

New Insights into the Controls and Mechanisms of Plankton Productivity in Coastal Upwelling Waters of the Northern California Current System

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ABSTRACT. During the lifetime of the National Science Foundation's Coastal Ocean Processes program, four experiments were conducted on the US West Coast in the northern California Current System. Although each project had a unique scientific focus, all four addressed the mechanisms causing eastern boundary current systems in general, and the California Current System in particular, to be biologically rich, from phytoplankton to apex predators. Taken together, findings from these projects provide new insights into the canonical view that upwelling systems are simple wind-driven "conveyor belts," bringing cold, nutrient-rich waters to the well-lit surface ocean where biological organisms flourish. We highlight new insights and advances gained from these programs, including recognition that (a) elements other than nitrogen, particularly iron, may limit the base of the food chain, and (b) the source of these nutrients is not solely a result of wind-driven Ekman transport. The importance of retentive features has clearly emerged, whether these are associated with topography, bathymetry, or more transient features such as river plumes. These new insights into the drivers and fate of this high biological productivity should greatly improve current and future generations of ecosystem models and provide a better understanding of the unique physical-biological coupling that makes the California Current System so rich.

INTRODUCTION

Coastal upwelling regions in Eastern Boundary Current (EBC) systems, such as those along the US West Coast, are some of the most productive regions in the world's ocean, from phytoplankton at the base of the food chain, all the way through fisheries, to apex predators, marine mammals, and birds. Indeed, these ecological regimes account for only 1% of the world's surface ocean, but they provide 35% of wild-caught fish annually (FAO, 2002). These biologically rich regimes are founded on the upwelling of nutrients due to wind-driven transport. Southward wind stress along the US West Coast drives an offshore surface Ekman layer flux, which is balanced near the coast by the vertical transport of cold, nutrient-rich waters from depth. This wind-driven flux provides nutrients to well-lit surface waters, but at the same time it changes the light climate for primary producers, as increased vertical mixing causes them to spend more time at deeper depths. Moreover, offshore transport of the resultant phytoplankton blooms and secondary production results in losses from the shelf waters.

Early analyses of the physics of coastal upwelling focused predominantly on straight coastlines (e.g., Barber and Smith, 1981; Beardsley and Lentz, 1987; Brink and Cowles, 1991). The dominant view of biological processes generally followed the concept of a two-dimensional "conveyor belt," in which upwelling results in cold, nutrient-rich water near the coast (Dugdale and Wilkerson, 1989). This circulation supports a coastal bloom composed primarily of diatoms, in turn fed on by mesozooplankton such as copepods and krill, which feed a rich

community of planktivorous fish, birds, and whales. As the water is transported offshore, planktonic organisms can catch a ride back to shore by sinking down into the upwelling return flow, completing the conveyor belt analogy (Figure 1).

This textbook view of coastal upwelling is a reasonable representation along straight coastlines, but a number of questions have arisen in the last 15 years about how these processes are regulated along real coasts with complex topography and freshwater input. On the US West Coast, four separate projects funded by the Coastal Ocean Processes (CoOP) program have provided a more complete view of the physical-biological coupling that leads to dramatic ecosystem productivity. In

1995, the Air-Sea Chemical Exchange (CASCEX) experiment took place in the vicinity of Monterey Bay, California; from 2000–2003, the Wind Events and Shelf Transport (WEST) project examined the role of upwelling in northern California, while Coastal Advances in Shelf Transport (COAST) carried out a similar project off Oregon in 2001–2003. COAST benefited from additional sampling and analysis in the northern California Current as part of the US Global Ocean Ecosystems Dynamics (GLOBEC) program. Finally, the River Influences on Shelf Ecosystems (RISE) project examined the influence of the Columbia River, the single largest West Coast discharge of freshwater, on the coastal upwelling ecosystem

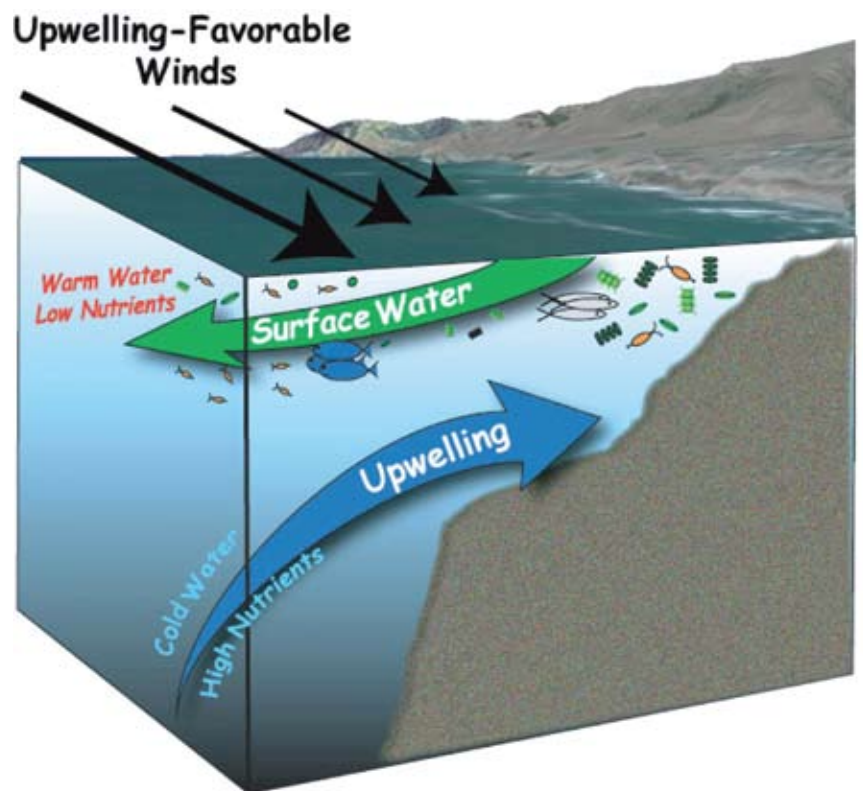


Figure 1. Coastal upwelling is often depicted as a two-dimensional process. Cold, nutrient-rich waters are transported to the surface due to divergence in offshore wind-driven Ekman transport. These waters support a rich biological community composed of diatoms and large zooplankton nearshore, with a gradual transition to smaller organisms offshore.

off Oregon and Washington during 2004–2006 (Figure 2). Although these CoOP projects had separate goals, methods, and outcomes, they all further informed our understanding of how EBC shelf regions maintain such high productivity, and they provided a more complete understanding of the influence of topography and runoff on physical-biological interactions.

Two fundamental questions all of these projects address are:

- How can high biological productivity be maintained in such a strongly advective physical regime?
- What factors set up the patchy mosaic of high and low biomass along the coast (Figure 2)?

Here, we present some of the new insights obtained from these projects, focusing on the role of nutrients, retention in an advective regime, and the biogeochemical consequences of these interactions.

