worked out using techniques from applied mathematics and mathematical physics. Process-oriented numerical models offer a conceptually similar way to study systems that are too complex to be solved analytically. Simulation-oriented models are aimed at reconstructing particular data sets using realistic hydrodynamic forcing pertaining to the space/time domain of interest. Generally speaking, such models tend to be quite complex because of the multitude of processes which must be included to simulate observations made in the natural environment. Of course, this complexity makes diagnosis of the coupled system more challenging. Nevertheless, the combination of models and observations provides a unique context for the synthesis of necessarily sparse data: space–time continuous representations of the real ocean which can be diagnosed term-by-term to reveal the underlying processes. Formal union between models and observations is beginning to occur through the emergence of inverse methods and data assimilation in the field of biological oceanography.

Although the field is more than a half-century old, modeling of plankton patchiness is still in its infancy. The oceanic environment is replete with phenomena of this type which are not yet understood. Fortunately, the field is perhaps better poised than ever to address such problems. Recent advances in measurement technologies (e.g., high-resolution acoustical and optical methods, miniaturized biological and chemical sensors, and genomic approaches) are beginning to provide direct observations of plankton on the scales at which the coupled processes operate. Linkage of such measurements with models is likely to yield important new insights into the mechanisms controlling plankton patchiness in the ocean.

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