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Overview Article

Disturbance ecology in a pelagic upwelling biome: Lagrangian frameworks for studying succession

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Abstract

Disturbance ecology is underdeveloped in marine pelagic ecosystems relative to terrestrial and aquatic benthic habitats, in part because, when measured relative to a fixed location, postdisturbance recovery involves the advection of entire communities in addition to biotic interactions. A Lagrangian frame-of-reference perspective alleviates this issue. Using results from the California Current Ecosystem, we highlight three approaches: *in situ* Lagrangian, synthetic Lagrangian, and simulated Lagrangian studies. Within a Lagrangian context, extratropical marine heatwaves and El Niños represent press disturbances or alterations to the disturbance regime. Individual upwelling events are more appropriately viewed as pulse disturbances. Upwelling disturbances stimulate rapid growth of pioneer species (diatoms), with herbivores (copepods) lagging these blooms by approximately 3 weeks. The climax community is an assemblage of small low-nutrient specialists with high Shannon diversity. We suggest that pelagic ecosystems can be ideal systems for investigating disturbance recovery because of the rapid response times of marine primary producers and herbivores.

Keywords: disturbance ecology, succession, plankton, California Current Ecosystem, LTER network

Disturbance ecology has a long and rich history as a framework for understanding ecosystem change (Sousa 1984, Pickett and White 1985, Pulsford et al. 2016, Burton et al. 2020, Gaiser et al. 2020). A *disturbance* is typically defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). In this context, which events are considered *discrete* can be a judgment call, but the term is often defined relative to the response time of the ecosystem and dominant biota (Connell and Sousa 1983, Goericke 2011a, Peters et al. 2011). Disturbances also vary substantially in their spatial extent, ranging from the meter scales of bioturbation caused by walruses digging in marine sediments or a single tree fall to wildfires or marine heatwaves that can extend over thousands of kilometers. Although disturbances are often thought of as negative events in common parlance, ecological disturbances are often natural events that play critical roles in maintaining the diversity and function of ecosystems.

Disturbance ecology is most thoroughly developed in terrestrial and aquatic benthic environments in which distinct communities can be temporally revisited to quantify recovery timescales and population dynamics. Such studies have demonstrated the necessity of disturbance for ecosystem maintenance (Parsons and DeBenedetti 1979, Gibson 1989, Belsky 1992) and the roles of succession in creating new niches and habitat space (McAuliffe 1984), have developed the concept of a successional mosaic across the landscape and related these concepts to biodiversity patterns (Denslow 1980, Clark 1991, Chambers et al. 2013), and have given rise to the (heavily debated) intermediate disturbance hypothesis, which posits that biodiversity will be highest in ecosystems experiencing moderate levels of disturbance (Connell 1978, Weithoff et al. 2001, Fox 2013). These studies have also developed quantitative frameworks for investigating the magnitude of a disturbance and its biotic response, as well as the resilience of ecosystems to perturbation (Yi and Jackson 2021). Theory also differentiates between *press* and *pulse* disturbances, which differ on the basis of whether the disturbance agent is acute or continuous in time (Bender et al. 1984, Glasby and Underwood 1996, Harris et al. 2018), whereas state-and-transition models are used to investigate alternate ecosystem states and the transitions between them (Bestelmeyer et al. 2017). Disturbance studies have elucidated important determinants that affect recovery responses including material (or biological) legacies that remain after a disturbance (Kopecky et al. 2023), the role of facilitation (positive species interactions) in shaping recovery trajectories (Bruno et al. 2003), and the utility of functional trait-based ecology as a way to understand responses to disturbance (Díaz et al. 2007, Laughlin 2014, De Battisti 2021). However, many of these topics suffer from a lack of replication because of the long time scales of recovery in many ecosystems (Buma 2021). The limited realizations of ecosystem recovery in slowly responding ecosystems can make it difficult to assess generalizability or to determine how specific characteristics of a disturbance (e.g., spatial extent, disturbance intensity, duration,

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material legacy) may alter the subsequent biotic response and recovery.

Despite a relative paucity of studies, marine pelagic ecosystems are ideal systems for studying disturbance ecology. Primary producer response times are incredibly rapid, with phytoplankton growth rates typically on the order of 0.1–1.0 per day (Laws 2013), allowing studies to be conducted over time spans of days to weeks rather than years. This can enable multiple replicated studies over comparatively short time spans and alleviates common problems associated with studying disturbance responses in other environments, including the lack of replication and generalizability of disturbance responses (Buma 2021). Common marine pelagic disturbance types (such as mixing events, upwelling pulses, or marine heatwaves) also occur with highly varying frequency, duration, and spatial extent enabling statistical analysis of the relationships between scale and biotic response. In addition, robust rate measurement techniques are available and widely used for accurately quantifying processes such as net primary production and zooplankton grazing rates (Steeman-Nielsen 1951, Landry and Hassett 1982), whereas the comparatively well-mixed state of plankton communities (relative to benthic or terrestrial ecosystems) enables efficient community characterization using modern environmental DNA approaches (Dupont et al. 2010, Bucklin et al. 2016, James et al. 2022). Nevertheless, with the exception of studies relating disturbance frequency to diversity and the paradox of the plankton (the finding of high plankton diversity in the marine pelagic despite supposedly homogeneous environmental conditions; Hutchinson 1961, Reynolds CS et al. 1993), disturbance ecology is relatively underdeveloped in marine pelagic systems. For instance, a recent long-term ecological research (LTER) synthesis study (Gaiser et al. 2020) investigated recovery from disturbance, disturbance legacies, and human feedback loops to disturbance ecology across a suite of ecosystems from grasslands to coastlines but included no studies of pelagic ecosystems.

Marine ecosystems can be affected by disturbances in numerous ways. Marine heatwaves of widely varying intensity and duration are caused by multiple phenomena with variable biotic responses (Santora et al. 2020, Oliver et al. 2021, Capotondi et al. 2024, Chen et al. 2024a). Rainfall and associated riverine runoff introduce limiting nutrients, dilute ocean salinity, and alter water column stratification and therefore light availability for phytoplankton (Alpine and Cloern 1992). Tropical cyclones and other storms and mixing events stir the ocean, simultaneously diluting surface ocean communities, introducing nutrients, and reducing surface temperatures (Babin et al. 2004, Lin 2012, Shropshire et al. 2016, Diaz et al. 2021, Chen et al.2024b). Hypoxic events can lead to sublethal effects or mass mortality events (Ekau et al. 2010, Stauffer et al. 2013). Coastal wildfires have been found to stimulate phytoplankton blooms, although the full impacts of ash deposition are still poorly understood (Kramer et al. 2020, Tang et al. 2021, Liu et al. 2022). Oil spills, which can occur at all depths in the ocean and range from massive events such as the *Deepwater Horizon* blowout to small leaks from moving vessels, set off successional cascades among microbial communities while affecting organisms across trophic levels (Mason et al. 2012, Ladd et al. 2018, Meurer et al. 2023, Brock et al. 2025). Mesoscale eddies are large swirling currents of water ranging in diameter from tens to hundreds of kilometers that substantially alter ecological, chemical, and physical ocean characteristics (Brown et al. 2008, Chenillat et al. 2015b, McGillicuddy 2016, Abdala et al. 2022). Similarly, meso- and submesoscale fronts and filaments can drive transient or sustained changes in vertical and horizontal ocean transport, substantially altering ecological and biogeochemical conditions (Levy and Martin 2013, Nagai et al. 2015, Stukel et al. 2017, Forsch et al. 2023). Although the above examples have been focused on abiotic disturbances, biotic disturbances are also numerous. These include such events as biological invasions (Shiganova 1998, Amalfitano et al. 2015), harmful algal blooms (Bates et al. 1998, Brand et al. 2012, Anderson et al. 2021), stochastic blooms of gelatinous taxa including cnidarian jellies and pelagic tunicates (Smith et al. 2014, Fuentes et al. 2018, Décima et al. 2023), and viral pathogens that can terminate phytoplankton blooms (Bratbak et al. 1993, Fuhrman 1999, Brum et al. 2015). (See box 1.)

In this article, we review the current understanding of disturbance ecology in the California Current Ecosystem (CCE), a large marine biome on the eastern edge of the North Pacific Subtropical Gyre (Bograd et al. 2003, Ohman et al. 2013a). We then highlight the limitations that arise from studying disturbance ecology using fixed (Eulerian) frames of reference when the community is transported rapidly by the currents. We suggest multiple approaches (experimental, observational, and modeling) for investigating disturbance ecology in advective systems using a Lagrangian frame of reference and present examples of each approach in the CCE. We focus on pelagic responses to pulse disturbances arising from individual upwelling events and show that a Lagrangian framework allows us to quantify disturbance–recovery processes and identify robust ecosystem responses.