THE ROLE OF NUTRIENTS

Classically, phytoplankton in the ocean are considered to be primarily limited by the element nitrogen (N), provided as nitrate during coastal upwelling events (Ryther and Dunstan, 1971). However, with the introduction of trace-metal clean sampling techniques, it became apparent that much of the world's ocean

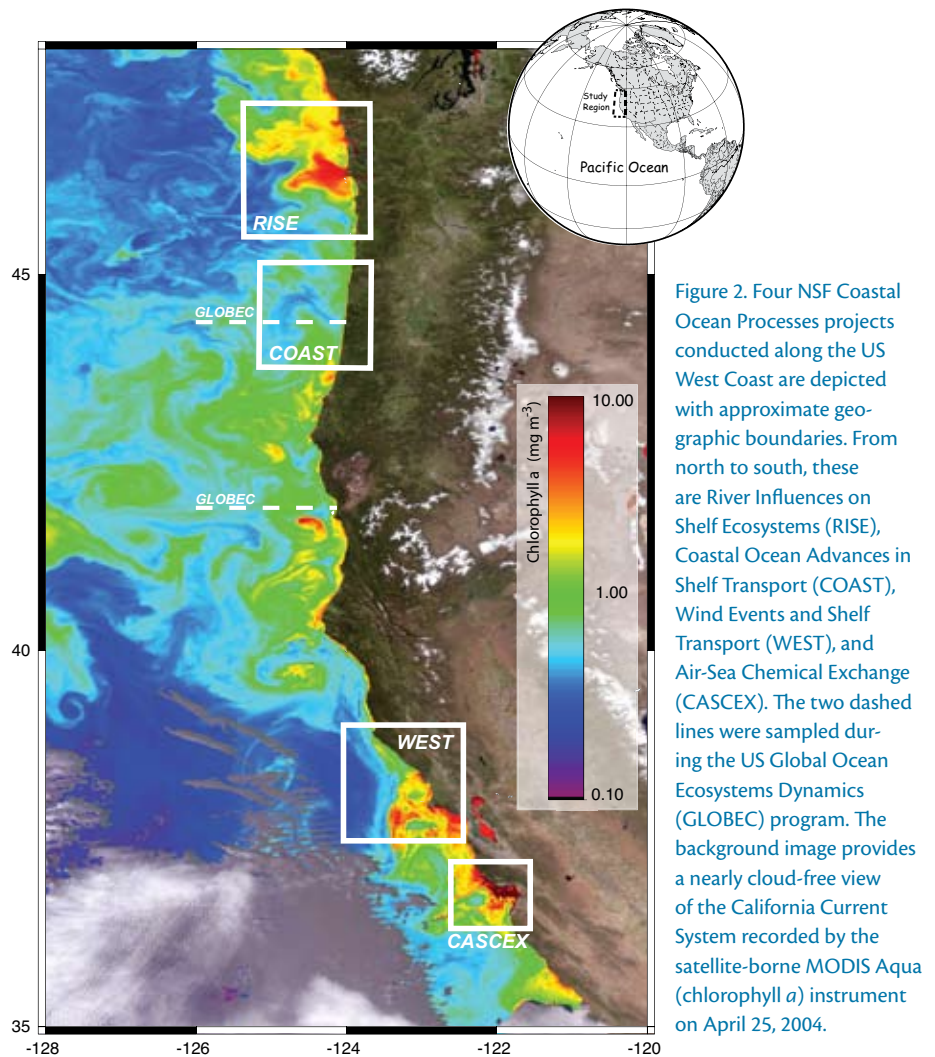


Figure 2. Four NSF Coastal Ocean Processes projects conducted along the US West Coast are depicted with approximate geographic boundaries. From north to south, these are River Influences on Shelf Ecosystems (RISE), Coastal Ocean Advances in Shelf Transport (COAST), Wind Events and Shelf Transport (WEST), and Air-Sea Chemical Exchange (CASCEX). The two dashed lines were sampled during the US Global Ocean Ecosystems Dynamics (GLOBEC) program. The background image provides a nearly cloud-free view of the California Current System recorded by the satellite-borne MODIS Aqua (chlorophyll *a*) instrument on April 25, 2004.

is primarily limited or co-limited by the element iron (Fe) (e.g., Martin and Fitzwater, 1988; Fung et al., 2000). Nevertheless, the nitrogen-limitation hypothesis continued to be applied in coastal regions, which are considered

to be iron-rich, owing to contact with metal-rich sediments and inputs from aeolian and fluvial deposition. This viewpoint was challenged in central California at about the same time as the start of three of the West Coast CoOP

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projects (Hutchins and Bruland, 1998; Hutchins et al., 1998; Bruland et al., 2001; Johnson et al., 2001). The role of iron has been directly or indirectly addressed in all of these CoOP projects.

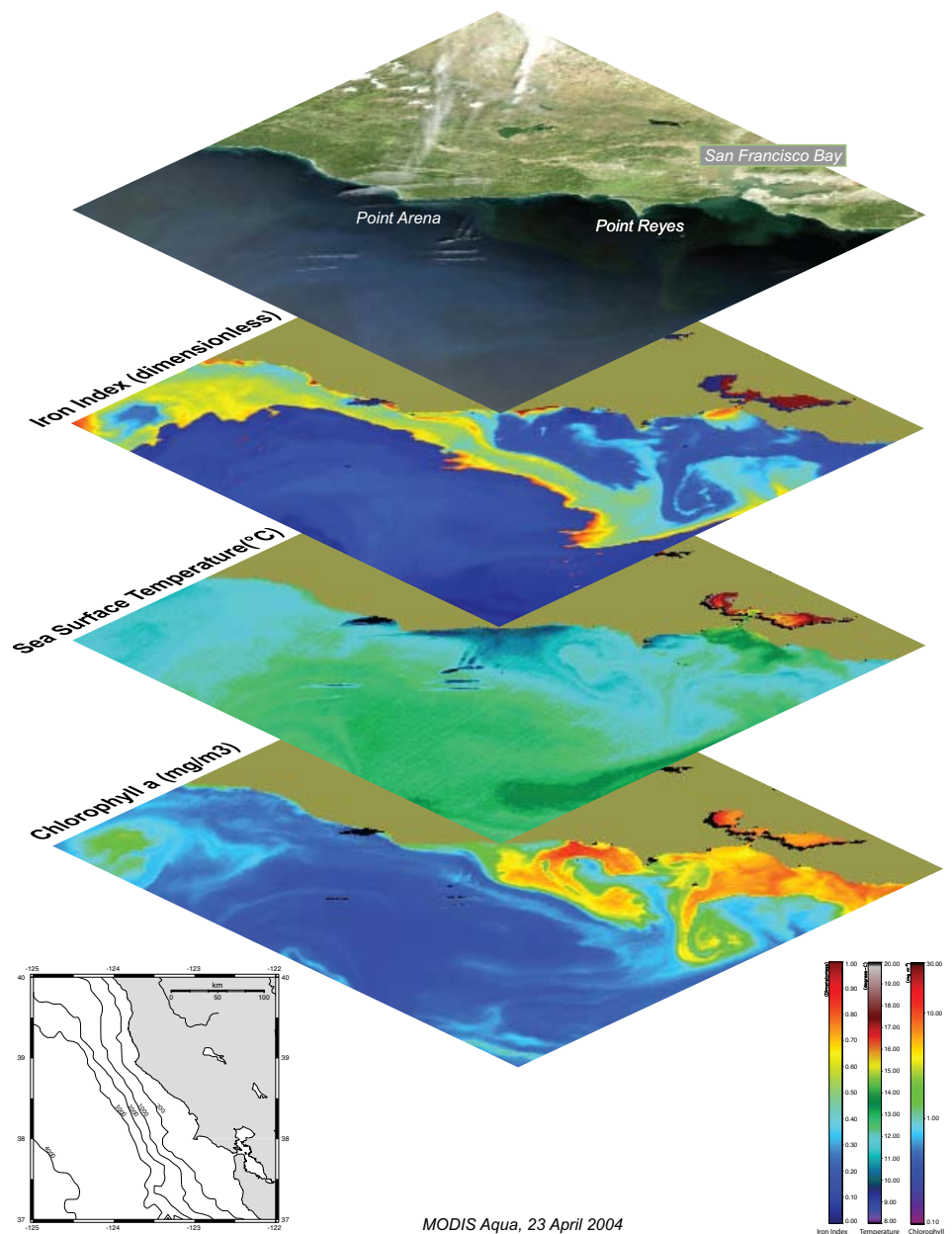
Based on the results from central California, Hutchins et al. (1998) proposed the idea of an “iron limitation mosaic,” with diagnostic indicators being a shift in particulate silicon:carbon (Si:C) and silicon:nitrogen (Si:N) ratios away from Redfield proportions. In particular, elevated Si:N ratios in diatoms were identified as a biological indicator of iron stress or limitation (Hutchins and Bruland, 1998). This “iron limitation mosaic” was predicted to occur in both space and time as a function of the variable sources and sinks of iron and macronutrients. This pattern was clearly evident in WEST, where Kudela et al. (2006) identified an “iron curtain” effect at the edge of the continental shelf (Figure 3). Inshore of approximately 200-m water

