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A Satellite-Based Lagrangian View on Phytoplankton Dynamics

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Keywords

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Abstract

The well-lit upper layer of the open ocean is a dynamical environment that
hosts approximately half of global primary production. In the remote parts
of this environment, distant from the coast and from the seabed, there
is no obvious spatially fixed reference frame for describing the dynamics
of the microscopic drifting organisms responsible for this immense pro-
duction of organic matter—the phytoplankton. Thus, a natural perspective
for studying phytoplankton dynamics is to follow the trajectories of water
parcels in which the organisms are embedded. With the advent of satellite
oceanography, this Lagrangian perspective has provided valuable informa-
tion on different aspects of phytoplankton dynamics, including bloom ini-
tiation and termination, spatial distribution patterns, biodiversity, export of
carbon to the deep ocean, and, more recently, bottom-up mechanisms that
affect the distribution and behavior of higher-trophic-level organisms. Up-
coming submesoscale-resolving satellite observations and swarms of autono-
mous platforms open the way to the integration of vertical dynamics into the
Lagrangian view of phytoplankton dynamics.

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1. INTRODUCTION

In contrast to terrestrial ecosystems, where environmental conditions are spatially constrained by almost static physical features (such as topographic and bathymetric reliefs; Turner 1989) that change over timescales that are much longer than the biological ones, organisms in the open ocean interact with a highly dynamical landscape (Lévy et al. 2015). Although this landscape involves processes that span a wide range of spatial and temporal scales (Ferrari & Wunsch 2009), when looking at ecological processes, the mesoscale and submesoscale (~1–100 km, hereafter referred to as the fine scale; McGillicuddy 2016, Mahadevan 2016) emerge as dominant structuring regimes for populations of marine organisms. A major reason for this association is that the typical timescales of the dynamical processes (days to months) encompass key biologically relevant processes, such as plankton division times and bloom durations or foraging trips and behavioral switches of marine predators. The notion of dynamical landscape is especially relevant for drifting organisms (plankton) that are advected and dispersed by the ocean currents (McManus & Woodson 2011). Accordingly, the temporal resonance between fine-scale dynamics and ocean biology is at the core of plankton patchiness, which inherits the whirling and filamentary form of the subjacent physics (Martin 2003).

Since the launch of the Coastal Zone Color Scanner (CZCS) in October 1978 (Yoder et al. 1987) and the Geodetic Satellite (GEOSAT) in 1985 (Le Traon et al. 1998), ocean color and altimetry satellites have provided a continuous and spatially synoptic view of the planktonic ecosystem and the oceanic flow in which it is embedded. This unique perspective has opened the way to detailed characterization of phytoplankton variability and its association with fine-scale ocean dynamics (Siegel et al. 2008, Chelton et al. 2011, Gaube et al. 2013). A common feature in these satellite-based observations is the presence of fine-scale patches of elevated phytoplankton concentrations, which coincide with mesoscale eddies and filaments (**Figure 1**). These fine-scale patches constitute what can be referred to as drifting forests, in which the pelagic life of primary producers, grazers, and predators—including fisheries and endangered species—takes place.

Because the planktonic system is embedded within a dynamical landscape with overlapping timescales, a major challenge when using satellite data to study phytoplankton dynamics is to untangle the footprint of biological processes (such as primary production, grazing, and mortality) from that of physical processes (such as advection, stirring, and mixing). In recent years, much progress has been made in addressing this challenge through Lagrangian analysis methods that describe the changes in water properties along particle trajectories. Because the dynamics of phytoplanktonic cells occurs in drifting water parcels, a Lagrangian viewpoint that takes into account the effect of advection by the currents is approximating a fixed-in-space (Eulerian) viewpoint on the dynamics of terrestrial ecosystems.

This article reviews the ways in which the application of Lagrangian concepts to the analysis and interpretation of satellite data contributes to our understanding of phytoplankton dynamics and its interaction with the oceanic flow. We first review some of the principles behind Lagrangian diagnostics of satellite-derives oceanic flows. We then demonstrate how Lagrangian methods are used to study processes that control the spatial and temporal evolution of fine-scale planktonic systems and to characterize bottom-up mechanisms that affect the distribution and behavior of higher-trophic-level organisms. Limitations of Lagrangian methods and avenues for future research are discussed at the end.

2. LAGRANGIAN DETECTION OF STIRRING STRUCTURES

The 1–100-km ocean dynamics (fine scale) is associated with a peak in the energy spectrum of ocean turbulence (Ferrari & Wunsch 2009). How does this peak translate in biotic or abiotic
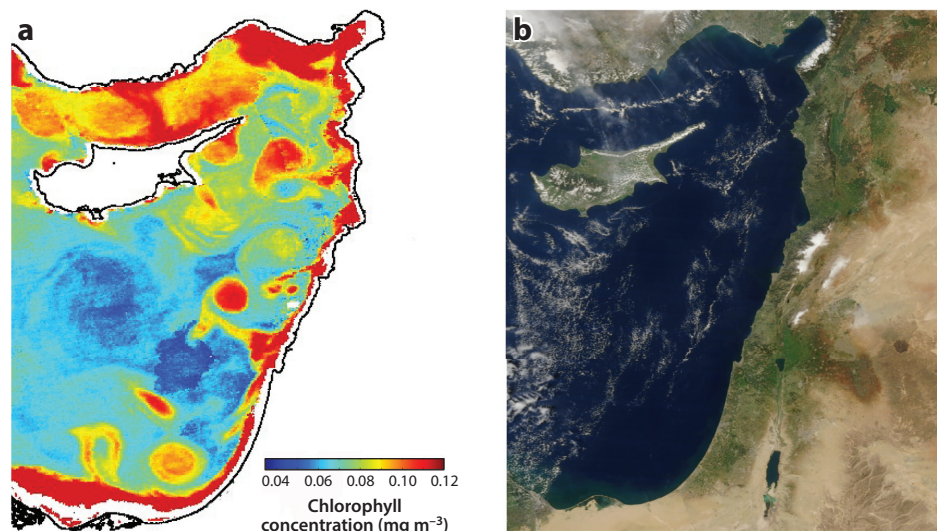
Figure 1

Two images of the eastern Mediterranean. Panel *a* shows a satellite-based map of surface chlorophyll concentrations, with patches of elevated phytoplankton biomass embedded within the ultra-oligotrophic waters. The morphology of these patches is dictated by the ocean currents, thus reflecting dynamical features as eddies and fronts. The typical lifetime of the plankton patches is weeks to months. A terrestrial analogue to these phytoplankton patches would be regions of elevated biomass surrounded by desert, as observed in the true-color satellite image from the same region shown in panel *b*. The plankton patches are advected and deformed by the currents, whereas their terrestrial equivalents are stationary over timescales of hundreds to thousands of years.

tracer variability? Part of the answer lies in the way in which the fine-scale dynamics determines the trajectories of the water parcels, redistributing their biotic and abiotic content in space and time. The study of these transport mechanisms has a natural framework with Lagrangian methods, which provide a description of the flow along its particle trajectories. This approach is similar to describing the property of the flow following an object that does not have active motion and therefore drifts, transported along current trajectories. Lagrangian methods saw a giant leap forward to oceanographic applications in the 1990s, when the retrievals of surface currents from satellite altimetry data (Le Traon et al. 1998) started to provide information with the spatial and temporal continuity required for computing numerical particle trajectories. The availability of these observational data has opened the way to the application of dynamical system theory (Ottino 1989, Wiggins 2005) as a way to understand the mechanisms behind the distribution patterns of oceanic tracers (Abraham & Bowen 2002, Waugh & Abraham 2008).

