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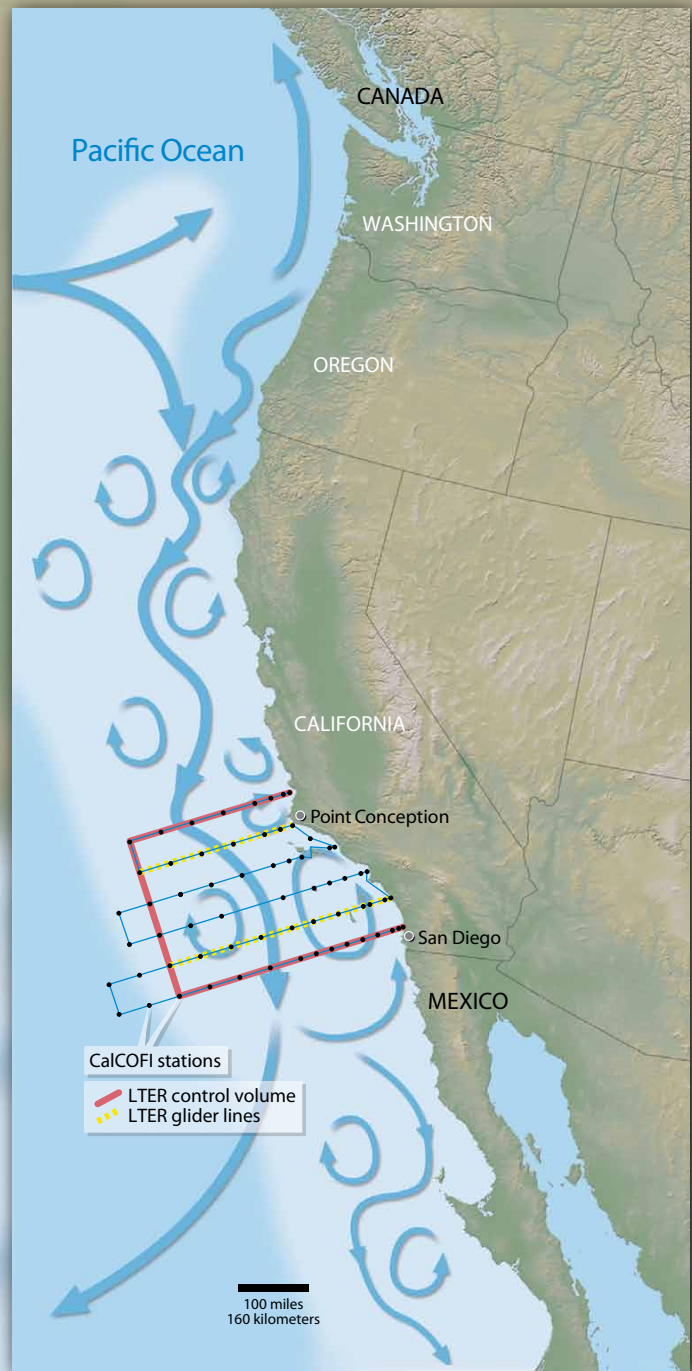
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Ecological Transitions in a Coastal Upwelling Ecosystem

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ABSTRACT. The southern California Current Ecosystem (CCE) is a dynamic eastern boundary current ecosystem that is forced by ocean-atmosphere variability on interannual, multidecadal, and long-term secular time scales. Recent evidence suggests that apparent abrupt transitions in ecosystem conditions reflect linear tracking of the physical environment rather than oscillations between alternative preferred states. A space-for-time exchange is one approach that permits use of natural spatial variability in the CCE to develop a mechanistic understanding needed to project future temporal changes. The role of (sub)mesoscale frontal systems in altering rates of nutrient transport, primary and secondary production, export fluxes, and the rates of encounters between predators and prey is an issue central to this pelagic ecosystem and its future trajectory because the occurrence of such frontal features is increasing.



INTRODUCTION

Disentangling climate-related changes from intrinsic variability in natural ecosystems is a major scientific challenge for the twenty-first century. Not only do measurement systems need to be in place for many decades, but a firm understanding must be developed of the causal mechanisms underlying natural and forced variability. Coastal upwelling ecosystems on the eastern edge of the major ocean basins are key regions of high productivity where differentiating climate-forced and intrinsic variability is especially important for establishing the scientific basis for forecasting future states of these ecosystems and the myriad services they provide to humans.

The California Current Ecosystem (CCE) is a coastal upwelling biome that forms the eastern limb of the large-scale gyral circulation of the North Pacific Ocean. The CCE Long Term Ecological Research (CCE LTER) site is located in the southern sector of the CCE where there is an exceptional record of ocean observations, thanks to CalCOFI (the California Cooperative Oceanic Fisheries Investigations), now in its seventh decade of sampling. Ecosystem dynamics in the CCE region are influenced by oceanic and atmospheric processes acting on spatial scales that vary from Pacific basin-wide, to regional-scale forcing, to energetic mesoscale (of order 30–300 km in horizontal dimension) and submesoscale (1–10 km) processes.

CalCOFI and other measurement programs have uncovered important sources of pelagic ecosystem change at varying temporal scales. These changes include:

- Progressive long-term trends, including changes in ocean temperature (Roemmich, 1992; Field et al., 2006), vertical stratification (Kim and Miller,

2007), dissolved oxygen (Bograd et al., 2008; McClatchie et al., 2010), wind-stress curl upwelling (Rykaczewski and Checkley, 2008), and plankton populations (Kahru et al., 2009; Lavaniegos and Ohman, 2007; Aksnes and Ohman, 2009; Ohman et al., 2012b)

- Multidecadal variability associated with the Pacific Decadal Oscillation (PDO; Miller et al., 1994; Mantua et al., 1997; Di Lorenzo and Ohman, 2013) and the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al., 2008)
- Interannual variability, dominated by the El Niño-Southern Oscillation (ENSO), that can be at least as strong as the temporal trends and multi-decadal variations (Todd et al., 2011; Ohman et al., 2012a) in the southern CCE region

Understanding the changing ocean ecosystem requires resolving these different scales of forcing and their interactions with intrinsic biological variations.