depth, biologically available iron was abundant, while offshore, iron concentrations rapidly decreased. Although iron was only measured during one field season, a proxy for bio-available iron was developed that used bio-optical variables. Using this proxy, there was good evidence for sharp gradients in iron, phytoplankton biomass, and productivity associated with the shelf edge and strong interannual variability related to both upwelling intensity and the number

of upwelling/relaxation events (Kudela et al., 2006; Wilkerson et al., 2006). Based on these results, it was hypothesized that the WEST region is strongly controlled by the input of iron from the continental shelf (Kudela et al., 2006), by the availability of upwelled nitrate (Dugdale et al., 2006), and by the modulating effect of wind forcing (Botsford et al., 2003, 2006; Wilkerson et al., 2006).

As part of COAST, Chase et al. (2005) directly measured iron in the Oregon

Figure 3. As part of WEST, Kudela et al. (2006) developed a bio-optical proxy for biologically available iron. Depicted here are (top to bottom) true-color, iron proxy, sea surface temperature, and chlorophyll images from April 23, 2004, for the WEST region. Kudela et al. (2006) suggested that iron is largely injected to the coastal ocean from shelf-upwelling processes, resulting in high and variable chlorophyll over the shelf with much lower biomass and productivity seaward of the 200-m isobath except where squirts and eddies export the shelf biomass. The iron proxy is based on the backscatter/fluorescence ratio (Kudela et al., 2006), applied here to MODIS 443-nm backscatter and fluorescence line height data. No simultaneous calibration iron data are available, so the proxy is a relative index from 0 (low bio-available iron) to 100 (high iron); these patterns are consistent with results reported by Buck et al. (2007) and Hurst and Bruland (2007). Note that the Fe index is generally low where chlorophyll is elevated, a result of biological drawdown (and subsequent blooming of phytoplankton) of the iron injected into the surface mixed layer.



upwelling system. They identified steep gradients both latitudinally and cross shelf, with relatively more iron being present in regions of “simple” bathymetry. Seasonally, they observed higher surface concentrations of iron in spring and greater particle-associated iron at depth in summer. During this study, there was no evidence for iron limitation of phytoplankton production, in contrast to what was observed in California. In a subsequent study, Chase et al. (2007) suggested that there is a poleward gradient in iron availability due to a combination of increasing river runoff and increasing shelf width moving from northern California to Washington. They postulated that while iron limitation is generally more likely to develop in northern and central California (with the exception of the Gulf of the Farallones), it is unlikely to be observed off Oregon and Washington. Although outside the scope of this review, iron limitation has also been documented

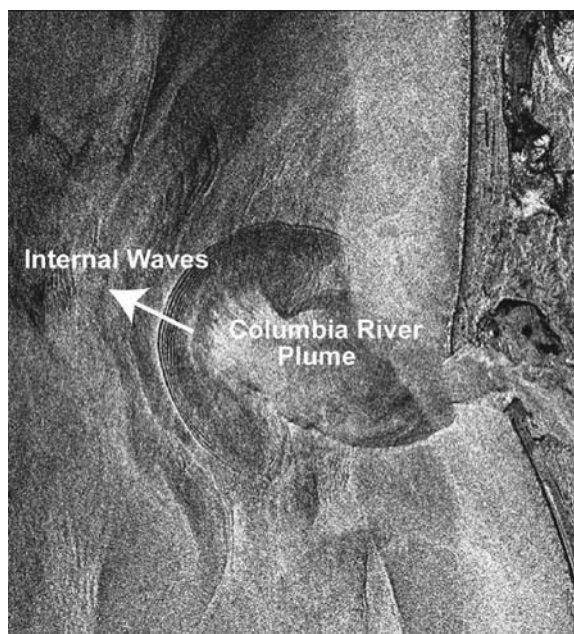
in the Southern California Bight, consistent with this general pattern (King and Barbeau, 2007).

A central hypothesis of RISE was that the iron limitation mosaic observed off California might also be seen along the Oregon and Washington coasts. However, as suggested by Chase et al. (2007), Bruland et al. (2008) also found no evidence for iron limitation off Oregon and Washington. Further, these authors declared the Washington shelf a “double winner” because it receives both iron and nitrogen (nitrate) from the Columbia River, in addition to the wide, iron-rich shelf sediments. Buck et al. (2007) also demonstrated that strong iron-binding ligands associated with the plume regulate the transfer of biologically available iron from particulates into the dissolved phase. The Columbia River thus more than compensates for the weaker upwelling-favorable winds off Washington, and helps to explain the observed increase in phytoplankton productivity moving from

Oregon to Washington (e.g., Ware and Thomson, 2005). Furthermore, plume frontal convergence is stronger, and nonlinear internal wave generation more common, north of the Columbia River mouth (Figure 4; Orton and Jay, 2005; Jay et al., in press), leading to a higher nutrient supply off Washington.

Evidence thus suggests that iron becomes less important in controlling phytoplankton production toward the north. The question remains whether nitrogen is the ultimate limiting nutrient controlling total productivity while iron controls the pattern of the mosaic. There is good evidence for this in Monterey Bay (Brzezinski et al., 1997; Kudela et al., 1997), the WEST region (Dugdale et al., 2006), the COAST region (Huyer et al., 2005), and the RISE region (Bruland et al., 2008; Kudela and Peterson, in review). However, results from these projects also highlight the perils of making broad-brush statements about the entire California Current System. In COAST, Ruttenberg and Dyhrman (2005) demonstrated substantial spatial and temporal variability in the dynamics of dissolved inorganic phosphorous (P) and dissolved organic phosphorous. Variability in both pools and rates is associated with equally rapid and small-scale changes in bacterial and phytoplankton assemblages, driven by physical variability. Kudela and Peterson (in review) suggest that the Columbia River plume could easily be pushed into P-limitation with small changes in N:P source ratios, while Nicholson et al. (2006) suggest that P-limitation may differentially impact dinoflagellates in central California. Although Brzezinski et al. (1997) concluded that silicic acid is unlikely to limit productivity, there was

Figure 4. A Synthetic Aperture Radar (SAR) image of the Columbia River plume on April 30, 2003, shows the formation of intense internal wave activity at the western boundary of the plume in the CoOP RISE study site. These plume-generated internal waves are large compared to the water depth (Nash and Moum, 2005); Zaron and Jay (2008) identified this plume mixing as a key component for explaining the entrainment of nutrients in the coastal ocean, likely leading to enhanced productivity on the Washington shelf.



evidence for reduced Si-production rates at ambient silica concentrations less than about 10 μM in Monterey Bay. Given the potential for Fe limitation in California waters, and the expected enhancement of Si:N ratios in diatoms under Fe stress, this reduced Si production could be indicative of incipient co-limitation by Si, N, and Fe during the 1995 Monterey Bay experiment.