Because the ocean is a turbulent and chaotic system, plotting trajectories of arrays of virtual drifters advected by the satellite-derived velocity field results in a so-called spaghetti diagram—a set of convoluted lines that appear to be random. Nevertheless, computing statistical quantities over single trajectories or ensembles of trajectories can provide an accurate description of the velocity field transport properties. An important concept in the study of the transport properties of oceanic flows is that of Lagrangian coherent structures, which refers to core geometrical features around which Lagrangian trajectories organize (Haller & Yuan 2000, Beron-Vera et al. 2008; for a review, see Haller 2015). A widely used application of the Lagrangian coherent structure concept is the identification of transport barriers (Boffetta et al. 2001)—also called, in this context, Lagrangian fronts (Prants et al. 2014a,b)—which often coincide with tracer fronts and confluence lines (Haller

& Poje 1998, Shadden et al. 2005, Lehahn et al. 2007, Mathur et al. 2007, Haller 2011, Haller & Beron-Vera 2012). Other features that can be detected by following real or virtual trajectories and quantifying their statistical properties are retention regions (regions whose content is slowly exchanged with the surrounding waters; d'Ovidio et al. 2013), regions where strong dispersion occurs (Carlson et al. 2010, Haza et al. 2012, Poje et al. 2014), and transport pathways (Sandulescu et al. 2006, Rossi et al. 2008, d'Ovidio et al. 2015; in particular, see the review Griffa et al. 2013).

Lagrangian analysis of satellite altimetry data, in particular the extraction of Lagrangian coherent structures, can thus provide valuable information about the transport properties of fine-scale oceanic velocity fields. Borrowed from atmospheric studies (Pierrehumbert & Yang 1993, Koh & Legras 2002), a widespread mathematical technique for extracting this Lagrangian information and applying it to investigate different aspects of ocean ecology and biogeochemistry is the calculation of the Lyapunov exponent. The Lyapunov exponent, calculated over finite time or finite size (Boffetta et al. 2001, d'Ovidio et al. 2004, Shadden et al. 2005), quantifies exponential rates of deformation of water parcels. When computed backward in time, it permits one to identify the parcels that have undergone strong filamentation, which typically occurs along fronts and at the peripheries of eddies. A map of Lyapunov exponents typically shows Lyapunov maxima organized in ridges, which can be interpreted as regions where stirring is maximal. Ridges of Lyapunov maxima serve to identify tracer fronts and transport barriers. Other mathematical methods for computing Lagrangian coherent structures have also been proposed (Mancho et al. 2004, Mendoza & Mancho 2010, Haller & Beron-Vera 2012, Mundel et al. 2014).

In addition to satellite-based retrievals, Lagrangian information for phytoplankton studies is commonly derived from surface drifters that consist, at a minimum, of a floating body with a positioning system [typically a Global Positioning System (GPS) device]. Lagrangian drifters are often equipped with hydrographic instruments and in some cases include a subsurface drogue (Niiler et al. 1995, LaCasce 2008, Lumpkin et al. 2017). Nowadays, thousands of drifters occupy the global ocean at a given time, with an increase in number during periods of extensive regional studies [e.g., the Grand Lagrangian Deployment (GLAD) and Consortium for Advanced Research on Transport of Hydrocarbon in the Environment (CARTHE) experiments; Olascoaga et al. 2013, Mariano et al. 2016]. However, surface drifters can be considered the ground truth of numerical trajectories in Lagrangian studies, with some caveats. Because of the chaotic nature of the ocean and the fact that ocean currents include components that are not resolved in model or satellite data, individual drifter trajectories are expected to diverge from the trajectories of their numerical analogues, even at the mesoscale (as, in fact, two numerical trajectories starting at the same position also do if noise is added when they are generated). Altimetry-derived features and real trajectories, however, are consistent when drifters are released in the vicinity of attractive Lagrangian coherent structures (Poje et al. 2002, Resplandy et al. 2009, Nencioli et al. 2011, Schroeder et al. 2012, Olascoaga et al. 2013), usually remaining collocated at a distance of ∼10 km for several days. Even better results may be obtained when high-resolution radar observations are available (Shadden et al. 2009). Another useful way of quantitatively comparing drifter information with altimetry data or model output is to extract statistics over a large number of trajectories (Lacorata et al. 2001, Poje et al. 2014, Beron-Vera & LaCasce 2016, Berta et al. 2016).

3. SPATIAL STRUCTURING OF THE PHYTOPLANKTONIC LANDSCAPE

3.1. Spatial Distribution Patterns

It has long been acknowledged that horizontal stirring and mixing control, to a large extent, fine-scale phytoplankton distribution (Gower et al. 1980). Taking an Eulerian approach, many works
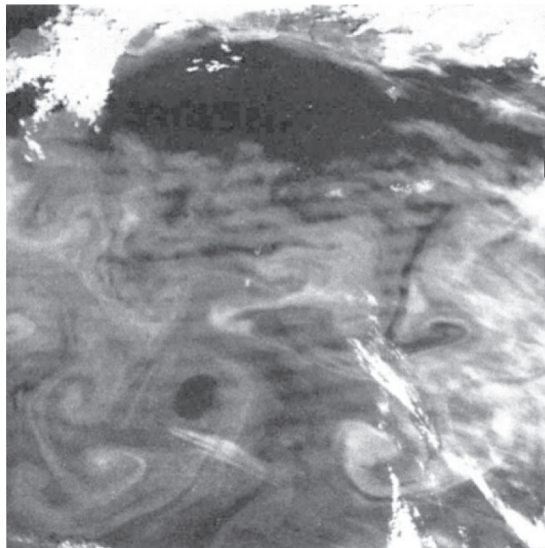
Figure 2

A Landsat image from June 1976, showing fine-scale patterns of enhanced sea surface reflectance over the North Atlantic. Based on the power spectrum slope, the reflectance patterns were interpreted as being associated with phytoplankton blooms advected by the turbulent oceanic flow. This Eulerian diagnostic provided some of the first satellite-based evidence of the structuring role of the surface currents. Reproduced from Gower et al. (1980) with permission.

have identified this dependency by characterizing spatial heterogeneity in phytoplankton distribution, as observed in discrete snapshots of satellite data. Useful methods for such characterization include spectral analysis, semivariogram analysis, autocorrelation analysis, and patchiness analysis (Platt & Denman 1975; Gower et al. 1980; Yoder et al. 1987, 1993; Denman & Abbott 1988; Piontkovski et al. 1997; Washburn et al. 1998; Mahadevan & Campbell 2002). Spatial characteristics of phytoplankton are often compared with those of nonbiological scalars such as sea surface temperature, thus providing information on the contribution of other processes to spatial structuring of phytoplankton distribution (Mahadevan & Campbell 2002). In their pioneering work, Gower et al. (1980) identified fine-scale patterns of surface chlorophyll in images taken by the high-resolution satellite Landsat (**Figure 2**). Based on the power spectrum slope of the remotely sensed chlorophyll field, the authors deduced that phytoplankton distribution is controlled by advection by the currents and is not affected by the biological process of reproduction.

