REVIEW ARTICLE

Biophysical interactions in the plankton: A cross-scale review

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Abstract

In plankton ecology, biological and physical dynamics are coupled, structuring how plankton interact with their environment and other organisms. This interdisciplinary field has progressed considerably over the recent past, due in large part to advances in technology that have improved our ability to observe plankton and their fluid environment simultaneously across multiple scales. Recent research has demonstrated that fluid flow interacting with plankton behavior can drive many planktonic processes and spatial patterns. Moreover, evidence now suggests that plankton behavior can significantly affect ocean physics. Biophysical processes relevant to plankton ecology span a range of scales; for example, microscale turbulence influences planktonic growth and grazing at millimeter scales, whereas features such as fronts and eddies can shape larger-scale plankton distributions. Most research in this field focuses on specific processes and thus is limited to a narrow range of spatial scales. However, biophysical interactions are intimately connected across scales, since processes at a given scale can have implications at much larger and smaller scales; thus, a cross-scale perspective on how biological and physical dynamics interact is essential for a comprehensive understanding of the field. Here, we present a review of biophysical interactions in the plankton across multiple scales, emphasizing new findings over recent decades and highlighting opportunities for cross-scale comparisons. By investigating feedbacks and interactions between processes at different scales, we aim to build cross-scale intuition about biophysical planktonic processes and provide insights for future directions in the field.

Keywords: plankton distributions, plankton dynamics, turbulence, biomixing, interdisciplinary, coupling, technology

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Introduction

[1] Interdisciplinary work, spanning both biology and physics, has improved our understanding of marine plankton ecology (Kiørboe 2008). Developments in methodology as well as increased interest have rapidly advanced the study of planktonic biophysical interactions across spatial and temporal scales. Increased resolution of instrumentation has allowed for sampling on smaller scales than previously possible, while the creation of ocean observing systems and improvement of remote sensing technologies have advanced views of plankton and physical processes at large scales. New studies emphasize the importance of behavior *and* physics in shaping both plankton distributions and the surrounding fluid environment, challenging the paradigm of plankton as passive tracers (e.g., Fuchs et al. 2004; Katija 2012).

[2] Since the scope of plankton ecology is broad, progress tends to be scale specific, and connections between scales tend to be underappreciated. However, a holistic view of biophysical plankton interactions across scales is important for two reasons: (1) biological dynamics and patterns are not isolated to specific scales but are transferred across scales (e.g., microscale interactions may affect global-scale ecological processes and vice versa) (Wiens 1989; Levin 1992), and (2) methods or insights from one scale often can be applicable to problems at different scales (e.g., acoustics used to measure submesoscale plankton distributions can be used to study plankton in smaller-scale thin layers and internal waves) (Holliday et al. 2003; Warren et al. 2003; Lavery et al. 2010). Although there are several reviews on specific topics concerning biophysical interactions among plankton (e.g., Peters and Marrasé 2000; Durham and Stocker 2011; Katija 2012), no recent review has bridged different scales and sampling approaches (for older reviews, see Denman and Powell 1984; Denman and Gargett 1995; Estrada and Berdalet 1997).

[3] This review provides insight into the rapidly advancing field of plankton biophysics at different scales while drawing cross-scale comparisons. We highlight ways that fluid dynamics affect plankton, with an emphasis on spatial distributions, and include recent work that suggests plankton behavior can influence fluid motion across a range of scales. Given the broad scope of this field, it is impossible to cover every topic, and this review is not meant to be all-encompassing. We have partially or completely omitted some subjects that merit entire reviews themselves, most notably, temporal plankton dynamics, chemical signals, the biomechanics of plankton swimming and feeding (see Guasto et al. 2012), particle aggregation and sedimentation, the fluid dynamics of turbulence-plankton interactions (see Jumars et al. 2009), and processes occurring at ocean basin scales. Topics we included were chosen as examples of processes with cross-scale implications. This review is organized by spatial scale: from the microscale of individual plankton (millimeters to centimeters) to the mesoscale (tens to hundreds of kilometers), although many processes span a range of scales. The biophysical processes discussed in this review and their relevant spatial scales are depicted in Fig. 1.

It was our goal to cover a range of scales addressing both physical processes influencing biology and biological processes influencing physics. Finally, we discuss how biophysical processes in plankton transfer to scales larger and smaller than the process itself, with an emphasis on future research directions that may provide a cohesive understanding of biophysical interactions across scales.

Microscale

[4] Considerable progress in the study of biophysical interactions in plankton has been made at the microscale—the scale of centimeters and less—where individual plankton interact with each other and with their environment (Kiørboe 2008). Knowledge of how microscale fluid motion affects plankton has been restricted by methodological limitations, and early understanding was largely driven by theory and experimental studies. Recent advances in technology have allowed novel research in both the laboratory and the field, expanding our understanding of plankton-fluid interactions. Here we discuss how small-scale turbulence can affect plankton growth, community composition, and encounter rates, as well as how plankton can influence their physical environment by changing the local viscosity and inducing small-scale fluid motion.

The Effect of Turbulence on Plankton Growth and Community Composition

[5] To survive and grow, phytoplankton rely on nutrient uptake by diffusion. Nutrient uptake and lack of flow at the cell surface result in a region of reduced nutrients around the cell—the concentration boundary layer (Kiørboe 2008; Nishihara and Ackerman 2009). Processes that reduce concentration boundary layer thickness, thereby increasing the flux of nutrients to a plankter's surface, will result in enhanced nutrient uptake and growth, with the potential to strongly affect phytoplankton population dynamics. Microscale turbulence can thin concentration boundary layers (Arin et al. 2002; Peters et al. 2006), in addition to sinking or swimming, which increase flow adjacent to the organism (Karp-Boss et al. 1996; Kiørboe et al. 2001). These processes can significantly increase nutrient uptake and phytoplankton growth.
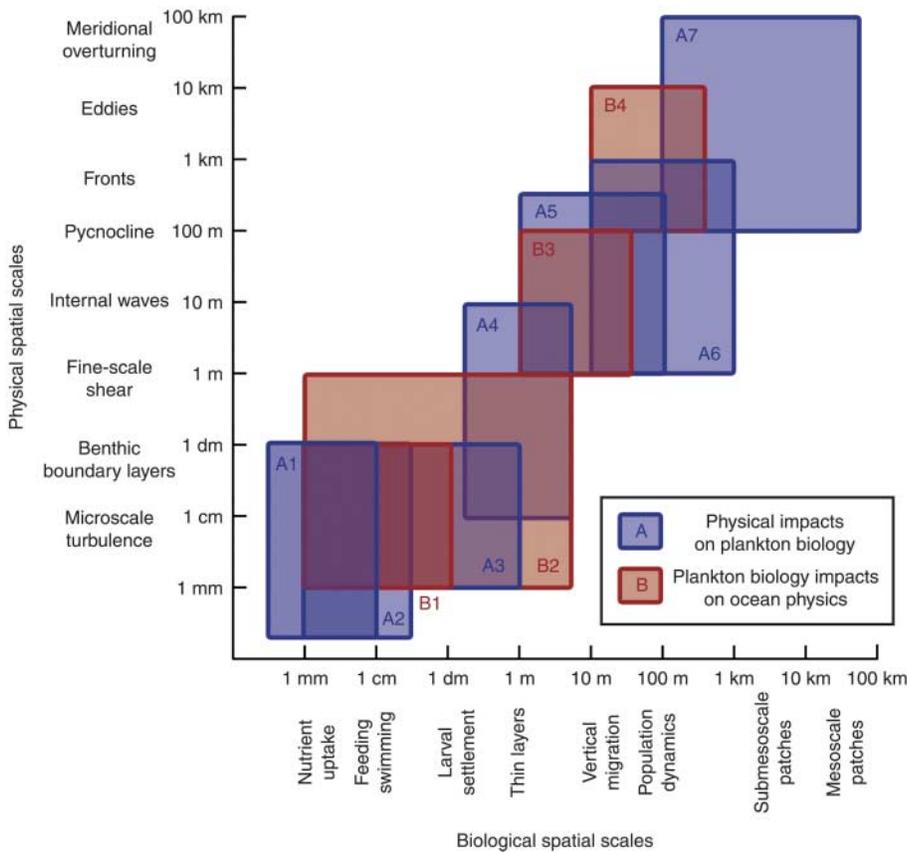
Fig. 1 Scales of interactions and overlap between biological and physical processes relevant to plankton ecology discussed in this review. Blue boxes (labeled A) represent physical processes that affect plankton dynamics or distributions. Red boxes (labeled B) represent ways that plankton biology influences ocean physics. A1 — The effect of turbulence on plankton growth and community composition. A2 — Turbulence and plankton encounter rates. A3 — Impact of benthic boundary layers on plankton dynamics and distributions. A4 — Plankton thin layers. A5 — Horizontal plankton patchiness induced by internal waves. A6 — Planktonic interactions with coastal flow. A7 — Fronts and submesoscale to mesoscale plankton patchiness. B1 — Effects of plankton on seawater viscosity. B2 — Microscale plankton-generated fluid motion. B3 — Aggregations and plankton stirring. B4 — Large-scale effects of biology on ocean physics.