NITROGEN SUPPLY

Another shift in our understanding of the control mechanisms in the shelf waters of EBC systems relates to the source of nitrogen. Although classic upwelling over the mid/inner shelf (Figure 1) does account for a large fraction of the total nitrogen supply, we now know that it is augmented by other sources. In particular, it has been suggested that upwelling due to Ekman divergence near the coastal boundary can be extended further offshore due to curl in the wind stress (Enriquez and Friehe, 1995; Munchow, 2000; Oke et al., 2002). This mechanism was clearly demonstrated in WEST, where Dever et al. (2006) estimated that the nitrate flux per unit coastline driven by Ekman transport from the 40-m isobath to shore was $0.30 \mu\text{M}\cdot\text{m L}^{-1} \text{ s}^{-1}$ compared with a value of $0.74 \mu\text{M}\cdot\text{m L}^{-1} \text{ s}^{-1}$ between the 40- and 90-m isobaths due to curl-driven upwelling. Because curl-driven upwelling in the WEST region is found more than 25 km from shore, the implication is that the majority of nitrogen may be upwelled at mid shelf or further offshore, potentially decoupled from coastal inputs of iron.

In COAST, Hales et al. (2005a) obtained high-resolution observations of nitrate flux over the inner shelf. They document the importance of “irreversible

nitrate fluxes” associated with cross-isopycnal mixing, a process separate from vertical advection of a water mass (upwelling). They estimate that 25% of the net onshore transport of upwelled nitrate seaward of the 30-m isobath is injected into the well-lit surface waters through this mechanism. Although not directly measured, they suggest that shoreward of the 30-m isobath, vertical irreversible flux may be even more important, and point out that this mechanism provides nitrate during both upwelling and relaxation events.

In RISE, wind-driven upwelling of nitrogen and irreversible turbulent fluxes of nitrogen are further augmented by the Columbia River. Bruland et al. (2008) document the importance of river-derived nitrogen, particularly during periods of reduced upwelling, when this may be the dominant source of nitrogen to near-coastal waters. In addition, the river outflow entrains pelagic nitrogen from horizontal transport and vertical mixing near the lift-off point (Zaron and Jay, in review) and at times may also entrain significant amounts of pelagic nitrogen through internal wave activity at the plume front (Nash and Moum, 2005; Pan and Jay, 2008; Figure 4). Taken together, results from CoOP projects suggest multiple nitrogen-supply mechanisms interacting in a complex three-dimensional system that exhibits variability in time and space associated with headlands, banks, and river inflow.

THE IMPORTANCE OF RETENTION OVER THE SHELF

Given sufficient nutrients and adequate light, phytoplankton will rapidly bloom in the coastal ocean. A central question of WEST, however, was to explain the

apparent paradox of high phytoplankton biomass in coastal upwelling regions—although upwelling winds provide nutrients, they also result in increased export of plankton from the shelf (Largier et al., 2006). This fundamental question was addressed directly or indirectly by these projects. What are the optimal conditions allowing phytoplankton blooms and subsequent secondary production in strongly advective upwelling systems? Part of the answer to this question is, of course, that the upwelling winds do not blow strongly all the time but rather pulse, yielding a series of upwelling-relaxation cycles. What is now better quantified is the importance of alternating between upwelling and relaxation conditions. Wilkerson et al. (2006) and Kudela et al. (2006) demonstrated that the size of the bloom is more or less proportional to the intensity of upwelling and the length of the relaxation phase. Too little wind results in low productivity because of a lack of nutrients, while too much wind, or not enough relaxation, does not allow the phytoplankton assemblage to fully draw down the available nutrients due to advective loss and light limitation. Botsford et al. (2003) formalized this concept by applying cross-shelf transport rates and surface mixed-layer deepening to a simplified nutrient-phytoplankton-zooplankton (NPZ) model in what they called a mixed-layer conveyor (MLC) model. This approach was subsequently extended to include realistic winds for the WEST region (Botsford et al., 2006). Results from the MLC model demonstrate the interactive effects of shelf width (narrower shelves are more likely to respond negatively to strong or prolonged upwelling-favorable winds in terms of plankton production) and

also of upwelling/relaxation oscillations (i.e., too much wind results in lower productivity), thus confirming the empirical results from WEST, which were largely constrained to the shelf and did not

fully assess the hypothesized advective losses from the shelf.

Using data from five summers along two coastal transects north (44.6°N) and south (41.9°N) off Cape Blanco, Oregon, Huyer et al. (2005) extended this type of analysis to a much larger spatial domain. They demonstrated that the northern line was predominantly nutrient-limited, while the southern line was predominantly light-limited, caused by the sharp gradient in wind stress north (weaker) and south (stronger) of Cape Blanco. The importance of upwelling was also dramatically illustrated during the 2005 “warm anomaly,” when a delay in upwelling-favorable winds resulted in dramatic declines in phytoplankton productivity, leading to dramatic impacts on fisheries, marine birds, and marine mammals (Kudela et al., 2006; Mackas et al., 2006; Sydeman et al., 2006; Weise et al., 2006).

Although wind relaxation and associated surface current reversals can provide one mechanism for retaining phytoplankton blooms (and zooplankton) on the shelf, it has long been recognized that variations in coastal bathymetry

and topography also play a key role in creating retention zones such as “upwelling shadows” (e.g., Graham and Largier, 1997). A similar feature has been recognized south of Point Reyes, California, through observations (Send et al., 1987) and modeling (Gan and Allen, 2002). This area is also well characterized in terms of zooplankton larval retention (Wing et al., 1995a, 1995b, 1998) and shows up as another region of warm, high-chlorophyll waters similar to northern Monterey Bay (Figure 1). Although perhaps less retentive than the Monterey Bay upwelling shadow, the importance of the northern Gulf of Farallones as a retention zone is enhanced by being the source of waters that flow poleward during relaxation events (Largier, 2004). An important finding from WEST was that a retentive feature is also found transiently on the north side of the Point Reyes headland during relaxation events (Kaplan and Largier, 2006; Vander Woude et al., 2006). This observation suggests that plankton may be retained by the combination of transient retention zones north and south of a promontory or headland as the wind and current reverse, allowing the plankton assemblage to maintain a coherent population in the region and perhaps allowing benthic populations with meroplanktonic larvae to be “self-seeding.” Vander Woude (2006) also demonstrated that, in addition to retaining plankton, these regions can serve as local sinks for atmospheric carbon dioxide as the phytoplankton blooms rapidly strip the high $p\text{CO}_2$ levels associated with freshly upwelled water, and that the relative balance of source versus sink switches rapidly (days) in response to upwelling and relaxation (Figure 5).

