

REVIEW

Plankton distribution and ocean dispersal

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Summary

Plankton are small organisms that dwell in oceans, seas and bodies of fresh water. In this review, we discuss life in the plankton, which involves a balance between the behavioral capabilities of the organism and the characteristics and movement of the water that surrounds it. In order to consider this balance, we discuss how plankton interact with their environment across a range of scales – from the smallest viruses and bacteria to larger phytoplankton and zooplankton. We find that the larger scale distributions of plankton, observed in coastal waters, along continental shelves and in ocean basins, are highly dependent upon the smaller scale interactions between the individual organism and its environment. Further, we discuss how larger scale organism distributions may affect the transport and/or retention of plankton in the ocean environment. The research reviewed here provides a mechanistic understanding of how organism behavior in response to the physical environment produces planktonic aggregations, which has a direct impact on the way marine ecosystems function.

Key words: persistent front, thin layer, plankton distribution.

Introduction

The spatial distribution of organisms in the ocean – from the smallest plankton to the largest predators – is determined by interactions between organism behavior and physical oceanographic structure and processes. The relative importance of physical structures and processes in driving organism distribution, and consequently dispersal, is directly related to the swimming and behavioral capabilities of an individual or species. Although it is clear that large predators such as sharks, marine mammals and large fishes can adjust to changes in their fluid environment with relative ease, plankton cannot. Life in the plankton involves a balance between behavior and the organisms' environment. Plankton is composed of viruses, bacteria, phytoplankton, zooplankton and the pelagic larvae of many marine invertebrates and fishes. This group displays a wide range of behavioral capabilities that bridge the transition from being a passive particle to being able to determine vertical and horizontal position in the ocean (Fig. 1). This species-specific transition often occurs at scales much smaller than traditionally recognized because of the organisms' ability to respond to ocean structure and processes.

In this contribution, we briefly review the physical characteristics and the dynamics of the ocean from the organism's point of view. We then review the known scales of interaction between plankton and physical processes, and how these interactions lead to observed patterns in the environment. Two specific oceanographic features – aggregations at persistent ocean fronts and aggregations in subsurface thin layers – are used as examples of interactions between organism behavior and physical oceanographic structure and processes. We then describe how these aggregations influence organism distribution, oceanic dispersal and, in some cases, larval recruitment. Finally, we discuss coupled biological–physical models being used to describe these interactions and some of the persistent features we observe in the sea.

Ocean physics: from the perspective of an organism

The dynamics of the ocean are highly variable and are driven by multiple forcing factors such as solar insolation, winds, tides and freshwater input. This variability in forcing leads to the development of distinct water masses of different hydrographic properties in both vertical and horizontal dimensions. For example, because of these forcing factors the upper ocean is generally regarded as being lower in density, well mixed and devoid of the nutrients needed for phytoplankton growth, while the deep ocean is generally regarded as being higher in density and nutrient rich. A boundary exists between these surface and bottom water masses that is referred to as a pycnocline (a region of rapid change in density). Because ocean density is largely dependent upon temperature and salinity, gradients in temperature (thermocline) and salinity (halocline) often coincide with the pycnocline. In general, the strength of the pycnocline increases and the vertical extent of the pycnocline decreases as one moves from an offshore ocean environment into the coastal ocean. In 'blue-water' offshore regions, there is little freshwater input. In the coastal ocean, not only can there be greater freshwater input, but also these are regions where the surface boundary layer (which responds to wind forcing) and the bottom boundary layer (which responds to tidal forcing) can interact. On a horizontal scale, ocean fronts develop where two spatially separated water masses with different hydrographic properties meet. Fronts are often characterized by sharp horizontal changes (or gradients) in temperature as well as other properties. These gradients, the pycnocline and the ocean fronts, are often regions that provide optimal growth conditions for organisms at the base of the food chain – the phytoplankton. There are frequently steep gradients in flow velocity and even reversals in flow direction associated with fronts and clines. Consequently, these regions are characterized by increased shear.

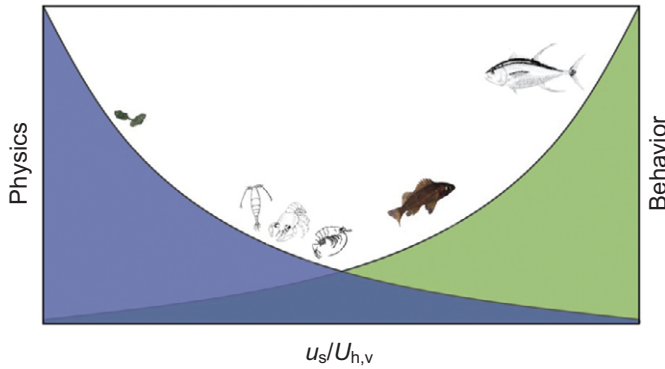


Fig. 1. Relative influence of physics and behavior in driving the distribution of organisms plotted against the ratio of swimming velocity (u_s) to characteristic velocity ($u_s/U_{v,h}$) where $U_{v,h}$ refers to vertical and horizontal flow, respectively. Organism groups are shown in approximate locations across this continuum.