Disturbances in the California Current Ecosystem pelagic environment

The CCE encompasses a productive coastal upwelling zone, a transitional zone with moderate and variable productivity, and an oligotrophic offshore domain that is contiguous with the oligotrophic North Pacific Subtropical Gyre (figure 1; Venrick 2002, Ohman et al. 2013a, Taylor et al. 2015). Phytoplankton growth and net primary production are predominantly nitrogen limited (Collier and Palenik 2003). Light limitation can be important during upwelling periods near the coast and iron at times limits phytoplankton in the transition zone and at chlorophyll maximum depths (King and Barbeau 2007, Hogle et al. 2018). Protistan zooplankton are typically the major grazers of phytoplankton (Landry et al. 2009, Connell et al. 2017, Landry et al. 2023), although a diverse suite of metazoan zooplankton including copepods, euphausiids, and pelagic tunicates are also important (Lavaniegos and Ohman 2007, Ohman et al. 2012, Morrow et al. 2018). The CCE is the site of one of the longest running spatially resolved oceanographic time series (CalCOFI, California Cooperative Oceanic Fisheries Investigations), which has collected samples spanning ocean physics to zooplankton at stations along the coast from 1949 to the present (figure 1). This time series has demonstrated that the CCE is subject to physical forcing on multiple timescales ranging from event scale to seasonal, interannual, decadal, and long-term climate change (Bond et al. 2003, Bograd et al. 2009, Jacox et al. 2015, Bograd et al. 2023, Kahru et al. 2023). Climatic drivers, including El Niños, the Pacific Decadal Oscillation and the long-term press of climate change, are linked to long-term changes in the abundances of many zooplankton and forage fish populations, which sometimes manifest as abrupt transitions in the ecosystem (Lavaniegos and Ohman 2007, Rykaczewski and Checkley 2008, Di Lorenzo and Ohman 2013, Lindegren et al. 2016, Miller et al. 2019).

These climatic drivers intersect with a suite of different disturbance types in the CCE. For instance, substantial research efforts have gone into understanding the impacts of the recent

Box 1. Definitions and terminology.

Climax community: the final stage of succession, characterized by a relatively stable community
Disturbance: any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment
Disturbance regime: the expected frequency, severity, and type of disturbances affecting an ecosystem
Eulerian framework: a spatial framework based on fixed spatial reference points (e.g., fixed latitude and longitude location)
Facilitation: positive interactions between species that affect successional patterns after a disturbance event
Lagrangian framework: a spatial reference frame that moves with the flow of the water
Marine heatwave: an event in which sea surface temperature anomalies exceed the ninetieth percentile for a period of at least 5 days
Material legacy: physical remnants remaining after a disturbance event that can shape ecosystem recovery
Nekton: organisms that can outswim a horizontal ocean current. Typically, nekton include fish and higher trophic levels
Pelagic: the open water column from the surface to above the sediments
Pioneer species: Rapidly responding species that colonize new habitat after a disturbance
Plankton: organisms that cannot outswim a horizontal ocean current. Plankton include bacteria, phytoplankton (floating algae), protistan zooplankton, and metazoan zooplankton (including herbivorous copepods and many predators from chaetognaths and ctenophores to siphonophores)
Press disturbance: a disturbance that persists over long durations relative to ecosystem response times
Pulse disturbance: a sudden short-term disturbance that does not persist in time
Resilience: the time required for a system to return to steady state following a disturbance
Return time: the duration between successive disturbance events

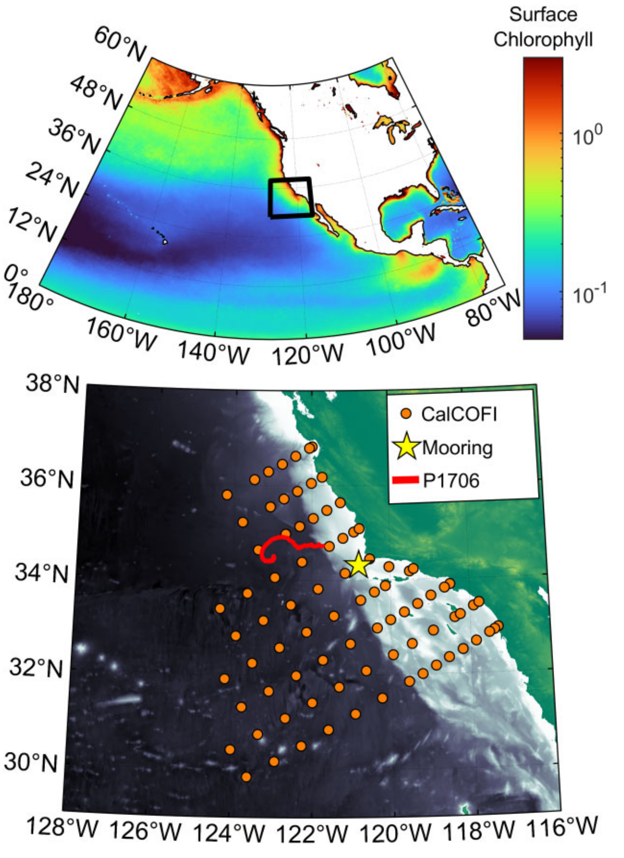

Figure 1. The top panel shows the North Pacific mean sea surface chlorophyll. Source: The data are from the NASA SEAWIFS satellite. The black inset outlines the CCE region, which is highlighted in the lower plot, which shows the regional bathymetry. The dots are standard CalCOFI stations. The star is site of the CCE2 mooring (CalCOFI station 80.55). The line shows the extended Lagrangian experiment conducted during CCE cruise P1706.

abundance increase of the large gelatinous grazer *Pyrosoma atlanticum* that began during the 2014–2015 Blob extratropical marine heatwave (Miller et al. 2019, O'Loughlin et al. 2020). Similarly, the increase in extreme fire frequency in Southern California has stimulated research into the effects of wildfire particulates on pelagic communities (Williams et al. 2019, Hulley et al. 2020, Kramer et al. 2020). Marine heatwaves are among the most studied pelagic disturbance agents globally (Hobday et al. 2018, Oliver et al. 2021, Capotondi et al. 2024). Marine heatwaves can originate as the result of many different phenomena, including El Niño, basin-scale extratropical events such as the 2014–2015 North Pacific Blob, and more ephemeral atmospheric phenomena (Holbrook et al. 2019, Oliver et al. 2021, Xu et al. 2021). Consequently, marine heatwaves vary widely in their characteristics and biotic responses (Hobday et al. 2016, Noh et al. 2022, Wyatt et al. 2022, Chen et al. 2024a). Within the CCE, El Niños are dominant drivers of interannual system variability with extensively studied biotic impacts (Kahru and Mitchell 2002, McClatchie et al. 2016, Lilly and Ohman 2021). More recently, prominent large-scale extratropical marine heatwaves have become common, with distinctly different physical forcing but often similar biotic responses (Leising et al. 2015, Gómez-Ocampo et al. 2017, Amaya et al. 2020). El Niños and large extratropical marine heatwaves have led to abrupt transitions and sustained changes in CCE pelagic communities (McGowan et al. 2003, Lindegren et al. 2016). However, at the multiple month to yearly time scale of these phenomena, which are long relative to the life spans of phytoplankton and many zooplankton, ecological postevent recovery is mostly rapid and tracks the physical forcing, albeit with biological lag times that reflect temporal integration of the underlying drivers (Hsieh and Ohman 2006, Bestelmeyer et al. 2011, Di Lorenzo and Ohman 2013).