[6] How organisms feel turbulence depends on their size relative to the Kolmogorov length scale, η (usually a few millimeters or less in turbulent environments), defined as

$$\eta = \left(\frac{\nu^3}{\varepsilon}\right)^{1/4}, \qquad (1)$$

where ν is the kinematic viscosity of seawater and ϵ is turbulent kinetic energy dissipation rate (Thorpe 2005). Since smaller plankton experience turbulence differently than their larger counterparts (Jumars et al. 2009), the effect of turbulence on phytoplankton growth is sensitive to organism size. Karp-Boss et al. (1996) found that a cell size of 60 μm (e.g., a large

centric diatom) is required for significantly increased nutrient uptake in turbulence, although this threshold is sensitive to turbulence intensity. Theoretical and laboratory studies have shown that the effects of flow on nutrient uptake are also sensitive to cell shape, physiology, and environmental nutrient conditions (Karp-Boss and Jumars 1998; Karp-Boss et al. 2000; Musielak et al. 2009), yet many questions about these relationships remain unanswered.

[7] Given that the interaction between turbulence and phytoplankton growth depends strongly on the size, shape, and physiology of the individual cell, it is a natural conclusion that environmental conditions can affect local phytoplankton community composition and size structure (Margalef 1997). Enhancement of nutrient uptake in turbulence is greatest for larger cells (Peters et al. 2006), and several experiments suggest that turbulent environments favor larger phytoplankton species, particularly diatoms (Estrada et al. 1987; Arin et al. 2002; Iversen et al. 2010); however, results from a recent series of mesocosm experiments do not support these conclusions (Guadayol et al. 2009). Developing a mechanistic understanding of how turbulence affects phytoplankton community composition is confounded by the numerous ways that turbulence interacts with plankton (Fig. 2). In addition to affecting nutrient uptake and growth, turbulence can affect grazing by enhancing encounter rates (Rothschild and Osborn 1988) and can even affect plankton sedimentation rates (Ruiz et al. 2004; Ross 2006).
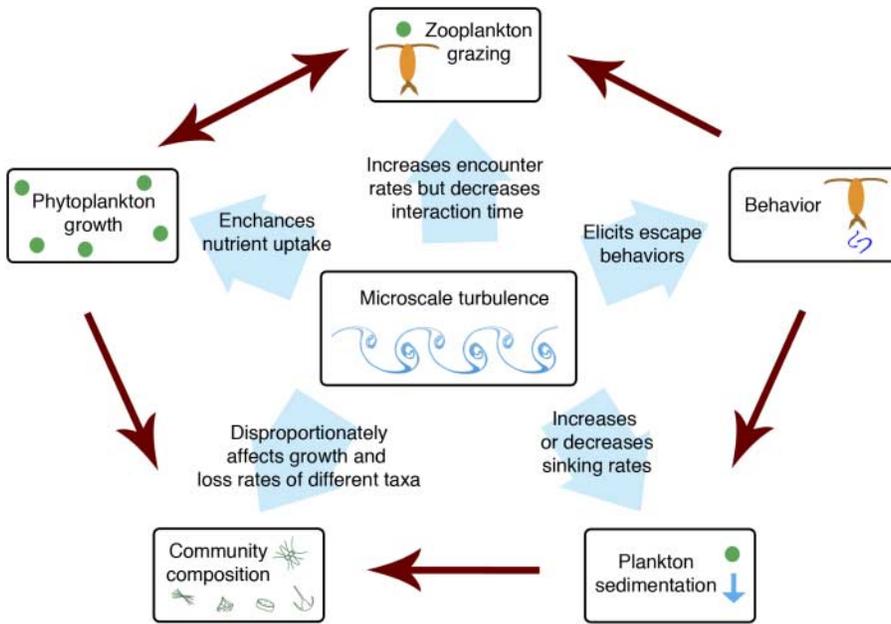
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Fig. 2 Schematic diagram illustrating potential impacts of microscale turbulence on small-scale plankton processes and interactions between the small-scale plankton processes. Microscale turbulence and community composition graphics by Tracey Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.um-ces.edu/imagelibrary/).

Turbulence and Plankton Encounter Rates

[8] Turbulence at the scale of individual plankton can affect the rates of key ecological processes such as zooplankton grazing and aggregate formation, previously thought to depend solely on organism concentrations (Gerritsen and Strickler 1977), by enhancing plankton contact rates (Rothschild and Osborn 1988). Increased encounter rates between predator and prey have been observed in the laboratory for zooplankton from several groups (microzooplankton, mesozooplankton, and planktonic larvae) when exposed to moderate levels of turbulence (MacKenzie et al. 1994; Peters and Gross 1994; Saiz and Kiørboe 1995). The magnitude of this effect varies depending on the species and feeding strategy of the planktonic predator (MacKenzie and Kiørboe 1995; Saiz and Kiørboe 1995; Shimeta et al. 1995).

[9] Although turbulence may increase plankton encounter rates, evidence suggests that at times turbulence can negatively affect ingestion (MacKenzie et al. 1994; Dolan et al. 2003). Whereas turbulence can increase the *rate* of contact, it also decreases the *time period* of contact. Since most predators require a minimum amount of time to react to and capture prey, increased turbulence can reduce the probability of a successful capture (MacKenzie et al. 1994), resulting in decreased ingestion and a dome-shaped response of ingestion rates to turbulence (MacKenzie et al. 1994; Dower et al. 1997). High levels of turbulence can also directly affect a plankter's ability to sense and capture its prey. Reductions in feeding rate for some copepods are likely the result of fluid motion interfering with hydromechanical signaling used to locate prey (Saiz and Kiørboe 1995; Visser 2001; Robinson et al. 2007). Turbulence may also erode feeding currents, leading to decreased feeding rates of planktonic suspension feeders (Saiz and Kiørboe 1995). Finally, whereas increased encounter rates may enhance foraging rates for planktonic grazers, these grazers will also experience increased contact with predators and thus higher mortality risk, at times outweighing any enhanced foraging success (Visser et al. 2009).

[10] Further hypotheses regarding interactions between small-scale turbulence and plankton have been explored with models. Models that include intermittent turbulence (Seuront et al. 2001), complex predator morphology (Strathmann and Grünbaum 2006), or a nonspherical predator sensory field (Lewis 2003; Lewis and Bala 2006) demonstrate significant changes in the effect of turbulence on plankton encounter rates. Organism size also structures the effect of turbulence on plankton contact rates, with the greatest effects predicted for meso-sized zooplankton predators (millimeter to centimeter size) (Kiørboe and MacKenzie 1995; Kiørboe and Saiz 1995).