Recent findings related to the coupling of long-term variability of zooplankton and climate in the CCE region highlight the importance of mechanistic understanding. Relatively abrupt transitions in pelagic organisms can be recognized in these long-term observations, as illustrated by changes in abundance (e.g., 1977 and 1999) of the subtropical euphausiid *Nyctiphanes simplex* (Figure 1). Such transitions have been interpreted to be ecosystem shifts between alternative persistent system states (or “regime shifts,” e.g., deYoung et al., 2008), though it is now clear that

the functional relationship between euphausiids and the environment does not change at these times (Bestelmeyer et al., 2011), as would be implied by a nonlinear regime shift concept. As Figure 1 illustrates, variations of the euphausiid and an integrated index related to the PDO are closely related, where the PDO effect is modeled with a natural damping time scale set by the euphausiids’ lifespan (Di Lorenzo and Ohman, 2013). That is, the zooplankton are merely tracking changes in the physical environment (Hsieh and Ohman, 2006). Di Lorenzo and Ohman (2013) suggest that this tracking occurs through a two-step integration of environmental forcing: first, a time-lagged response of ocean circulation to atmospheric forcing, followed by a time-lagged response of zooplankton population growth to changing ocean circulation. This double integration mechanism provides a new null hypothesis that needs to be considered before more complicated nonlinear mechanisms are invoked.

FOUR CENTRAL MECHANISMS

We have advanced four mechanisms that would explain ecological transitions such as those depicted in Figure 1. They include: (1) anomalous alongshore advection of different plankton assemblages, (2) changes in cross-shore transport and loss/retention of organisms, (3) altered predation pressure, and (4) in situ food web changes in response to altered stratification and nutrient supply. Different experimental, observational (Ohman et al., 2013, in this issue), and modeling

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approaches (Franks et al., 2013, in this issue) are being used to explore these different mechanisms. Here, we briefly mention approaches to address three mechanisms, then focus primarily on one: in situ changes in response to altered stratification and nutrient supply.

The importance of sustained, anomalous alongshore advection as a process leading to altered assemblages is being addressed by time series analyses (e.g., Di Lorenzo and Ohman, 2013), numerical hindcast models, and quarterly calculations of north-south volume transports. Higher frequency sampling at the CCE-1 and CCE-2 moorings along CalCOFI line 80 as well as at the CORC (Consortium for the Ocean's Role in Climate) moorings along CalCOFI line 90 (http://mooring.ucsd.edu/index.html?/projects/cce/cce_data.html) permit finer temporal resolution of

variations in alongshore transport. Altered cross-shore transport as a mechanism leading to altered rates of retention of organisms in the nearshore zone is being addressed by ROMS (Regional Ocean Modeling System) models of nearshore circulation, including both offshore-propagating eddies and Ekman transport (Combes et al., 2013), as well as mooring-based measurements. The sources of predation of primary interest are zooplanktivorous fishes and carnivorous zooplankton. Variations in zooplanktivorous fish stocks (sardines, anchovies, jack mackerel) can be combined with bioenergetic models to estimate consumption under conditions of high and low prey availability (e.g., Nonacs et al., 1998) that may result from changes in stratification. Variations in abundance of carnivorous zooplankton (especially jellyfish, siphonophores,

chaetognaths, predatory copepods) are assessed from the CalCOFI zooplankton samples, paying attention to temporal changes in the occurrence of mesoscale eddies and fronts and the associations of predators with such features (cf., McClatchie et al., 2012).

In addressing the role of altered stratification and nutrient supply, we use a space-for-time exchange approach. This approach makes the assumption that spatial variations in food web structure and rate processes can be analyzed as an analog of how structure and rates of the pelagic community will respond to change over time.

For example, consider the spatial variability in depth of the nitracline (the depth where NO_3 first exceeds $1 \mu\text{M}$) from west to east across the CCE region (Figure 2a). Nitracline depth is closely related to the vertical distribution (Figure 2a) and concentration (Figure 2a,b) of phytoplankton chlorophyll *a* (Chl-*a*), and to the concentration of the picoautotroph *Synechococcus* spp. in our region (Figure 2c, note the nonlinear relationship). Numerous other characteristics of food web structure are expected to covary with such changes at the base of the food web (e.g., Landry 1977; Duarte et al., 2000). In the time domain, interannual variations in the nitracline depth also covary with both the vertical distribution and concentration of Chl-*a* (Figure 2d). The magnitude of variability in nitracline depth is similar in both space and time. We therefore expect that targeted experiments in water parcels representing the range of conditions that exist contemporaneously in space will give us the ability to forecast how temporal changes in ocean forcing may affect the food web in the future.

