

WEST: A northern California study of the role of wind-driven transport in the productivity of coastal plankton communities

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Abstract

The “Wind Events and Shelf Transport” (WEST) program was an interdisciplinary study of coastal upwelling off northern California in 2000–03. WEST was comprised of modeling and field observations. The primary goal of WEST was to better describe and understand the competing influences of wind forcing on planktonic productivity in coastal waters. While increased upwelling-favorable winds lead to increased nutrient supply, they also result in reduced light exposure due to deeper surface mixed layers and increased advective loss of plankton from coastal waters. The key to understanding high levels of productivity, amidst these competing responses to wind forcing, is the temporal and spatial structure of upwelling. Temporal fluctuations and spatial patterns allow strong upwelling that favors nutrient delivery to be juxtaposed with less energetic conditions that favor stratification and plankton blooms. Observations of winds, ocean circulation, nutrients, phytoplankton and zooplankton off Bodega Bay and Point Reyes (38°N) were combined with model studies of winds, circulation and productivity. This overview of the WEST program provides an introduction to the WEST special issue of Deep-Sea Research, including the motivation for WEST, a summary of study components, an integrative synthesis of major research results to-date, and background on conditions during field studies in May–June 2001 (the upwelling period on which this special issue is focused).

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1. Introduction

The Coastal Ocean Processes (CoOP) “Wind Events and Shelf Transport” (WEST) program was

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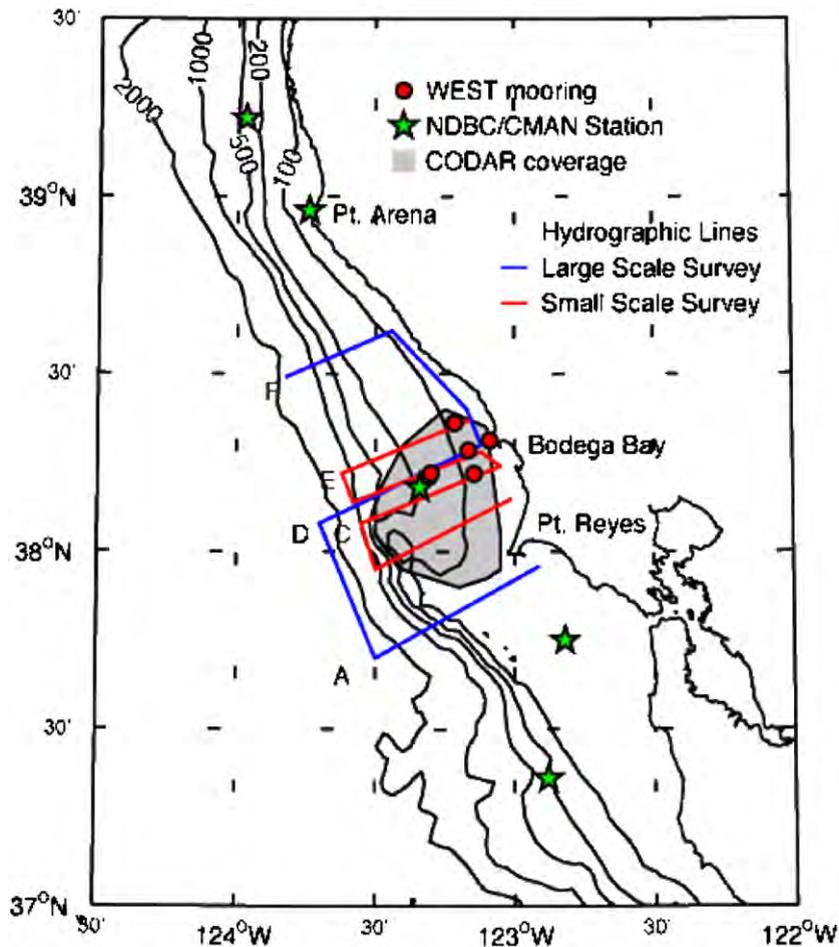


Fig. 1. The northern California region in which WEST studies were conducted. Isobaths are shown for 100, 200, 500, 1000 and 2000 m. WEST moorings are shown as red dots (central mooring is D090), while the long-term NDBC moorings are shown as green stars (NDBC 46013 is off Bodega Bay). The large-scale ship survey was comprised of lines F, D and A (cross-shore blue lines), while the small-scale ship survey was comprised of lines E, D and C (cross-shore red lines). On occasion line B was occupied (southernmost red line). The gray-shaded area off Pt. Reyes and Bodega Bay roughly demarcates the area for which surface currents were obtained in 2001 from the initial two HF radar nodes deployed at Bodega Bay and Pt. Reyes.

established to study the role of wind-driven transport in plankton productivity over the shelf, specifically in the context of wind-driven coastal upwelling. Wind-driven transport plays three key roles in shelf productivity—nutrient supply to the euphotic zone, light control through vertical mixing of primary producers, and offshore export of near-surface plankton—but, while the first process yields a strong positive biological response to upwelling winds, the other two influences lead to negative productivity responses to increased wind. The central challenge of our study has been to explain this apparent paradox: in the presence of reduced light and increased export during strong winds, how

do phytoplankton achieve such remarkable blooms, and how is so much of this primary production available to secondary consumers over the shelf? Underlying this general interdisciplinary conundrum are several more specific questions that are the focal topics of papers in this special volume.

WEST was funded by the National Science Foundation, under the CoOP program (<http://starbuck.skio.peachnet.edu/coop/>). Field studies were conducted in 2000–03 off northern California, in the vicinity of Bodega Bay (Fig. 1), and this special volume contains a multi-disciplinary set of papers focused on May–June 2001. A companion CoOP study off Oregon, known as COAST (Barth

and Wheeler, 2005), included more focus on spatial pattern, specifically as related to Hecate Bank, Oregon, and less emphasis on rate processes.

Shelf waters off northern California are subject to very strong wind forcing, with strong southward winds during the summer and reversing winds with weak means during the winter. During summer, maximum west coast winds are recorded in the vicinity of Bodega Bay (Dorman and Winant, 1995). The strong summer winds are observed from the spring transition in March or April through to July, and on into August or September in some years. Strong southward winds may last for a few to several days before slackening—this period of weaker winds being known as a relaxation period.