[11] Because laboratory experiments may interfere with organism behavior (Franks 2001), it is essential to

understand which effects of turbulence manifest in nature. However, less progress has been made to understand turbulence and plankton encounter rates in the field, and results have been inconclusive. Although there is evidence of a positive correlation between wind speed (a proxy for turbulence) and larval feeding rates (Dower et al. 1997), there have also been observations of negative relationships between turbulence and feeding rate for several species of copepods (Irigoien et al. 2000; Visser et al. 2001). In addition to influencing contact rates, small-scale turbulence may elicit escape behaviors evolved to avoid predators, which may also affect foraging ability (Fields and Yen 1997). Turbulence avoidance behaviors have been observed on larger scales through downward shifts in the vertical distributions of copepods in response to turbulent field conditions (Incze et al. 2001; Maar et al. 2006). This effect further complicates interpretation of field observations and the relationship between turbulence and plankton ingestion rates (Franks 2001).

[12] The effect of turbulence on encounter rates, although most studied for predator–prey interactions, applies to any process that depends on contact between particles, such as aggregate formation, the spread of infection by parasites, and mating (Kiørboe 1997; Riffell and Zimmer 2007; Llaveria et al. 2010). Aggregate formation, in particular, represents an individual-scale phenomenon sensitive to changes in turbulence that has been the focus of recent research: mesocosm studies and models have helped elucidate the biophysical interactions that influence particle coagulation (e.g., Jackson 1990; Alldredge et al. 1995; Kiørboe 2001), and a full discussion is covered in recent reviews (e.g., Burd and Jackson 2009).

Effects of Plankton on Seawater Viscosity

[13] Although seawater viscosity is usually assumed to vary due to physical factors (e.g., temperature and salinity), biological factors may also be important in increasing viscosity on small scales (Jenkinson 1986; Jenkinson and Sun 2010). This elevated viscosity arises from mucus exopolymers that are secreted from both phytoplankton and bacteria (Decho 1990). A positive correlation between elevated seawater viscosity and chlorophyll *a* concentration or phytoplankton abundance has been observed in the field (Jenkinson 1993; Jenkinson and Biddanda 1995), and in some cases heterotrophic bacteria may play an important role (Seuront et al. 2010). Biologically enhanced viscosity depends on the temporal dynamics of phytoplankton blooms, with the strongest effects occurring during bloom formation and maintenance (Seuront et al. 2006, 2007). Changes in viscosity are also influenced by the composition of the phytoplankton community (Jenkinson and Biddanda 1995; Seuront et al. 2010).

[14] Seawater in phytoplankton blooms with elevated viscosity becomes a non-Newtonian fluid, with shear stress no longer linearly related to strain rate (Jenkinson 1986), which may have important implications for understanding the small-scale physics of the ocean. For example, increased seawater viscosity can modify the spectrum of shear rate that in turn affects the Kolmogorov length scale (Jenkinson 1986). Increased seawater viscosity may also lead to additional acoustic absorption, with the potential to affect many in situ acoustic measurements (Rhodes 2008). There may be biological implications as well, such as higher energetic cost for fish to irrigate their gills, at times resulting in fish mortality (Jenkinson 1989). Microscale planktonic processes, such as plankton encounter rates and nutrient uptake, are likely sensitive to changes in viscosity, but the direct link between biologically elevated viscosity and its impact on microscale planktonic interactions remains largely unstudied.

Microscale Plankton-Generated Fluid Motion

[15] Plankton structure their microenvironment at the individual scale as part of two fundamental activities: swimming and feeding (e.g., Strickler 1982; Yen et al. 2003; Costello and Colin 1995). For many organisms, manipulation of the fluid environment is critical to their way of life. The application of flow visualization techniques, including dye visualization (Fig. 3A), particle tracking and Schlieren optics (e.g., Strickler 1977), particle image velocimetry (Fig. 3B; e.g., Stamhuis and Videler 1995), planar laser-induced fluorescence (e.g., Koehl and Reidenbach 2007), and three-dimensional holography (Malkiel et al. 2003), has advanced our ability to measure fluid structures created by aquatic organisms.
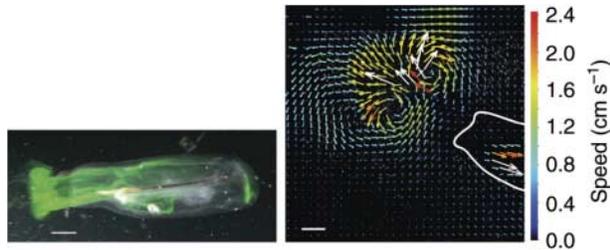
Fig. 3 Swimming wakes produced by the salp, *Cyclosalpa affinis*, visualized using in situ dye (A) and two-dimensional particle image velocimetry (B). Scale bars: 5 mm.

[16] Swimming organisms modify the background fluid by adding rearward momentum to the fluid to produce forward thrust, displacing fluid as they translate through it. These swimming motions create characteristic hydrodynamic structures that are distinguishable from ambient background fluid motion (Fig. 3). Different species of jellyfish and salps, for example, create unique vortex ring structures during swimming (Dabiri et al. 2010; Sutherland and Madin 2010). In addition to influencing the fluid environment for locomotion, a number of organisms create feeding currents to bring fluid and associated food particles in contact with feeding structures. Feeding currents generated by a stationary organism influence a larger adjacent volume of seawater than those generated by a cruising organism and therefore increase vulnerability to mechanosensory detection by predators (Kiørboe and Visser 1999).

[17] The size of the fluid structure created by a moving planker—termed the "zone of influence" (van Duren et al. 2003)—can be much larger than the organism itself. Models show that the strength of the flow field signal is inversely related to the distance from a stationary organism and distance^2 from a swimming organism (Visser 2001). Several ways in which the flow fields produced by individuals structure the physical environment and ecological interactions are discussed in the following examples.

[18] Individual flow fields can influence predator–prey interactions. Some plankton can detect and respond to organism-induced fluid motions by attacking; others respond by escaping. Work with protists (Jakobsen 2001) and copepods (Fields and Yen 1997;

Kiørboe et al. 1999) suggests that fluid shear deformation acts as the proximate cue for predator-induced escape responses. The presence of fine-tuned mechanosensory structures and a repertoire of behavioral responses provide strong evidence that organism-specific fluid signatures have structured predator–prey interactions over evolutionary time. The ability to detect the fluid signal of a predator may mean the difference between life and death; mortality increases when the potential escape response of copepods is diminished due to damping of the relevant fluid-mechanical cue by background turbulence (Robinson et al. 2007).

[19] Individual flow fields can also affect the organization of conspecifics into schools or swarms. Within aggregations of the same species, fluid signatures can be used to communicate with conspecifics, establish spacing patterns between neighbors, and potentially confer a hydrodynamic advantage (Leising and Yen 1997; Patria and Wiese 2004; Liao 2007). Schooling krill, for example, respond to the flow fields of neighbors by beating swimming appendages in synchrony (Patria and Wiese 2004) and may gain a hydrodynamic advantage from neighbors via flow refuging (exploiting regions of slower flow) or vortex capture (gaining energy from vortex rings generated by neighbors) (Liao 2007).

Fine Scale

[20] In addition to being heterogeneous on the scale of kilometers, plankton distributions in the ocean can also be patchy on much smaller scales. In this section we discuss benthic boundary layers (BBLs) and their effect on plankton dynamics, thin plankton layers on the scale of meters, and horizontal bands of increased plankton concentration due to internal waves. We also examine the potential of plankton aggregations at these scales to influence ocean mixing.

Impact of BBLs on Plankton Dynamics and Distributions

[21] BBLs form over the seafloor due to lack of fluid flow adjacent to a surface, fluid viscosity, and friction imposed on the ambient current, creating a velocity gradient normal to the substrate (Denny 1988). These velocity gradients typically follow a logarithmic form whose character depends on the roughness of the

bottom resulting in turbulent boundary layers (on the order of centimeters to meters for rough bottoms and as velocity increases), which influence the exchange of momentum, nutrients, and plankters (Nowell and Jumars 1984; Grant and Madsen 1986). The physical factors that influence the character of BBLs, such as bottom roughness and turbulence, therefore affect plankton dynamics and distributions. BBLs may affect food supply for filter feeders because slower flows adjacent to the substrata limit delivery of phytoplankton. If grazers deplete phytoplankton faster than they are delivered through ambient currents or turbulent transport, then concentration boundary layers form with low abundances of phytoplankton near the bed (Tweddle et al. 2005). Rapid velocity fluctuations due to water movement interacting with roughness elements increase turbulence and enhance the flux of plankton to the bottom (Koehl and Hadfield 2010), leading to a correlation between grazing rate and bed shear stress (Jones et al. 2009). Benthic organisms exploit filtering mechanisms, such as exhalant jets, to biomix near-bottom waters, increasing turbulence and the flux of phytoplankton to the benthos (Lassen et al. 2006).