The application of Lagrangian analysis methods to study the structuring effect of horizontal stirring is often based on tracking of distinct chlorophyll patches, as observed in series of ocean color satellite images (Toner et al. 2003, Lehahn et al. 2007, Olascoaga et al. 2008, Calil & Richards 2010, Calil et al. 2011, Guidi et al. 2012, Huhn et al. 2012, d'Ovidio et al. 2015). These patches are characterized by a typical length scale of between ∼100 and ∼1,000 km (**Figure 3**). The pattern formation mechanism is characterized by comparing the time-varying morphology of the chlorophyll patches with the spatial distribution patterns of synthetic particles that are numerically advected by the observed or modeled velocity field. A complementary diagnostic is based on comparing colocalization of chlorophyll fronts and Lagrangian coherent structures calculated from the satellite-derived velocity field. These diagnostic methods are useful in tracing horizontal pathways of nutrient delivery. Specifically, nutrient dispersion pathways are spatially structured by Lagrangian coherent structures, as indicated by the fact that they match in satellite
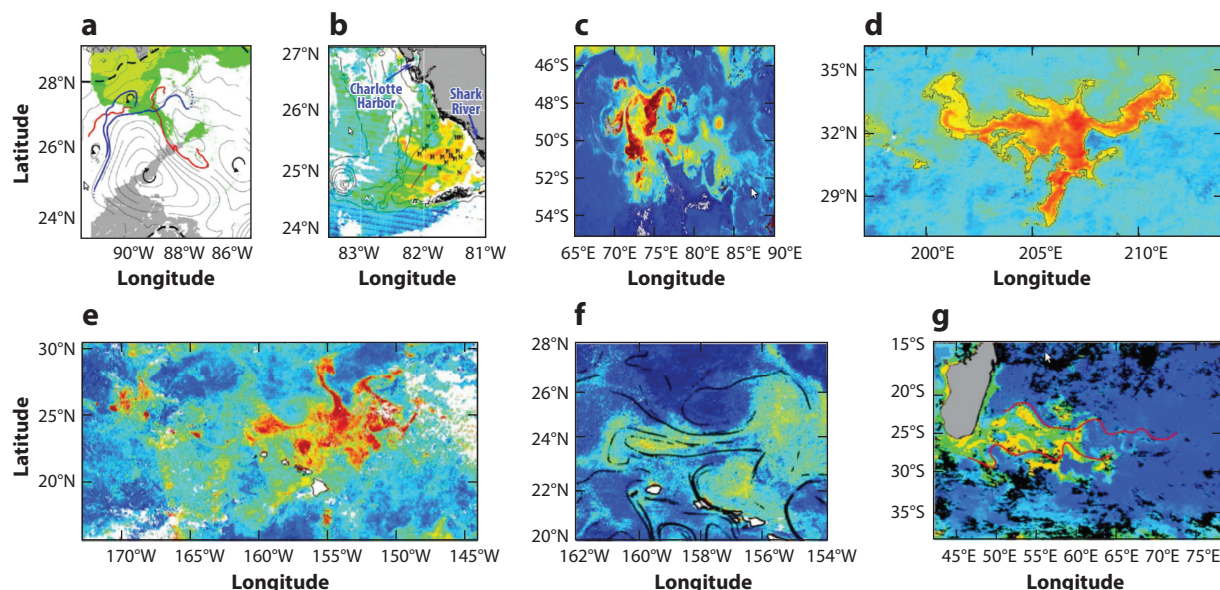
Figure 3

Examples from Lagrangian studies that analyzed the spatiotemporal evolution of phytoplankton patches, as observed in maps of satellite-derived surface chlorophyll concentrations from (*a*) the Gulf of Mexico, (*b*) the west Florida shelf, (*c*) the Kerguelen Plateau, (*d–f*) the North Pacific Subtropical Gyre, and (*g*) a western section of the Indian Ocean. The images show snapshots from the evolution of patches. These studies quantified the structuring effect of horizontal stirring by comparing the morphology of the patches with spatial distribution patterns of synthetic particles advected by the surface currents (see **Figure 4**). Colors are scaled to regional minima and maxima. Panels *a*, *b*, *e*, and *g* adapted from Toner et al. (2003), Olascoaga et al. (2008), Calil et al. (2011), and Huhn et al. (2012), respectively, with permission; panel *c* adapted from d'Ovidio et al. (2015) under the Creative Commons Attribution 3.0 Unported license (**https://creativecommons.org/licenses/by/3.0**); panel *d* adapted from Lehahn et al. (2017) under the Creative Commons Attribution 4.0 International license (**https://creativecommons.org/licenses/by/4.0**); panel *f* adapted from Guidi et al. (2012) under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported license (**https://creativecommons.org/licenses/by-nc-nd/3.0**).

data patches of high chlorophyll concentrations (Toner et al. 2003; Lehahn et al. 2007, 2017; Olascoaga et al. 2008; Calil et al. 2011; Huhn et al. 2012; Efrati et al. 2013; d'Ovidio et al. 2015) (see **Figures 3** and **4**).

The generation of particle trajectories by Lagrangian methods mimics the direct cascade to smaller scales as induced by a mesoscale eddy field for any advected tracer, including nutrients and phytoplankton (Abraham 1998). Thus, Lagrangian methods are often able to simulate the formation of submesoscale distribution patterns even from purely mesoscale velocity fields, such as the ones derived from satellite altimetry data. One example of this downscaling capability of Lagrangian techniques is the characterization of stretching of initially large-scale tracer patches that are filamented in strain regions, like at the periphery of mesoscale eddies (Lehahn et al. 2007, Beron-Vera et al. 2008).