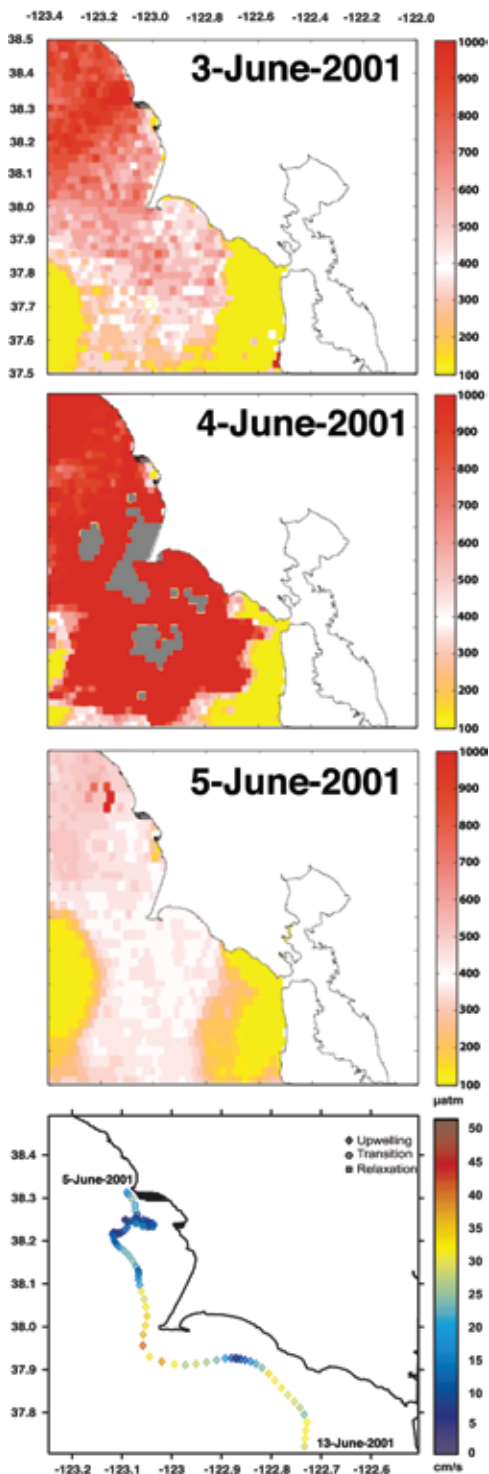


Figure 5. Retentive regions are critical because they allow newly upwelled waters to bloom fully. Although the importance of upwelling shadows equatorward of headlands has been highlighted previously, as part of CoOP WEST, Vander Woude (2006) developed a remote-sensing-based model of carbon dioxide concentrations ($p\text{CO}_2$) and demonstrated that these retentive regions can occur equatorward or poleward of a promontory, such as Point Reyes (depicted here). Relatively small coastal regions oscillate rapidly between $p\text{CO}_2$ sources to the atmosphere (red) and $p\text{CO}_2$ sinks due to biological drawdown (yellow). The lower panel depicts a surface-drogued drifter trajectory for a smaller spatial region near Point Reyes, demonstrating that drifters slow down (are retained) both north and south of the headland (Vander Woude et al., 2006).

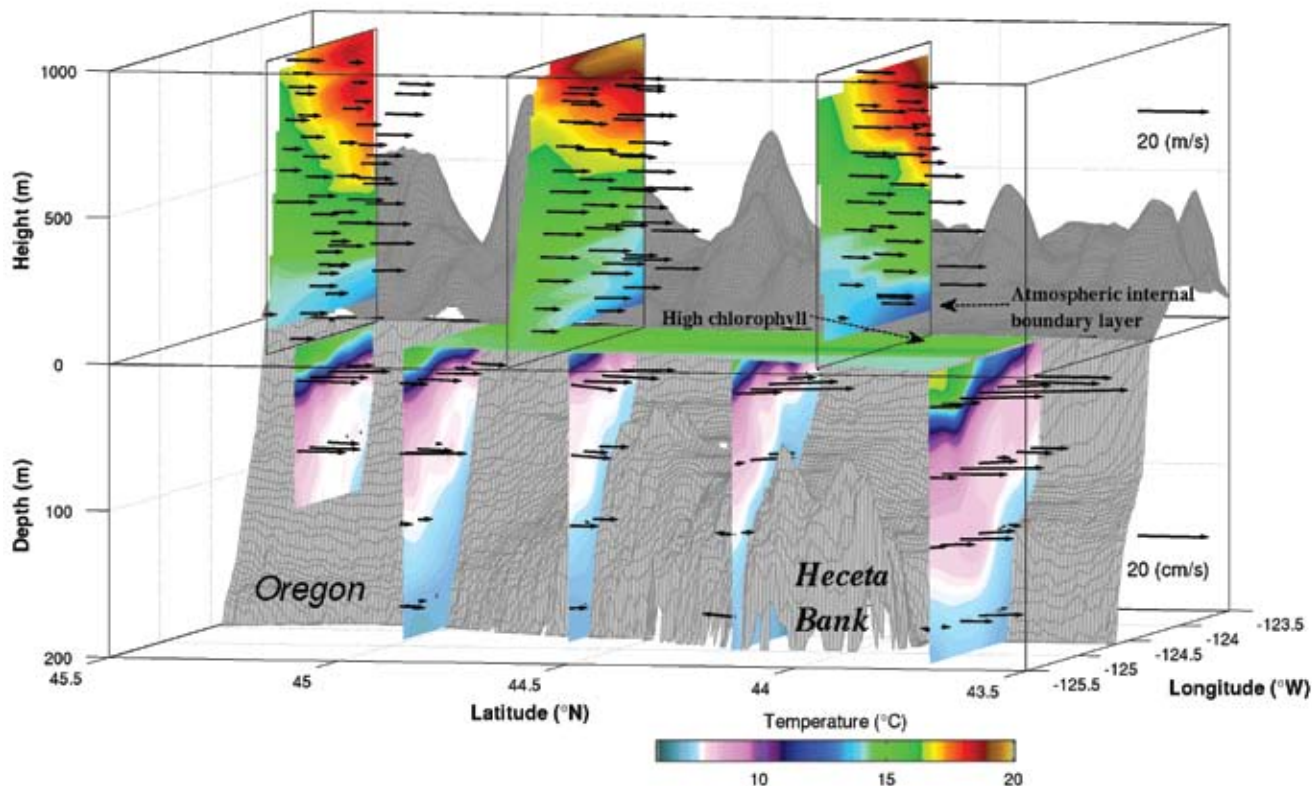
THE WIND-DRIVEN COASTAL OCEAN: NOW IN HIGH-DEF

By John A. Barth, John M. Bane, Stephen D. Pierce, and Sara M. Haines

New observational tools and coordinated interdisciplinary research conducted during the CoOP program greatly expanded our understanding of wind-driven coastal ocean ecosystems. These tools allowed us to probe the entire water column, the air-sea interface, and the atmosphere above with unprecedented spatial and temporal resolution. A new “high-definition” view of the time-varying coastal ocean has emerged. During the Coastal Ocean Advances in Shelf Transport (COAST) CoOP project (<http://damp.coas.oregonstate.edu/coast>), sampling of the coastal ocean with a ship-towed, underwater, undulating vehicle and a shipboard acoustic Doppler current profiler was done simultaneously with profiling of the overlying atmosphere from an instrumented twin-engine airplane. This detailed view revealed the interaction of a wind-driven coastal upwelling jet with a submarine bank, and the impact of this flow-topography interaction on the coastal marine ecosystem. Disruption of the strong, along-shelf, oceanic coastal upwelling jet by Heceta Bank creates a “lee” region close to shore where near-surface phytoplankton

thrive. As the oceanic jet flows around the bank, plankton, nutrients and cold, saline water are swept off the continental shelf, enriching the offshore northern California Current marine ecosystem. The region of cooler air temperature inshore and below about 200 m is a stable atmospheric internal boundary layer, created by contact with cold, upwelled water; this internal boundary layer, in turn, alters the alongshore coastal wind field. (See Volume 110 (C10) of the *Journal of Geophysical Research* for more details.)

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Visualization of atmospheric potential temperature and oceanic temperature (vertical sections), winds and ocean currents (arrows), and surface chlorophyll (green shades at sea surface) off central Oregon on August 19, 2001. Surface chlorophyll concentrations are scaled to use the color bar such that light blue is about 1 mg m^{-3} and dark green is 20 mg m^{-3} . The highest phytoplankton concentrations are found over Heceta Bank (see also the article by Kudela et al., this issue). The four southern oceanic sections combine temperature data from ship-towed and air-deployed sensors.