[22] Larger-scale processes, such as waves, mediate background flow conditions and influence planktonic distributions in and near BBLs. Wave-current interactions increase shear stress and the apparent roughness of the bottom (Grant and Madsen 1986; Nittrouer and Wright 1994; Gaylord et al. 2006). An oscillatory wave-driven boundary layer on the order of centimeters is nested within a larger boundary layer that forms from wind-driven or tidal currents (Nittrouer and Wright 1994). These interactions enhance mixing of plankton, and recent attempts to combine wave and current boundary layers in dispersal models have given more accurate representations of transport in the coastal ocean (Gaylord et al. 2006).

[23] BBLs are critical to meroplankton settlement (Abelson and Denny 1997; Koehl 2007). Turbulence generally increases inshore and may be used as a settling cue by some coastal invertebrates (Fuchs et al. 2004). Boundary layer flows influence encounters with the substrate and, in addition to being a settlement cue themselves, can mediate other habitat-associated cues (Abelson and Denny 1997). Planktonic larvae can also exploit

lower velocities in BBLs to decrease dispersal distances (Marliave 1986; Shanks 2009a).

Plankton Thin Layers

[24] Plankton can be heterogeneous in their vertical distribution in the water column on meter scales, as evidenced by recurring observations of plankton thin layers, which are persistent vertical regions less than 5 m thick where plankton concentrations occur at 1.5−3 times that of the background concentration and may extend horizontally for kilometers (Dekshenieks et al. 2001; Benoit-Bird et al. 2009; Durham and Stocker 2011). Thin layers can consist of various taxa of phytoplankton, in addition to zooplankton or marine snow (Alldredge et al. 2002; McManus et al. 2003), and their occurrence, formation, and maintenance are driven by a combination of physical and biological processes (Dekshenieks et al. 2001; McManus and Woodson 2012).

[25] Thin layers are often associated with the pycnocline or other locally stratified regions (Dekshenieks et al. 2001; McManus et al. 2003; Prairie et al. 2010) and appear to require stable regions of the water column (i.e., regions of low mixing) to develop (Cowles et al. 1998; Dekshenieks et al. 2001; Wang and Goodman 2010). Our mechanistic understanding of the link between mixing and thin layers has been expanded in models that describe plankton layer formation, maintenance, and destruction and allow predictions for thin layer occurrence under various conditions. Such models have explored the balance between mechanisms of layer formation and turbulent diffusion, which acts to dissipate plankton layers (Stacey et al. 2007; Birch et al. 2009; Prairie et al. 2011).

[26] Although mechanisms of thin layer formation are often biological, such as increased local growth or directed swimming (Durham and Stocker 2011), physical factors can also act as mechanisms of thin layer formation (Franks 1995; Cheriton et al. 2010). Slowing or ceasing of plankton sinking at density discontinuities could explain observed accumulations at density gradients (MacIntyre et al. 1995; Alldredge et al. 2002). Layers can also occur when slabs of water that are locally rich in plankton are advected into the middle of the water column (Cheriton et al. 2010; Steinbuck et al. 2010a). In

addition, vertical shear can strain existing horizontal plankton patches, resulting in thin vertical layers (Eckart 1948; Franks 1995; Birch et al. 2008). Shear can also form layers by interacting with plankton motility; some plankton may respond behaviorally to shear (Rakow and Graham 2006), and vertically migrating plankton may become trapped in areas of high shear due to morphology–fluid interactions (Durham et al. 2009).

Horizontal Plankton Patchiness Induced by Internal Waves
[27] For decades, observations of long, narrow sea slicks and bands have been attributed to plankton patchiness in association with internal waves (Shanks 1983; Franks 1997). Models have demonstrated that patches arise both at and beneath the ocean's surface as plankters with directed swimming behavior (e.g., depth-keeping) encounter high-frequency internal waves (Lennert-Cody and Franks 1999). These predictions have been supported by observations of plankton patches associated with internal waves in the field (Kushnir et al. 1997; Macías et al. 2010). One study noted that changes in fluorescence along isotherms indicated that observed patches were shaped by interactions between phytoplankton swimming behavior and internal wave motion, and not just vertical advection of phytoplankton gradients (Lennert-Cody and Franks 1999, 2002). Swimming behavior also plays a role in the taxonomic composition within internal-wave associated bands, because composition may result from differences in organism swimming strength (Macías et al. 2010).

[28] In addition to affecting plankton distributions, internal waves can produce changes in planktonic processes and physiologies. Primary production can be altered by internal wave activity, since vertically advected phytoplankton will experience fluctuating irradiance levels (Holloway and Denman 1989; Evans et al. 2008). In addition, as phytoplankton are transported vertically by internal wave motion, they experience changes in the ratio of fluorescence to chlorophyll *a*—a process known as "nonphotochemical quenching" (Lennert-Cody and Franks 2002). This phenomenon can mimic changes in cell concentration by causing apparent increases in phytoplankton biomass in internal wave troughs when biomass is estimated via fluorescence.

[29] The capacity for internal waves to change local plankton concentrations may have implications for their transport toward shore in coastal environments (Woodson et al. 2011). This is important for benthic suspension feeders, which may receive a temporally varying food supply (Witman et al. 1993; Leichter et al. 1998), and even more so for planktonic larvae of near-shore invertebrates and fish that rely on shoreward transport to settle in suitable environments (Shanks 1983; Pineda 1991). Simple, linear internal waves cannot transport plankton even when interacting with swimming organisms (Franks 1997); however, large-amplitude nonlinear internal waves, which are common in coastal waters, can transport plankton shoreward (Lamb 1997). The potential for transport of larvae by internal waves has been supported by observations of periodic larval settlement and associations between internal waves and increased larval concentrations (Pineda 1991; Roegner et al. 2007; Shanks 2009b). Larvae found near the surface can experience cross-shore transport via slicks associated with internal waves (Shanks 1983; Shanks 1988; Shanks 2006). Unlike plankton thin layers, patches from high-frequency internal waves are relatively ephemeral, no longer than the period of the waves (Lennert-Cody and Franks 1999), and thus unlikely to be important for predator–prey interactions, except for the fastest swimming predators (Haney 1987; Silber and Smultea 1990).

Aggregations and Plankton Stirring
[30] Recently, there has been renewed interest in the possibility that organisms can influence fluid motion and vertical water column structure on scales much larger than the organisms themselves. Three mechanisms have been proposed by which organisms might influence fluid motion on the scale of meters. First, the wakes of swimming organisms, in aggregate, may produce kinetic energy comparable to environmental sources (e.g., Huntley and Zhou 2004). However, the potential for plankton to have a substantial influence on overturning has been challenged by the suggestion that turbulence generated by most swimming animals in the sea dissipates rapidly as heat (Visser 2007), since it occurs at small length scales, below the Ozmidov scale, L_0, defined

as

$$L_0 = \sqrt{\frac{\varepsilon}{N^2}}, \qquad (2)$$

where N is the buoyancy frequency, a measure of vertical density stratification. More recently, a second mechanism of ocean mixing has been proposed; Darwinian induced fluid drift involves transport of viscous fluid that is carried along by swimming organisms as they move through a stratified ocean (Katija and Dabiri 2009). The amount of fluid transport is related to the shape of the organisms and the viscosity of the fluid. A third approach involves consideration of all the sources of energy derived from biological inputs, including mechanical energy released by movements of nekton and migrating plankton, as well as metabolic energy release (Dewar et al. 2006). Regardless of the mechanism of biomixing, it is likely that large numbers or aggregations of zooplankton are required for significant stirring. As discussed earlier, plankton frequently aggregate in layers through both physical and biological mechanisms. Because these layers are often associated with sharp density gradients (Dekshenieks et al. 2001; Prairie et al. 2010), there is the potential for plankton to disrupt stratification.