Predictions of subgrid phytoplankton features from mesoscale velocity fields by Lagrangian methods are far from perfect, largely because they neglect the effect of unresolved submesoscale components of the velocity field on the advection and dynamics of tracers. Nevertheless, in regions where the oceanic flow has a strong mesoscale component that suppresses or entrains submesoscale current instabilities, Lagrangian diagnostics of mesoscale satellite-derived currents do remarkably well in resolving the formation of submesoscale distribution patterns because
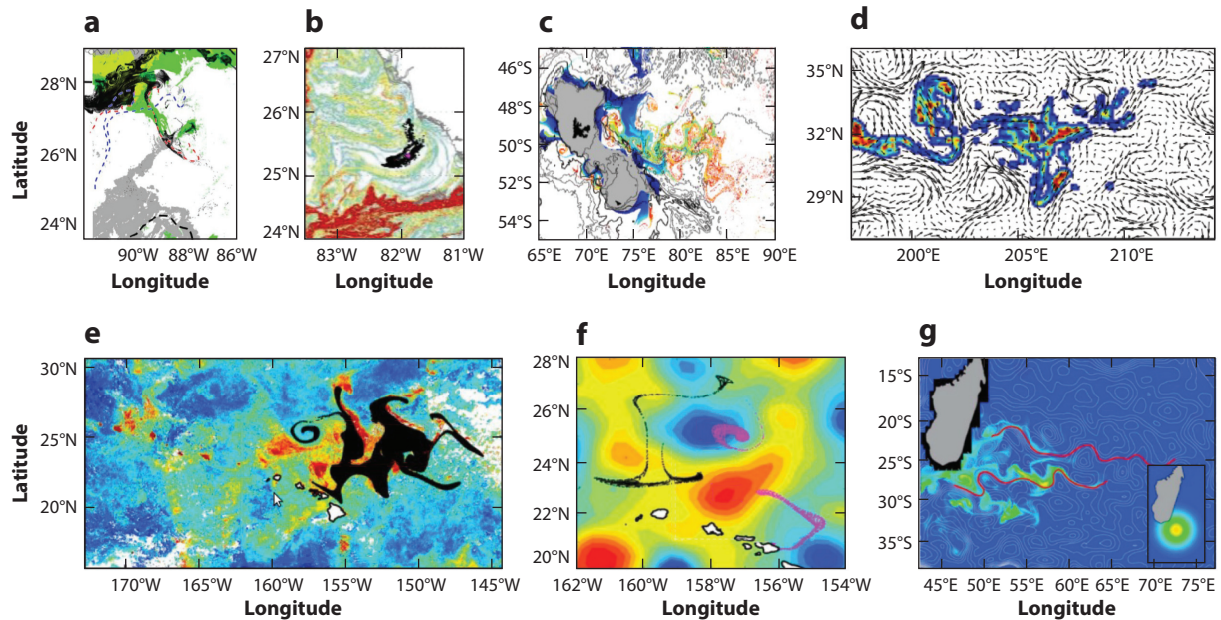
Figure 4

Snapshots from numerical experiments used to quantify the structuring effect of horizontal stirring on the chlorophyll patches shown in **Figure 3**: (*a*) the Gulf of Mexico, (*b*) the west Florida shelf, (*c*) the Kerguelen Plateau, (*d–f*) the North Pacific Subtropical Gyre, and (*g*) a western section of the Indian Ocean. The role of stirring is estimated by comparing the spatial distribution of the synthetic particles with the changing morphology of the chlorophyll patches. Colors are scaled to regional minima and maxima. Panels *a*, *b*, *e*, and *g* adapted from Toner et al. (2003), Olascoaga et al. (2008), Calil et al. (2011), and Huhn et al. (2012), respectively, with permission; panel *c* adapted from d'Ovidio et al. (2015) under the Creative Commons Attribution 3.0 Unported license (**https://creativecommons.org/licenses/by/3.0**); panel *d* adapted from Lehahn et al. (2017) under the Creative Commons Attribution 4.0 International license (**https://creativecommons.org/licenses/by/4.0**); panel *f* adapted from Guidi et al. (2012) under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported license (**https://creativecommons.org/licenses/by-nc-nd/3.0**).

Lagrangian trajectories integrate the temporal variability of the currents. In principle, trajectories that are generated by a time-invariant velocity field follow current streamlines, thus remaining trapped forever within closed tracks, as is the case at the interiors of eddies. However, because Lagrangian methods take into account that the velocity field evolves while particles are advected, when a particle completes a loop, the currents are not exactly the same as they were when the loop was initiated. Complex patterns arise from this coupling between particle motion and the temporal variability of the velocity field, rooted in dynamical systems and chaos theory (Wiggins 2005, Prants et al. 2017). Tracer leakage from recirculating features as mesoscale eddies can then be estimated by Lagrangian methods. Leakage corridors, typically in the shape of a spiral, can be identified and used to estimate the dilution rates of eddy retentive cores (Lehahn et al. 2011, Smetacek et al. 2012, d'Ovidio et al. 2013) or the connection pathways among multiple eddies (d'Ovidio et al. 2010).

One can expect that elongated nutrient pathways or phytoplankton filaments induced by horizontal stirring would eventually be mixed with their ambient waters by turbulent diffusion. Accordingly, an inverse-cascade scenario in which horizontal stirring and mixing disperse fine-scale patches over relatively large areas, thus acting to homogenize phytoplankton distribution, is also expected, a scenario that was recently observed by Lehahn et al. (2017). Based on a Lagrangian diagnostic of multisatellite data and an ecosystem model, this study showed that by reducing concentrations of nutrients, phytoplankton, and zooplankton, this dispersion or dilution process may

regulate interactions within fine-scale planktonic systems and enhance accumulation of phyto-plankton biomass in low-nutrient environments. The effect of this stirring-induced dilution can be regarded as a horizontal analogue to the effect of dilution resulting from vertical dynamics (Behrenfeld 2010, Zarubin et al. 2017).

3.2. Effects on Phytoplankton Community Structure

The structuring effect of fine-scale dynamics across upper-ocean marine ecosystems has profound consequences for the biogeochemical functioning of the ocean and the way in which we observe it. A dramatic and well-known effect is the local modulation of the vertical velocities, and therefore of the nutrient fluxes, that occurs over filaments or when mesoscale eddies dome isopycnals, or when eddies and fronts interact with the wind field. Reviews of these mechanisms can be found elsewhere (Lévy et al. 2012, Mahadevan 2016, McGillicuddy 2016). Here, we focus on a Lagrangian class of processes—namely, the way in which contrasting patches of water (generated, for example, by the nutrient flux modulation induced by the fine-scale vertical processes described above) are stirred together, keeping some of their integrity for timescales relevant to the phytoplanktonic demography. The mosaic of stirred water patches with contrasting physicochemical characteristics is inherited by the plankton community (d'Ovidio et al. 2010, Wilkins et al. 2013, Lévy et al. 2015).

Fine-scale patches with contrasting characteristics are first segregated, favoring the taxa that are best adapted to the local conditions by competition. The ocean turbulence eventually mixes these patches on timescales of days to weeks, possibly creating new assemblages and environmental conditions and therefore interfering with competition and exclusion processes. One expected result is therefore a change in the microbial community structure and, in turn, a change in the local biogeochemical functioning. Patterns resulting from this process can be explored with satellite data; several algorithms now exist that extract information on the phytoplankton community from spectral anomalies in the water-leaving radiance (Ciotti & Bricaud 2006, Uitz et al. 2006, Alvain et al. 2008, Raitsos et al. 2008, Kostadinov et al. 2009, Brewin et al. 2010, Mouw & Yoder 2010, Kurekin et al. 2014). Indeed, a mosaic of contrasting planktonic functional groups clearly driven by horizontal stirring is commonly seen at confluence regions when stirring patterns from altimetry are compared with information about phytoplankton types from ocean color satellite data (d'Ovidio et al. 2010) (**Figure 5**).