Currents over the northern California shelf have been studied extensively over the past 20 years as an archetypal wind-driven upwelling system. The most extensive experiment, the Coastal Ocean Dynamic Experiment (CODE), acquired observations from 1981 to 1983 with an emphasis on summer upwelling conditions (Beardsley and Lentz, 1987). Since CODE, several other major observational experiments have been conducted over the shelf in the vicinity of Bodega Bay: Northern California Coastal Circulation Study (NCCCS) 1987–89 (Largier et al., 1993); Shelf Mixed Layer Experiment (SMILE) 1988–89 (Dever and Lentz, 1994); and Sediment Transport Events over the Shelf and Slope (STRESS) 1988–89 and 1990–91 (Trowbridge and Lentz, 1998). These studies have given insight into the importance of coastal-trapped waves and local wind forcing of along-shelf flow (Chapman, 1987; Davis and Bogden, 1989), the identification of surface Ekman layer transport at the mid-shelf (Lentz, 1992; Dever, 1997), the asymmetry between upwelling and downwelling conditions in the bottom boundary layer (Trowbridge and Lentz, 1991), and the importance of offshore forcing of shelf flows (Largier et al., 1993).

Numerical modeling of wind-driven upwelling has grown out of these extensive observations, with Haidvogel et al. (1991) and Moisan et al. (1996) developing larger-scale models that resolve filaments and mesoscale eddies in the California Current System. Gan and Allen (2002a, b) resolved the spatio-temporal detail of wind-driven upwelling events over the shelf—specifically for the region between Pt. Reyes and Pt. Arena. They resolved realistic spatial structure associated with capes and embayments, and also with relaxation events (Send et al., 1987).

Off northern California more descriptive studies have pointed out enhanced upwelling in the vicinity of capes such as Mendocino, Arena, Reyes and Ana Nuevo (Huyer and Kosro, 1987; Largier et al., 1993; Rosenfeld et al., 1994; Steger et al., 1999). Although the larger-scale upwelling filaments have been the focus of recent interest (Brink and Cowles, 1991; Strub et al., 1991), contemporary attention on embayments and relaxation has led to renewed interest in upwelling centers and plumes, typically associated with headlands and periods of active upwelling. Much of this interest has stemmed from questions about transport patterns posed by the need to understand better biological responses and distributions, which are strongly affected by water motion. Prior to WEST, studies designed to link winds, coastal circulation, and plankton production and distribution over the northern Californian shelf have been limited to modest field efforts. Nevertheless, studies like Wing et al. (1995a, b, 1998) on meroplankton and Wilkerson and Dugdale (1987) on nutrients and phytoplankton have shown some of the links between spatio-temporal coastal circulation patterns and plankton responses.

The strong primary production response to upwelling lags the physical process of wind-driven upwelling, and the peak phytoplankton population available to secondary consumers (e.g., grazing by zooplankton) lags the physical upwelling process further. During upwelling, seed stocks of algal cells in high-nutrient water at depth over the shelf are raised into the well-lighted near-surface waters. This newly upwelled water is characterized by low chlorophyll concentrations, high nutrients, low temperatures, and rate processes that are low/minimal (Slawyk et al., 1997). As the water is brought into the euphotic zone, algae respond to high light and nutrients by switching on nutrient uptake mechanisms and starting to photosynthesize. Balanced growth is reached when carbon:nitrogen (C:N) uptake equals Redfield proportions (Kudela et al., 1997). This aging upwelled water is characterized by high chlorophyll, low or rapidly declining nutrients, increased water temperature, and phytoplankton rate processes that are high/maximal. Further downstream, and after more time has elapsed, the nutrients become depleted and rate processes slow down. Typically the cycle from upwelling to nutrient depletion takes about 5–7 days (e.g., MacIsaac et al., 1985; Dugdale et al., 1990).

This time-structured biological response to upwelling is embedded within a characteristic pattern of water movement away from upwelling centers, and it is thus observed as a spatial pattern in productivity, with low-chlorophyll waters in upwelling centers and high-chlorophyll waters downstream along the upwelling plume. This observation is common to a number of coastal upwelling regions (Brown and Hutchings, 1985; Bricaud et al., 1987; Dugdale et al., 1989), with downstream high-chlorophyll waters being found both nearshore (e.g., Graham and Largier, 1997; Pitcher, 1988) or offshore. This idealized upwelling structure has been described as a “conveyor belt”, with upwelled dissolved inorganic nitrogen (DIN) being converted to particulate organic nitrogen (PON) as aging upwelled waters move along near-surface transport pathways. The speed of biological response to high nutrients and light is taxon-specific and also may be influenced by initial macro-nutrient concentrations (i.e. “shift-up” dynamics described by Dugdale et al., 1990) and the presence of micro-nutrients (Hutchins et al., 1998). Satellite imagery has provided an unprecedented degree of spatial resolution, with reasonable temporal resolution of upwelling spatial structures (Feldman et al., 1989). In addition to the complexity introduced by heterogeneous physical and biological processes, productivity also may be complicated by patchy iron limitation (Hutchins et al., 1998; Bruland et al., 2001) with constantly shifting boundaries of iron replete and deplete waters, as well as seasonal depletion of iron in coastal waters (Johnson et al., 2001).

Zooplankton represent the key trophic link between primary producers and higher trophic levels such as fish, and are thus essential to an understanding of the flow of energy and material in pelagic ecosystems. Variations in wind-driven shelf circulation are known to cause variations in the distribution, growth, and recruitment of many holoplanktonic and meroplanktonic species (e.g., Peterson et al., 1979; Parrish et al., 1981; Pillar, 1986; Botsford et al., 1994; Wing et al., 1995a, b, 1998; Peterson, 1998). However, less is known about how zooplankton with longer population time scales interact with flow and phytoplankton fields that reflect the synoptic time scales of wind-driven upwelling. Further, the degree to which primary production and zooplankton grazing are coupled is still not clear and neither is the role of mesozooplankton, which appear to make direct use of a

substantial portion of the primary production, as much as 15–50% in non-tropical shelf areas (Walsh, 1983; Baars and Fransz, 1984; Landry and Lorenzen, 1989; Bathmann et al., 1990). Subject to water-borne transport, zooplankton exhibit changes in distribution over diurnal and synoptic time scales (e.g., Smith et al., 1981; Dorman et al., 2005), but questions remain about the net advection of zooplankton over time scales of life expectancy and how effective zooplankton populations are in holding their position over the shelf (e.g., through ontogenetic migration, Peterson et al., 1979, or diel vertical migration, Wroblewski, 1982) or becoming concentrated in bays (e.g., Graham et al., 1992; Wing et al., 1998; Roughan et al., 2005).