[31] A large proportion of planktonic species, including some copepods, euphausiids, dinoflagellates, mysids, jellyfish, and salps, engage in diel vertical migration, which is a major mechanism for aggregating plankton. Migrations can be over several hundreds of meters and may include multiple trophic levels, resulting in complex assemblages, which can have a particularly profound impact on the vertical transport of material through the water column (Bollens et al. 2011). Can organisms also transport fluid in the same way that migrating organisms can transport organic material vertically through the water column (Bochdansky et al. 2010)? If so, plankton aggregations could potentially homogenize a sharp density gradient, with ramifications for mixing and nutrient delivery. Few investigators have tested the hypothesis that migrating plankton aggregations influence physical structure, but a number of field and laboratory studies provide evidence that strong-swimming zooplankton can overwhelm local physics. Swimming aggregations of micronekton and zooplankton are capable of overcoming physical forcing so that

distributions of biomass are independent of physical structure (Gallager et al. 2004; Benoit-Bird and Au 2006; McManus et al. 2008). For example, jellyfish in a stratified lake can transport viscous fluid that adheres to the animal for several body lengths as they swim upward (Katija and Dabiri 2009).

[32] On the other hand, field and laboratory studies have also shown that vertical plankton migration ceases in regions associated with density discontinuities, leading to accumulations in distinct layers. Maintenance in these layers may be driven by difficulty in osmoregulation or by behavioral responses to physical cues, including gradients in density, velocity, or chemicals. Specifically, changes in swimming speed or turning frequency can lead to accumulation in layers (Menden-Deuer and Grünbaum 2006; Woodson et al. 2005). In controlled laboratory studies of migrating plankton in stratified tanks, starting and ending density gradients are often unaltered over the course of an experiment (Harder 1968; Clay et al. 2004; Woodson et al. 2005), suggesting that even at small scales plankton may not consistently influence physics.

[33] Measurements within aggregations show that turbulence levels generated by the organisms can be higher than background environmental turbulence (Kunze et al. 2006; Farmer et al. 1987; Gregg and Horne 2009), but in other cases swimming organisms do not boost turbulence appreciably (Rousseau et al. 2010; Lorke and Probst 2010). Ultimately, the capacity of animal aggregations to influence larger-scale physics depends on two factors: (1) whether the energy is injected above the Ozmidov scale; and (2) the mixing efficiency, γ, defined as

$$\gamma = \frac{KN^2}{\varepsilon}, \qquad (3)$$

where K is the turbulent diffusivity of heat. Although turbulence measurements within large fish schools in Monterey Bay, California, were 100-fold higher than measurements taken outside, mixing efficiency was 100-fold lower ($\gamma = 0.0022$ inside; $\gamma = 0.23$ outside) (Gregg and Horne 2009). On the other hand, mixing efficiencies generated by fish ($\gamma = 0.22$) in a stratified lake were similar to measurements taken in the absence of fish ($\gamma = 0.21$), indicating that mixing efficiencies

were not diminished in fish aggregations and that turbulence generated by fish could be important when background environmental turbulence is weak (Lorke and Probst 2010).

Submeso- and Mesoscale

[34] Large-scale interactions between plankton and ocean physics have been studied intensively for more than a century. Satellite images of chlorophyll reveal complex patterns, with heterogeneous distributions on the scale of $\sim 1-10$ km (submesoscale) and the scale of tens to hundreds of kilometers (mesoscale). Whereas recent progress has been made toward understanding physical mechanisms structuring plankton distributions at these scales, novel research on planktonic distributions has revealed that these patterns are not the result of physics alone but can be mediated by plankton behavior. We discuss several submeso- and mesoscale phenomena: planktonic interactions with coastal flow, plankton accumulations at fronts and eddies, and behaviorally driven large-scale stirring by plankton.

Planktonic Interactions with Coastal Flow

[35] Coastal environments are productive regions that exhibit high abundances of plankton and are nurseries for fish and invertebrate larvae, many of which settle in nearshore regions. Near the coastal boundary, topographic features interact with currents in a variety of ways that affect transport and retention of plankton. Recirculation zones in the lee of headlands increase retention times and can lead to high standing stock of phyto- and zooplankton (Graham and Largier 1997; Roughan et al. 2005; Mace and Morgan 2006). Island wakes and associated recurrent eddies enhance mixing via shear zones and in some cases lead to local retention of plankton (Wolanski and Hamner 1988; Swearer et al. 1999; Tseng 2002), with the amount of retention mitigated by island size and shape (Hernández-León 1991). Mesoscale eddies shed from coastal areas due to flow-topography interactions can also transport coastal micronutrients to nutrient-deplete oceanic waters (Whitney and Robert 2002).

[36] As the predominant coastal currents move alongshore, they interact with the coastal boundary and result in an increased effect of bottom friction as depth decreases closer to shore. Over submesoscales, coastal eddies transport high concentrations of nitrate, and presumably plankton, to the inner shelf (Bassin et al. 2005). On smaller scales (hundreds of meters to a few kilometers), the influence of bottom friction and lateral shear on the inner shelf decreases mean alongshore velocity close to shore in a region termed the "coastal boundary layer" (Nickols et al. 2012), and these slower flows close to shore have the potential to decrease alongshore transport of plankton. In addition, physical structures of reefs within shallow waters have a significant impact on water movement and plankton distributions. Impinging currents on reef structures and canopies (coral and rocky reefs, seagrass beds, and kelp forests) must be redirected, leading to acceleration and flow separation around edges of reefs as well as flow attenuation in the core (Hamner and Hauri 1981; see Gaylord et al. 2012 for a review of biophysics and kelp forests). Such hydrodynamic features can lead to accumulation of zooplankton (Hamner and Hauri 1981).

[37] Coastal winds and waves can affect cross-shore transport of coastal plankton, redistributing plankton patches. Fronts associated with alongshore upwelling winds have been found in nearshore waters and can act as a barrier to mixing, preventing phyto- and zooplankton offshore from moving into nearshore waters while also concentrating inshore zooplankton in very nearshore waters (McCulloch and Shanks 2003; Shanks and McCulloch 2003). Cross-shore winds can drive two-dimensional circulation in the inner shelf, while wave forces moderate the symmetry of cross-shore transport (Fewings et al. 2008). In addition, recent measurements suggest that cross-shore transport due to wave-induced Stokes drift, the net movement of wave propagation due to surface gravity waves, is comparable to that due to cross-shore current velocities and provides an additional mechanism for cross-shore movement of plankton (Monismith and Fong 2004; Lentz and Fewings 2012). As discussed earlier, the interaction between planktonic behavior and internal waves may result in a significant source of plankton delivery to the nearshore (Lamb 1997; Leichter et al. 1998; Woodson et al. 2011).

[38] Surf zone mixing is another potentially important physical driver of coastal plankton distributions

and transport. Limited research has been conducted on plankton distributions in the surf zone; however, the surf zone has been invoked as an important semipermeable membrane for delivery of planktonic larvae to shore (Rilov et al. 2008; Shanks et al. 2010). The balance of on- and offshore transport at the coastal boundary requires vertical circulation within the surf zone that can lead to accumulation of plankton (McPhee-Shaw et al. 2011). New research on rip currents indicates a large degree of retention within the surf zone, which may have important implications for plankton distributions (MacMahan et al. 2010). Since dynamics within the surf zone are often decoupled from those of the inner shelf, the meeting of these two water masses can lead to significant cross-shore shear and front generation (Storlazzi et al. 2006).