Shear has been hypothesized to have a significant influence on the spatial structure of plankton patches in the ocean. Velocity shear (defined as the change in flow speed from one point in the ocean to another, divided by the distance between the two points) imparts strain on a scalar patch in the ocean (Eckhart, 1948). Vertical velocity shear, S (with units of s^{-1}), is defined as:

$$S = \partial u / \partial z \tag{1}$$

In this formulation u is the horizontal flow and z is the vertical dimension. In a two-dimensional flow with vertical variation in velocity (Fig. 2), a patch of plankton with initial dimensions (length) of L_x in the horizontal and L_z in the vertical (Fig. 2) is transported at different depth-dependent rates. The differences in transport result in the patch being strained by the sheared velocity profile and tilted (Stacey et al., 2007). Therefore, L_x grows in time. Continuity (conservation of mass) in the flow then requires that the patch be thinned vertically, as the product of L_x and L_z must be constant in the absence of changes in fluid density or mixing. It has been hypothesized that broad patches of plankton may be thinned by vertical shear due to current jets, frontal dynamics, internal waves or horizontal intrusions (Kullenberg, 1974; Franks, 1995; Stacey et al., 2007; Ryan et al., 2008). Most organisms, especially those in the plankton, cannot perceive the large-scale dynamics of the ocean. However, gradients in ocean properties at the scale of meters can be exploited through distinct behavioral responses. These behaviors, such as foraging and avoidance, when common to a population, can lead to distinct patterns in distributions across large areas of the ocean. In the following section, the important scales of organism behaviors and swimming capabilities are discussed in relation to organism size, as they transition from being passive particles to being able to determine their vertical and horizontal positions in the ocean.

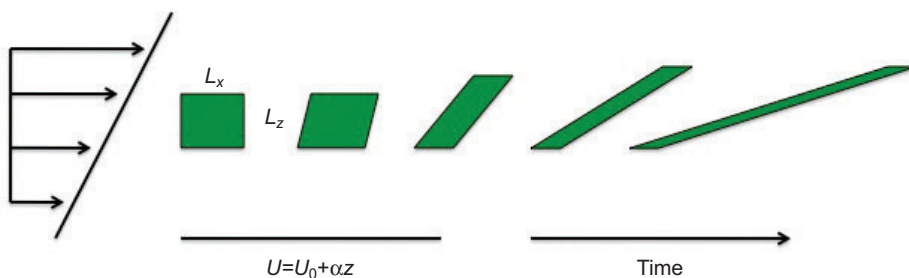


Fig. 2. A sketch of the effect of velocity shear on a patch of fluid. In a two-dimensional flow with vertical variation in velocity, a patch of plankton with initial dimensions of L_x in the horizontal and L_z in the vertical is transported at different depth-dependent rates. Redrawn from Stacey et al. (Stacey et al., 2007).

Scales of organism behavior

At microscopic scales, small organisms (e.g. viruses and bacteria) are dominated by viscous forces. Swimming speeds of these small organisms are much lower than ambient fluid velocities, and, consequently, behavioral movements have little effect on their larger scale distribution patterns. In these cases, physical processes and structure drive the observed distribution patterns. For all organisms in a fluid environment, Reynolds numbers (Re):

$$Re = u_s L / \nu \tag{2}$$

where u_s is the organism's swimming velocity, L is the organism's length and ν is kinematic viscosity, describe the relative importance of inertial ($u_s L$) and viscous (ν) forces. Similarly, characteristic velocity ratios:

$$\text{Velocity ratio} = u_s / U_{v,h} \tag{3}$$

where $U_{v,h}$ refers to vertical and horizontal flow, respectively, define the ability of an organism to swim against a flow. At the smallest scales mentioned above, Reynolds numbers and velocity ratios are typically orders of magnitude less than unity. However, as organism size and motility increase, the interaction of organism behavior with physical processes becomes more complex (Fig. 1).

Even at the modest scales of phytoplankton, interactions between behavior and hydrodynamics begin to affect the larger scale distribution patterns of the population. In these cases, Reynolds numbers and characteristic velocity ratios are still less than one. As an example, vertically swimming dinoflagellates, which are less than 0.5 mm in length and have sustained swimming speeds of less than 0.5 mm s^{-1} , can be trapped in a layer of elevated shear by gyrotactic trapping (Durham et al., 2009). In gyrotactic trapping, a weakly negatively buoyant, vertically swimming organism with a non-symmetric center of mass may encounter a critical strain rate that prevents the organism from maintaining a vertical orientation. If this critical strain rate is exceeded, the swimming behavior leads to a spiraling pattern and aggregation of multiple organisms. Even if the critical strain rate is not exceeded, accumulation of phytoplankton in regions of low flow (e.g. Stacey et al., 2007; Ryan et al., 2008) and diel migration of dinoflagellates between light and nutrient resources can lead to significant changes in the spatial structure and vertical location of entire phytoplankton populations (Cheriton et al., 2009; Sullivan et al., 2010b). For example, in 2005 a team of oceanographers participating in the Layered Organization in the Coastal Ocean Program in northern Monterey Bay, CA, USA, observed vertical movement of the distribution of an entire population of dinoflagellates. The highly motile dinoflagellate species *Akashiwo sanguinea* exhibited a diurnal vertical migration pattern, with daytime distributions near the surface where light levels were sufficient for photosynthesis, and night-time distributions at the pycnocline where nutrient levels were increased relative to the surface (Cheriton et al., 2009; Sullivan et al., 2010b).