4. PROCESS STUDIES AND LAGRANGIAN TIME SERIES

A major challenge in plankton research is to extract observational time series, either from in situ measurements or from remotely sensed satellite retrievals, that reflect ecological and biogeochemical processes. Eulerian time series extracted over fixed locations provide highly useful information on low-frequency processes, such as regular basin-scale seasonal cycles in the state of the marine ecosystem (e.g., Behrenfeld 2010). However, the interpretation of higher-frequency variability patterns in these spatially fixed time series is often ambiguous, largely owing to the impact of mesoscale and submesoscale dynamics that can induce episodic events with strong contrasts occurring at temporal scales of days to weeks. Because the planktonic systems in which ecological processes occur are advected by the currents, fixed time series often do not reflect internal changes in the state of the system, but rather provide a glimpse into the state of the water parcel transported into the sampling location at the time of the measurements (e.g., Bagniewski et al. 2011, Villar et al. 2015). Lagrangian tools that follow trajectories of water parcels provide an extremely useful platform for addressing this challenge.
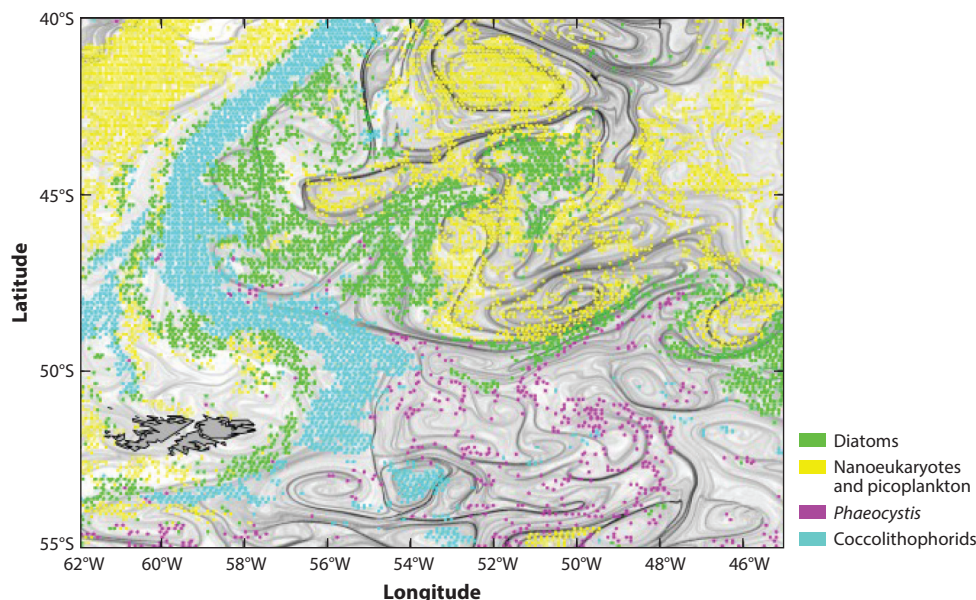
Figure 5

Patterns of putative dominant phytoplankton types as detected in satellite ocean color by the PHYSAT algorithm (Alvain et al. 2008) compared with Lagrangian fronts (*gray lines*) derived from altimetry. Green is used for diatoms, purple for *Phaeocystis*, cyan for coccolithophorids, blue for *Synechococcus*, red for *Prochlorococcus*, and yellow for nanoeukaryotes. The ecological frontiers between the patches of dominant types match well with the Lagrangian fronts, providing a strong indication of the role of stirring in structuring a mosaic of water patches with contrasting biogeochemical functioning. Adapted from d'Ovidio et al. (2010).

The most straightforward approach in this direction is the extraction of Lagrangian time series using drifting autonomous platforms that are equipped with physical, chemical, and bio-optical sensors (Lumpkin et al. 2017). However, the above-described advancements in our ability to quantify transport properties of the ocean currents have opened a way to extract Lagrangian information on bio-optical properties from satellite data. Jönsson et al. (2009, 2011) and Jönsson & Salisbury (2016) have introduced a concept that is based on integrating bio-optical data from sequential satellite images with a modeled velocity field in order to quantify changes in biogeochemical properties along particle trajectories. The approach is based on tracking virtual particles and assigning the relevant satellite data to a given particle whenever it intersects with a coincident observation. Despite possible mismatches between real and simulated water parcel trajectories (see Section 6), this methodology was successfully used to quantify variations in phytoplankton productivity over spatiotemporal scales of days and tens of kilometers, emphasizing the potential importance of episodic events in controlling phytoplankton production in coastal waters (Jönsson & Salisbury 2016).

An alternative approach for extracting Lagrangian information on bio-optical properties of phytoplankton is based on tracking distinct chlorophyll patches as observed in series of ocean color satellite images (Abraham et al. 2000; Chelton et al. 2011; Gaube et al. 2013; Lehahn et al. 2014b, 2017). The guiding principle for extracting these satellite-based Lagrangian time series is the identification of distinct water patches whose time-varying spatial characteristics can be tracked over timescales that are comparable with those of the biological processes of interest.

Under the condition that the boundaries of the patch are accurately delineated throughout its lifetime, consecutive satellite images can be used to document temporal changes in the internal physical and bio-optical properties of the water patch. Recently, applications of this approach allowed the characterization of the demise phase of phytoplankton blooms and its association with viral infection (Lehahn et al. 2014b) as well as the quantification of bloom responses to horizontal dilution (Lehahn et al. 2017).

Because both ocean color and altimetry satellite data are, in general, available in near-real time, the application of Lagrangian tools allows the planning and execution of adaptive sampling strategies (Petrenko et al. 2017), pinpointed at specific locations within water patches that are tracked throughout their lifetime. Such a pinpointed sampling strategy may substantially reduce the spatiotemporal ambiguities that arise when spatial and temporal variability are intermingled because of stirring, for instance, when a contrasting patch drifts across a sampling station. Furthermore, taking this approach also allows the interpretation of in situ measurements with respect to the physical and biogeochemical history of the sampled water patch, as observed in the satellite data.

Adaptive sampling strategies are especially useful in natural and artificial iron fertilization experiments (Coale et al. 1996, Abraham et al. 2000, Blain et al. 2007, Boyd et al. 2007, Buesseler 2012), which represent an ideal case study for exploring the biogeochemical structuring effect of the ocean currents and quantifying the evolution in time of fine-scale planktonic systems. These fertilization experiments essentially aim at connecting oceanic primary production to the pathways of a limiting resource (iron) from its known artificial or natural source to its biogeochemical fate (Robinson et al. 2014). Following a hypothesis suggested by Martin (1990), during the 1999 Southern Ocean Iron Release Experiment (SOIREE) campaign (Boyd et al. 2000), iron was added to a patch of high nutrient and low chlorophyll concentrations, leading to the formation of an artificial phytoplankton bloom and highlighting the important impact of stirring on its development (Abraham et al. 2000). Other artificial and natural iron experiments followed, including the European Iron Fertilization Experiment (EIFEX), the Loha Fertilization Experiment (LOHAFEX), and Kerguelen Ocean and Plateau Compared Study 2 (KEOPS2). These experiments attempted to track the evolution of the iron-enriched patches using Lagrangian methods that combine information from drifters with altimetry-based numerical trajectories in order to estimate various parameters of plankton dynamics and, in some cases, even the efficiency of iron fertilization in terms of carbon export to the deep ocean (Smetacek et al. 2012, Martin et al. 2013, d'Ovidio et al. 2015).