El Niños and large extratropical marine heatwaves have distinctly different climatic drivers (Strub and James 2002, Bond et al. 2015, Amaya et al. 2020), resulting in some important differences in the mechanisms by which they affect pelagic communities (Lilly and Ohman 2021). Nevertheless, both phenomena can be

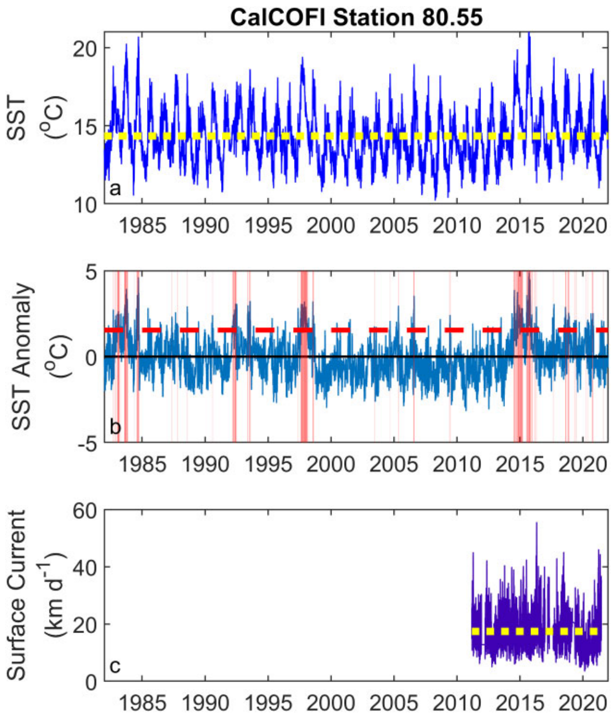

Figure 2. Marine heatwaves at CalCOFI Station 80.55 near Point Conception (figure 1). (a) Sea surface temperature time series at the station derived from AVHRR satellite data (Steeman-Nielsen 1951, Reynolds RW et al. 2007). (b) Sea surface temperature anomaly. The pink vertical lines delineate marine heatwave events, defined as 5-day or longer periods in which temperature anomaly exceeds the ninetieth percentile (which is shown by the horizontal dashed line). (c) The daily average near-surface current speed was measured by acoustic doppler current profiler mounted on the CCE2 mooring at station 80.55 (Ohman et al. 2013b). The yellow dashed lines in panels (a) and (c) show the mean values.

seen as having extremely strong magnitudes and long durations within the marine heatwave continuum (Xu et al. 2021, Amaya et al. 2023). Indeed, most marine heatwaves in the CCE last 10 days or less (Chen et al. 2024a), highlighting the fact that marine heatwaves can be either press or pulse disturbances. We can illustrate marine heatwave variability by looking at sea surface temperature near the Point Conception upwelling center (star in figures 1b and 2a) where 74 distinct marine heatwaves occurred from 1982 to 2021 (figure 2b). The median duration of these marine heatwaves was only 8.5 days; these can therefore typically be considered discrete events, although the longest marine heatwave lasted 120 days, which is certainly long relative to the life span of phytoplankton. We can also investigate the return time—or expected duration between subsequent disturbance events—an important characteristic of disturbance regimes. The median return time between marine heatwave events was 22 days, with a range of 2–1845 days. Although that median return time is relatively short, 23 of the 72 marine heatwaves were preceded by a marine heatwave–free period of at least 3 months, whereas 10 were preceded by a period of more than a year. This suggests highly variable return times between events, mediated by large-scale climatic drivers that alter the disturbance regime. Marine heatwaves were very frequent, with short return times, during the 2014–2015 North Pacific Blob marine heatwave and the strong El Niño of 1998. Marine heatwaves were infrequent, with long return times, during the long period of predominantly negative Pacific Decadal Oscillation from approximately 1999 to 2014.

In many ways, however, this analysis of marine heatwave event frequency and return time at a fixed location in time is not representative of the disturbance frequency experienced by plankton communities drifting with the flow. At this station, median surface velocities are 16.6 kilometers per day (figure 2c). Therefore, using a median marine heatwave return time of 22 days, we would expect the community to be transported hundreds of kilometers away before the next marine heatwave occurs. The Eulerian (fixed point in space) framework can therefore confound the understanding of disturbance ecology in pelagic ecosystems. If we see rapid recovery in, for instance, chlorophyll concentrations measured by the CCE2 mooring after cessation of a marine heatwave event, this does not necessarily imply rapid growth rates and recovery of the phytoplankton community present at this location during the marine heatwave. Instead, it may simply reflect the advection of a new patch of water and associated community from cooler water with a high phytoplankton biomass. To understand recovery processes from disturbance events, we must adopt a planktonic perspective and Lagrangian framework (box 2).

Such a Lagrangian perspective is equally important for investigating another important type of disturbance: upwelling events. Upwelling introduces cold, nutrient-rich water to the sunlit surface ocean, while diluting surface communities. This typically stimulates blooms of large phytoplankton, such as diatoms, and lagged growth of their consumers (Venrick 2002, Gangrade and Mangolte 2024, Lampe et al. 2025). Upwelling in the CCE is typically driven by either coastal upwelling, which leads to very high vertical velocities in a narrow area along the coast, or wind stress curl upwelling, which is much weaker but acts over a much larger area (Rykaczewski and Checkley 2008). Upwelling pulses and the percentage of water that has been recently upwelled are correlated with atmospheric drivers, such as El Niño–Southern Oscillation and the North Pacific Gyre Oscillation (Chabert et al. 2021, Miller et al. 2025). Importantly, both coastal and wind stress curl upwelling are associated with offshore advection of water; therefore, as communities evolve in response to a pulse of upwelling, they are also transported away from the upwelling source (Miller et al. 2025). Studying the ecological response requires a similarly moving framework.

Lagrangian framework for pelagic disturbance ecology

In contrast to terrestrial and aquatic benthic ecosystems, the marine pelagic is a fluid environment, and communities drift with the ocean currents. Although some large organisms (referred to as *nekton* and typically at trophic level 3 or above) can outswim a horizontal ocean current, lower trophic level populations are typically at the mercy of ocean circulation. As a result, in a fixed (Eulerian) coordinate system, the rates of change of the abundances, biomasses, and concentrations of organisms and biogeochemical properties (e.g., nutrients) are governed by the advection–diffusion equation.

$$\frac{\partial B}{\partial t} = \underbrace{-\frac{\partial}{\partial x}(\vec{u}B) - \frac{\partial}{\partial y}(\vec{v}B) - \frac{\partial}{\partial z}(\vec{w}B)}_{\text{Three-dimensional advection}}$$

$$\underbrace{+\frac{\partial}{\partial x}\left(K_x\frac{\partial B}{\partial x}\right) + \frac{\partial}{\partial y}\left(K_y\frac{\partial B}{\partial y}\right) + \frac{\partial}{\partial z}\left(K_z\frac{\partial B}{\partial z}\right)}_{\text{Three-dimensional diffusion}} + S \qquad (1)$$

This equation states that the rate of change (∂/∂t) of any ecological or biogeochemical property (*B*) is equal to the sum of three-dimensional advective and diffusive fluxes, as well as

Box 2. Eulerian and Lagrangian frameworks.

We use the terms Eulerian and Lagrangian to refer to stationary and moving frames of reference, respectively. A Eulerian study is one in which fixed locations relative to the surface of the earth are sampled repeatedly. For instance, if phytoplankton abundance is sampled daily from a pier, this would be a Eulerian frame of reference. CalCOFI is a Eulerian time series program, because the same stations are sampled each quarter. A Lagrangian framework is one in which sampling is done along a moving frame of reference by, for instance, deploying a float (drifter) in the ocean and following that float as it drifts with the current. Lagrangian studies are particularly powerful tools for studying plankton, because plankton experience the world in a Lagrangian framework as they drift with the flow. Repeat sampling of phytoplankton abundance in a Lagrangian framework therefore allows investigators to calculate the net rates of change of phytoplankton (net growth) or other measured variables. Rates of change of different properties (temperature, biomass, etc.) often differ when measured in Eulerian or Lagrangian frameworks as is shown in figure 3.

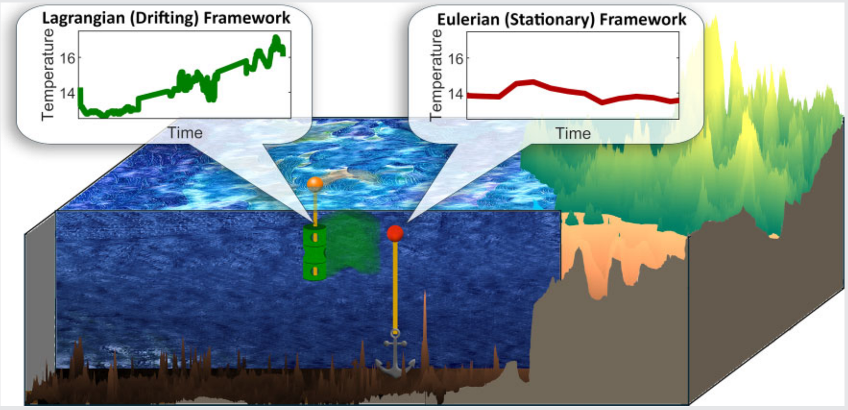

Figure 3. An example of a Lagrangian (drifting mooring) and an Eulerian (mooring anchored to the bottom of the ocean) framework.

biological sources and sinks (S) of the property being investigated. In equation 1, x and y are the two horizontal dimensions (with associated velocities u and v), whereas z is the vertical dimension (with vertical velocity w). K_x and K_y are the horizontal diffusivity coefficients, which are typically equal to each other but orders of magnitude greater than K_z (the vertical diffusivity coefficient). In many marine environments and especially eastern boundary current upwelling systems with high offshore velocities combined with strong cross-shore gradients, the advective and diffusive terms are often larger than the biological sources and sinks. In a Eulerian framework, the rates of change of nutrients, organic carbon, and populations are therefore determined more by physical circulation than by biological sources and sinks. As a result, the adoption of a Lagrangian framework (i.e., moving frame of reference, the green drifter in box 2) is strongly preferred for investigating the ecological processes (e.g., biological sources and sinks) driving change in plankton communities.