Models of nutrient-phytoplankton-zooplankton (NPZ) dynamics range from simple three-box models (one box for each component, as in Franks et al., 1986, Franks and Walstad, 1997) to models that partition the NPZ components into additional boxes (e.g., Wroblewski, 1977) or models of increasing complexity (and boxes) that include the microbial web (e.g., Fasham et al., 1990; Moloney and Field, 1991). These models have been coupled with a variety of upwelling circulation models, depending on the focus of study, ranging from simple “conveyor belt” models to fully 3-dimensional simulations. A number of previous model studies have pointed to the importance of the time scale of upwelling, both in the coupling between primary and secondary production (Hofmann and Ambler, 1988; Peña, 1994; Spitz et al., 2003) and in the dominant pathways of carbon and nitrogen utilization (Painting et al., 1993; Carr, 1998).

2. The studies that comprise WEST

Fieldwork was conducted over the strongly wind-driven shelf and slope off Bodega Bay, California (Fig. 1), obtaining observations of physical, chemical and biological parameters from fixed time-series sensors, ship surveys, drifters, high-frequency (HF) radar, and satellites. In addition, models were used to obtain a more general understanding of the observed upwelling processes.

- Wind studies include modeling topographic effects on the marine boundary layer (Koraćin et al., 2004, 2005) and model estimates of wind stress (Kochanski et al., 2006), as well as direct observations of wind stress and curl (Dorman et al., 2006).

- Surface circulation studies include direct observations of the Ekman transport response (Dever et al., 2006), satellite-observed retention zones (Vander Woude et al., 2006), and HF radar maps of the spatially structured response to time-dependent wind forcing (Kaplan et al., 2005) and the trajectories of surface waters (Kaplan and Largier, 2006).
- Three-dimensional circulation is investigated using data from the ship surveys (Roughan et al., 2006) and the regional ocean modeling system (ROMS; Kuebel-Cervantes and Allen, 2006) with a focus on the shelf response during upwelling and subsequent relaxation.
- Phytoplankton studies include observations of nutrient levels and primary production rates (Dugdale et al., 2006; Kudela et al., 2006), bloom events (Wilkerson et al., 2006), and phytoplankton taxa (Lassiter et al., 2006), as well as modeling of the effect of wind strength and duration on bloom characteristics (Botsford et al., 2003, 2006).
- Zooplankton studies include estimates of mesozooplankton grazing rates (Slaughter et al., 2006) and studies of changes in distribution, abundance and composition of copepods (Papastephanou et al., 2006) and euphausiids (Dorman et al., 2005) over cruise periods.

2.1. Observing temporal variability—moored instruments

The core shelf region was instrumented with five multi-disciplinary moorings during the two main field years 2001–03 (Fig. 1). The ‘central’ mooring D090 also was deployed during the pilot field year 2000. Moored instruments resolved time scales from tidal-diurnal to seasonal and extended from 1.5 to 28 km offshore (Dever et al., 2006). The coherent mooring array was designed to resolve the scale of along-shelf and cross-shelf structure in velocity, and thus to evaluate first differences (i.e. divergence and shear).

Moorings were equipped with downward-looking acoustic Doppler current profilers (ADCPs), which covered the water column from 5 m below the surface and temperature loggers, which were spaced at 5-m intervals over the uppermost 25 m (to resolve the surface mixed layer and thermocline) and 10–15 m over the remainder of the water column. In addition, each mooring was equipped with an anemometer 3 m above sea level and conductivity-

temperature loggers at 10 m depth in combination with transmissometers and fluorometers. Similar packages were deployed at 1, 50 and 78 m depth on D090. A near-surface WS Oceans NAS-2E nitrate monitor returned values every 2 h at 1 m depth on D090 and also from D040 during cruise periods. The surface buoy on D090 included sensors for humidity, solar insolation, and air temperature and additional wind measurements were available (Dorman et al., 2006). These instruments and data are more fully described in Dever et al. (2006).

2.2. Observing surface spatial pattern—satellite, HF radar, drifters

Hourly maps of surface current velocity have been available for the WEST region since May 2001 when two HF radar units (13 MHz CODAR Seasondes) were deployed at Pt. Reyes and Bodega Marine Lab (Kaplan et al., 2005; Kaplan and Largier, 2006). During 2001, coverage extended over 40 km offshore and from Pt. Reyes north to Gerstle Cove (Figs. 1 and 2). An expanded array continues as part of the Bodega Ocean Observing Node (bml.ucdavis.edu/boon). Vander Woude et al. (2006) and Kudela et al. (2006) describe concurrent data on surface temperature and chlorophyll-*a* levels available from satellite sensors such as AVHRR, SeaWiFS, and MODIS (Fig. 2). In addition, 62 surface drifters were deployed during WEST (6 m WOCE ‘‘holey-sock’’ drogues centered at 7.5 m depth—see Kaplan et al., 2005). A combination of HF radar, drifter and satellite data yield an improved knowledge and understanding of transport routes, including the origin and destination of waters (Kaplan and Largier, 2006) and the development of chlorophyll levels in a water parcel being advected offshore (Vander Woude et al., 2007).