One application of the space-for-time

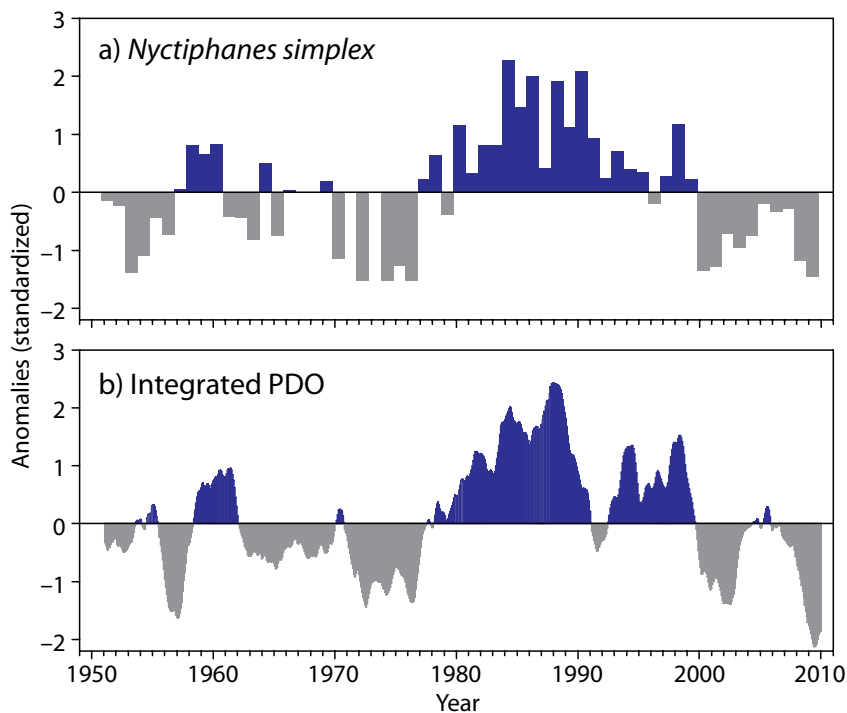


Figure 1. Temporal variability of (a) the euphausiid *Nyctiphanes simplex* in the California Current Ecosystem Long Term Ecological Research region over 60 years and (b) an autoregressive 1 model of the Pacific Decadal Oscillation with damping time scale $\tau = 2 \text{ y}$ (Di Lorenzo and Ohman, 2013). The y-variables in both graphs are standardized anomalies. Note the relatively abrupt, coincident changes, particularly those in 1977 and 1999.

exchange can be seen in our quasi-Lagrangian studies of phytoplankton growth and grazing process in different water parcels across the CCE LTER region (Figure 3). Each of five “cycles” of experimental activity was positioned relative to specific hydrographic features that were located from CalCOFI cruise, satellite ocean color data, *Spray* ocean glider data (Davis et al., 2008), and Moving Vessel Profiler (Ohman et al., 2012a, 2013, in this issue) profiles of physical and biotic variables. In situ seawater dilution experiments were performed at eight light depths suspended from a satellite-tracked holey sock drift array (Figure 3), with mesozooplankton grazing calculated from net samples using the gut fluorescence method. The results (Figure 3; Landry et al., 2009) reveal onshore-to-offshore spatial declines in phytoplankton specific growth rates (μ), accompanied by shifts in the phytoplankton assemblage from diatoms and dinoflagellates onshore to offshore dominance of pico- and nanophytoplankton. Microzooplankton grazing (m) was relatively similar across the region, while mesozooplankton grazing (M) declined progressively from inshore to offshore (Figure 3). The net community growth rate—the resultant of $\mu - (m + M)$ (white bars in Figure 3)—agreed well with the net rate of change of phytoplankton concentrations observed in ambient waters on successive nights (red bars in Figure 3), suggesting the quasi-Lagrangian method was successful in following the plankton community in a water parcel, whether the net rate of phytoplankton change was positive (increasing population) or negative (decreasing population). Numerous other processes have been investigated concurrently with these experiments, including the effects of iron and iron-light co-limitation (Hopkinson and Barbeau,