[39] Recent studies indicate that planktonic larvae over continental shelves appear to be concentrated close to shore (Borges et al. 2007; Shanks and Shearman 2009), even in strong upwelling regimes (Morgan et al. 2009; Morgan and Fisher 2010). Ontogenetic and diel vertical migration contribute to nearshore retention of larvae and avoidance of offshore transport via the Ekman layer (Morgan and Fisher 2010). In addition, cross-shore circulation can be weakened over the inner shelf during both up- and downwelling periods, when the mid and outer shelves are stratified (Lentz and Fewings 2012). The coastal boundary layer, cross-shore shear, front generation, and surf zone retention may further enhance nearshore retention and decrease cross- and alongshore transport of plankton.

Fronts and Submesoscale to Mesoscale Plankton Patchiness

[40] Fronts—manifested as sharp spatial gradients in hydrographic properties such as temperature, salinity, and nutrient concentrations (Belkin et al. 2009)—contribute to spatial heterogeneity in the ocean (Owen 1981). Several physical mechanisms lead to formation and maintenance of ocean fronts, including thermal boundaries, wind-driven upwelling, tides, internal waves, Langmuir circulation, river plumes, mesoscale eddies, and topography. In convergent zones, buoyant particles remain at the surface despite weak downwelling vertical currents, leading to accumulation at fronts (Franks 1992; Yoder et al. 1994; Genin et al. 2005). When individual behaviors are important, such as for vertically migrating zooplankton, the combination of upwelling and downwelling currents with plankton behavior (swimming against the flow to maintain depth) results in plankton accumulations (Genin et al. 2005). Biophysical accumulation at fronts and tolerance to high turbulence by dinoflagellates in these regions may serve as pelagic seed stock for subsequent blooms (Smayda 2002).

[41] Mesoscale eddies are another source of heterogeneity influencing plankton processes in both the open ocean and coastal regions (Garçon et al. 2001). Upwelling produced from eddies alters local nutrient concentrations, allowing for enhanced primary productivity (Sweeney et al. 2003). Elevated food concentrations may also alter diel vertical migration of zooplankton (Eden et al. 2009), which has the potential to influence the availability of prey to surface-oriented predators. Eddies can be an important mechanism in the transport of organisms (Sweeney et al. 2003); coastal plankton and larval fish trapped in eddies can be displaced into the open ocean (Lobel and Robinson 1986; Keister et al. 2009) or vice versa.

[42] Recent research on mesoscale plankton processes has focused on applying advanced technologies to study both larger and smaller scales than previously was possible. New tracking and detection methods have bolstered awareness of the role of jets (or squirts) and filaments in coastal transport (Lévy et al. 2001; Nieto et al. 2012). These features are intense areas of offshore transport formed in hydrostatic balance with isopycnals and may be persistent features around topographic headlands (Barth et al. 2000). Advances in the study of eddies has resulted from use of satellite altimetry to quantify temporal patterns of eddy variability and track eddy propagation (Morrow and Traon 2011) in an effort to understand their importance in ocean biogeochemistry (Lévy 2008). Satellite remote sensing is routinely used to characterize ocean surface properties at the mesoscale and for mapping the persistence and spatial extent of mesoscale features (Kostianoy et al. 2004; Belkin et al. 2009; Nieto et al. 2012). Recent research using a combined multisatellite data set has revealed the importance of mesoscale physical variability on structuring phyto-

plankton communities by creating unique niches along evolving fronts (d'Ovidio et al. 2010).

Large-Scale Effects of Biology on Ocean Physics

[43] Although several recent studies have addressed the ability of planktonic organisms to affect fluid flow at the scale of meters, as discussed previously, the spatial extent of biologically induced mixing and its potential to overturn stratification remain unclear. Global climate is intimately related to meridional overturning, which transfers heat from the equator to the poles. Is biologically mediated stirring comparable to the overturning generated by mechanical mixing (e.g., wind, tides)? Munk (1966) first proposed the notion that the marine biosphere might generate mixing on scales comparable to mechanical sources. More recent reviews of the topic (Huntley and Zhou 2004; Dewar et al. 2006; Katija 2012), as well as field studies of aggregations described earlier, have arrived at different conclusions regarding mechanisms and relative scales of plankton-generated mixing.

[44] Recent modeling studies based on the Darwinian drift mechanism proposed and experimentally validated by Katija and Dabiri (2009) have also arrived at different interpretations, although all but one (Subramanian 2010) have concluded that biomixing by numerous small plankton is significant. Varying interpretations of these models relate to disparate model assumptions, for example, presence of background turbulence (Leshansky and Pismen 2010), unsteady (Leshansky and Pismen 2010) versus steady swimming, potential flow (Dabiri 2010; Thiffeault and Childress 2010) versus inclusion of viscous effects (Subramanian 2010), and migratory behavior across isopycnals (Dabiri 2010). These inconsistencies suggest a need for more field and experimental observations for model input and validation.

[45] Stratified regions with a high biomass of migrating plankton have the greatest potential for biologically enhanced mixing. Roughly 80% of the area of the ocean and 83% of the global ocean biomass falls in the permanently stratified region between 50° N and 50° S (Bogorov et al. 1968; Longhurst et al. 1990). The proportion of vertically migrating zooplankton can be as high as 90% (Wiebe et al. 1979), but a more typical range is between 10% and 20% (Angel 1986; Longhurst et al. 1990; Ianson et al. 2004). Moving forward, an inherent challenge in estimating biological impacts on diapycnal mixing is the necessity of scaling up from smaller-scale, direct observations. Large-scale estimates of biogenic mixing will require a careful consideration of the relative biomass, vertical distribution, and swimming behavior of plankton compared with the physical forces on a region-by-region basis.

Cross-Scale Comparisons

[46] Biophysical interactions in the plankton span scales from millimeters or less to hundreds of kilometers, and the interacting biological and physical processes generally operate at similar scales (Fig. 1). For example, modulation of concentration boundary layers around individual cells directly influences nutrient flux and organism-scale physiology (Kiørboe 2008). Likewise, transport of fluid via Darwinian drift by vertically migrating plankton (Katija and Dabiri 2009) would be expected to occur on scales similar to the distance traveled by the organisms. However, a critical next step is to understand how processes can connect across scales in order to build intuition about plankton ecology (Ballantyne et al. 2011). Next, we discuss the potential for biophysical interactions to affect plankton processes at much larger scales and for large-scale dynamics to influence processes at smaller scales (see Fig. 4). We also examine the application of new methods to cross-scale investigations of interactions between plankton and ocean physics, as well as new ways of combining previous methodology (see Fig. 5). Finally, we discuss the significance of this research area for furthering an interdisciplinary understanding of plankton dynamics across scales.

Consequences of Planktonic Processes for Larger Scales

[47] The scale-specific processes discussed in this review often have larger-scale implications, with the potential to influence higher-order plankton dynamics (Fig. 4). Spatial heterogeneity in plankton distributions can affect grazing rates and trophic dynamics on much broader scales than those of the patches themselves. For example, plankton thin layers act as hot spots for zooplankton foraging, because many grazers have the
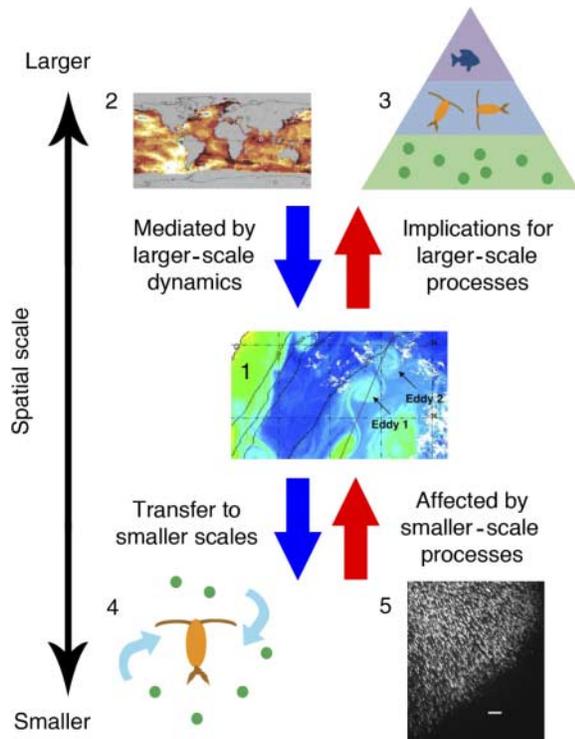
Fig. 4 Schematic diagram demonstrating how biophysical processes in the plankton can interact across scales, using an example of cross-scale connections for plankton patches in eddies (1; image from Garcia et al. 2004), which can be mediated by global changes in ocean temperature (2; image from Hansen et al. 2006), can affect global trophic dynamics (3), can influence plankton encounter rates (4), and can be affected by mixing due to plankton aggregations (5; image from Hamner and Hamner 2000). Blue arrows represent implications of processes for smaller scales, and red arrows represent effects of processes on larger scales.