2.3. Observing three-dimensional spatial structure—shipboard surveys

Five major ship surveys were conducted during WEST: two in winter (January 2002 and 2003) and three in the spring–summer upwelling season (May–June 2000–2002). Summer surveys consisted of two 2-week segments, each designed to start and end with a large-scale survey (Fig. 1: blue lines A, D, and F), while the intervening period was comprised of repeated small-scale surveys (Fig. 1: red lines C, D, and E) and time-series ‘‘anchor stations’’

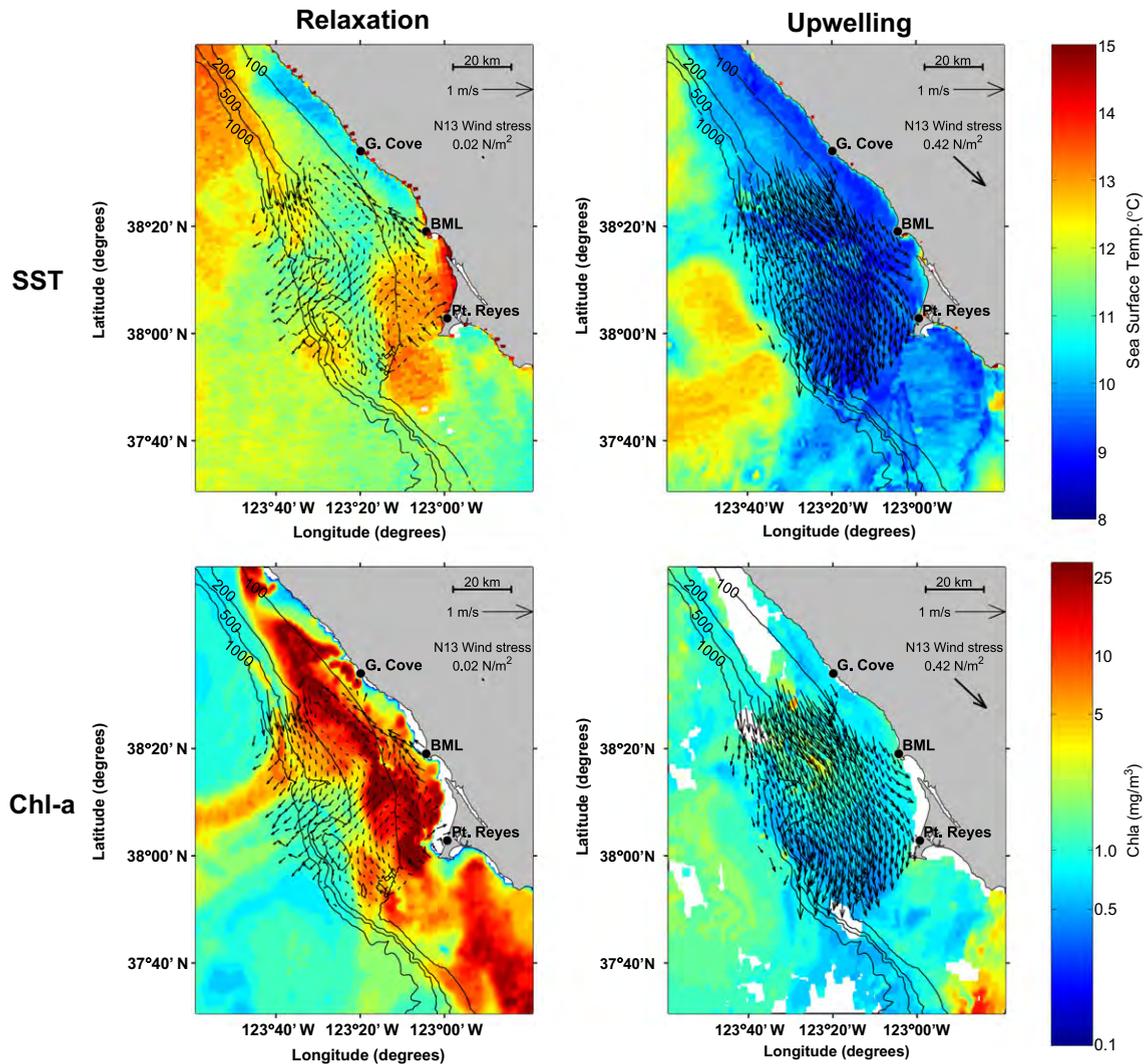


Fig. 2. Maps of surface current (HF radar) overlaid on satellite-derived sea-surface temperature (upper panels) and chlorophyll (lower panels) patterns in June 2003. Left panels: Typical relaxation conditions are represented by HF radar data from 10 June 2003 and satellite data from 2 to 3 days later, showing the transport effect of observed flow on these tracer distributions (SST composite for 12–13 June; chlorophyll composite for 11–14 June). Right panels: Typical upwelling conditions are represented by HF radar data from 17 June 2003 and satellite data from 2 to 3 days later, showing the transport effect of observed flow on these tracer distributions (SST and chlorophyll composites for 19–20 June).

designed to observe day–night differences at stations along the D-line. The D-line was occupied about every other day, resolving synoptic variability.

Plankton and nutrient samples were collected on station, concurrent with CTD/fluorometer/transmissometer casts (Roughan et al., 2006). Samples were analyzed for nitrate, silicate, phosphate and ammonium (Dugdale et al., 2006), chlorophyll concentration (Wilkerson et al., 2006), phytoplankton size and species (Lassiter et al., 2006), bio-optical properties (e.g., CDOM, particulate absorp-

tion spectra; Kudela et al., 2006) and copepod nauplii concentrations (Papastephanou et al., 2006). In addition, net zooplankton were collected using vertical tows of a ring net (1-m diameter, 73- μ m mesh) for mesozooplankton such as copepods (Papastephanou et al., 2006; Slaughter et al., 2006) and double oblique tows of bongo nets (333 and 500 μ m mesh) for meso/macrozooplankton such as euphausiids (Dorman et al., 2005). Measurements of primary production were obtained daily (Dugdale et al., 2006), as well as midday bio-optical

profiles (Kudela et al., 2006). During anchor station time-series, depth-stratified zooplankton samples were obtained with a MOCNESS tow.

Data also were collected underway. Current velocities (ADCP), surface water properties (temperature, salinity, chlorophyll fluorescence) and wind velocity were collected routinely. In addition, on selected transect lines a “Scanfish” tow-fin was deployed (Roughan et al., 2006) to obtain tow-yo profiles of temperature, salinity, fluorescence, and optical plankton counts.