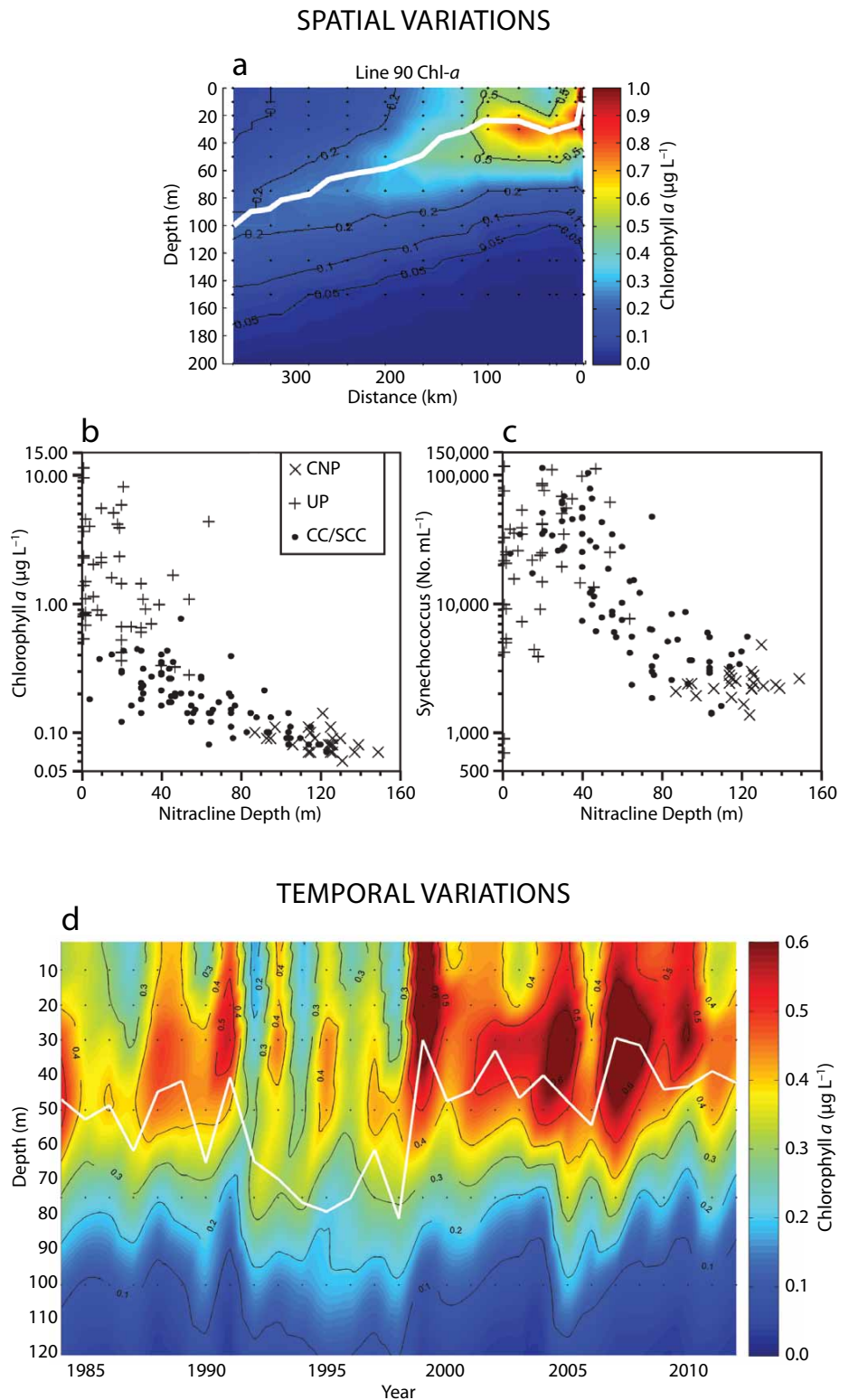


Figure 2. Nitracline variations in space and time. Variations in space: (a) Nitracline depth (NCD; white line) increases with distance from shore, moving east (right) to west (left) along California Cooperative Oceanic Fisheries Investigations (CalCOFI) line 90. Other biological properties often covary with NCD, including Chl-*a* concentration (contours in a, symbols in b), and (c) abundance of the cyanobacteria *Synechococcus* spp. Variations in time: (d) areally averaged NCD (white line) varies significantly from year to year and is inversely related to Chl-*a* concentration (contours) in the California Current proper regions of the study area. Panels b,c modified from Collier and Palenik (2003); see also Aksnes et al. (2007); all data from CalCOFI cruises

2008), export fluxes measured both by ^{234}Th and sediment traps (Stukel et al., in press), characterizations of dissolved organic matter (Lihini Aluwihare, Scripps Institution of Oceanography, *pers. comm.*,

April 2013), microbial communities (Samo et al., 2012), silicic acid cycling (Mark Brzezinski, UC Santa Barbara, and Jeffrey Krause, Daupin Island Sea Lab, *pers. comm.*, April 2013), selective

grazing by mesozooplankton (Décima, 2011), changes in vertical habitats of mesozooplankton (Romagnan, 2007), and changes in mesopelagic fish communities (Lara-Lopez et al., 2012). With a sufficient number of such experiments that exploit natural spatial variations in the ecosystem, we intend to parameterize models to forecast changes in food web structure, predator-prey interactions, and particle export processes with projected future changes in ocean density stratification and nutrient supply.