ability to seek out and remain in regions of high prey concentration (e.g., Tiselius 1992; Menden-Deuer and Grünbaum 2006). Enhanced foraging in thin layers could be intensified under turbulence, where small-scale fluid motion combined with high particle concentrations will elevate encounter rates. Since in situ grazing rates have been shown to be higher within plankton layers (Menden-Deuer and Fredrickson 2010), ignoring this small-scale plankton patchiness may result in significantly underestimating global grazing rates. It has even been suggested that without the presence of highly concentrated patches of prey, zooplankton would not be able to sustain observed population sizes (Mullin and Brooks 1976; Davis et al. 1991). Similarly, although the impact on global scales is still largely unknown, fronts are important in shaping local trophic dynamics by

altering the distribution of marine plankton at convergence zones. Plankton aggregations at fronts play an important role in determining the distributions of larger predators, by providing important foraging grounds for penguins (Boersma et al. 2009), seabirds (Schneider 1990; Russell et al. 1999), marine mammals (Weise et al. 2006), and fish (Fiedler and Bernard 1987).

[48] Small-scale features can also affect larger-scale carbon cycling. Increased particle encounter rates from small-scale turbulence could enhance aggregation rates, resulting in higher carbon flux (Jackson 1990; Kiørboe 1997). Zooplankton-produced hydrodynamic disturbances might also play an important role in particle fragmentation and elemental cycling (e.g., Steinberg et al. 1997). Shear stress generated by the pleopods of swimming euphausiids can fragment marine snow particles, leading to smaller mean particle sizes, thereby reducing sinking rates (Goldthwait et al. 2004). This process has important ramifications for the biological pump since smaller particles are more likely to remain in surface waters, allowing increased opportunity for remineralization. Likewise, particles settling through sharp vertical density gradients may significantly decrease their settling velocity, resulting in layer formation (MacIntyre et al. 1995; Alldredge et al. 2002); this may decrease carbon export, since these accumulations may act as hot spots for bacterial remineralization. At the submeso- and mesoscale, eddies, jets, squirts, and eddy-associated filaments likely play a significant role in ocean-scale biogeochemistry (Lapeyre and Klein 2006; Peterson et al. 2011). These features may be spatially constrained, yet they contribute significantly to the offshore and vertical transport of coastal waters and biota, facilitating the biological pump of carbon due to their intensity (Lapeyre and Klein 2006).

[49] Since many coastal invertebrate and fish species depend on biophysical mechanisms for successful settlement, small-scale processes have implications for biogeography. Boundary layer flows allow larvae to escape higher velocity flows and can promote retention to natal sites. Distributions of meroplankton are further modified by small-scale behaviors of individual plankters, which allow larvae to choose water masses, potentially controlling whether they are retained near their natal site or transported offshore (Shanks and Brink
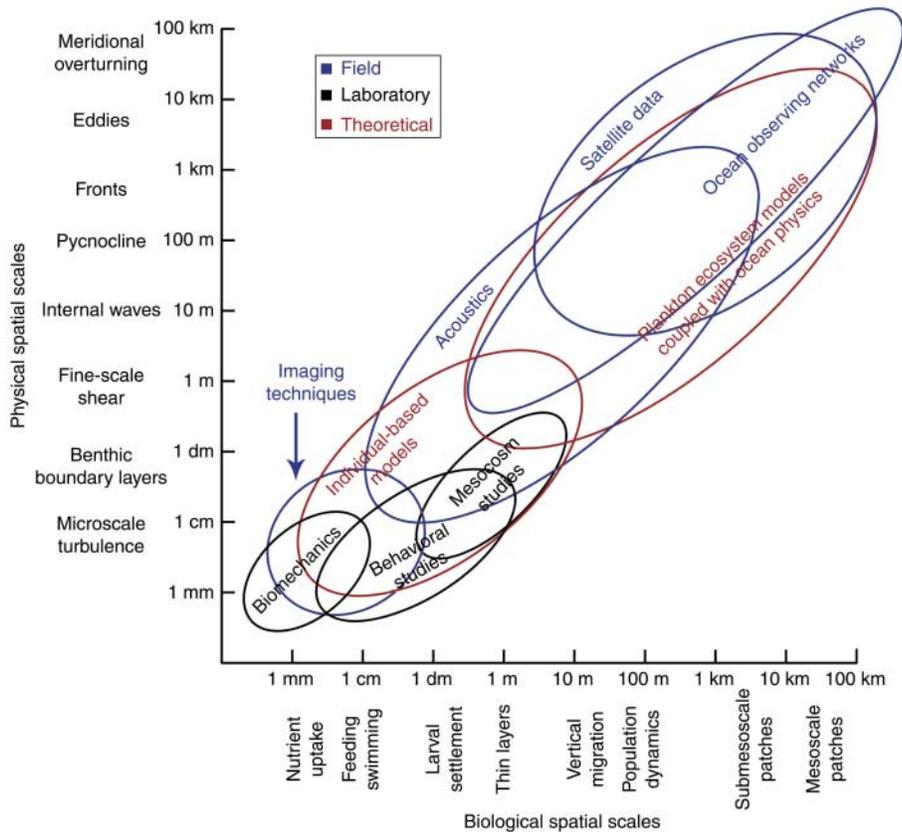
Fig. 5 Plot showing field (blue), laboratory (black), and theoretical (red) techniques in plankton ecology that can be used to study a range of biological and physical scales.

term patterns in plankton community composition, and interact with background conditions to influence plankton evolution (Margalef 1997). Whereas some plankton have evolved to take advantage of turbulence to enhance growth, other plankters have evolved escape behaviors in the presence of turbulence (Fields and Yen 1997; Maar et al. 2006), which may lead to different survival rates among species depending on background conditions. Plankton have also evolved sensory structures tuned to detect and respond to hydrodynamic signals produced by mates and prey in addition to predators (Jakobsen 2001; Kiørboe et al. 1999). These planktonic adaptations in response to physical cues may govern the composition of local plankton communities and give insights to evolution in a changing environment, with important ramifications for future planktonic distributions.

2005; Morgan and Fisher 2010). These small-scale biophysical interactions can therefore affect the degree to which populations are connected. In addition, persistent spatial fronts are associated with high levels of shoreline recruitment, which is likely driven by small-scale biophysical interactions associated with fronts such as enhanced shear, accumulation of plankton, and increased encounter rates, thereby increasing larval growth and survival (Woodson et al. 2012).

[50] Last, small-scale phenomenon can influence plankton community dynamics and evolution. As discussed previously, swimming or small-scale turbulence can thin concentration boundary layers around individual phytoplankton, resulting in enhanced nutrient uptake and subsequent growth (Karp-Boss et al. 1996). Since these effects occur disproportionately for organisms of different size, shape, and taxonomic group, microscale processes can lead to large-scale and long-

Effects of Large-Scale Dynamics on Smaller Scales

[51] Large-scale phenomena can also cascade down to influence interactions that occur at much smaller scales (Fig. 4). Large-scale patterns can affect smaller-scale interactions between biology and physics since many of them—including thin layer and BBL formation, biogenic mixing, and transport of plankton—are sensitive to background environmental parameters such as stratification, background flow, and nutrient availability (Dekshenieks et al. 2001; Tweddle et al. 2005; Jones et al. 2009). For example, turbulence and fluid transport mediated by aggregations of plankton can potentially occur on scales of hundreds of meters (Gregg and Horne 2009) but will have implications for centimeter-scale vertical density gradients and individual

plankton encounter rates. Similarly, increased background levels of phytoplankton concentrations at the mesoscale will influence the effect of turbulence on encounter rates or the potential for phytoplankton to enhance local seawater viscosity. Coastal fronts may also be responsible for creating horizontal discontinuities in smaller-scale features such as plankton thin layers (Holliday et al. 2010).