Lagrangian studies have a long history in oceanographic research (Gould 2005, Griffa et al. 2007, Dickey et al. 2008, Prants et al. 2017, Lehahn et al. 2018, Van Sebille et al. 2018). For instance, neutrally buoyant floats were used to discover and map deep ocean currents (Swallow 1955, Swallow and Worthington 1957), satellite-enabled floats were used to quantify surface ocean circulation patterns (Poulain and Niiler 1989, Haynes and Barton 1991), and Lagrangian models were used to study phytoplankton and zooplankton transport by ocean currents (Dippner 1993, Miller et al. 1998). Lagrangian perspectives have also been used to understand sinking particle flux variability (Deuser et al. 1988, Siegel et al. 1990), to investigate pollutant and debris dispersal (Al-Rabeh et al. 1989, Maximenko et al. 2012), and to conduct large-scale marine carbon dioxide removal experiments (Coale et al. 1998, de Baar et al. 2005). This rich history of diverse experimental and modeling approaches provides a scaffolding for studying ecological disturbance and succession in a fluid environment.

Considering ecological change using this Lagrangian perspective—and thinking from the perspective of organisms with life spans of days to weeks—also gives us a different viewpoint for disturbance ecology. For such a plankton community, an El Niño event or even a short, month-long marine heatwave cannot be viewed as a pulse disturbance, because it persists over many generations. Rather, such an event is better seen as either a press disturbance or a modification to the disturbance regime. In this context, the press disturbance (warming surface temperatures) intersects with the pulse disturbances from upwelling events that are experienced by the drifting community. Specifically, warmer sea surface temperatures increase stratification and decrease vertical mixing during El Niño events, whereas altered atmospheric patterns simultaneously lead to decreased upwelling-favorable winds (Jacox et al. 2015).

Whether the upwelling pulse or the marine heatwave press is the main disturbance agent in the system depends, in part, on the difference between Eulerian and Lagrangian frameworks. Upwelling peaks along the California coastline in spring and is therefore considered (from a Eulerian perspective) part of the seasonal cycle, rather than a discrete disturbance. However, from the perspective of a drifting plankton community, upwelling is a stochastic event controlled by variable currents that determine whether and when the plankton patch enters an upwelling location (Strub and James 2000, Keister and Strub 2008). For instance, Stukel and colleagues (2023) found that, although most water parcels in the CCE at a depth of 100 meters would return to the surface within 2 years, the arithmetic mean return time was 102 years, implying a strongly skewed distribution of return times and substantial variability in the trajectories of different plankton communities.

Therefore, from a Lagrangian perspective, we must consider the dynamics of communities that drift with ocean currents, experiencing a series of disturbances that alter community structure often against internal pressures that move the community toward a climax state. An upwelling event could be considered a pulse disturbance that dilutes the surface community with deep water, cooling temperature and injecting nutrients and even subsurface diatom cysts (i.e., algal resting stages). This upwelling pulse typically leads to rapid phytoplankton growth and communities dominated by large cells and especially diatoms (Venrick 2002, Goericke 2011a, 2011b, Taylor et al. 2015, James et al. 2022). In this context, rapidly growing diatoms can be considered pioneer species that first colonize the habitat after disturbance. Lampe and colleagues (2021) further hypothesized that sinking by large coastal diatoms (e.g., *Thalassiosira*) may aid in their dispersal into newly upwelled water parcels, an assertion that is supported by sediment trap studies in the region that often find this taxa to preferentially contribute to sinking flux (Preston et al. 2019, Valencia et al. 2022). Notably, this taxon has also been shown to be digestion resistant (Fowler and Fisher 1983), suggesting that transport within zooplankton fecal pellets may play a role in this cycle (Valencia et al. 2021). Lin and colleagues (2024) further showed that disturbance responses can be mediated, in part, by the biomass and physiological state of subsurface phytoplankton communities brought into the euphotic zone. Once the upwelling ends (or the parcel of water is advected away from the upwelling center), the nutrients will start to be exhausted, and later successional species will begin to dominate, often with a gradual transition toward smaller cells and a higher proportion of cyanobacteria (Goericke 2011a, Taylor et al. 2015). As community succession occurs, however, the water parcel will be subjected to further disturbances. For example, additional pulse upwelling events could occur if the water parcel returns to the coastal upwelling zone or is influenced by weaker upwelling that occurs in the offshore zone of wind stress curl (Checkley and Barth 2009, Song et al. 2011). Press disturbance events associated with marine heatwaves may also influence the water parcel, as will biotic disturbances such as pathogen outbreaks, incursions of vertical-migrating euphausiid swarms, or salp or pyrosome blooms. Considering the history of this moving water parcel therefore provides an interesting opportunity to investigate the impacts of multiple intersecting disturbances.

An additional important question arises from this discussion: Given the Eulerian framework used by most ocean time series programs, when is a Eulerian framework appropriate for disturbance ecology and when is a Lagrangian approach necessary? Another way to frame this question is to ask where the local effects of the disturbance on community dynamics (e.g., growth and mortality rates) override the advective and diffusive transport signals that are inherent to pelagic ecosystems. This can be framed mathematically, by considering the advection–diffusion equation that governs the rate of change of any property (e.g., a taxon of interest) in the ocean. When the biologically driven rates of change (S in equation 1) are large relative to the advective and diffusive components of equation 1, a Eulerian framework is likely sufficient. This generally occurs when spatial scales of disturbance are large relative to horizontal spatial gradients and the velocities of horizontal currents. It will also, of course, be true when studying nekton that can swim against currents and therefore not be as affected by advection and diffusion. In figure 4, we provide a flow chart for diagnosing when a Eulerian perspective would be sufficient for studying disturbance ecology. Among other things, a Lagrangian perspective is particularly important for studying lagged recovery after a disturbance, whereas a Eulerian perspective will often be sufficient to investigate the immediate impacts of ongoing (press) or recently concluded (pulse) disturbances. In the following sections, we outline three different approaches for Lagrangian investigations of disturbance ecology: *in situ* Lagrangian studies, synthetic Lagrangian analyses, and simulated Lagrangian models.

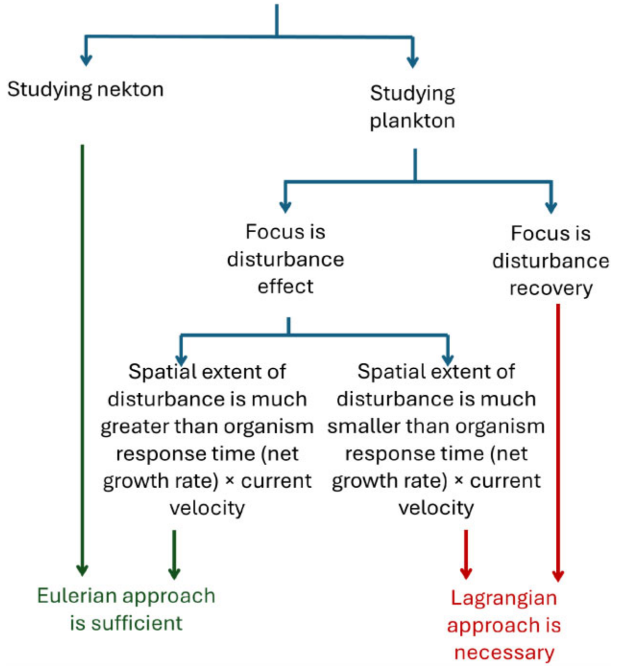

Figure 4. Flow chart providing guidance about when a Eulerian approach is sufficient and when a Lagrangian approach is necessary.