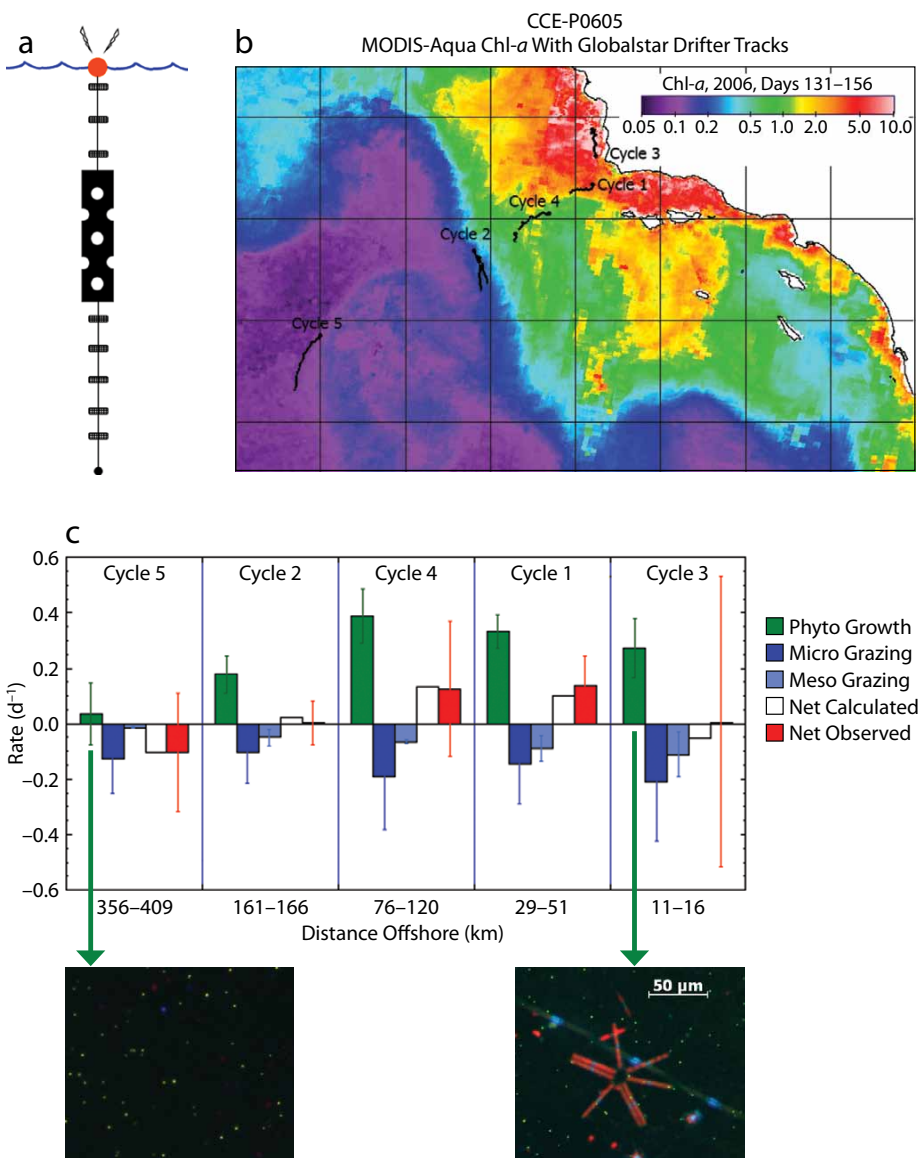


Figure 3. (a) Holey sock drift array with Globalstar tracking. (b) Overlays of experimental cycle drifter tracks (black lines) on cruise-averaged MODIS-Aqua images of surface Chl-*a* for a California Current Ecosystem process cruise off of Pt. Conception, California. *Figure courtesy of Mati Kahru, Scripps Institution of Oceanography* (c) Instantaneous rates of change of Chl-*a* due to phytoplankton growth and micro- and mesozooplankton grazing for Lagrangian drifter experiments (cycles). Cycles are arranged from west (left) to east (right). Phytoplankton specific growth rates (μ , green) and microzooplankton specific grazing rates (m , dark blue) are determined from in situ seawater dilution experiments incubated at eight light depths (cf. panel a). Mesozooplankton-specific grazing (M , light blue) is calculated from size-fractionated gut fluorescence. The net calculated change (k' , white) is the resultant of $\mu - m - M$. The net observed change (red) is from daily measurements in the ambient water column. Epifluorescence images indicate phytoplankton assemblages in the offshore and inshore cycles (dark boxes; both images to the same scale). *Figure modified from Landry et al. (2009)*

WIND-STRESS CURL VS. COASTAL BOUNDARY UPWELLING

While upwelling influences much of the CCE LTER region directly or via lateral advection, two rather different types of upwelling have distinctive ecological impacts. Studies of coastal upwelling have classically focused on upward vertical velocities and nutrient supply associated with alongshore, equatorward winds and Ekman transport near the continental boundary (coastal boundary upwelling, thick blue arrow in Figure 4a). However, along most of the west coast of North America, the east-to-west gradient in wind stress gives rise to another form of vertical motion called wind stress curl-induced upwelling (thin blue arrows in Figure 4a), which is displaced offshore of the coastal boundary. The occurrence of wind stress curl upwelling in boundary currents has long been known (e.g., Chelton, 1982; Pickett and Paduan, 2003), but its ecological significance has recently received renewed attention. Working in the CCE region, Rykaczewski and Checkley (2008) pointed out that although the vertical velocities associated with offshore wind-stress curl upwelling are much lower than with coastal boundary upwelling, the area of ocean

associated with curl upwelling is much larger; hence, the nutrient flux associated with curl-driven upwelling is usually greater. Moreover, in the weaker curl upwelling zone, smaller phytoplankton cells and smaller-bodied zooplankton tend to dominate the size composition of the plankton, in contrast to the larger diatoms and mesozooplankton in the coastal boundary upwelling (Rykaczewski and Checkley, 2008; see Figure 4a). These authors argued that differential plankton size structure in the two zones leads to food webs that favor different types of planktivorous fish. Because of different gill-raker spacing and prey size preferences (van der Lingen et al., 2006), Pacific sardines can more effectively utilize the smaller-bodied prey in the curl upwelling zone, while northern anchovies can more effectively capture the larger-bodied prey in the coastal boundary upwelling. Temporal changes in the coastal boundary upwelling zone over the last six decades have been relatively weak, in contrast to the clear temporal trend of increased curl-driven upwelling (Figure 4b), explaining an increasing trend in sardine biomass and surplus production. Hence, differential use of these distinct upwelling habitats can lead co-occurring consumers to show markedly different responses to ocean changes.

The offshore, more stratified part of the CCE domain shows a classical deep Chl-*a* maximum layer (Venrick et al., 1973). In such regions, the availability of nitrogen typically is thought to limit phytoplankton growth in surface waters, while the deep Chl-*a* maximum has been considered light-limited. However, CCE process studies indicate that waters near the base of the euphotic zone can have modest NO₃ availability but insufficient Fe, leading to subsurface regions of Fe-light co-limitation (Hopkinson and

Barbeau, 2008). Such subsurface layers develop in stratified regions offshore. Fe limitation has also been documented in near-surface waters in the CCE region in locations displaced slightly downstream

from nearshore upwelling zones, and in the wind-stress curl dominated transition zone between nearshore and offshore waters, where Fe is depleted relative to NO₃ (King and Barbeau, 2007, 2011).