Moving up a trophic level, at the sizes of small zooplankton, Reynolds numbers and characteristic velocity scales are transitional and of similar order to unity (0.1–10.0). For these organisms active behaviors, such as vertical movement to maintain depth and foraging in the vertical, can form aggregations (Wolanski and Hamner, 1988; Turchin, 1991; Genin, 2004). Many species of copepods exhibit elaborate hierarchical foraging behaviors involving specific responses to velocity shear, density gradients and food resources. Such behavioral hierarchy suggests that copepod foraging is cued into the oceanographic mechanisms that lead to plankton patchiness (Woodson et al., 2005; Woodson et al., 2007). Such behaviors suggest that copepods can utilize physical cues to identify regions where there is higher probability of prey resources. However, shear does not induce feeding behavior, and additional cues (e.g. chemical exudates from photosynthesis, food presence, etc.) are required to induce feeding (Woodson et al., 2007). Foraging behaviors can lead to aggregation in food resource patches (Menden-Deuer and Grunbaum, 2006; Woodson et al., 2007), and to movement into regions with reduced flows. Organisms that maintain their position in regions of reduced flow would be transported horizontally shorter distances than those organisms outside regions with reduced flow (McManus et al., 2005) (reviewed by Woodson and McManus, 2007).

The vertical characteristic velocity ratio (u_s/U_v) for small zooplankters, including marine invertebrate larvae, is typically one or larger. These organisms can actively swim against vertical flows to maintain their position near convergent fronts, propagating internal tidal bores, within pycnoclines or near the bottom (Forward and Tankersley, 2001; Pineda, 1999; Genin, 2004; Genin et al., 2005). Such behaviors can lead to aggregation and distinct distribution patterns among zooplankton. This ability also allows zooplankters to exploit flows associated with tides and other periodic motions to enhance directed transport (Forward and Tankersley, 2001; Naylor, 2006). The ability to maintain vertical position will also be influenced by the amount of turbulence in the water column (McManus et al., 2003). In a study undertaken in a small fjord off the coast of Washington State, researchers observed persistent subsurface aggregations of mysids (see section entitled ‘Thin plankton layers’). The authors suggested that the mysids were actively migrating to the pycnocline to produce this aggregation. The subsurface aggregations were temporarily dispersed only when turbulence was enhanced as a consequence of the passage of solitons (e.g. solitary internal waves). In other words, the aggregations were maintained when the mysid migration speeds were greater than the vertical velocities associated with active mixing and turbulence, and the animal aggregations broke down when the vertical mixing was greater than the animal’s migration speed. The disturbance by the passage of solitons was only temporary and the aggregations of mysids reformed in less than an hour (McManus et al., 2003).

For larger animals living at larger spatial scales, behavior may drive observed patterns in organism distribution. For these organisms, Re and velocity ratios are much greater than unity. Most small fishes can sustain a swimming speed of tens of cm s^{-1} except during very early pelagic life stages. These velocities are orders of magnitude larger than the observed sustained vertical velocities in the ocean (which are on the order of 1 mm s^{-1}), with rare exceptions observed during intermittent large surface wave events, internal waves and intense wind-driven turbulence (e.g. D’Asaro et al., 2007). For these larger organisms, behaviors ranging from foraging to predator avoidance, mating and migration are the dominant factors influencing population distributions (Fig. 1). It should be

noted, however, that foraging responses of larger organisms to lower trophic level prey tie these distributions to the ocean physics that drive patterns at smaller scales, the importance and prevalence of which are described in the next section.

Pattern and distribution in the ocean

Even with its immense productivity, the oceans of the world have relatively low production across much of their domain. Basic scaling of the ocean environment suggests that a well-mixed euphotic zone could not support the high levels of production observed (Mullin and Brooks, 1976). From micro-organisms to phytoplankton, nutrient resources would be too low to support substantial growth. At increased spatial and temporal scales, if the ocean properties were homogeneous, small grazing organisms (e.g. copepods, krill, sardines, anchovies) would not be able to meet energetic requirements (Mullin and Brooks, 1976). For example, if the ocean were well mixed, individual prey items for many zooplankton would be of the order of 10–100 cm apart with no cues for the detection of additional prey particles given an encounter with an initial prey item. An individual copepod needs to locate of the order of 1000 prey items each day just to meet energetic requirements. Fortunately, for marine organisms (and fisherfolk), the ocean is highly structured as a result of basic hydrodynamics, and it is this structure, coupled with organism behavior, that drives the patchiness of predators and prey alike (e.g. Wolanski and Hamner, 1988; Daro, 1988; Genin, 2004), which in turn fuels the bountiful productivity of marine ecosystems.

In addition to the high level of patchiness across multiple scales in the ocean, spatial scaling is not isotropic because vertical scales are highly compressed relative to horizontal scales. This asymmetry in spatial scales is due to the fact that (1) ocean basins are broad and shallow (e.g. with dominant width scales of ~10,000 km and mean depths of 4 km), (2) changes in density caused by variations in temperature and salinity can confine vertical fluid motion, and (3) photosynthetically active radiation (PAR), which is the light that photosynthetic organisms use for growth, decays exponentially from the surface with depth. Consequently, patchiness and ocean structure in the vertical is of the order of meters. Small organisms in the ocean have evolved to exploit this asymmetry such that most zooplankton and smaller organisms forage using vertical migrations and larger organisms often employ both vertical and horizontal searches for prey and resources. Ocean structure that provides an environment for biological patchiness is common in the vertical as well as the horizontal despite the disparity in spatial scales. This disparity simply implies that organisms of different size and behavioral capabilities exploit vertical and horizontal structure differently. As an example, ocean fronts develop where two spatially separated water masses with different hydrographic properties meet. These areas are known as biological hotspots for many higher trophic level organisms. We expand upon this example in the following section.