In situ shipboard Lagrangian studies

In situ Lagrangian studies have been a hallmark of CCE-LTER process cruises (Landry et al. 2009). These Lagrangian studies are conducted by tagging a parcel of water with a 1-meter-diameter, 3-meter-long holey sock drogue (essentially a wind-sock designed to have high drag in the water) that is centered at 15 meters depth in the water and connected by a line to a surface float that communicates via satellite (Niiler et al. 1995). The research vessel follows the drifting array while conducting sampling as necessary for the project's goals. Although this approach allows daily replicability of sampling and experiments, the number of independent water parcels that can be sampled on a cruise is limited and it adds substantial logistical challenges. Nonetheless, the strategy provides unique opportunities for investigating cross-trophic level interactions and relating ecosystem properties to transient changes in plankton communities (Landry et al. 2009, Stukel et al. 2015). For instance, Landry and colleagues (2009) tracked eight water parcels, each for a period of 3–5 days, while measuring net growth rates along the Lagrangian trajectory and simultaneously quantifying phytoplankton growth rates, phytoplankton mortality due to protistan grazing, and phytoplankton mortality due to mesozooplankton grazing (figure 5a). These results demonstrated that phytoplankton net rates of change *in situ* were well explained

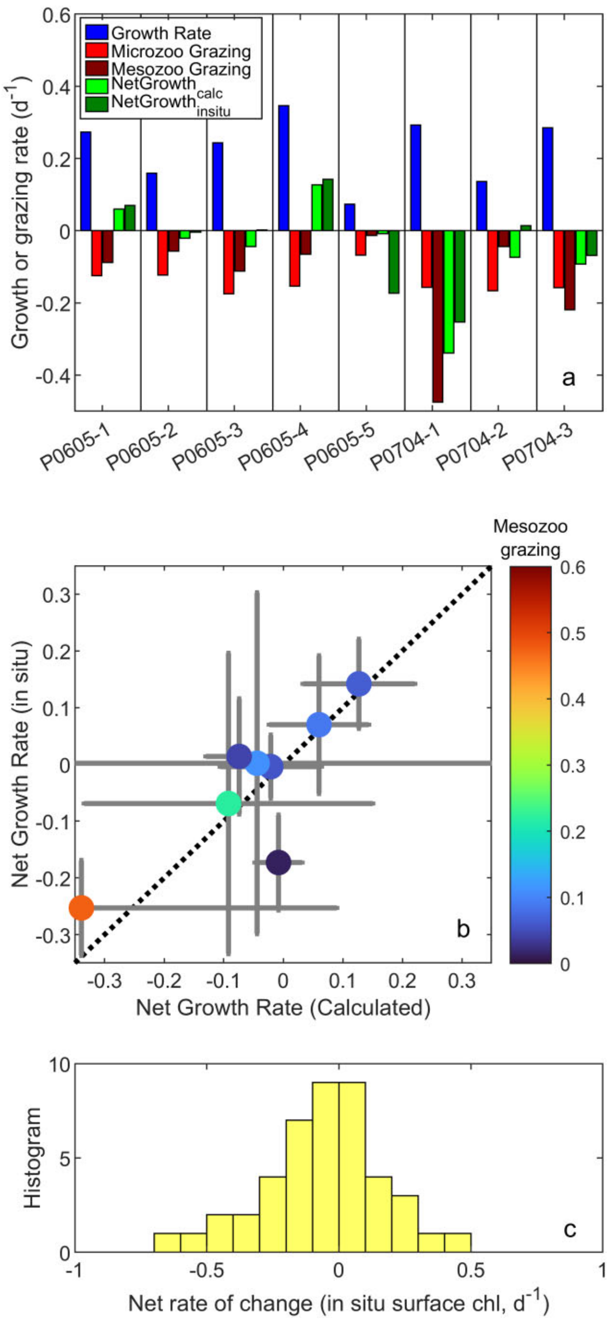

Figure 5. Growth, grazing, and net phytoplankton rates of change. (a) Vertically integrated phytoplankton growth rate, phytoplankton mortality due to protistan (microzooplankton) grazing, phytoplankton mortality due to mesozooplankton grazing, net phytoplankton growth rate calculated as growth minus protistan-grazing mortality minus mesozooplankton-grazing mortality, and net phytoplankton growth rate measured on the basis of rates of change along Lagrangian trajectories. (b) Net calculated phytoplankton growth rate compared with net measured phytoplankton growth rate with mesozooplankton grazing as the color axis (units of per day). Source: Landry and colleagues (2009). (c) Histogram of net rates of change of surface chlorophyll along 2- to 5-day Lagrangian trajectories across 10 CCE-LTER cruises.

by the balance between intrinsic phytoplankton growth rates and their losses to zooplankton grazing (figure 5b).

These results allow us to investigate some aspects of the dilution–recoupling hypothesis, as they pertain to disturbance dynamics in the CCE. Behrenfeld (2010) suggested that deep-mixing events in the subarctic Atlantic may primarily affect phytoplankton by disrupting the close growth–grazing balance that often forms between phytoplankton and protistan zooplankton during climax community conditions. This dilution-mediated disruption allows growth to exceed grazing and enables bloom formation. The data from Landry and colleagues (2009) suggest similarities in coastal upwelling systems. Growth is typically closely balanced by grazing (figure 5a), with protistan grazing usually exceeding mesozooplankton grazing and strongly correlated with phytoplankton growth rates (supplemental figure S1e). However, net growth imbalances were driven less by changes in the phytoplankton–protist balance than by variability in mesozooplankton grazing rates (figure S1d). This highlights the importance of metazoan grazers (especially copepods and euphausiids) in determining phytoplankton dynamics in the CCE and necessitates their inclusion in studies of disturbance ecology in coastal upwelling biomes.

Using these results but also incorporating sinking particle and net primary production measurements, Stukel and colleagues (2011) further demonstrated that vertical export of organic carbon could be explained using estimates of fecal pellet production. They also showed that nitrate-fueled new production is often spatially decoupled from sites of vertical export production, whereas many investigators assume these two processes are locally balanced. Other interesting results from this experimental approach include different community-level grazing impacts on *Prochlorococcus*, *Synechococcus*, and heterotrophic bacteria (Landry et al. 2023); silicon to carbon stoichiometric changes in diatoms in response to iron limitation (Brzezinski et al. 2015); the importance of mesoscale fronts for the biological carbon pump (Stukel et al. 2017); quantification of iron transport and consumption within coastal filaments (Forsch et al. 2023); and the impacts of ocean acidification on phytoplankton iron use (Lampe et al. 2023). Nevertheless, these short-term (typically 3–5 day) experiments afford little time for observing community responses to a disturbance, given that typical *net* rates of change of phytoplankton biomass (as estimate from chlorophyll *a*) are usually between –0.3 per day and 0.3 per day (figure 5c).

On the CCE-P1706 process cruise (June 2017), a longer Lagrangian experiment was conducted to investigate the dynamics of a water parcel that was being advected away from the coastal upwelling domain within a coastal filament after an upwelling event (Kranz et al. 2020, Wang et al. 2020, Forsch et al. 2023). The results therefore allowed investigation of recovery following the upwelling pulse. The nutrient and chlorophyll concentrations were high at the beginning of the experiment (figure 6a), and chlorophyll was initially restricted to approximately the upper 25 meters (figure 6b). During the first 4 days, the chlorophyll decreased by more than 50%, although macronutrient (nitrate and phosphate) concentrations remained more than 5 micromoles per liter. The net primary production exceeded 3000 milligram per carbon per square meter per day for the first 3 days but declined rapidly on days 4 and 5, likely because of iron limitation (Forsch et al. 2023). Protistan grazing on phytoplankton was initially approximately 3000 milligrams of carbon per square meter per day but declined more rapidly than net primary production while remaining higher than mesozooplankton grazing throughout the experiment. The initial decrease in chlorophyll despite high primary production suggests that at least part of the phytoplankton biomass decline was due to dilution (i.e., mixing) with lower chlorophyll surrounding water patches or subsurface waters. Because diffusive mixing (equation 1) is related to the gradient of biological properties (i.e., the spatial scale of the disturbed patch), this highlights the importance of