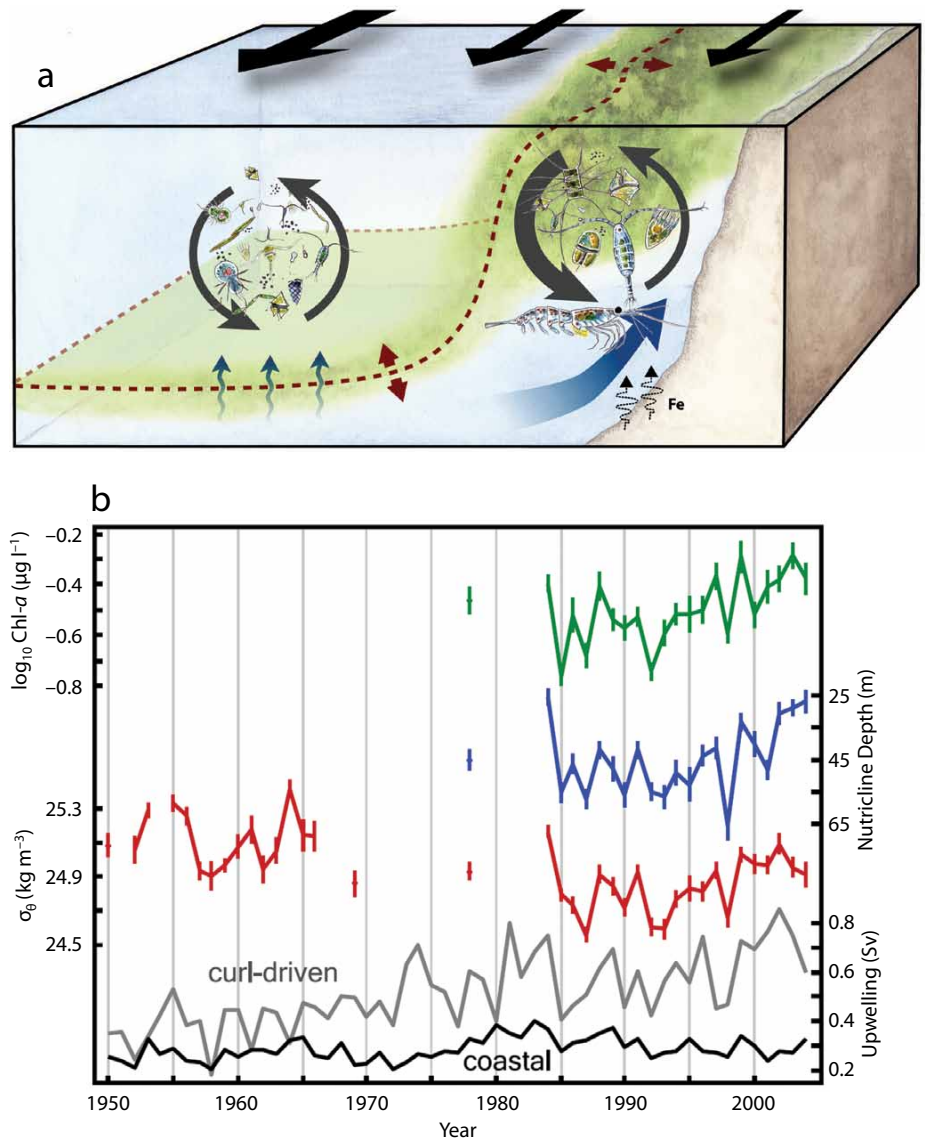


Figure 4. (a) Conceptual diagram of general spatial distributions and food web relationships associated with wind-driven upwelling in the California Current Ecosystem study region. Bold upper black arrows depict the onshore-to-offshore gradient in equatorward wind stress. Large blue arrow represents strong upwelling at the coastal boundary. Small blue arrows represent weaker offshore wind stress curl upwelling. Red arrows indicate onshore-offshore and vertical movements of the nitracline. Circular arrows depict relative magnitudes and balance of phytoplankton growth and grazing loss processes in eutrophic and oligotrophic food webs, dominated by large and small plankton, respectively. Figure courtesy of Mike Landry and Kristin Carlson, Scripps Institution of Oceanography (b) Temporal changes in summer upwelling and other properties in the California Current Ecosystem Long Term Ecological Research region. Upper water column density = σ_{θ} , red, Nitracline depth = blue, and Chl-*a* concentration = green. After 1970, these water column characteristics are better correlated with curl-driven upwelling (gray) than with coastal upwelling (black). Prior to 1970, σ_{θ} is correlated with coastal upwelling and not offshore curl-driven upwelling. From Rykaczewski and Checkley (2008)

MESOSCALE AND SUBMESOSCALE FRONTS

Evidence from the CCE LTER region suggests that the incidence of satellite-detectable ocean fronts has increased over the past 29 years (Kahru et al., 2012), perhaps related to greater hydrodynamic instabilities resulting from increasing wind stress and associated increases in numbers of filaments and eddies. This increasing trend leads to

questions about how these mesoscale and submesoscale frontal features modify ecological processes such as nutrient supply, primary and secondary production, export fluxes, biotic gradients, and predator-prey interactions. Ecosystem processes at fronts have attracted the interest of many previous investigators in the California Current System (e.g., Mackas et al., 1991; Haury et al., 1993; Venrick, 2000). A recent study in

the CCE study domain revealed striking ecological changes at an oceanic frontal system (Landry et al., 2012; Figure 5). A stable, deepwater frontal system designated the A-Front showed pronounced biotic transitions, including predominance of the picophytoplankters *Prochlorococcus* to the south, *Synechococcus* to the north, and diatoms at the front itself (Figure 5; Chekalyuk et al., 2012; Taylor et al., 2012). The local