We would like to emphasize that the goal of this manuscript is to convey the notion that the spatial distributions of organisms in the ocean (from the smallest plankton to the largest predators) are determined by interactions between organism behavior and physical oceanographic structure and processes. We discuss two examples (thin layers and persistent fronts) that demonstrate these interactions; however, there are numerous other examples that could have been used, for example ocean eddies or aggregations of organisms at the interface of the internal tidal bores. We have chosen thin layers and persistent fronts as examples because over the past two decades we have played crucial roles in the discovery and quantification of these features.

Persistent fronts

Fronts, common features of all marine ecosystems from estuaries to the open ocean, are formed by a variety of physical mechanisms. For many decades, the scientific community has known that life forms as diverse as phytoplankton, crustaceans, fish, marine mammals and birds alter their distribution in the presence of oceanic fronts (Pingree et al., 1975; Owen, 1981; Le Fevre, 1986). However, it has been shown only recently that ocean fronts [which have previously been linked to larval recruitment (Roughgarden et al., 1991; Wing et al., 1995)] when ‘persistent’ can drive recruitment patterns across large spatial scales over time scales of nearly a decade (Woodson et al., 2012). Persistent ocean fronts, which are common in upwelling regions near changes in topography and bathymetry, can have gradients in physical, chemical and/or biological properties. Persistence through time leads to both passive and behavioral accumulation of organisms. These persistent ocean fronts play important roles in the connectivity of marine populations and, in turn, the spatial distribution of entire marine ecosystems.

Many intertidal and benthic marine species have a planktonic larval phase, and populations in the intertidal zone are heavily influenced by the supply of these larvae (Paine, 1966; Dayton, 1971; Caley et al., 1996; Connolly and Roughgarden, 1998). Larvae are released into the water where they are transported and dispersed by oceanographic processes. Larvae then return to adult habitats after a planktonic stage, which may range from a few hours to several months depending upon the species and the environmental conditions. Convergent fronts, which are present in many coastal waters, have been shown to aggregate organisms that are passive or have weak swimming capability (e.g. phytoplankton). Because of reduced mixing, elevated nutrients and adequate light levels, ocean fronts can also be regions of enhanced phytoplankton growth. The resulting increased phytoplankton biomass at ocean fronts can lead to the active aggregation of stronger swimming organisms searching for food [e.g. larvae, zooplankton and larger predators (Bjorkstedt et al., 2002; Genin, 2004; Genin et al., 2005; Landaeta and Castro, 2006; Woodson and McManus, 2007)]. Because of the increased food resources at ocean fronts, stronger swimming organisms spend a longer percentage of time foraging in these regions and, as a result, their relative dispersal distances can be decreased (Woodson and McManus, 2007).

Using 8 years of satellite sea surface temperature (Fig. 3) and chlorophyll *a* imagery (which is a standard proxy for phytoplankton concentration), in addition to an 8 year time series of recruitment data for both barnacle and rockfish larvae from the Partnership for Interdisciplinary Studies of Coastal Oceans program, Woodson et al. (Woodson et al., 2012) found that coastal ocean fronts that maintained their average spatial location over periods of years are correlated with regions of high chlorophyll concentration, as well as increased recruitment of invertebrate and fish species across the entire California Current Large Marine Ecosystem (CCLME). The CCLME is located along the west coast of the US, in the eastern Pacific. It extends between 32°N and 46°N, covering a distance of 1810 km. Woodson et al. (Woodson et al., 2012) found positive correlations between the long-term (8 year) location of persistent fronts and the recruitment of the larvae of important community-building and commercially important species. The novel part of this study is the ability to identify regions with fronts that recur across time scales of nearly a decade, and to relate these features to the dispersal and recruitment of plankton. This type of long-term assessment was not previously possible. With new knowledge of the long-term persistence of these features, combined with our understanding of the behavioral response of larvae (and other

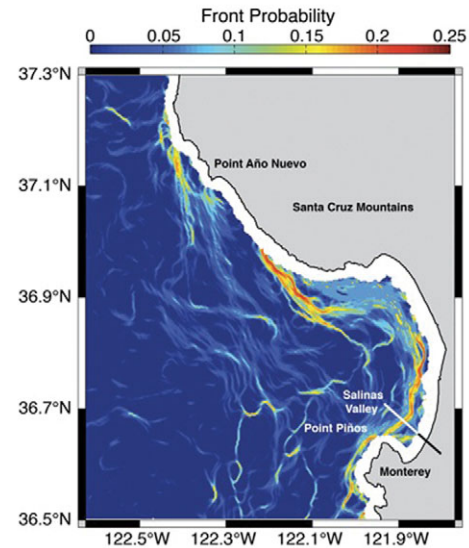


Fig. 3. Front probability for Monterey Bay region for a 2 week period in June 2007 computed using the probabilistic method described in Woodson et al. (Woodson et al., 2012).

organisms) to these features, we can make a better estimate of the dispersal patterns of plankton and recruitment of larvae in the marine environment, and the resilience of marine ecosystems.

Thin plankton layers

It is common to have a subsurface stratified region (or a pycnocline) trailing estuarine fronts, near-shore upwelling fronts and tidal mixing (shelf-sea) fronts. Within the coastal marine environment, planktonic organisms frequently congregate below the surface in the base of the pycnocline in vertically thin layers (Fig. 4). While of limited vertical extent (usually <3 m), these thin plankton layers can persist in the marine environment over large temporal and horizontal spatial scales and often contain concentrations of organisms several orders of magnitude greater than those above and below the layer (Sullivan et al., 2010a).