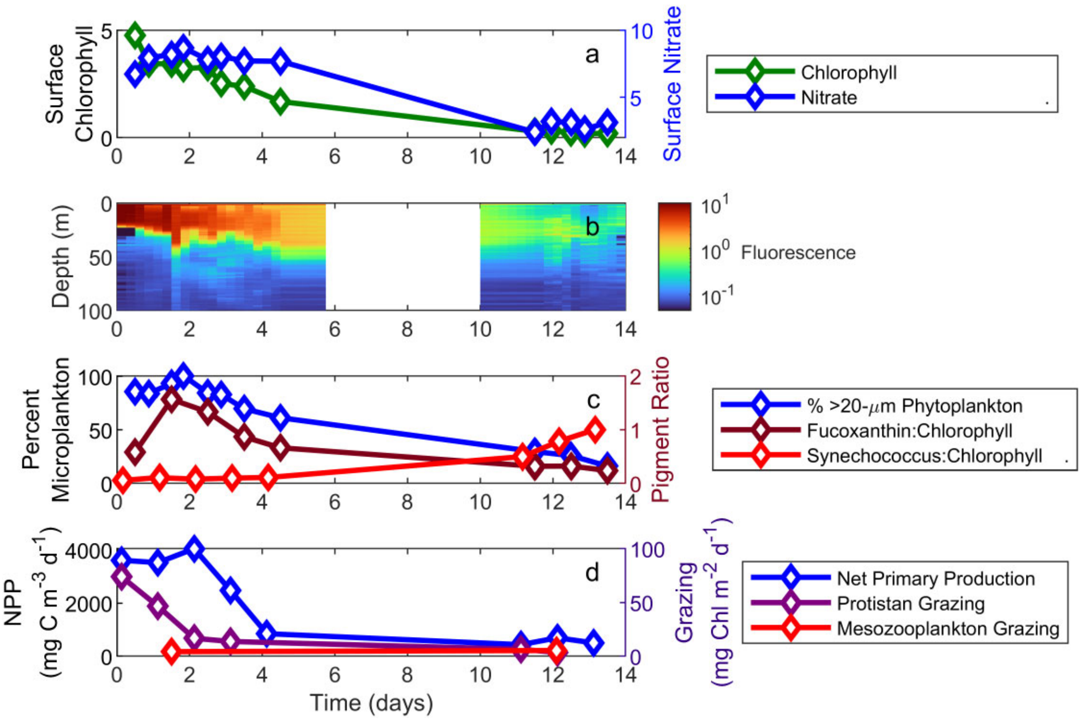

Figure 6. Ecosystem change during Lagrangian analyses of a coastal upwelling filament. Filament was tracked for 2 weeks using satellite-enabled surface floats tethered to a 3- × 1-meter holey sock drogue centered at 15-meter depth in the mixed layer (Kranz et al. 2020, Forsch et al. 2023). (a) Surface chlorophyll a and nitrate concentration. (b) Fluorescence (proxy for chlorophyll a) vertical structure. (c) Phytoplankton community changes as quantified by the proportion of chlorophyll a retained on a 20-micrometer pore-size filter, the ratio of fucoxanthin (diagnostic pigment for diatoms) to chlorophyll a, and the ratio of ***Synechococcus*** cell abundance to chlorophyll a (Chen et al. 2024a). (d) Net primary production measured by bicarbonate ($H^{14}CO_3^-$) uptake, vertically integrated protistan grazing rates measured by the dilution method, and mesozooplankton grazing rates measured by the gut pigment method (Landry et al. 2009, Morrow et al. 2018, Kranz et al. 2020). See figure 1 for the location of the experiment. No samples were collected from days 6–10.

patch size in determining recovery time following a disturbance (e.g., Angelini and Silliman 2012). Other clear patterns observed during recovery were a strong shift from dominance by diatoms (figure 6c) to the cyanobacterium *Synechococcus*, a substantial decrease in the proportion of large phytoplankton (figure 6c), and a gradual deepening of the depth of the chlorophyll maximum (figure 6b) over the 2-week study. Taken together, these results show rapid recovery from a community dominated by large coastal diatoms (i.e., rapidly growing species) to a community dominated by cyanobacteria (slower growing taxa). Notably, however, even after 2 weeks, *Prochlorococcus*, the most dominant phytoplankter under nutrient-depleted stratified conditions in the CCE, was still not abundant (not illustrated). Although this is only a single realization of postdisturbance recovery in the CCE, it provides a potential path forward for documenting multiple occurrences of postdisturbance recovery in the pelagic community. We also note that such Lagrangian approaches have been used in other ocean regions (e. g., Benitez-Nelson et al. 2007, Landry et al. 2016, Morison et al. 2019, Landry et al. 2021, Siegel et al. 2021, Décima et al. 2023), and therefore, there is potential for broader global syntheses.

Synthetic Lagrangian approaches

A serious limitation of the above approach for conducting Lagrangian experiments is the substantial cost of ship time needed to follow a drifting plankton community for days or weeks. This limits the number of such studies that can be conducted, contributing to the n = 1 problem in disturbance ecology (Buma 2021). Synthetic Lagrangian approaches (i.e., approaches that combine Lagrangian trajectory analyses with Eulerian sampling) provide a cost-effective way to use shipboard sampling for replicated sampling of disturbance recovery in pelagic ecosystems. In these approaches, a Lagrangian particle advection model is used to trace the trajectory of a sampled water parcel backward in time to determine its history with respect to disturbance events. Such a Lagrangian model can be forced with multiple ocean circulation products, including ocean model reanalysis products and satellite-derived surface currents. The goal is to leverage biological measurements made during standard Eulerian time series programs (e.g., CalCOFI) and then relate the measured ecosystem properties to the prior disturbance history of the water parcel (e.g., time since disturbance, type of disturbance, intensity of disturbance). We illustrate such an approach below.

Chabert and colleagues(2021) used satellite-derived surface currents to model the previous path of water parcels and determine the duration of time since they exited the upwelling region (i.e., time since upwelling disturbance). The resulting mosaics of water ages were highly spatially complex and resembled spatial maps of the varying impacts of fire, flood, or hurricane disturbances across a terrestrial landscape. By mapping this water mass age product onto CCE-LTER Process cruise study locations, Chabert and colleagues (2021) were able to investigate rates of nutrient drawdown postupwelling event. New production (supported by upwelled nitrate) typically exceeded export production (nitrogen loss from the euphotic zone in sinking particles) for the first 2–3 weeks after an upwelling events but export production exceeded new production after approximately 40 days.

The Chabert and colleagues (2021) analysis can be mapped to any sampling locations to investigate ecosystem recovery following an upwelling event, including the extensive data set from CalCOFI/Augmented CCE-LTER quarterly time series cruises (figure 7). This synthetic Lagrangian approach shows us that net primary production and chlorophyll are typically maximal, as was expected, in the vicinity of upwelling (figure 7a, 7b). However, they also allow us to calculate ecosystem recovery rates after disturbance, with primary producers returning to low-productivity background levels on the order of approximately 3 weeks. We also see distinct community shifts over these timescales. The largest phytoplankton represent approximately 30% of the chlorophyll in recently upwelled water, whereas tiny picoplankton become dominant 40–80 days after upwelling. *Prochlorococcus*, a cyanobacterium well adapted to warm low-nutrient conditions, was especially responsive (figure 7d) and increased with time after a disturbance, despite the overall decrease in phytoplankton biomass. In contrast with the immediate response of primary producers to the upwelling disturbance, dominant large herbivores lagged upwelling, peaking around 2 weeks later (figure 7f).

Protistan diversity also showed a strong response to upwelling disturbances. The Shannon Diversity Index (*H′*, which is a measure of alpha diversity that incorporates both species richness and evenness from a single sample) increased approximately monotonically from a minimum in the recently upwelled water to a maximum in the offshore climax community. The results therefore do not align with the intermediate disturbance hypothesis (Dial and Roughgarden 1998), which predicts a diversity peak at an intermediate stage of disturbance recovery. We note however, that this is not a direct test of that hypothesis as it does not account for beta diversity (i.e., the difference in species composition between samples taken along an environmental gradient) or whether individual trajectories were associated with periods of weaker or stronger disturbance frequency. Furthermore, insight might be gleaned by investigating whether systematic differences exist between low-disturbance frequency regimes (e.g., El Niños or extratropical marine heatwaves with infrequent upwelling pulses) versus high-disturbance frequency regimes (e.g., La Niñas with frequent upwelling pulses). Such a synthetic Lagrangian approach could easily be extended to test predictions from other studies, such as faster recovery of ecosystem function (i.e., primary and secondary production, nutrient cycling) relative to community composition following disturbances (Hillebrand and Kunze 2020).

Synthetic Lagrangian approaches have been used for multiple other purposes in CCE-LTER research. For instance, de Verneil and Franks (2015) were able to determine water parcels that had been repeatedly sampled during underway surveys of a frontal region and therefore calculate phytoplankton net growth rates in regions influenced by this front. Gangrade and Franks (2023) linked phytoplankton patches within a frontal system to discrete upwelling events near the coast that preceded the (offshore) shipboard sampling by 11–16 days. They estimated net phytoplankton growth rates of 0.28–0.4 per day for the initial 2 week period after upwelling pulses. Gangrade and Mangolte (2024) subsequently estimated that phytoplankton abundance peaked at approximately 2 weeks and copepod abundance at approximately 1 month after the upwelling events (figure 8a), which is notably longer than estimated from the Chabert and colleagues (2021) analysis (figure 7) and may be the result of different definitions for the beginning of an upwelling pulse or to specific dynamics occurring during the single cruise studied by Gangrade and Mangolte (2024). Gangrade and Mangolte (2024) also showed that phytoplankton