Application of Lagrangian tools to achieve a process-level understanding of planktonic systems is mostly efficient when the analysis is restricted to cores of retentive eddies (Chenillat et al. 2015, 2016), which preserve their content by minimizing exchanges with ambient waters (Provenzale 1999, d'Ovidio et al. 2013, Gaube et al. 2013). Although they are rare, highly retentive eddies (Haller & Beron-Vera 2013) with expected trapping times of several months that may overlap the entire eddy lifetime may occur, for example, when a meander of an energetic current pinches off. Such retentive eddies create a distinct transport barrier in the shape of a ring inside the energetic eddy, which in some cases delineates the boundaries of a distinct chlorophyll patch bounded within the eddy (Doglioli et al. 2006, Lehahn et al. 2011). Quasi-isolated planktonic environments trapped within retentive mesoscale eddies (Lehahn et al. 2011, 2014b) offer great opportunities for in situ experiments because they represent a case of a coherent water mass that can be tracked over a period that is comparable with that of key ecological and biogeochemical processes. In this regard, retentive mesoscale eddies can be seen as a giant equivalent of mesocosm experiments, or megacosm.

5. HIGHER TROPHIC LEVELS

The important role of horizontal stirring and Lagrangian features in structuring the spatial vari-
ability of oceanic primary producers—the phytoplankton—also translates to higher trophic levels.
As for studies of phytoplankton, application of Lagrangian approaches has proven extremely useful
when studying the ecology and behavior of higher-trophic-level marine organisms. An obvious
reason for using a Lagrangian approach to identify foraging sites stems from the fact that a lag has
to be expected between primary and higher production. This lag in time—which can vary from a
few days for aggregation processes to several months for ecosystem maturation—is reflected in a
displacement in space of the foraging site with respect to the regions where primary production
had occurred and may be tracked by Lagrangian trajectories.

Although mainly qualitative, observational evidence of this mechanism has started to emerge
in the last few years, in particular thanks to the development of animal telemetry techniques.
A dramatic example is provided by a long-range predator, the elephant seal *Mirounga leonina*,
which in the Southern Ocean during late summer forages intensively on a water mass that shows
no signature in terms of satellite-derived chlorophyll. However, tracking of the water mass using
altimetry-derived Lagrangian tools indicated that it had supported a distinct phytoplankton bloom
several months earlier. The water mass had drifted along the Antarctic Circumpolar Current for
more than 1,000 km with respect to the blooming site before it was foraged by the elephant seal
(Cotté et al. 2015) (**Figure 6**).

At a smaller scale, the association of top predators with Lagrangian coherent structures—
possibly foraging sites—is a recurrent finding across different taxa. Tew Kai et al. (2009) compared
for the first time fine-scale, Lyapunov-derived fronts with positions of a marine top predator (the
great frigatebird, *Fregata minor*) in the Mozambique Channel and found a remarkable association.
Similar relationships with Lagrangian coherent structures were also observed for frigatebirds
that were engaged in intensive foraging activity (De Monte et al. 2012). The spatial linkage
between Lagrangian features and top predators has also been observed in other species, including
Mediterranean whales, fur and elephant seals (Cotté et al. 2011, 2015; Nordstrom et al. 2013; Della
Penna et al. 2015), penguins (Bon et al. 2015, Della Penna et al. 2017), and other seabirds (Scales
et al. 2014). Lagrangian features seem to also be associated with larger catches for commercial
fisheries (Prants et al. 2014a), although it is difficult to assess how much this relationship depends
on the use of satellite images by the fishermen themselves.

The reason that predators target Lagrangian structures remains unclear. Predators consistently
forage at the fronts marking the edges of bloom patches (Polovina et al. 2001, 2017; Cotté et al.
2011; Bon et al. 2015). Besides the classic picture of enhanced production and convergence (Franks
1992, Yoder et al. 1994, Polovina et al. 2017), fronts marking the edge of a bloom may be regions
where the ecosystem is older and possibly had a longer time to mature. Another possibility is the
entrainment effect of Lagrangian fronts, which can attract trajectories of predators—even fast-
swimming ones—when the animal is engaged in intensive prey search. During this phase, which can
last for several days, the predator concentrates its active movement in diving and therefore drifts
horizontally in a quasi-planktonic way, becoming entrained by attractive Lagrangian coherent
structures (Della Penna et al. 2015).

However, the role of Lagrangian fronts as foraging sites clashes with the common idea of
mesoscale eddies as oases of biomass (Godø et al. 2012). Indeed, considering that retention occurs
at eddy cores and dispersion occurs at eddy peripheries, where Lagrangian fronts are located, one
should expect that the most favorable conditions for large prey concentration are inside eddies.
Nevertheless, to our knowledge there has not been a single unambiguous (i.e., high-resolution)
case reported in the literature of predation in the center of an eddy. Reconciling the front paradigm
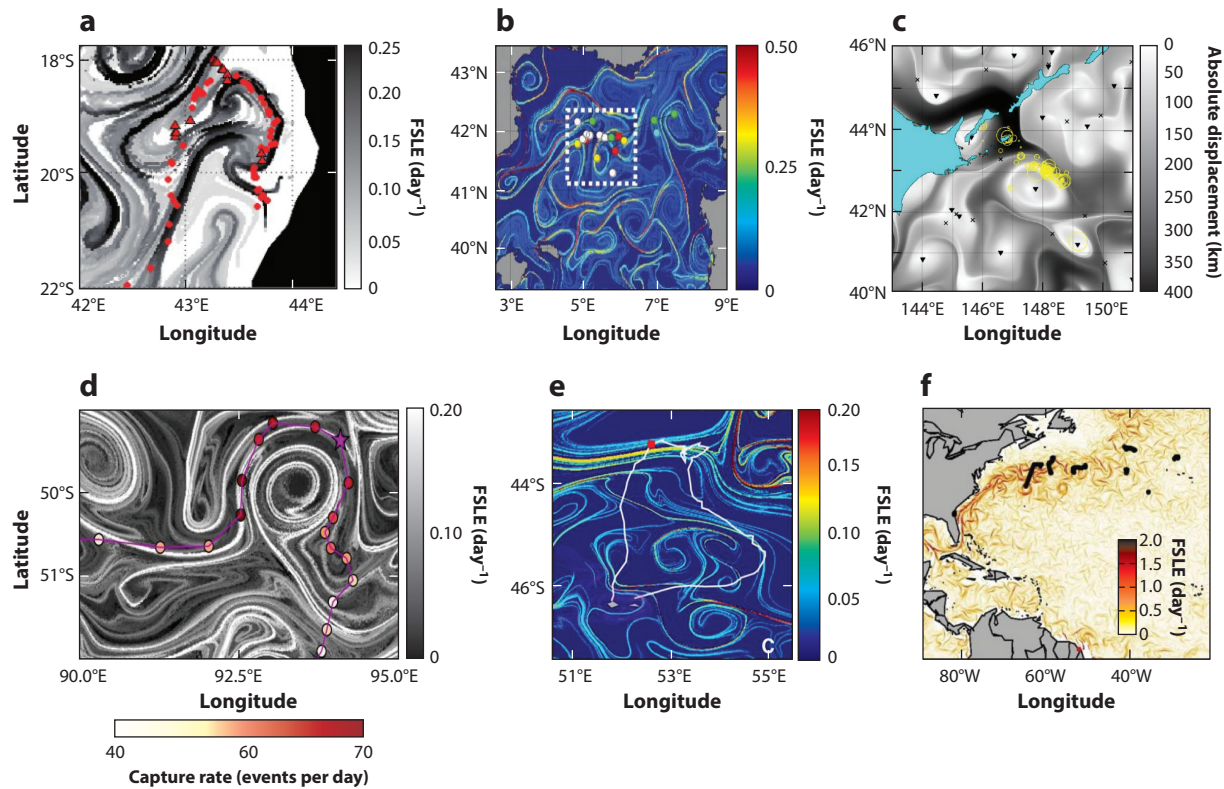
Figure 6