2.4. Modeling winds, currents and plankton productivity

High-resolution atmospheric simulations of the northern California coastal region were performed during WEST, using the Mesoscale Model 5 (MM5; Grell et al., 1995). The model was run for May–July, 2001 with a multiple-nest setup and 1-km horizontal resolution, showing the persistent flow expansion fan that develops in the lee of Point Arena with a deceleration area further downwind (Koraćin and Dorman, 2001; Koraćin et al., 2004).

Three-dimensional ocean circulation was modeled using the primitive-equation ROMS—a hydrostatic model with terrain-following vertical coordinates (Kuebel-Cervantes and Allen, 2006). The simulations use realistic topography and

temporally varying but spatially uniform wind stress and heat flux values as measured at the D090 mooring. The model results are compared with observations of currents and water temperatures from moorings, ship surveys and HF radar. Three-dimensional Lagrangian tracks are calculated from the model flow field, allowing insight on potential origins and destinations of upwelled water.

Ecological modeling during WEST was comprised of an idealized mixed layer conveyor (MLC) model that addressed the importance of wind strength and variability in terms of phytoplankton and zooplankton productivity (Botsford et al., 2003, 2006). The model includes the rate of nutrient upwelling, offshore advective loss, and reduced light exposure in deeper surface mixed layers. Productivity is modeled in terms of nitrogen, the limiting nutrient (Wilkerson et al., 2006). This model is run for observed 2001 wind conditions as well as for observed winds for the preceding 20 years.

3. Upwelling and relaxation events

May–June 2001 was one of the two most intensive upwelling study periods in WEST, combining ship-board survey, moorings, drifters, HF radar, satellite imagery and modeling. This period is presented here as an example of typical wind-forced variability off northern California and because it is the focus of

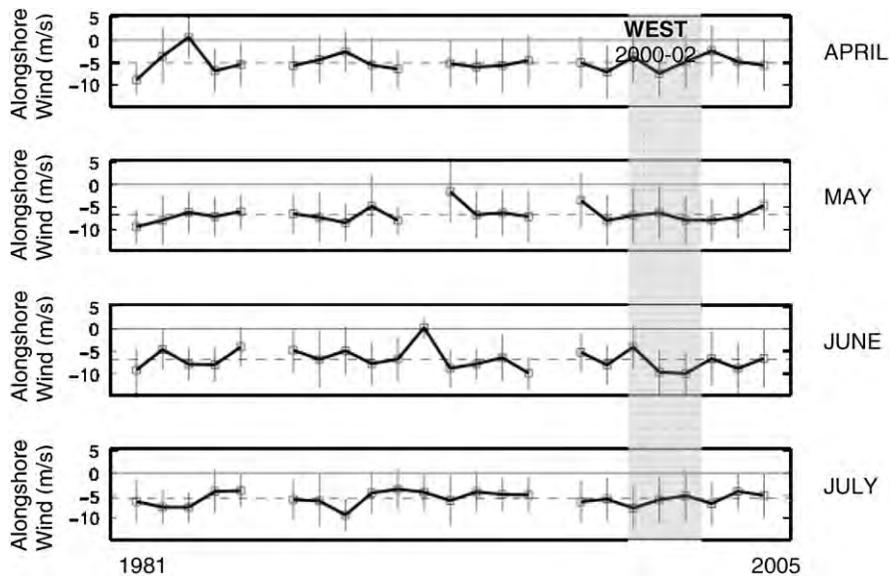


Fig. 3. Monthly mean along-shelf wind (and standard deviation) at NDBC 46013 (Fig. 1). Top panel shows mean wind for April for each year from 1981 to 2005, with monthly standard deviation shown as whiskers on symbol. The long-term 22-year mean for April is shown as a dashed line across the upper panel. Second panel is data for May. Third panel is for June, and the bottom panel is for July. The WEST years 2000–02 are shaded.