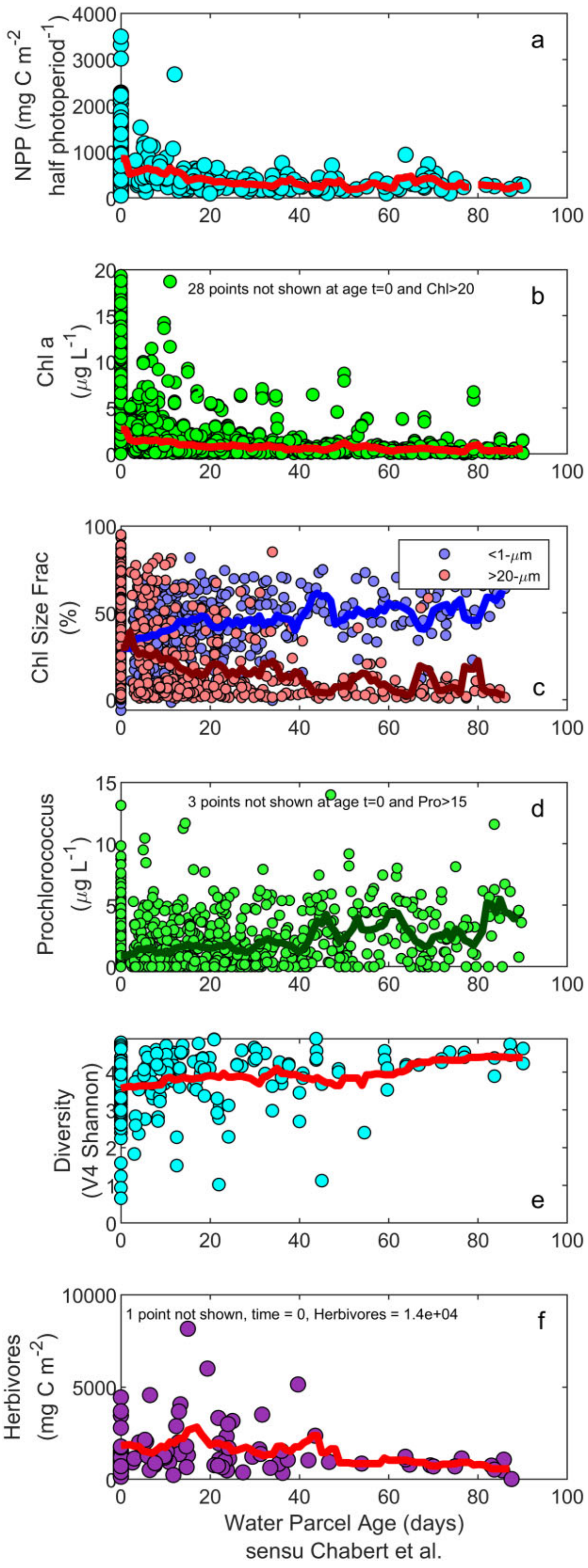

Figure 7. Ecosystem recovery following an upwelling event. The ***x***-axis is the age of the water parcel with respect to the recent upwelling disturbance event, defined as the time since the parcel of water exited the less than 500-meter isobath zone (Chabert et al. 2021). Vertically integrated net primary production (a, Mantyla et al. 1995) and surface chlorophyll a (b) peak inside the 500-meter isobath (age = 0 days since upwelling), and decrease with e-folding scales of 12.1 and 7.3 days, respectively. Distinct community shifts are evident during successional processes: The proportion of surface chlorophyll contained in microplankton

Figure 7. (Continued.) (less than 20-micrometer; Goericke 2011a) averaged 30% in freshly upwelled water but declined substantially over the first 3 weeks (the red line in panel (c)). Conversely, the percentage of chlorophyll contained in cells larger than 1-micrometer (blue in panel (c)) increased from 30 (standard deviation [SD] = 17%) at time **t** = 0 to 60 (SD = 7%) from 80–100 days after the upwelling. This community shift was further reflected in ***Prochlorococcus*** biomass (d) (source: Taylor et al. 2015), which increased with time after the disturbance, despite the overall decrease in phytoplankton biomass. Shannon diversity of protists based on amplicon sequencing of the V4 region of the 18S rRNA gene (e, Lampe et al. 2024) were minimum in the upwelling region (3.6, SD = 0.8) and reached a maximum value in the climax community (4.4, SD = 0.4). Similar results are found on the basis of assessing diversity using the V9 region or calculating diversity on the basis of richness instead of H' (see supplemental figure S2). (f) The biomass of suspension-feeding metazoans (calanoid copepods, euphausiids, and pelagic tunicates; Kenitz et al. 2019) exhibited a lag time before reaching maximum average biomass 17 days after upwelling. The solid lines in each panel are running means.

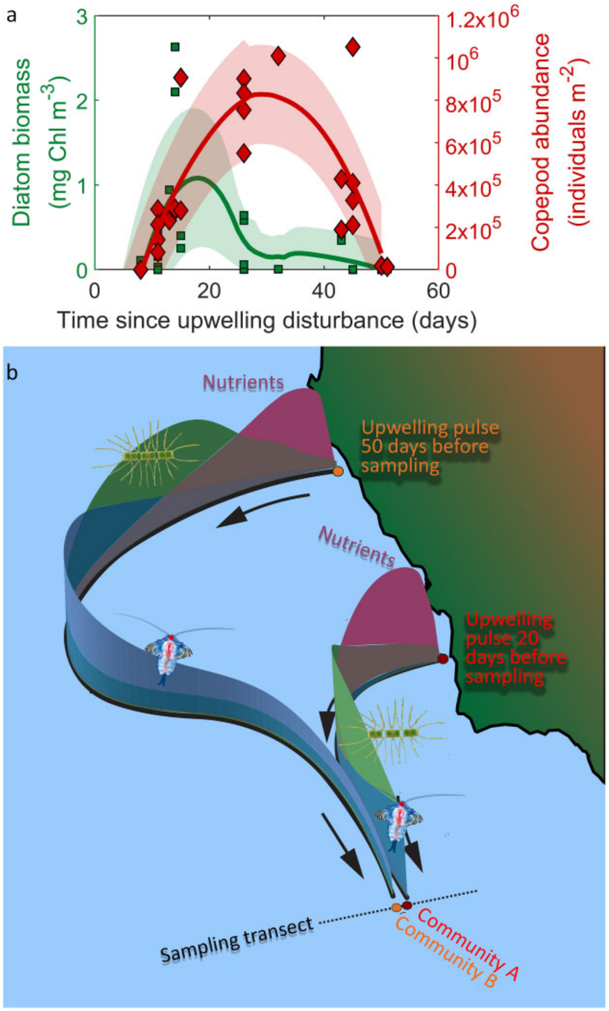

Figure 8. Diatom biomass and copepod abundance in a frontal region as a function of time since upwelling disturbance using a synthetic Lagrangian approach (a) and a schematic showing how different Lagrangian trajectories (i.e., water parcel histories) are brought together in the frontal region, leading to different ecological characteristics for geographically close communities (b). Source: Modified from Gangrade and Mangolte (2024).

patches at the front originated from multiple geographically distinct upwelling events, brought together by ocean circulation (figure 8b). This suggests interesting opportunities for studying the importance of edge effects in shaping disturbance recovery, by focusing on water parcels that are near or far from similarly disturbed patches. Addressing a very different issue, Lilly and colleagues (2022) simulated passive transport of euphausiids across different El Niño–Southern Oscillation phases. By linking the Lagrangian backward-in-time trajectories to euphausiid abundance data from CalCOFI cruises, they showed that changes in advection were strong drivers of population differences but also found differences in dynamics between subtropical fauna (which experienced transport of entire populations into the CCE domain) and cool-water species (with population structures suggesting growth within the region).

Synthetic Lagrangian approaches also afford an opportunity to connect pelagic disturbance responses to other aspects of ecological theory, such as the importance of material legacies. For instance, back trajectories could be used to relate successional patterns to the biogeochemical properties (e.g., nutrient stoichiometry) of upwelled water parcels or the ecological characteristics (e.g., prevalence or absence of different taxa) of the initial postdisturbance community. Although we have highlighted the combination of synthetic Lagrangian approaches with shipboard observations, this approach could also be applied to remote and autonomous observations. For instance, mapping Lagrangian trajectories onto phytoplankton community characteristics observed remotely by NASA's Plankton, Aerosol, Cloud and Ocean Ecosystems (PACE) satellite (which enables hyperspectral analysis of visible and ultraviolet ocean reflectance at approximately 1-kilometer resolution; Cetinić et al. 2024) might enable full trajectories of community succession to be constructed. More precise Lagrangian trajectories can also be mapped to ecological and biogeochemical observations through the use of large-scale drifter programs used to map surface currents and temperature (Zhang et al. 2019). Predictable changes to the disturbance regime mediated by climatic drivers such as the El Niño–Southern Oscillation or Pacific Decadal Oscillation may also provide natural laboratories for testing ecological theories, such as the impact of spatial correlation in disturbance on the prevalence of long-range dispersing species versus dispersal limited taxa (Liao et al. 2016). These synthetic Lagrangian approaches therefore offer a fruitful approach for further research and may yield exciting new insights as they are applied more widely and to more diverse pelagic ecosystems.