Previously undetectable, thin layers are now observable as a result of advances in high resolution sampling methods and technology. Results from two decades of research reveal that thin plankton layers are a crucial component of marine ecosystem dynamics. Far from being unusual or rare, thin layers of plankton are common features and can be found in a wide variety of environments (Bjornsen and Nielsen, 1991; Donaghay et al., 1992; Cowles and Desiderio, 1993; Dekshenieks et al., 2001; Cowles, 2003; McManus et al., 2003; McManus et al., 2005; Cheriton et al., 2007; McManus et al., 2008; Ryan et al., 2008; Cheriton et al., 2009; Ryan et al., 2010). Thin plankton layers have been shown to contain up to 75% of the total biomass in the water column (Holliday et al., 2010; Sullivan et al., 2010b). Thus, they can be concentrated areas of intense biological activity (Sullivan et al., 2010a).

In order to understand the formation, maintenance and dissipation of a thin planktonic layer, one must consider the physical, chemical and biological mechanisms acting in concert on a layer. For thin layers to form and persist in the marine environment, the divergent processes acting on the layer cannot exceed the convergent processes (Osborn, 1998; McManus et al., 2003; Stacey et al., 2007). Convergent and divergent processes can be physical or biological. Some examples of convergent processes

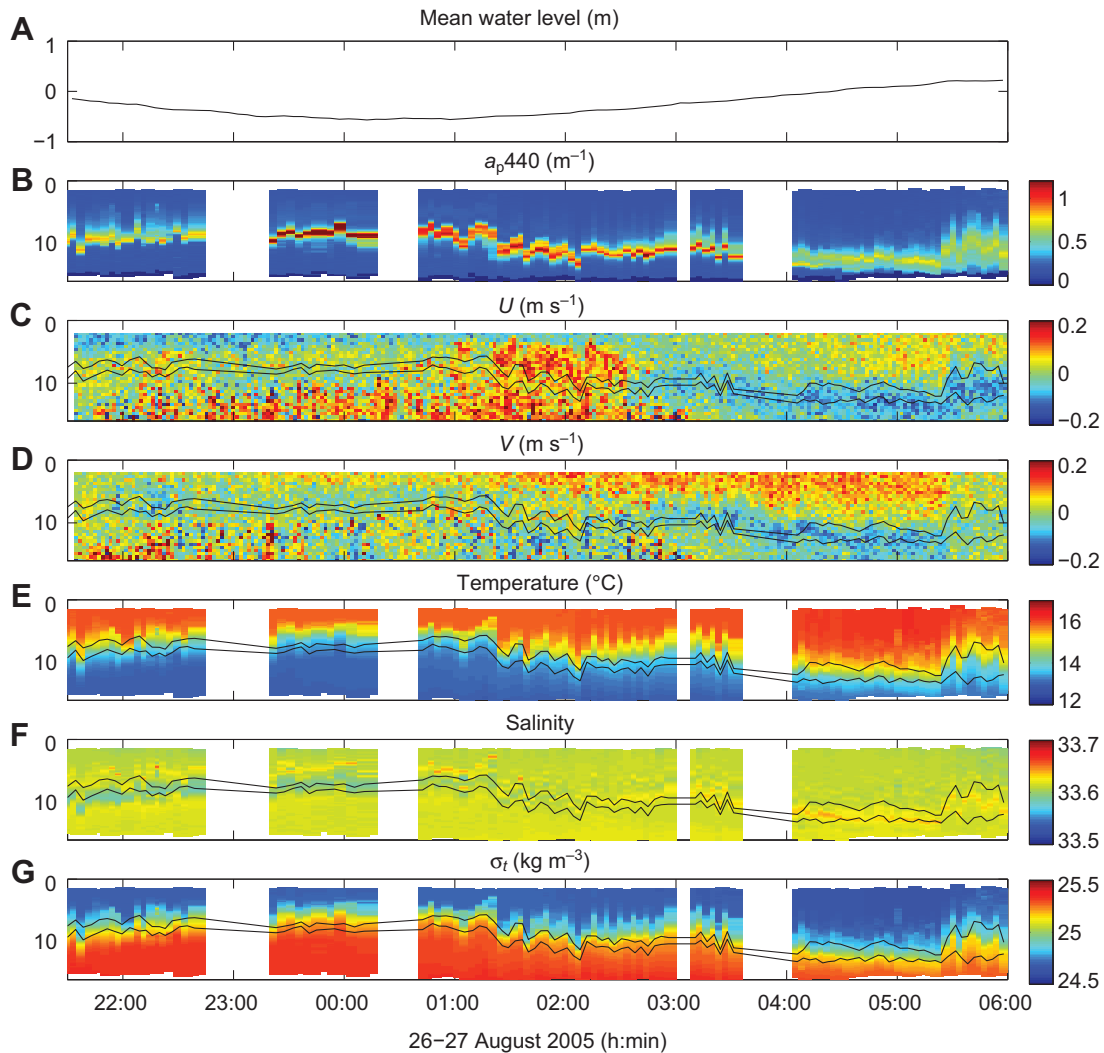


Fig. 4. Time series of data from 21:30 h on 26 August to 06:00 h on 27 August 2005. (A) Water level (m) from a bottom-mounted acoustic Doppler current profiler (ADCP), (B) a_{p440} (m^{-1}), a proxy for phytoplankton biomass from 99 consecutive profiles (~ 4 min each) with a high-resolution profiler, (C) eastward (U) and (D) northward (V) current velocity (m s^{-1}) measured by a vessel-mounted ADCP, and high-resolution profiler measurements of (E) temperature ($^{\circ}\text{C}$), (F) salinity and (G) density (σ_t ; kg m^{-3}). Solid black lines indicate the upper and lower boundaries of the a_{p440} layer. For B–G, y-axis is depth (m). Redrawn from Cheriton et al. (Cheriton et al., 2009).

are straining by shear, as well as active swimming to physical, chemical and/or biological gradients on the part of both phytoplankton and zooplankton. Some examples of divergent processes are turbulent mixing and behavioral movement away from physical disturbances in the water column.