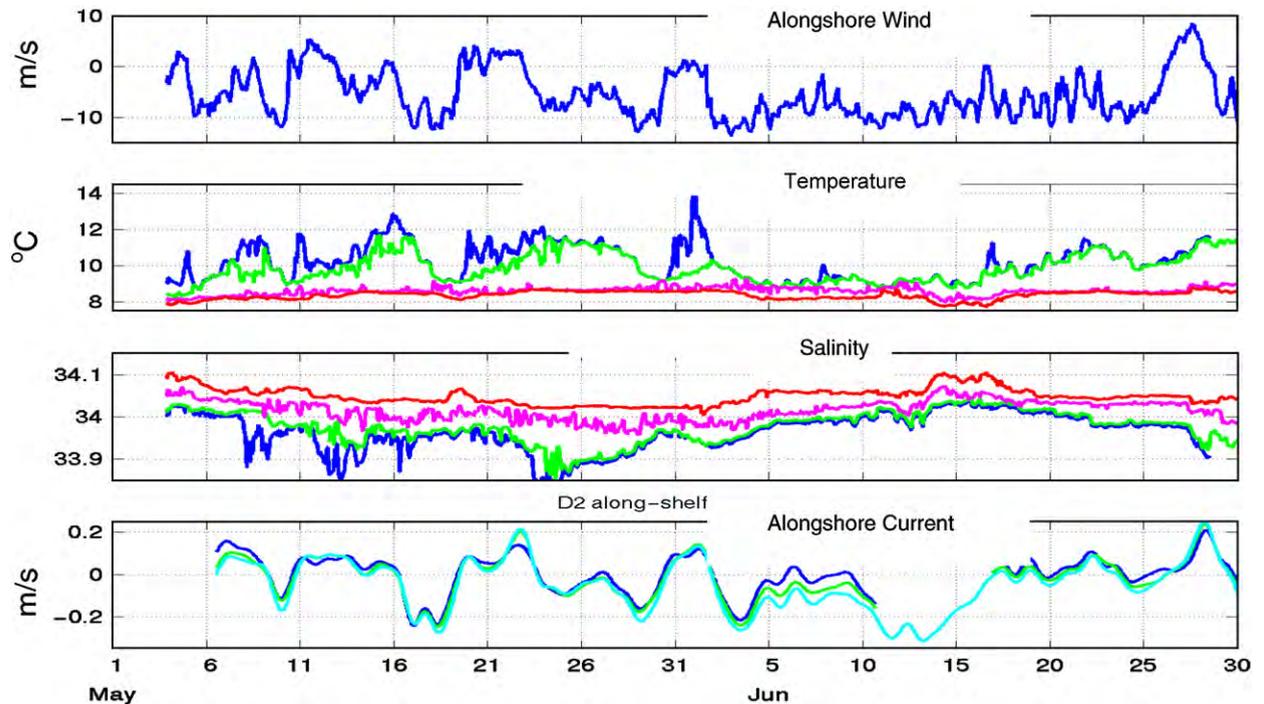


Fig. 4. Observations of wind, temperature, salinity and currents at mooring D090 (Fig. 1). Top panel: Along-shelf wind speed, at an orientation of 320° T. Second panel: Water temperature at depths of 1 m (blue), 10 m (green), 50 m (magenta), and 80 m (red). Third panel: Salinity at depths of 1 m (blue), 10 m (green), 50 m (magenta), and 80 m (red). Bottom panel: Subtidal along-shelf current speed, at orientation 320° T and at depths of 5 (cyan), 25 (green) and 75 m (blue).

most of the papers in this special issue. While other ship surveys in May–June 2000 and 2002 allow detailed year-to-year comparison, we inspect longer-term wind records to assess the WEST period in the context of interannual variability (Fig. 3). Wind data are available from NDBC buoy 46013 since 1981 and have been used as the primary index of wind forcing in prior studies like CODE (1981–82) and NCCCS (1988–89). One can see that mean monthly winds during WEST upwelling surveys reasonably represent typical wind forcing over the shelf off northern California. During May 2001 (and 2000 and 2002) the mean wind was close to the 25-year mean for the month of May, while in June 2001 upwelling winds were persistent (Fig. 4) and the mean is about 10 m/s, notably stronger than the 25-year mean for June. Again in 2002, June was characterized by strong winds, but during the pilot cruise in June 2000 winds were unusually weak.

The characteristic pulses of upwelling wind and ocean response are evident during May–June 2001 (Fig. 4) and other spring–summer seasons off northern California. We identify active “upwelling

events” as periods during which the equatorward along-shelf component of the 36-h low-passed wind at NDBC 46013 exceeds 5 m/s. Not only are NDBC 46013 winds a good index (correlated with winds observed nearshore and extensively used in previous studies; e.g., CODE), but they also exhibit a clear bimodal distribution in 2001 (and most years) so that one obtains the same events if one chooses a value as low as 3 m/s or as high as 6 m/s. Between upwelling events are periods of weaker wind—“relaxation events”—periods in which the 36-h wind is less than 5 m/s. Transitions between relaxation and upwelling, and vice versa, are sudden—hence the bimodal wind distribution.

Upwelling events occurred 1–3 May (3.5 days), 5–10 May (6 days), 13–14 May (1.5 days), 16–19 May (3.5 days), 23–31 May (7.5 days), 1–26 June (24.5 days) and 28 June–7 July (8.5 days). Fig. 4 illustrates the decreasing water temperature, increasing salinity and equatorward along-shelf currents that are observed in response to these northerly wind events. Further, nitrate concentrations increase and chlorophyll fluorescence decreases during upwelling.

Relaxation events occurred 3–4 May (1 day), 10–13 May (2 days), 15 May (1 day), 19–23 May (3.5 days) and 31 May–1 June (1.5 days). Also, an unusual summer downwelling event was observed 26–28 June (2.5 days), demarcated by poleward winds in excess of 5 m/s. Fig. 4 illustrates the increasing water temperature near-surface (and thus increasing stratification), decreasing salinity (after a few days) and poleward along-shelf currents that are observed during these periods of weak wind. Further, nitrate concentrations decrease and chlorophyll fluorescence increases during relaxation.

The 2001 upwelling survey cruise started 19 May, at the end of a well-defined upwelling event (16–19 May), which was followed by a well-defined relaxation event (19–23 May). These two events are described below in more detail, providing examples of typical upwelling and relaxation events.

During the 16–19 May event, equatorward winds at NDBC 46013 remained over 5 m/s for 3.5 days (generally over 10 m/s, and peaking at 15 m/s), allowing full development of upwelling conditions (Fig. 4). Near the coast, winds were also upwelling-favorable, but weaker—remaining below 10 m/s at D040. This typical structure accounts for positive wind-stress curl (stress ~ 0.1 Pa at D040 and ~ 0.5 Pa at NDBC 46013) and upwelling across the shelf (Dorman et al., 2006; Dever et al., 2006). Stratification disappeared and the surface mixed layer deepened rapidly, reaching 30 m by 19 May. Offshore Ekman transport of order $1\text{--}2\text{ m}^2/\text{s}$ ($u \sim 0.05$ m/s) was observed at D090, but weaker at D040 and stronger at D130 (Dever et al., 2006). Averaged over the 11 km between D090 and the shore, this transport divergence corresponds to upwelling of order 10 m per day. Cold waters ($\sim 9^\circ\text{C}$) were observed at the surface of the D090 mooring and a modest 0.03 increase in salinity was observed near bottom (78 m), indicating upwelling of deeper waters onto the shelf towards the end of the upwelling event. About a day after the start of upwelling winds, equatorward along-shelf flow developed, with depth-averaged subtidal along-shelf velocity exceeding 0.25 m/s over the middle and outer shelf (D090 and D130) and slightly weaker inshore at D040, especially later in the upwelling event. Consistent with the upwelling of colder waters ($< 12^\circ\text{C}$), nitrate levels increased 17–18 May, lagging the wind by about a day. Peak surface nitrate levels of $24\ \mu\text{M}$ were observed on the D090 mooring by 18 May, 2 days after the start of wind forcing. Concurrent with this increase in nitrate and

decrease in temperature was a rapid decrease in near-surface chlorophyll fluorescence, consistent with the offshore transport of pre-upwelling surface waters. Fluorescence dropped close to zero by 18 May, and these newly upwelled waters exhibited light transmission of over 90%. Nearshore, in the presence of weaker winds at D040, weak stratification persisted throughout this upwelling event, and surface temperatures did not drop below 10°C . Offshore, in the presence of stronger winds, a deeper surface mixed layer (> 40 m) was observed at D130.