Nevertheless, there are trade-offs associated with using synthetic Lagrangian approaches. Most notably, the efficacy of synthetic Lagrangian approaches is inherently tied to the accuracy of the numerical scheme used to compute the trajectories and the ocean circulation products used (Van Sebille et al. 2018, Prants 2025). Unfortunately, the accuracy of such products can be difficult to quantify because of a paucity of direct *in situ* ocean velocity measurements, and there is no simple heuristic for determining which products to use. In coastal upwelling biomes, such as the CCE, it is clear that circulation products including ageostrophic flows (i.e., wind-driven surface upwelling and other flows that are not driven by the balance of horizontal pressure gradients and the Coriolis force) should be prioritized. The relative utility of products derived from remotely sensed surface flows (e.g., geostrophic flows derived from satellite altimetry and ageostrophic flows from scatterometers) or from three-dimensional ocean reanalysis products likely depends on the goal (e.g., studying evolution of surface communities versus three dimensional dynamics) and the location (coastal regions often have more complex dynamics but better remote sensing data from high-frequency coastal radar) of the study. There is clearly a concerted need for more intercomparison studies that validate numerical Lagrangian trajectories with *in situ* float data. Furthermore, an additional limitation of most synthetic Lagrangian approaches is that a full trajectory of recovery is typically not available (e.g., figure 7); a single observation along a Lagrangian trajectory cannot be matched to previous observations along that trajectory. This can make it impossible to disentangle the ways in which early successional variations can shape future patterns.

Simulated Lagrangian approaches

Simulated Lagrangian approaches provide another method for investigating pelagic disturbances. Although there is some overlap between simulated Lagrangian approaches and the synthetic Lagrangian approaches outlined above, we differentiate them on the basis of whether Lagrangian trajectories are explicitly compared with *in situ* observations as a part of the analysis (synthetic Lagrangian approach) or whether the results are derived solely from simulations (simulated Lagrangian approach). We note, however, that it is very common for simulated Lagrangian studies to nevertheless include observations as model validation tools.

Simulated Lagrangian analyses can take many different forms. For instance, an ecological or biogeochemical model can be run within a zero-dimensional (0-D) framework simulating a discrete water parcel as it is advected on a Lagrangian trajectory through the ocean (Kida and Ito 2017, Messié and Chavez 2017, Ser-Giacomi et al. 2023). Lagrangian analyses can also be combined with Eulerian modeling approaches, such that the three-dimensional model is run in a Eulerian framework and a Lagrangian model is used to sample within the Eulerian model to understand temporal changes within a moving ocean feature (Stukel et al. 2014, Chenillat et al. 2015a, Cetina-Heredia et al. 2018). Finally a wide range of studies have coupled individual-based models for phytoplankton (Yamazaki et al. 2014, Baudry et al. 2018, Wu et al. 2022), zooplankton (Miller et al. 1998, Dorman et al. 2015), and fish (Johnson et al. 2013, Shropshire et al. 2022) to Lagrangian models to simulate the dynamics of individual organisms as they move through the ocean.

We highlight in the present article an example of a Lagrangian model in which a simple biogeochemical model is used to simulate ecosystem change following an upwelling event as the water parcel is advected through the ocean. Messié and Chavez (2017) developed a simple model including two phytoplankton and two zooplankton groups, along with nitrate and ammonium. The model is forced by upwelling-driven nutrient pulses, which initiate a bloom of large phytoplankton and a lagged bloom of large zooplankton (figure 9). This biogeochemical model is essentially a 0-D model in which the simulated parcel is isolated from the surrounding water. However, the parcel is advected by surface currents derived from satellite products such as OSCAR (the Ocean Surface Current Analysis Real-Time product; Johnsonet al. 2007) or GlobCurrent (Rio et al. 2014). The model therefore predicts two-dimensional time-varying nutrient, phytoplankton, and zooplankton fields. Despite its relative simplicity, this model (and subsequent models building on this framework; e.g., Messié et al. 2022, 2025) accurately predicts hotspots of high zooplankton abundance and sinking carbon export. An additional value of such approaches is that, if they simulate observations accurately, the mechanistic understanding built into the model can help to diagnose processes driving ecosystem changes. For instance, the diagnostic equations in Messié and Chavez (2017) show that different dynamic balances between nutrient-limited growth and adaptive grazing pressure explain the starkly different responses of large and small phytoplankton to upwelling pulses.

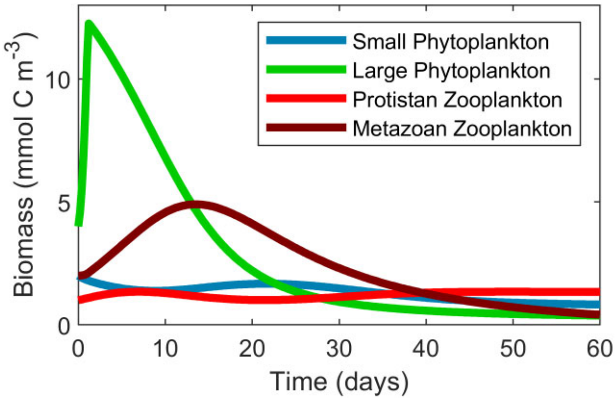

Figure 9. Biomasses of different plankton functional groups along a Lagrangian trajectory during upwelling in the Messié and Chavez (2017) model.

Chenillat and colleagues (2015a) provided an example of a combined Eulerian–Lagrangian modeling approach that uses a coupled physical–biogeochemical model (ROMS+NEMURO) to simulate three-dimensional time-varying plankton and biogeochemical distributions in the CCE. They released simulated Lagrangian floats within mesoscale eddy structures in the Eulerian model to trace temporally evolving dynamics within the features. Initially elevated plankton biomasses within the eddies were found to be the result of trapping of rich coastal waters. Plankton biomass was maintained, however, by dynamic Ekman pumping of new nutrients into the eddy core. This altered temporal patterns and maintained longer blooms in the eddy relative to what would be expected in—for instance, the analysis of Messié and Chavez (2017), which assumed that water parcels were isolated from upwelling after leaving the coastal zone. Such Eulerian–Lagrangian approaches could be adapted for investigating responses to multiple disturbance types, with the caveat that accuracy of the results will depend on how accurately the dynamics of the system are simulated. The most effective path forward may be to combine several of the approaches outlined in the present article and leverage the different strengths and weaknesses of *in situ* Lagrangian approaches, synthetic Lagrangian approaches, and different flavors of simulated Lagrangian approaches.

Conclusions

Although we have focused in the present article on responses to upwelling pulse disturbances, the approaches outlined above could also be fruitfully applied to investigating other pelagic disturbances such as marine heatwaves, hypoxic events, ocean acidification events, and marine carbon dioxide removal experiments. The increasing accuracy and higher resolutions of modern ocean circulation products are likely to further increase the efficacy of both synthetic Lagrangian and simulated Lagrangian approaches. The availability of autonomous platforms also opens new avenues for less expensive *in situ* Lagrangian studies (Dickey et al. 2008), albeit with substantially lower sampling capabilities and especially limited ability to quantify rate processes. Recent remote sensing advances (e.g., the hyperspectral radiometer on the PACE satellite) will also greatly enhance synthetic Lagrangian approaches to reconstructing postdisturbance succession within pelagic communities. The fast response times of phytoplankton communities allow Lagrangian studies to be supplemented with short-term manipulative experiments that simulate disturbance in a controlled system (i.e., bottle or mesocosm experiments). In addition, the vast range of different spatial and temporal scales of disturbances in the marine pelagic (and the ability to identify many of these disturbances remotely) enables interesting scale-dependent ecological research. For these reasons, we believe that a greater focus on pelagic environments as model systems for investigating disturbance ecology is justified and could potentially yield rapid advances.

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Supplemental data

Supplemental data are available at *BIOSCI* online.

Author contributions

Michael R Stukel (Conceptualization, Funding acquisition, Investigation, Visualization, Writing – original draft), Andrew E. Allen (Funding acquisition, Investigation, Writing – review & editing), Katherine A. Barbeau (Funding acquisition, Investigation, Writing – review & editing), Pierre Chabert (Investigation, Writing – review & editing), Shonna Dovel (Investigation, Writing – review & editing), Shailja Gangrade (Investigation, Writing – review & editing), Sven A. Kranz (Investigation, Writing – review & editing), Robert H. Lampe (Investigation, Writing – review & editing), Michael R. Landry (Funding acquisition, Investigation, Writing – review & editing), Pierre Marrec (Funding acquisition, Investigation, Writing – review & editing), Monique Messié (Investigation, Writing – review & editing), Arthur J. Miller (Funding acquisition, Investigation, Writing – review & editing), Grace M Wilkinson (Funding acquisition, Investigation, Writing – review & editing), Mark David Ohman (Funding acquisition, Investigation, Writing – review & editing).

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