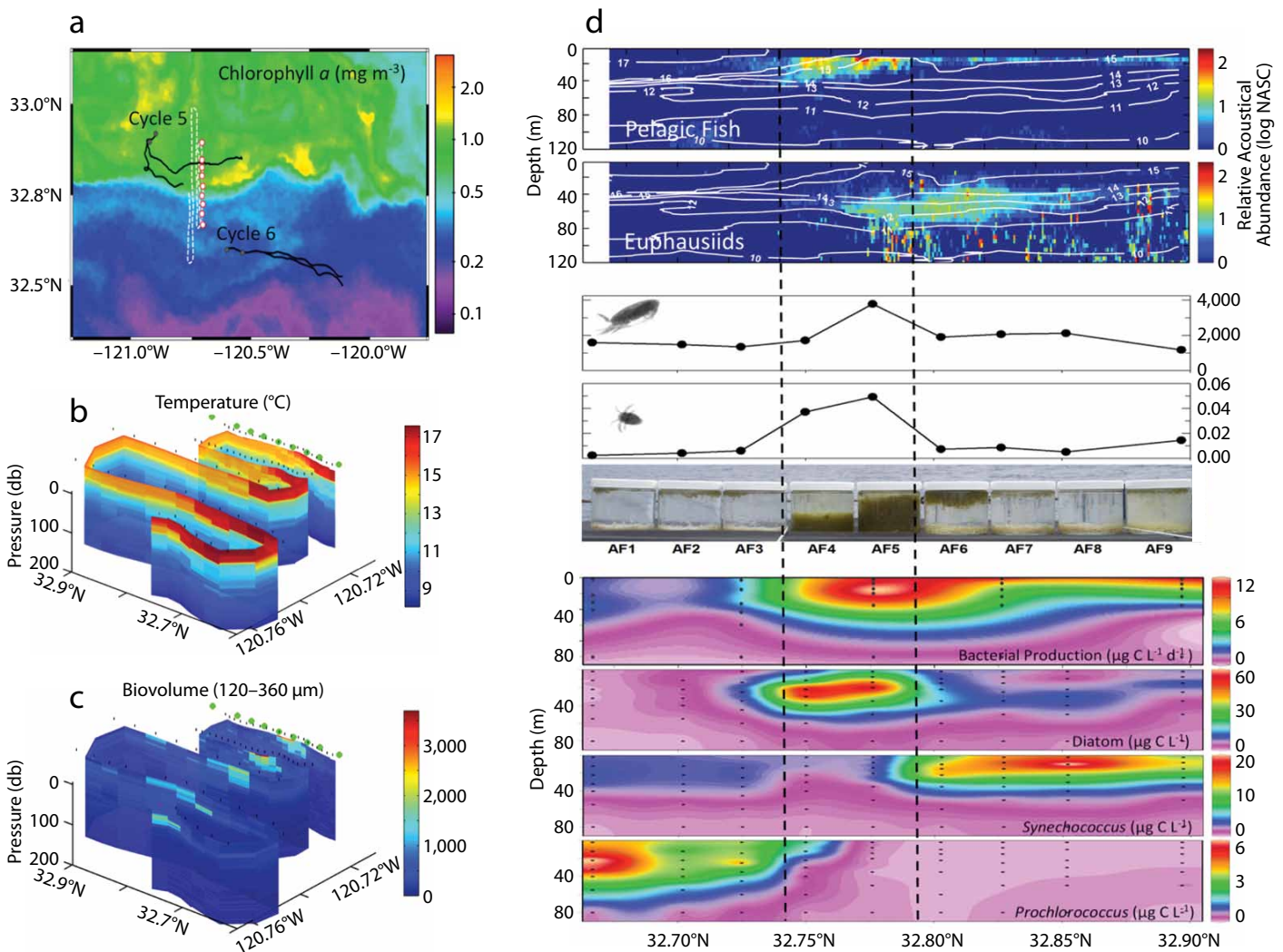


Figure 5. Changes in properties across the A-Front (a deepwater frontal system in the California Current), Oct. 2008. (a) Merged MERIS, MODIS-Aqua, MODIS-Terra, and SeaWiFS image of the study region, indicating drifter tracks (black lines), ship track (dotted line), and sampling stations (red dots). *Figure courtesy of Mati Kahru, Scripps Institution of Oceanography.* Moving Vessel Profiler survey of (b) temperature and (c) particle biovolume in the 120–360 μm ESD (equivalent spherical diameter) size range (green dots indicate sampling stations for panel d; Ohman et al., 2012a). (d) From bottom to top, vertical sections across the A-Front of carbon biomass of *Prochlorococcus*, *Synechococcus*, and total diatoms (Taylor et al., 2012); bacterial carbon production rate (Samo et al., 2012); photograph of composition of net tows from 100–0 m (202 μm mesh); vertically averaged abundance of nauplii (free-swimming copepod larvae) per adult copepod and total calanoid copepods (Ohman et al., 2012a); vertical sections of acoustically derived estimates of euphausiid and fish acoustic backscatter (Lara-Lopez et al., 2012). In panel (d), stations are oriented from south (left) to north (right). Vertical band delineates the front. *Modified from the cover of the Journal of Plankton Research, September 2012 (see Landry, Ohman et al., 2012)*

maximum in diatoms was associated with elevated nitrate fluxes (Li et al., 2012), peak phytoplankton variable fluorescence (Chekalyuk et al., 2012), elevated bacterial production (Samo et al., 2012), increased concentrations of organic aggregates (Ohman et al., 2012a), elevated abundance of calanoid copepods and of naupliar recruitment (Ohman et al., 2012a), and increases in both euphausiid and pelagic fish populations (Lara-Lopez et al., 2012). We hypothesize that such ecological “hot spots,” while limited in spatial extent, may come to play a disproportionately greater role in ecological processes, and affect ecosystem transitions in the California Current Ecosystem in the future.

Another example of the ubiquitous ocean fronts in the CCE LTER region, which are often associated with westward-propagating eddies (Chelton et al., 2007; Combes et al., 2013), is a recent study that identified an eddy dipole (anticyclonic eddy flanked by two cyclonic eddies; Figure 6a) with associated frontal gradients due west of Pt. Conception. An in situ survey with a towed vehicle (SeaSoar; Figure 6b,c), combined with acoustic Doppler profiler measures of ocean currents, revealed a pronounced density front with an associated southward jet (Figure 6c). The effects of this feature on primary and secondary production, export fluxes, trace metal and silica cycling, and other processes in the ocean water column are topics of intensive ongoing analyses.

There can be secondary circulation associated with the meandering boundaries of fronts that markedly alter the directions of vertical motions. For example, anticyclonic frontal meanders can displace fluid elements (and entrained nutrients and plankton) upward, while cyclonic meanders can displace fluids

and organisms downward, due to the conservation of potential vorticity. In order to understand the net fluxes associated with frontal features, it is desirable to resolve such meanders and the integrated contribution they make along the spatial extent of the feature.