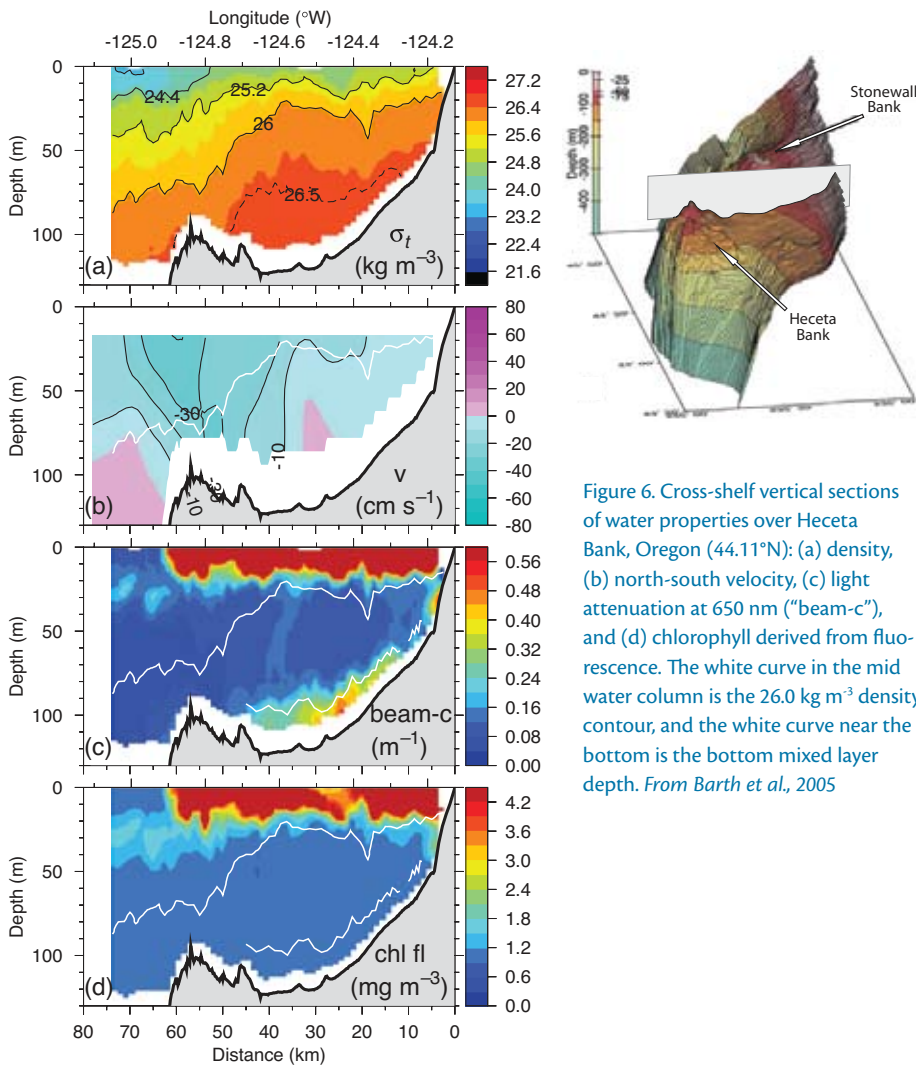


Figure 6. Cross-shelf vertical sections of water properties over Heceta Bank, Oregon (44.11°N): (a) density, (b) north-south velocity, (c) light attenuation at 650 nm ("beam-c"), and (d) chlorophyll derived from fluorescence. The white curve in the mid water column is the 26.0 kg m⁻³ density contour, and the white curve near the bottom is the bottom mixed layer depth. From Barth et al., 2005

Alongshore variations in bottom topography can also lead to the formation of "shadow" regions on the shelf where retention is enhanced. In the COAST region off central Oregon where the coastline is relatively straight, a large submarine bank rises to over 50% of the surrounding water column depth (Figures 2 and 6; Barth and Wheeler, 2005). The strong alongshelf, equatorward upwelling jet follows the bottom topography around Heceta Bank, leaving a more quiescent region closer to shore (Figure 6). High chlorophyll biomass (> 15 mg m⁻³) is found in this "lee" region created by Heceta Bank and time-

varying wind can lead to a counterclockwise recirculation over the bank with a time scale of about 10 days (Figure 6) (Barth et al., 2005).

Hales et al. (2005b) similarly identified coastal Oregon as a strong local sink for pCO₂ during summer upwelling, contrary to the notion that upwelling waters are always an atmospheric source. They further identified a deep-water sink for carbon from the atmosphere due to the vertical export of biogenic material through sinking late in the summer, and concluded that the North Pacific's eastern boundary could account for 5% of the annual basinwide uptake of pCO₂. Wet-

and Wheeler (2003) provide indirect evidence for the mechanisms allowing coastal Oregon to become a strong carbon sink; from on-deck incubations, they showed that carbon is drawn down at greater-than-Redfield proportions after the depletion of inorganic nitrogen, presumably due to the continuation of photosynthesis and the release of carbon-rich carbohydrates by the plankton community. Taken together, the results from COAST and WEST suggest that small-scale variability in biological drawdown of carbon can have a significant impact on the biogeochemistry of these shelf regions. The presence of Heceta Bank in the COAST region (Figures 2 and 6) also provided spatial-scale variability in retention and associated biological responses, strongly modulating the biogeochemical coupling in this region.

Equally important retentive features were identified in RISE, but rather than being associated with headlands or subsurface topography, they were caused by the presence of the buoyant Columbia River plume, already identified as a potential source of iron and nitrogen to the coastal ocean. Banas et al. (in review) demonstrate, using a coupled physical-biological model, that the Columbia River plume acts as a porous barrier to the dominant equatorward flow during the summer, slowing down and retaining the resident plankton communities in a shallow surface layer (Figure 7). The net effect is to shift primary production offshore of the 100-m isobath, resulting in an approximately 20% increase offshore and 20% decrease nearshore under weak to moderate upwelling, and to increase microzooplankton grazing losses dramatically due to the increased residence time in the vicinity of the plume.