During the 19–23 May relaxation event, equatorward winds remained below 5 ms^{-1} for 3.5 days at buoy NDBC 46013, allowing full development of relaxation conditions. In fact, winds were poleward during this event, but they remained weak ($< 5\text{ ms}^{-1}$) and exhibited negligible wind-stress curl. Stratification appeared immediately following weakening of the upwelling wind and the surface mixed layer disappeared. Near-surface cross-shelf velocities were weak during relaxation conditions, but the along-shelf velocities were notably poleward (Fig. 4). Along-shelf velocities at D040 and D090 reversed immediately, concurrent with the end of upwelling-favorable winds, and depth-averaged poleward velocities in excess of 0.1 m/s were observed after a few days. Further offshore, the D130 depth-averaged velocity reversed later and remained weaker (< 0.05 m/s poleward) while at distances > 40 km offshore HF-radar-observed surface currents remained weakly equatorward throughout the event. At the end of the relaxation event, poleward flow continued over the shelf for a day following the return of upwelling winds, so that poleward transport persisted for almost 5 days. While surface temperatures showed an immediate increase following the demise of upwelling winds, the initial temperature increase at 10 m was weak and the decrease in salinity was negligible, characteristic of surface warming of recently upwelled waters. During this initial phase of the relaxation event, nitrate levels decreased to about $10\ \mu\text{M}$, consistent with an increase in chlorophyll fluorescence to levels between 5 and $10\ \mu\text{g l}^{-1}$. Three days after the demise in upwelling winds, however, a sharp drop in salinity was observed at the surface, and, soon after that, also at 10 m depth on the D090 mooring (Fig. 4). Concurrent with this was an increase in temperature at 10 m and re-appearance of a surface mixed layer on 23–24 May, as well as a sudden decrease of nitrate to undetectable concentrations, a sudden increase in chlorophyll

fluorescence from less than $5 \mu\text{g l}^{-1}$ to about $15 \mu\text{g l}^{-1}$, and a sudden decrease in light transmission from about 90% to about 75%. This second phase of the relaxation event followed two days of strong poleward flow and represents the arrival of a different water mass from the south. This low-salinity water was observed during other relaxation events as well (Fig. 4), consistent with northward transport of surface waters from the Gulf of Farallones (cf., Send et al., 1987; Wing et al., 1995a, b, 1998).

4. Overview of results

This introduction to the WEST special volume addresses links between papers and developments in our integrative understanding of the role of wind forcing in primary and secondary production in coastal plankton communities.

4.1. Spatial structure in wind forcing and ocean response

The persistent flow expansion fan that develops in the lee of Point Arena is evident in the MM5 modeling by Koraćin and Dorman (2001) and Koraćin et al. (2004). While accelerated winds tend to be found south of Arena, over the outer shelf (e.g., off Bodega Bay), a thicker marine layer with slower winds is typically found at the coast. As the extent and strength of the expansion fan vary so do gradients of the wind stress in the Bodega Bay area, resulting in shifting patterns of wind-stress curl and upwelling in the WEST region. These patterns are reflected in the observations of strong and persistent wind-stress offshore, while inshore winds are much weaker at times (Dorman et al., 2006). This cross-shelf shear in the along shelf wind accounts for most of the observed wind-stress curl, varying between 0 and $3 \times 10^{-5} \text{ Pa m/s}$ inshore of the D090 mooring (11 km offshore) and weaker further offshore. Agreement between observations and modeling in WEST indicates that models can now be used to resolve and represent the small-scale structure in wind stress that is so important to determining when, where and how strongly surface divergence occurs.

This spatial structure in wind stress results in the upwelling of waters not only at the coast due to the adjustment of cross-shelf Ekman transport to the presence of the coast, but also away from the coast where positive curl in the wind stress produces areas

of divergent Ekman transport (Enriquez and Friehe, 1995; Koraćin et al., 2004). The five-mooring array yielded direct observations of near-surface Ekman transport, calculated by integrating velocity measurements down to the surface boundary layer depth (Dever et al., 2006). This observed transport is highly correlated with Ekman transport calculated from buoy wind stress, and thus there is good agreement between divergence estimates from wind observations and direct calculation from current observations, being similar in strength and well correlated. Upwelling driven by the adjustment to the coastal boundary condition occurs primarily inshore of the D040 mooring (1.5 km offshore) with vertical advection up to $8 \times 10^{-4} \text{ m/s}$ (Dever et al., 2006). Curl-driven upwelling rates are weaker, but extend over a larger area: about $3 \times 10^{-4} \text{ m/s}$ between D040 and D090 and decreasing to about $1.5 \times 10^{-4} \text{ m/s}$ between D090 and D130. This curl-driven upwelling thus extends well offshore and it is evident in surface velocity divergence estimates from HF radar data, extending about 40 km offshore (Kaplan and Largier, 2006). The integrated curl-driven upwelling flux is thus at least as large as that due to adjustment of Ekman transport to the coastal boundary.

Although the numerical modeling of wind-forced circulation in the WEST region did not include spatially structured wind stress, significant along-shelf variability in circulation due to variations in coastline shape and bottom topography is well represented (Kuebel-Cervantes and Allen, 2006). This is demonstrated by comparisons of model results with moored, shipboard and CODAR observations. These results suggest that resolving small-scale structure in wind forcing may not be critical for understanding the general flow response and along-shelf variability along the shelf in this region, although the spatial structure of wind stress is critical in determining where upwelling occurs, and thus probably key in understanding primary production and phytoplankton distributions.