[52] Quantifying interactions between plankton and their physical environment is increasingly important in light of rising surface ocean temperatures due to anthropogenic effects, which has further potential to mediate small-scale biophysical processes. Increasing temperatures due to global climate change will lower fluid viscosity. This will have implications for small-scale fluid processes such as turbulence generation, particle sinking, swimming, and encounter rates (Woodward et al. 2010). Increased stratification and stability will damp turbulent mixing and nutrient delivery (e.g., Manabe and Stouffer 1993), with implications for numerous oceanic processes. In particular, phytoplankton community composition is related directly to the stability of the water column (Falkowski and Oliver 2007; Peters 2008), since the extent of turbulent mixing and nutrient availability may favor certain groups and sizes of plankton and explain some of the current diversity of plankton (Hutchinson 1961). Furthermore, spatial patterns of plankton associated with stratification, such as thin layers (Dekshenieks et al. 2001), may become more common, with consequences for trophic dynamics.

New Approaches to Investigating Biophysical Processes in the Plankton across Scales

[53] The quickly expanding field of plankton biophysics has motivated new developments in methodology in addition to combining previous techniques to study problems across scales (Fig. 5). Questions concerning biophysical plankton interactions at small scales have been hampered by a lack of in situ data with the necessary resolution; however, novel technological advances now provide opportunities to sample biological and physical variables concurrently on appropriate scales (Holliday et al. 2003; Ross et al. 2007; Churnside and Donaghay 2009). One example is the study of microscale plankton distributions, which have been quantified

using bulk measures such as chlorophyll *a* fluorescence. However, the interpretation of these data can be obscured by the presence of large individual plankton at scales < 1 cm, which can be seen in the flattening of plankton spectra at these scales (Fig. 6A; Franks 2005; Yamazaki et al. 2006) and has been confirmed by spatial statistics on in situ plankton distributions (M. J. Doubell, pers. comm.; J. C. Prairie, unpubl.). These observations provide motivation for the use of advanced imaging techniques to study microscale plankton distributions (Fig. 6B; Jaffe et al. 1998; Katz et al. 1999; Steinbuck et al. 2010b), which may also uncover biotic and abiotic mechanisms that control these distributions. Progress in imaging technology has made it possible to resolve individual plankton interactions and the effect of turbulence in their natural environments, and some of the most promising technologies allow for simultaneous measurements of plankton behavior and physical structure in the field, such as in situ digital particle image velocimetry (Katija and Dabiri 2008).

[54] In addition to new technology, in situ plankton ecology has benefited from recent applications of existing technology. For example, bioacoustics, previously used to study biological patterns at submeso- and mesoscales, has been adapted to study biophysical interactions in internal waves (Warren et al. 2003), and high-frequency broadband acoustics can enumerate a broad range of targets, which allows differentiation of zooplankton and physical structure even at small scales (Lavery et al. 2010). Further, combining instrumentation in novel ways will allow better integration of studies across scales. For example, mounting a particle image velocimetry apparatus on a remotely operated vehicle would allow measurement of plankton−fluid interactions on a small scale along with concurrent measurements of physical structure, with the opportunity to sample multiple locations. Similarly, in situ and shipboard sampling using acoustic and optical instruments, such as bottom-moored acoustics (Kaltenberg et al. 2010), combined with current meters and satellite-derived data identifying the position of fronts (Venegas et al. 2008), could provide fine-scale resolution of biota across fronts necessary to investigate cross-scale plankton biophysical interactions (Genin et al. 2005).
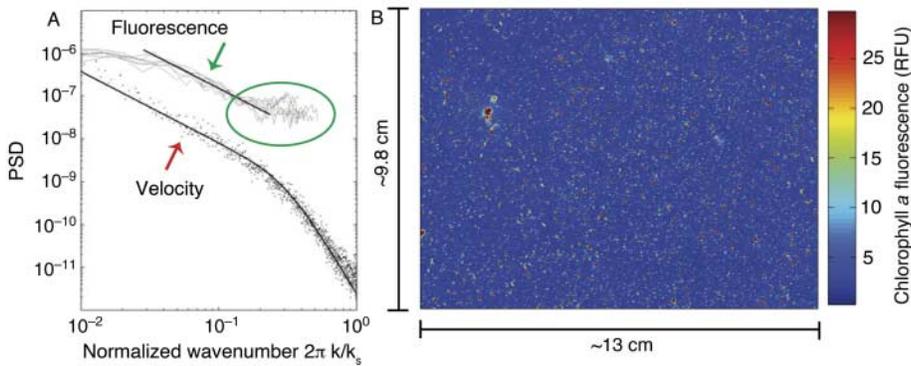
Fig. 6 A — Power spectra for normalized velocity and chlorophyll fluorescence, demonstrating that in the inertial subrange of turbulence, the spectra for both velocity and fluorescence exhibit a −5/3 slope. However, at the highest wavenumbers (i.e., the smallest spatial scales), the fluorescence spectrum flattens (indicated by the green circle), perhaps due to phytoplankton being discrete at these scales (image adapted from Yamazaki et al. 2006). B — An example image from a free-falling planar laser imaging fluorometer from the Santa Barbara Channel, California, September 2006, which shows in situ distribution of chlorophyll *a* fluorescence (Prairie et al. 2010). Discrete phytoplankton are visible from high fluorescence values (red range).

Additionally, applying molecular techniques will allow an understanding of how biophysical processes drive plankton diversity at a range of scales.

[55] Ocean circulation models, such as the Regional Ocean Modeling System, as well as large-scale observational systems, such as high-frequency radar networks and satellite technology, make it possible to visualize and predict larger-scale transport of plankton (Bassin et al. 2005; Siegel et al. 2008) while also providing an opportunity to embed smaller-scale processes. Progress is being made toward nesting these models to increase resolution, but key areas still remain unresolved near the coast and over small spatial scales (Helbig and Pepin 2002). Individual-based models allow ocean circulation models to be parameterized with biological parameters and individual behaviors and are fundamental to our understanding of biophysical interactions over large scales (Paris et al. 2007).

[56] Finally, continuous sampling will be needed to capture rare events and long-term trends, especially in the context of global climate change. The Ocean Observatories Initiative and other means of acquiring long time series and broad spatial coverage will be revolutionary for future approaches to measuring the relative contributions of biology and physics to ocean mixing on relevant time scales (Chave et al. 2009).

Significance to Aquatic Environments

[57] Plankton ecology is an inherently interdisciplinary subject, as demonstrated in this review by the many ways and scales at which plankton biology and physics interact. Dynamics and distributions of plankton are shaped by their physical environment, from microscale turbulence influencing plankton grazing rates to eddies forming mesoscale plankton accumulations. In addition, plankton can affect their fluid surroundings; plankton blooms can increase local seawater viscosity, and plankton motility can affect mixing at a range of scales. The examples of biophysical coupling in the plankton presented here illustrate not only the need for more interdisciplinary research but also a need for cross-scale research. Patterns and processes that occur at one scale are intimately connected with those at both smaller and larger scales. For example, interactions between turbulence and plankton at centimeter scales can affect global carbon cycling and plankton community dynamics. Meanwhile, large-scale changes in stratification and temperature driven by global climate change mediate background conditions for smaller-scale processes. The application of new technology and greater communication between researchers studying different scales will be necessary in future research in the field of ocean biophysics in order to achieve a more complete understanding of plankton ecology.

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