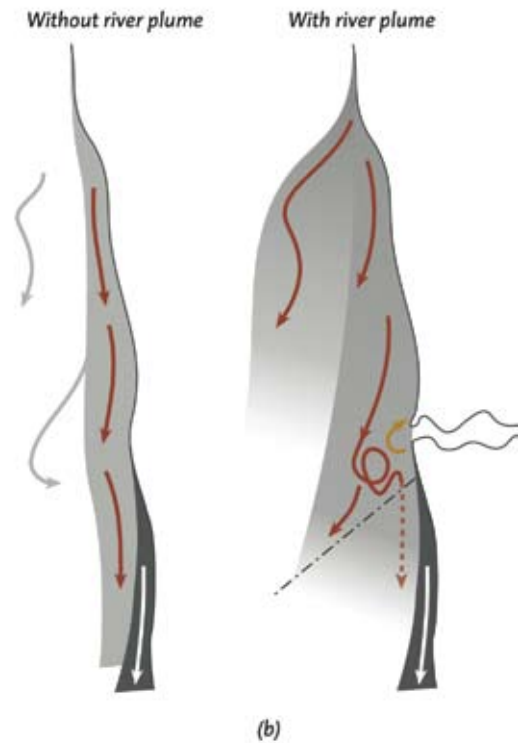
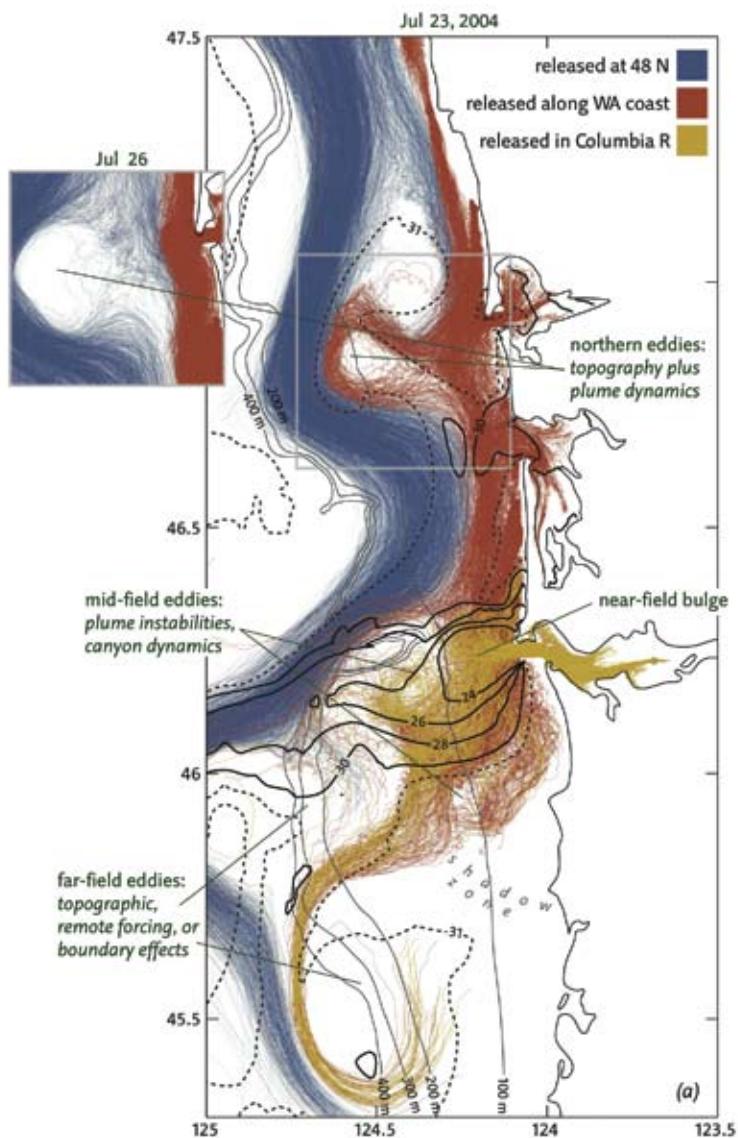


Figure 7. (a) Three-dimensional particle trajectories along on the Washington-Oregon coast calculated by Banas et al. (2008) from the model of MacCready et al. (2008). One day of upwelling circulation was looped for each particle map (July 23, 2004, main panel; July 26, inset) to highlight transient features: particle paths are akin to streamlines, although vertical diffusion is included. Thin black contours show the bathymetry, and thick black contours show the location of the Columbia River plume (24-, 26-, 28-, and 30-psu contours solid, 31-psu contour dashed). Particles released in the Washington upwelling zone (red) on July 23 are entrained into a transient topographic eddy at 46.8°N, in which aged northern plume water (31-psu contour) is also seen; on July 26 the eddy still exists but the northern plume has dissipated and coastal water is not entrained into it. Particles released in the Columbia River (yellow) highlight a complex field of transient eddies in the mid- and far-field upwelling plume as well. Both plume water and Washington coastal water are shunted offshore by this eddy field, creating a shadow zone on the northern Oregon shelf like that seen in the lee of headlands. (b) Schematic showing the net effect of these transient eddy entrainment processes. When the plume is turned off in the model (see Banas et al., 2008), water upwelled off Washington (red arrows) advects south along the inner-to-mid shelf and merges with the northern Oregon upwelling system (white arrow): topographic recirculation on the outer shelf (gray arrows) occurs but is relatively weak. In the presence of the plume, Washington water is episodically exported across the shelf and slope, both north and south of the river mouth. This dispersive process retards the southward advection of water along the inner shelf, such that the plume acts like a semipermeable barrier (black dashed line) in the along-coast direction.

PLANKTON COMMUNITY STRUCTURE

Associated with the schematic two-dimensional upwelling depicted in Figure 1 is the assumption that coastal upwelling communities are dominated by large phytoplankton (diatoms), which are

in turn grazed on by large zooplankton (e.g., copepods, krill), which in turn feed the rich and abundant higher trophic levels found in the California Current (Croll et al., 2005). The four CoOP West Coast projects provide further evidence for the dominance of diatoms in these

upwelling systems. In each case, direct observations support the idea that diatoms are the workhorses of these biological communities, accounting for the bulk of biomass and, more importantly, new and total production (Brzezinski et al., 1997; Kudela et al., 1997; Ruttenberg

and Dyrman, 2005; Eisner and Cowles, 2005; Lassiter et al., 2006; Frame and Lessard, in review; Kudela and Peterson, in review). That is not to say that smaller cells are not contributing to biomass and productivity, however. Frame and Lessard (in review) show that small cells (cyanobacteria, picoeukaryotes, and nanoflagellates $<5\ \mu\text{m}$), as well as larger dinoflagellates, are varying but sometimes substantial contributors to photosynthetic biomass on the Washington and Oregon shelves (Figure 8). Sherr

et al. (2005) documented an onshore-offshore gradient in the smallest cells off the southern Oregon coast, with this size class increasing in abundance and proportion seaward of the coastal upwelling front. Similarly, during the dramatic ecosystem collapse caused by the 2005 delayed onset of upwelling, an offshore, small-cell community largely replaced the characteristic nearshore diatom assemblage. As predicted, this smaller phytoplankton assemblage, despite healthy growth rates, simply did

not reach high levels of biomass (Kudela et al., 2006; Lassiter et al., 2006), resulting in the much-publicized negative impacts on higher trophic levels.

Although these studies largely confirmed the importance of diatoms, this roughly 15-year period also encompassed a dramatic shift in our understanding of the relative importance of micro- and mesozooplankton as grazers in coastal environments. Based on published studies from around the world that directly measured microzooplankton grazing,