IMPORTANCE OF THE SOUTHERN SECTOR OF THE CALIFORNIA CURRENT SYSTEM

The southern sector of the California Current System (SCCS) is an ideal region for understanding long-term forcing and response mechanisms of the pelagic

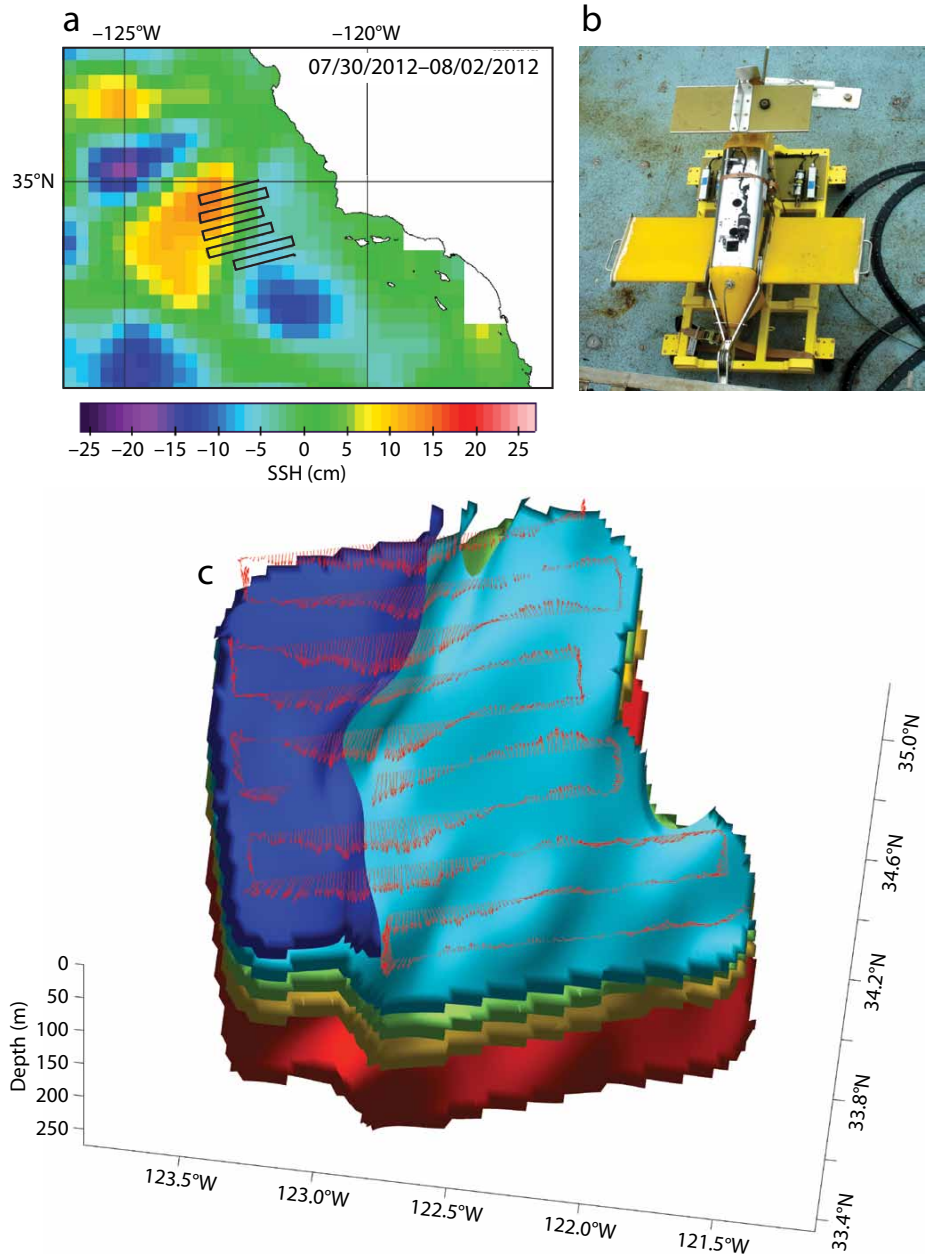



Figure 6. Survey of the region of the E-Front (a front in the California Current west of Pt. Conception), July to August 2012. (a) AVISO satellite image of sea surface height with overlay of SeaSoar survey 1 track (black dots) across the E-Front. Image courtesy of Mati Kahru, Scripps Institution of Oceanography (b) SeaSoar towed body. (c) SeaSoar vertical sections of density (σ_θ , color contours) with vertically averaged current vectors from 27–53 m depth from a 75 kHz acoustic Doppler current profiler (red lines), for the region identified in (a). Panel (c) courtesy of Alain de Verneil, Scripps Institution of Oceanography

ecosystem for several reasons. This is the site of the CalCOFI ocean time series, now in its 65th year. The Pt. Conception region is a biogeographic boundary region for many pelagic and benthic organisms, and displacements in this boundary represent an early sentinel of climate change. The SCCS is the preferred spawning site for the majority of epipelagic fish biomass in the California Current System, as well as for many near-shore fishes and benthic invertebrates. Low-frequency changes in the SCCS are correlated with changes in much of the Northeast Pacific. Over a relatively small geographic distance, there is a pronounced gradient of ocean conditions from productive to oligotrophic waters, encompassing much of the range of productivity in the world ocean. An integrated network of autonomous and shipboard measurements is currently in place (Ohman et al., 2013, in this issue). Advanced ROMS and other models have been developed and parameterized for this region (Franks et al., 2013, in this issue). And, proximity to the varved sediments of the Santa Barbara Basin makes it possible to reconstruct paleoceanographic variability extending back nearly two millennia, facilitating comparisons between ecosystem states in the pre-industrial era and the Anthropocene (e.g., Field et al., 2006).

In summary, the southern California Current Ecosystem is a dynamic eastern boundary current region that is forced by physical and biotic processes across a spectrum of temporal and spatial scales. Notable among these are multidecadal variations in ecosystem conditions, some of which are manifest as relatively abrupt changes that reflect linear tracking of the physical environment rather than oscillations between alternative preferred states. A space-for-time exchange is

one approach that permits the natural spatial variability in the CCE to be used to develop a mechanistic understanding needed to project future temporal changes. The contrasting ecosystem processes occurring in the offshore curl-driven upwelling zone and the near-shore coastal boundary upwelling zone appear to be of particular significance in this region. The role of frontal systems in altering rates of nutrient transport, primary and secondary production, export fluxes, and the rates of encounter between predators and prey is an issue central to this pelagic ecosystem and its future trajectory because occurrences of such frontal features are increasing.

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