Association between marine predators and Lagrangian coherent structures [finite-size Lyapunov exponents (FSLEs) except in panel *c*]:
(*a*) great frigatebirds (*Fregata minor*), (*b*) Mediterranean whales (*Balaenoptera physalus*), (*c*) leatherback turtles (*Dermochelys coriacea*),
(*d*) southern elephant seals (*Mirounga leonina*), (*e*) macaroni penguins (*Eudyptes chrysolophus*), and (*f*) Pacific saury (*Cololabis saira*) catch
over absolute Lagrangian drift maps. Panels *a*, *b*, *c*, *e*, and *f* adapted from Tew Kai et al. (2009), Cotté et al. (2011), Prants et al. (2014a),
Della Penna et al. (2017), and Chambault et al. (2017), respectively, with permission. Panel *d* adapted from Della Penna et al. (2015)
under the Creative Commons Attribution 4.0 International license (**https://creativecommons.org/licenses/by/4.0**).

with the core paradigm remains an interesting but open challenge for which we can at the moment
only formulate hypotheses, such as a mesoscale enhancement of nekton production inside the eddy
and the formation of fine-scale prey aggregation at the eddy periphery resulting from submesoscale
instabilities arising there.

At the global scale, these observations have motivated attempts to identify multispecies hot
spots of biodiversity by finding regions where different phytoplankton communities are stirred
together (De Monte et al. 2013). At the same time, detection of either fronts or ecologically rele-
vant Lagrangian structures—obtained with the integration of animal telemetry and multisatellite
analysis—has been proposed as a tool to support the design of pelagic marine protected areas
(Chassot et al. 2011, Scales et al. 2014, Della Penna et al. 2017).

6. LIMITATIONS OF THE LAGRANGIAN METHODS

The Lagrangian diagnostics discussed in this article are based largely on the calculation of trajec-
tories from two-dimensional horizontal velocity fields, commonly derived from satellite altimetry

data. This two-dimensional restriction is usually justified by assuming that on short timescales (days to weeks), the integrated effect of typical vertical velocities is not strong enough to displace a trajectory below the mixed layer, which in some cases is questionable (Sulman et al. 2013). Restricting the attention to the horizontal neglects the role of vertical mixing onto a key factor affecting phytoplankton abundance, which is light availability. As has been recently shown, in some cases this vertical effect may dominate chlorophyll variability through photoacclimation (Siegel et al. 2013, Behrenfeld et al. 2016).

On the horizontal, the representation of the ocean velocity field by altimetry is associated with several approximations and errors that reflect on the reliability of the Lagrangian analyses: Altimetry is currently based on nadir observations, which lead to two-dimensional maps of sea surface height in which mesoscale structures are rounder and smoother than they are in reality because of the necessary spatiotemporal interpolation process of the along-track observations (Le Traon et al. 1998, Pascual et al. 2006), structures below 70–100 km are not resolved (Xu & Fu 2012), ageostrophic currents and vertical processes as mixed-layer instabilities (Capet et al. 2008) and Ekman transport are neglected (with some exceptions, like in Sudre & Morrow 2008), and specific errors arise in the vicinity of the coastline (Cipollini et al. 2014). To these sources of error, one must add that phytoplanktonic gradients are not shaped by transport alone, but rather are strongly dependent on biological activity (Okubo 1978), so that their distribution is not determined purely by their initial condition and advection. As a consequence of these limitations, a mismatch between expected Lagrangian features and phytoplankton patterns is typically present.

Systematic comparisons of Lagrangian structures against ground-truth patterns are rare and typically consider physical tracers (Despres et al. 2011, Prants et al. 2016). By comparing in situ hydrography with the altimetry-derived Lagrangian structure of a mesoscale eddy near the Kuril Islands, Prants et al. (2016) found a precision of 7–20 km. Mismatches of 10–20 km are indeed typical when phytoplankton patterns as observed in satellite images are reconstructed with altimetry-derived Lagrangian techniques. Even larger errors arise when Lagrangian features are computed from altimetry in coastal regions. Here, standard altimetry products are notoriously unreliable (Cipollini et al. 2014) and, when used to compute Lagrangian features, may lead to spurious features. In such cases, the results of satellite-based Lagrangian diagnostics need to be carefully validated against those of specifically designed drifter release experiments (Nencioli et al. 2011). By contrast, Lagrangian information derived from satellite altimetry data is quite resilient in the presence of additive noise in the velocity field and to unresolved fine-scale features in the surface currents (see the mathematical arguments in Cotté et al. 2011, pp. 224–25; see also Hernández-Carrasco et al. 2011).

7. SUMMARY AND PERSPECTIVES

Providing glimpses into the changing properties of the ocean surface, satellite observations are Eulerian in nature. Nevertheless, integration of information from consecutive images allows interpretation of the satellite data in a Lagrangian manner that describes changes in seawater properties along particle trajectories. Because phytoplankton and the environment in which they are embedded are transported by the currents, taking a Lagrangian viewpoint when applying satellite data to study phytoplankton dynamics is a natural choice that allows the tracking of fine-scale spatiotemporal changes in properties of the planktonic system (**Figure 7**).