In 2005, Steinbeck and colleagues, working in northern Monterey Bay, examined thin subsurface layers of dinoflagellates and the small scale physical processes associated with these layers (Steinbeck et al., 2009). They found that a high dinoflagellate swimming speed was required during layer formation to overcome turbulent mixing and to match the observed formation time. However, after formation a reduced swimming speed was required to maintain the layer. Cheriton and colleagues point out that ephemeral vertical displacements of these layers caused by the passage of solitary internal waves can have a greater influence over layer maintenance than shear by straining or by organism swimming (Cheriton et al., 2009). Thus, for a model to accurately describe thin layer dynamics in an environment with internal waves, the convergent and divergent effects of the vertical

oscillations caused by internal waves must also be considered (Cheriton et al., 2009).

In a study undertaken in a small fjord off the coast of Washington State, researchers (McManus et al., 2003) observed thin subsurface layers of mesozooplankton. These researchers suggested that a biological mechanism involving migratory behavior brought mysids to the pycnocline where dense thin layers of phytoplankton were also located. The researchers observed that mesozooplankton layers were temporarily dispersed only when turbulence levels exceeded the speed of vertical migration during the passage of solitary internal waves (McManus et al., 2003). These fine-scale structures were shown to modify animal behavior. This modification of behavior and position, in turn, impacts the way marine ecosystems function.

In another undertaken in Monterey Bay in 2006, Benoit-Bird found that fish (the Pacific sardine *Sardinops sagax* and the northern anchovy *Engraulis mordax*) were attracted to zooplankton thin layers (Benoit-Bird, 2009). Fish were shown to spend significantly more time within zooplankton layers, modifying their

usual behavior when thin zooplankton layers were present. Tracks of individual fish revealed they were diving down through a zooplankton layer before spiraling slowly upwards through the layer. The upward portion of this behavior corresponded with a dramatic decrease in the intensity of acoustic scattering (a proxy for zooplankton density), resulting in the appearance of ‘holes’ in the layer, which reformed minutes after the fish departed (Benoit-Bird, 2009). The conclusion was that thin layers could have significant ecological effects throughout the food chain. As organisms increase in size, organism behavior becomes increasingly important for thin layer dynamics.

While Benoit-Bird (Benoit-Bird, 2009) discusses the temporary disruption of thin layers of zooplankton by individual predatory fish movements, she points out that the thin layers were resilient over time to the apparent foraging fish. Following the work of Huntley and Zhou (Huntley and Zhou, 2004), however, one must consider that large schools of fish might have the ability to produce enough turbulence to mix out these layered structures. Huntley and Zhou analyzed data on the hydrodynamics of swimming of 100 marine species, across a range of sizes from bacteria to blue whales (Huntley and Zhou, 2004). They concluded that turbulent energy dissipation in the presence of schooling animals could be three to four orders of magnitude greater than the background average rate of turbulent energy dissipation. Making concurrent observations of turbulence and organism distribution is quite difficult in the field (see Katija, 2012). Following the theoretical treatment of the subject by Huntley and Zhou (Huntley and Zhou, 2004), Kunze et al. (Kunze et al., 2006) and Katija (Katija, 2012) present evidence that vertically migrating organisms can enhance turbulent mixing in the water column. This could be an important source of fine-scale turbulent mixing in the ocean. It may be a key mechanism by which nutrients are periodically transported across the pycnocline of strongly stratified systems, thus providing the fuel for the lower trophic levels that the schooling fish require for sustenance (Kunze et al., 2006).

In the most spatially comprehensive study available, thin plankton layers were identified in 2000 km of over 80,000 km of airborne LIDAR data collected from a variety of oceanic and coastal waters. The characteristics of thin layers varied over this vast spatial expanse. Many of the observed layers were self-contained features consistently <3–4 m in vertical extent, and 1–12 km in horizontal extent. Other thin layers were portions of much more spatially expansive layers that had regions where the layer became thicker, and thus were no longer classically defined as ‘thin layers’ (Churnside and Donaghay, 2009). The areas surveyed were inclusive of upwelling regions, areas with significant freshwater inflow and warm core ocean eddies.

Organism transport in fronts and clines

In a 2002 study in northern Monterey Bay, researchers (McManus et al., 2005) found that zooplankton layers – most likely composed of one species of krill, *Thysanoessa spinifera* – were located near the base of the pycnocline, either within the layer of no motion or in regions with low current velocities (<6 cm s⁻¹). These organisms are active swimmers and were most likely associated with the pycnocline because of increased phytoplankton densities in this region. Because the majority of these organisms were located in regions of the water column with low current velocities, this vertical positioning may result in a decrease in the horizontal dispersal distance of these organisms within this system. An example of the spatial coincidence between thin layers and changes in direction of horizontal current velocity is given in Fig. 5.