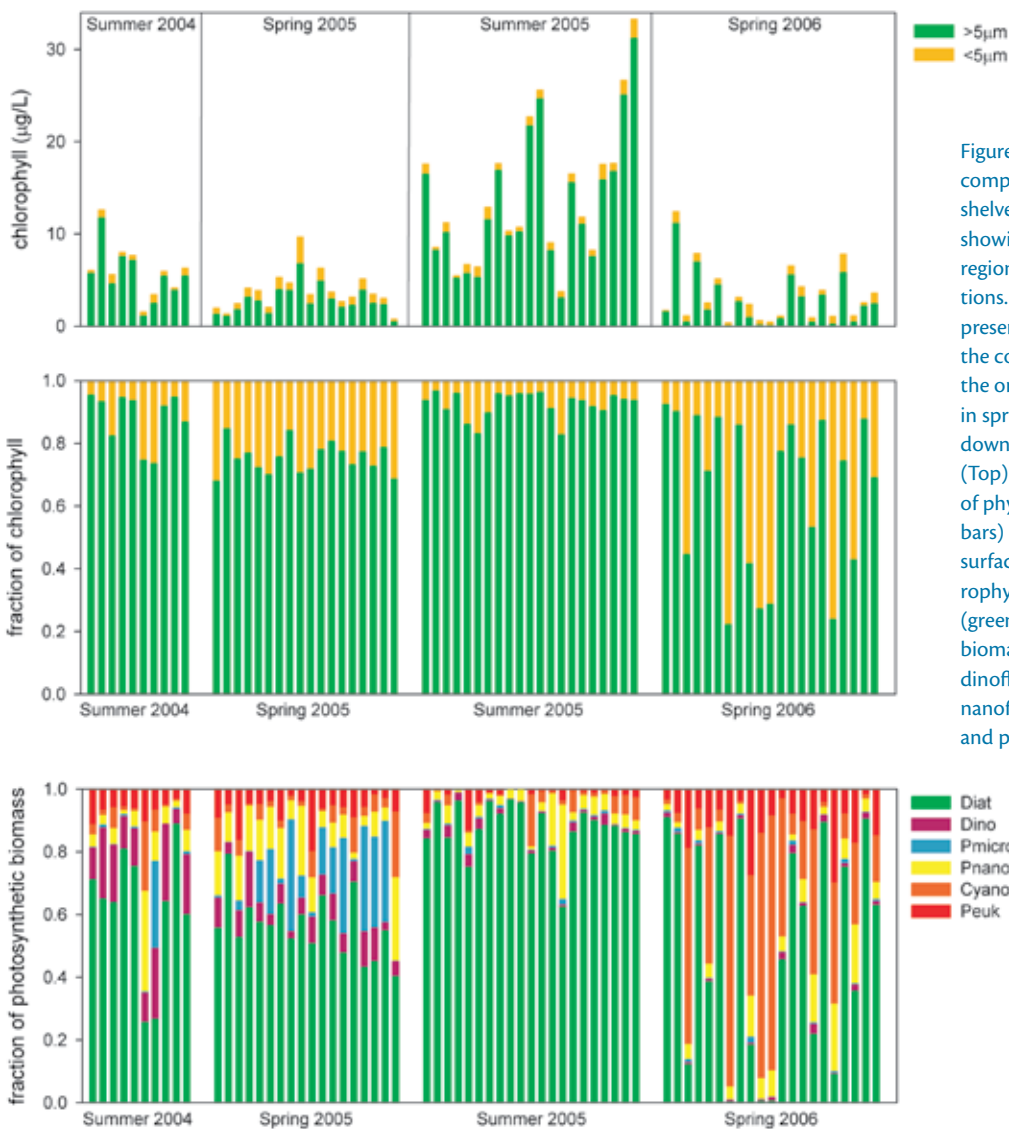


Figure 8. Phytoplankton community and size composition on the Washington and Oregon shelves during the 2004–2006 RISE cruises, showing that diatoms typically dominated the region under widely varying upwelling conditions. However, small cells ($<5\ \mu\text{m}$) were always present and were a much larger proportion of the community than usual in spring 2005, when the onset of seasonal upwelling was delayed, and in spring of 2006, during a period of extended downwelling that followed strong upwelling. (Top) The concentration of chlorophyll, an index of phytoplankton biomass, in the $<5\ \mu\text{m}$ (yellow bars) and $>5\ \mu\text{m}$ (green bars) size fraction in surface samples. (Middle) Fraction of total chlorophyll in the $<5\ \mu\text{m}$ (yellow bars) and $>5\ \mu\text{m}$ (green bars). (Bottom) Fraction of phytoplankton biomass in different taxa groups (diatoms [diat], dinoflagellates [dino], microflagellates [pmicro], nanoflagellates [pnano], cyanobacteria [cyano], and picoeukaryotes [peuk]).

Calbet and Landry (2004) estimated that microzooplankton consume 60% of primary production in coastal zones, making this size fraction the dominant grazing loss term. Despite the importance of microzooplankton, only two projects directly assessed this component. As part of RISE, over 60 grazer-dilution experiments were conducted (Lessard and Frame, 2008). Not surprisingly, microzooplankton consumed the smaller phytoplankton at rates equivalent to the phytoplankton production, but they also consumed a substantial portion (50%) of diatom production. Overall, microzooplankton consumed an average of 66% of the total phytoplankton production in this coastal upwelling region.

In energetic coastal upwelling areas, however, mesozooplankton may at times be significant grazers, including and particularly during wind-relaxation events. Dorman et al. (2005) reported from the WEST region that the krill *Euphausia pacifica* rapidly reproduced during short-term relaxation events and likely used diel vertical migration to ride the “conveyor belt” to minimize advective loss. Slaughter et al. (2006) estimated mesozooplankton grazing rates with the gut fluorescence method during WEST; they found that this community could account for greater than 100% of phytoplankton standing stock per day during prolonged wind relaxation, but more typically consumed 25–38% of standing stock per day during stronger upwelling events when a greater loss of phytoplankton from shelf waters would be expected. Similar to these results, Lamb and Peterson (2005) suggest that copepods and their prey are maintained over Heceta Bank by recirculating counterclockwise circulation over this submerged feature, but that strong

upwelling winds result in advective loss southward of the bank’s mesozooplankton community, highlighting another feature of physical retention in an advective flow. In the RISE study, Peterson and Peterson (in review) similarly found that mesozooplankton were preferentially associated with “aged” Columbia River plume waters, which they attributed to the formation of shallow, strong temperature and density gradients that kept the zooplankton in physical proximity to the phytoplankton, which in turn could reach maximal bloom conditions in part due to the enhanced retention caused by the plume.


As previously noted by others (e.g., Ware and Thomson, 2005), there is a gradient in phytoplankton biomass moving poleward. A key finding from RISE was very little difference in the phytoplankton assemblages (Frame and Lessard, in review) or physiological capacity (Kudela and Peterson, in review) between the two regions, but that, based on the grazer-dilution experiments (Lessard and Frame, 2008), modeling studies (Banas et al., 2008), and inferences from multi-day grow-out experiments (Kudela and Peterson, in review), microzooplankton grazing pressure is significantly higher on the Oregon shelf. Given the complex oceanography of these coastal waters, it is unwise to extrapolate from this result to the rest of the California Current, but it is clear that microzooplankton must be considered in any discussion of biological productivity along eastern boundary current regimes. As noted by Banas et al. (2008), “the microbial revolution in biological oceanography has not penetrated far enough into the ecosystem modeling community,” but we expect that results

from these CoOP projects will provide insight and guidance to future efforts.

SUMMARY

The four CoOP projects that took place on the US West Coast have both reinforced and modified our view of how coastal upwelling regions function. Although the two-dimensional view of coastal upwelling remains valid as a reasonable reduction of a complex process, CoOP has identified many important complexities and has also clarified some of them. We have learned that there is no single answer to explain how coastal upwelling and shelf oceanographic processes in the central and northern California Current System promote one of the richest biological communities in the Pacific. Some highlights include the recognition that elements other than nitrogen, particularly iron, may limit the base of the food chain, and that the source of these nutrients is not solely, or possibly even primarily, a result of wind-driven Ekman transport. Further, nitrogen is supplied to the euphotic zone through many transport mechanisms, and from different sources. The importance of a spatial pattern with retention zones interspersed with upwelling centers is also clear, whether these retention zones be associated with topography, bathymetry, or more transient features such as river plumes. Lastly, new insights into the fate of this biological productivity are emerging, and should greatly improve current and future generations of ecosystem models. Increased understanding of the more subtle features of upwelling systems will surely guide us to new and exciting research questions, and help us predict the consequences of future environmental change.

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Editor's Note: Oceanography does not usually permit citation of articles that are in review; however, because of the rapidly advancing nature of this issue's topics, we are making an exception. Updates on the status of manuscripts cited as in review here will be posted on the CoOP Web site (<http://www.skio.usg.edu/coop>).

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