Lagrangian diagnostics of satellite observations, which provide concomitant information on the spatial distribution of surface chlorophyll and geostrophic surface currents, has allowed us to understand the way in which fronts induced by mesoscale currents modulate the spatial distribution of primary production. The structuring effect also has an important effect on phytoplankton
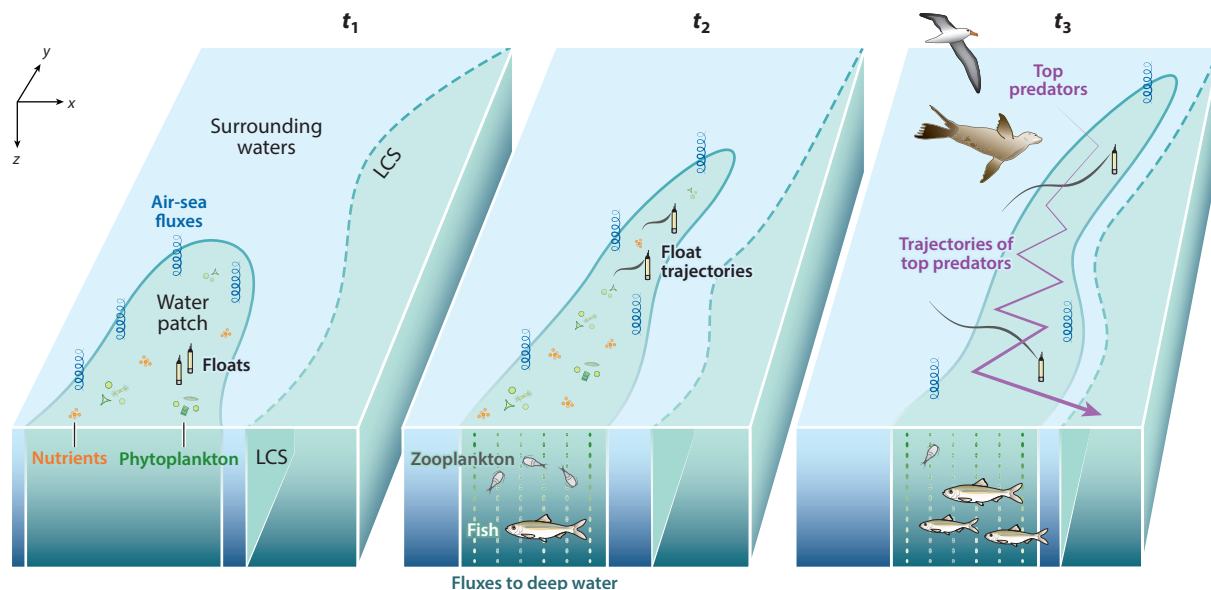
Figure 7

Schematics showing the evolution in space and time of a planktonic system embedded within a fine-scale water patch stirred by the ocean currents. The patch is enriched by a local injection of nutrients, making it biologically richer than the waters surrounding it. As time passes, the accumulated biomass transfers across trophic levels, from primary producers to top predators, with part of it sinking to the deep waters. Changes in water properties affect fluxes of gases and particles across the air-sea interface. Because of horizontal stirring, the patch is advected and stretched until it forms a filament whose boundary is delineated by Lagrangian coherent structures (LCSs). The stretching process is expressed by the spread of Lagrangian floats initiated at adjacent locations. Taking a Lagrangian viewpoint allows one to characterize the structuring effect of the oceanic currents and quantify internal changes within the planktonic system as it is advected and deformed.

diversity, either by enhancing competition in ephemeral retentive regions or, conversely, by merging contrasting communities in mixing regions. Although current satellite observations may provide useful information on phytoplankton community structure, this information remains difficult to trust without in situ concomitant observations (De Monte et al. 2013). In this regard, a breakthrough is expected from future hyperspectral ocean color missions such as PACE (Plankton, Aerosol, Cloud, Ocean Ecosystem). Applying Lagrangian diagnostic tools when interpreting these new satellite data should provide more accurate and reliable maps of plankton diversity, thus bridging the observational gap with phytoplankton biogeography as estimated from models (Follows et al. 2007).

One important application of Lagrangian interpretation methods is the execution of adaptive sampling strategies that are pinpointed at fine-scale patches based on real-time satellite observations. Such adaptive sampling strategies may be useful for detecting fine-scale variations in properties of boundary-layer aerosols (Lehahn et al. 2014a), thus allowing improved understanding of the way in which the marine ecosystem affects and is affected by fluxes of particles across the ocean-atmosphere interface (Quinn & Bates 2011, Guieu et al. 2014). Taking a Lagrangian perspective also allows one to design experiments that trace the origin of water masses that give rise to phytoplankton blooms and to disentangle changes associated with plankton dynamics from those associated with frontal systems drifting over sampling stations—the so-called synoptic problem.

An important limitation of current satellite-based Lagrangian studies of phytoplankton is their restriction to horizontal dynamics. This is a practical approximation that can be justified by

invoking the very high aspect ratio of three-dimensional trajectories (as assumed in d'Ovidio et al. 2004). Admittedly, as shown in model studies (Perruche et al. 2011, Sulman et al. 2013), this approximation—a necessity that stems from the fact that reliable estimations of vertical velocity fields at the required scales are largely unavailable—should not hold in all cases. This situation may change drastically in the coming years with data from missions such as Soil Moisture and Ocean Salinity (SMOS), Aquarius, and Surface Water and Ocean Topography (SWOT), which will bring higher-resolution observations of salinity and sea surface height (Fu & Rodriguez 2004). Although these are not direct observations of vertical velocities, together with improved sea surface temperature observations, these data are expected to feed assimilation schemes or theoretical frameworks (e.g., omega equation formalism) that will provide accurate estimates of the three-dimensional ocean dynamics.

In association with remote sensing, development of semi-Lagrangian drifters (D'Asaro et al. 2003, Harcourt & D'Asaro 2010) as swarms of autonomous underwater robots (Jaffe et al. 2017) are expected to provide three-dimensional trajectories in the near future. These novel observations will allow assessment of how Lagrangian coherent structures modulate nutrient and light accessibility in the vertical along the trajectories of planktonic organisms. Three-dimensional drifter trajectories will also confirm model studies that reported the presence of subsurface Lagrangian fronts capable of shaping the demise of phytoplankton that control the location and ventilation of oxygen minimum zones (Bettencourt et al. 2015). At the same time, the possibility of constructing ocean color images by composing multiple daily scenes from geostationary ocean color missions using instruments such as the Geostationary Ocean Color Imager (GOCI) and Optical Carbonaceous and Anthropogenic Aerosols Pathfinder Instrument (OCAPI) should strongly reduce cloud coverage issues and provide systematic synoptic images of phytoplankton distribution at (sub)mesoscale resolution.

Recent studies have demonstrated that coherent Lagrangian structures have a structuring role not only in phytoplankton distribution, but also in the displacement and behavior of top predators. In particular, trophic hot spots—regions where different levels of the trophic chain aggregate—appear to often be colocalized with Lagrangian structures. Although the mechanisms behind this focusing effect remain unclear, these observations on top predators suggest that the Lagrangian view provides a valid reference frame for end-to-end processes as well. Drifting platforms such as the PolarPod should provide ideal in situ observational systems for Lagrangian structures because they will largely follow the current systems and will be able to monitor, by active and passive acoustics, the central and upper trophic levels with minimal disturbance. In the future, the characterization of ecological hot spots in terms of Lagrangian features may provide a way to transpose the changes in circulation emerging from climate change scenarios into biogeographical information. In turn, this approach may help to form a scientific basis for the creation of pelagic marine protected areas whose boundaries take into account the drift of ecological hot spots in the wake of climate change.

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

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