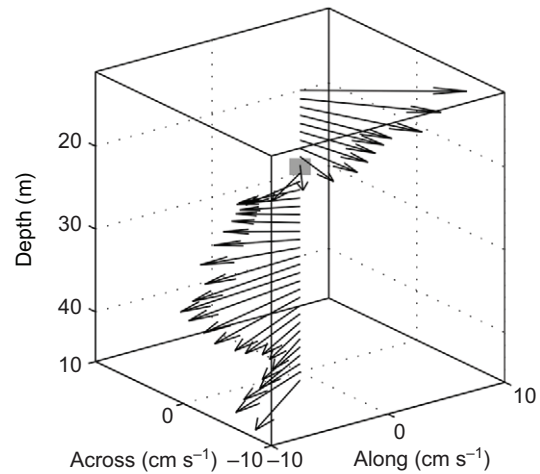


Fig. 5. An example of the spatial coincidence between thin layers and changes in the direction of horizontal current velocity in northern Monterey Bay on 6 September 2003 at 21:00 h. Velocity profiles are represented as vectors; thin layer vertical ranges are shown by the shaded bars. Redrawn from Ryan et al. (Ryan et al., 2008).

After a comprehensive review of the published literature, we (Woodson and McManus, 2007) presented a meta-analysis of horizontal dispersal distances from 59 historical oceanographic studies that concurrently documented oceanographic conditions and *in situ* organism distributions. Out of 59 studies that met their search criteria, 78% reported organism aggregations that were associated with fronts or clines (e.g. pycnocline, thermocline, halocline). These associations were consistent across multiple trophic levels, from phytoplankton to whales.

In spite of the presence of frontal jets associated with frontal features, biological accumulation is often focused at or near the region of reduced flow where high horizontal shear results from changes in flow direction. In some cases, such as shelf-break fronts, this condition extends to the sea floor and thus acts as a barrier to offshore transport throughout the water column (reviewed by Woodson and McManus, 2007). Association with such regions of low flow velocity reduces the transport and dispersal of plankton populations.

Flow reversals at fronts and clines are ubiquitous in coastal systems worldwide (Mann and Lazier, 2006). Because flows are often reduced in these regions of reversal, dispersal distances for larvae and zooplankton in these regions could be hundreds of kilometers less than many present-day dispersal estimates (Woodson and McManus, 2007). This pattern holds across several taxonomic groups of zooplankton including copepods (weak swimmers), krill (relatively strong swimmers), invertebrate larvae and fish larvae. Reduced transport implies that individual populations might be more isolated than currently accepted, and that patterns of dispersal and connectivity could be highly structured.

Modeling plankton distributions and oceanic dispersal

It has been established that marine organisms across a range of scales, from microscopic plankton to higher level predators, are located in regions of the ocean with strong physical gradients. These concurrent biological and physical distributions have tremendous implications for the physiological state of the marine organism, as well as for oceanic dispersal.

Because of their size and lifespan, it is possible to track larger predators. For example, loggerhead turtles with Argos satellite tracking tags have been followed as they traveled along a basin-wide chlorophyll front – the transition zone chlorophyll front, which is located at the boundary between the low chlorophyll subtropical gyre and the high chlorophyll subarctic gyre (Polovina et al., 2001). Because of the ability to track these animals, and locate the transition zone chlorophyll front with satellite remote sensing, we now understand that apex predators use this feature as a migratory pathway across the North Pacific (Polovina et al., 2001).

For microscopic plankton, like larvae, the task of tracking oceanic dispersal is much more complex. Coupled biological–physical oceanographic models provide one set of tools that are increasingly being used to predict larval dispersal patterns (Cowen and Sponaugle, 2009; Metaxas and Saunders, 2009). Physical oceanographic models calculate water movement and physical attributes within a study grid. Biological models, which range in complexity, attempt to mimic processes occurring during the larval lifespan. Results from coupled biological–physical numerical models show that pelagic larval duration, larval behavior and larval mortality have pronounced effects on larval distribution and dispersal patterns (Deksheniaks et al., 1996; Deksheniaks et al., 1997; Paris and Cowen, 2004; Pfeiffer-Herbert et al., 2007; North et al., 2008).

Because pelagic larval duration varies with environmental factors, species-specific models have been developed in which larval growth rate is a function of environmental factors (Deksheniaks et al., 1993). Environmental factors that have been shown to alter growth rate of a specific species in the laboratory include (but are not limited to) temperature and food concentration (Davis, 1958; Davis and Calabrese, 1964; Huntington and Miller, 1989; Olson and Olson, 1989; Pechenik, 1987; Scheltema and Williams, 1982). Model results suggest that the length of time larvae are in the water column can affect both dispersal and settlement patterns (Siegel et al., 2003).

A crucial component that is often neglected in coupled biological–physical oceanographic models is larval behavior. While many larvae are not capable of swimming against horizontal currents, they are capable of swimming vertically (Mileikovsky, 1973; Mann, 1986). The ability to change depth allows larvae to move into different strata of the water column, where current direction can differ significantly. Observations of larval behavior in the laboratory and observations of ontogenetic position in the field have been used to parameterize behavioral components for biological models (Deksheniaks et al., 1996; Pfeiffer-Herbert et al., 2007). Coupled biological–physical numerical models including larval behavior show that behavior significantly changes larval dispersal trajectories (Rothlisberg, 1983) and ultimately population connectivity (Paris et al., 2007). If larvae position themselves within fronts, and clines, it is highly likely that their dispersal distances will be much shorter than those hypothesized based upon pelagic larval duration alone (reviewed by Woodson and McManus, 2007).

The relative importance of different factors causing larval mortality (e.g. predation, starvation, physiological stress) is not known (Morgan, 1995). Mortality is often referred to as the ‘closure term’ in modeling studies (Steele, 1976; Steele and Henderson, 1992). Deksheniaks and colleagues developed a numerical model to assess the effect of different forms of size-specific and depth-dependent predation on larval survivorship (Deksheniaks et al., 1997). Three simulations were run, in which variable predation

with larval size was tested. In the first simulation, predation pressure decreased with increasing larval size. In the second simulation, predation pressure increased with increasing larval size. In the third simulation, predation pressure was constant across all larval sizes. Simulation one showed the highest survivorship when the predation pressure decreased with increasing larval size. Additional simulations showed that the interaction between vertical migration and predation determined the percentage of the cohort that survived to settlement size. The results from this modeling study reaffirm the assertion by Landry (Landry, 1976), and Steele and colleagues (Steele, 1976; Steele and Henderson, 1992) that the form of the mortality term used in models is crucial in determining the accuracy of the simulated distributions.

While coupled biological–physical oceanographic models are increasingly being used to calculate larval dispersal, there are shortcomings to this approach. First, many physical models under-resolve features of water flow that are important to community dynamics. Because of large horizontal and/or vertical grid sizes, and in some cases because of long time averaging, many physical circulation models under-resolve features like near-shore persistent fronts, vertical stratification and internal tidal bores. This is unfortunate because features like persistent fronts, vertical stratification and internal tidal bores have been associated with larval transport and recruitment in observational studies (Pineda, 1999; McManus et al., 2005; Woodson et al., 2012). In addition, because physical flows become non-linear close to shore, many physical circulation models do not extend into the inner shelf and near-shore regions. Thus, processes that would transport larvae from the shoreline to 1–2 km offshore (and back again) are not included in many modeling studies. Second, the biological components of these coupled models rarely incorporate species-specific organism behaviors that contribute to distribution patterns. This can happen for a variety of reasons. As one example – many models of basin-scale processes produce daily-averaged output. These models cannot resolve higher frequency processes like diurnal migration or foraging behavior. Another reason that these coupled models rarely incorporate species-specific organism behavior is that the behaviors are simply not known. The scientific community should make an effort to understand and quantify these behaviors, whenever possible. For, without these capabilities, calculated larval dispersal patterns may be incorrect. It is important to remember that this is an iterative process, which requires ongoing discussions between ecologists, oceanographers and modelers. With each new study, our scientific community gets a step closer to the answer (Galindo et al., 2010).

Review and conclusions

In this contribution, we have highlighted how persistent mesoscale and fine-scale physical structures in the ocean, coupled with passive and active organism responses, lead to persistent structures in marine populations (Deksheniaks et al., 2001; Woodson and McManus, 2007; Sullivan et al., 2010a; Woodson et al., 2012).

The ocean is highly structured as a result of basic hydrodynamics, both horizontally and the vertically – this structure is most pronounced in coastal waters. For example, in a horizontal plane when two water masses with different hydrographic properties meet, there is a high probability one will encounter an ocean front. Because of reduced mixing, elevated nutrients and adequate light levels in these areas, ocean fronts can be regions of enhanced phytoplankton growth. The resulting increased phytoplankton biomass at ocean fronts can lead to the active aggregation of stronger swimming organisms searching for food

(Bjorkstedt et al., 2002; Genin, 2004; Genin et al., 2005; Landaeta and Castro, 2006). As a second example, it is common to have a vertically stratified region (e.g. a pycnocline) trailing many types of fronts. These regions, which also provide optimal conditions for phytoplankton growth, can be regions of enhanced phytoplankton biomass as a result of both passive and active organism responses (Pingree et al., 1975; Sullivan et al., 2010a). Stronger swimming organisms, like zooplankton, spend a longer percentage of time foraging in these regions of enhanced phytoplankton biomass. In both examples, it is a combination of physical processes, and both passive and active biological responses that create structured planktonic populations (Sullivan et al., 2010a; Sullivan et al., 2010b). Larger predators respond to planktonic aggregations in fronts and clines, creating biological hotspots (Owen, 1981; Polovina et al., 2001; Woodson and McManus, 2007; Benoit-Bird, 2009).

Flow reversals at fronts and clines are ubiquitous in coastal systems worldwide (Mann and Lazier, 2006). Because flows are often reduced in these regions of reversal, dispersal distances for larvae and zooplankton in these regions could be hundreds of kilometers less than many present-day dispersal estimates (Woodson and McManus, 2007). Reduced transport implies that individual populations might be more isolated than currently believed, or that patterns of dispersal and connectivity may be highly structured (Woodson et al., 2012). Because of this research, we now have a mechanistic understanding of how organism behavior in response to the physical environment produces fine-scale and mesoscale planktonic aggregations, which has a direct impact on the way marine ecosystems function.

This mechanistic understanding can be applied to coupled biological–physical oceanographic models, which are one set of tools increasingly being used to predict larval dispersal patterns. A crucial component needed to more accurately predict larval dispersal patterns is larval behavior (Galindo et al., 2010). While many larvae are not capable of swimming against horizontal currents, they are capable of swimming in the vertical (Mileikovsky, 1973; Mann, 1986). The ability to change depth vertically allows larvae to move into different strata of the water column, where current direction can differ significantly. Coupled biological–physical numerical models including larval behavior show that behavior significantly changes larval dispersal trajectories (Rothlisberg, 1983), and ultimately population connectivity (Paris et al., 2007).

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