4.2. Ocean circulation and transport patterns

Surface currents in this area are dominated by synoptic-scale wind-forced variability (Largier et al., 1993; Kaplan et al., 2005) and reflect a marked cross-shelf structure (Kaplan et al., 2005; Dever et al., 2006; Roughan et al., 2006; Kuebel-Cervantes and Allen, 2006). Along-shelf currents within about 15 km of the shore exhibit a tendency towards

poleward flow, while currents farther out over the shelf are clearly equatorward, as on CODE and NCCCS mooring lines deployed some 50 km to the north (Winant et al., 1987; Largier et al., 1993). During relaxation (Send et al., 1987), near-surface poleward flows up to 0.3 ms^{-1} may be observed within 15 km of the coast (Dever et al., 2006; Kaplan et al., 2005), and similar equatorward currents are observed during upwelling winds. This inshore poleward flow is warmer and can result in a significant drop in salinity as water from the Gulf of Farallones is advected past the moorings at D040 and D090 (Fig. 4). These poleward relaxation flows are thus stratified, and while the near-surface mean current is weakly poleward inshore (order 0.01 m/s), the depth-averaged mean current is weakly equatorward (order 0.01 m/s). Owing to the common occurrence of stratification at moorings D040 and D090, these locations are generally offshore of the “inner shelf” (*sensu stricto*), as discussed by Dever et al. (2006). While circulation modeling resolves this inshore feature in spite of homogeneous wind forcing, it does not appear as well developed in the model as in reality.

Farther offshore over the mid/outer shelf, the equatorward jet is strongly correlated with fluctuating winds (Kaplan et al., 2005; Dever et al., 2006). However, lower-frequency oceanic forcing is also important at the offshore mooring D130 (Dever et al., 2006), consistent with results from a 130-m mooring deployed near the F-line during NCCCS (Largier et al., 1993). ADCP transects extending yet further offshore on the D-line indicate that a second equatorward flow feature can be found off the shelf, consistent with model results (Kuebel-Cervantes and Allen, 2006) and persisting through relaxation periods (Roughan et al., 2006). Both data and model describe a single along-shelf jet over the shelf and slope on the F-line, and show that the two-jet structure forms north of the D-line (perhaps due to an upstream influence of Cordell Bank: Kuebel-Cervantes and Allen, 2006) and continues south to the A-line. At the A-line, one jet is over the shelf, close to the tip of Point Reyes, and the other jet is found 60–70 km offshore, well beyond the slope and at times offshore of the shoaling undercurrent. The direct interaction of the offshore jet with the California Undercurrent results in strong shear and mixing (Roughan et al., 2006).

The transport effect of observed surface currents is estimated through an integration of HF radar data (Kaplan and Largier, 2006), and transport

patterns are also modeled (Kuebel-Cervantes and Allen, 2006), revealing a bimodal pattern with equatorward transport throughout the shelf during upwelling winds and poleward transport over the inner/mid-shelf during relaxation. During upwelling, surface waters in the WEST/Bodega shelf region come from the north, are advected south between Cordell Bank and Point Reyes, and are exported from the shelf by the upwelling jet that separates from the shore at Point Reyes. Consistent with drifter data, HF radar data show that surface waters move through the 50-km domain in about 4–5 days, comparable with bloom response times for diatoms. During relaxation, nearshore waters off Bodega Bay flow in from the south, importing waters from the Gulf of Farallones and also entraining in this some offshore waters and some upwelled waters from the outer shelf. The strength of northward flow past Point Reyes results in a separation eddy on the north side of the point and onshore flow between Point Reyes and Bodega, evident in HF radar data and confirmed by drifter data (Kaplan et al., 2005; Kaplan and Largier, 2006). Surface divergence associated with this eddy suggests that sub-surface waters are also entrained vertically into this northward relaxation flow. In addition to observed surface transport patterns, three-dimensional model Lagrangian analyses reveal the potential for cross-shelf, along-shelf and vertical transport during upwelling wind events (Kuebel-Cervantes and Allen, 2006). Modeled water parcel displacements suggest fundamentally different upwelling responses north and south of Pt. Reyes, with local water upwelled near the coast on the A-line and deeper water upwelled north of Pt. Reyes.

Patterns of transport are also reflected in surface properties, with newly upwelled waters being cold and clear while aged upwelled waters are warmer and with higher chlorophyll content (Kudela et al., 2006). Analysis of satellite imagery shows nearshore retention sites, where aged upwelled waters are found at times—even during active upwelling. Vander Woude et al. (2006) find that surface waters may be retained or retarded allowing surface aging of upwelled waters in nearshore zones both north (upstream) and south (downstream) of the Point Reyes promontory. Although warmest waters with highest chlorophyll are seen on the north side of Point Reyes during relaxation periods, even during upwelling these waters may be warmer and higher in chlorophyll than waters further north (Vander

Woude et al., 2006). HF radar observations indicate that a zone of convergence in surface velocity may exist upstream of this headland (Kaplan et al., 2005), and onshore winds (Dorman et al., 2006) suggest that upwelling may be suppressed along this shoreline between Pt. Reyes and Tomales Point. These results indicate that the persistence of high biomass coastal waters in this strongly advective and wind-dominated system is at least partially explained by the presence of physically retentive features associated with headlands and embayments.

4.3. Primary production and phytoplankton distributions

WEST was motivated by the need for a deeper understanding of the interplay of multiple responses to upwelling winds (nutrient supply, plankton export, and light exposure). The pulsed nature of upwelling winds is key, with high-nutrient upwelling events being followed by stratified relaxation events and weak/reversed surface currents over the shelf. In observations and models of blooms (Wilkerson et al., 2006; Botsford et al., 2006), it is apparent that maximum phytoplankton productivity occurs when wind variability matches phytoplankton bloom time scales. Wilkerson et al. (2006) suggest that a 3–7 day relaxation is optimal, following an upwelling pulse. Through modeling, Botsford et al. (2006) show how productivity integrated over an event depends on the nature of wind variability. For example, all upwelled nitrogen is converted to phytoplankton over the shelf for upwelling events interrupted by relaxation events in May 2001, whereas only half of the available nitrogen is utilized over the shelf during persistent upwelling in June 2001.

A corollary of the time-dependence of blooms is that high levels of phytoplankton will be observed at locations where 3-to 7-day old upwelled waters are found, as in the retention zones identified by Vander Woude et al. (2006). The basis for this spatial pattern is also apparent in the modeling results of Botsford et al. (2003, 2006): high levels of shelf productivity are found for scenarios where the shelf is broad enough to accommodate 3-to 7-day old waters (i.e., upwelled waters are not exported prior to a full phytoplankton bloom occurring). These spatial patterns of aging upwelled waters may explain high levels of secondary production in coastal upwelling regions characterized by headlands and bays, or by broad shelves.

Wilkerson et al. (2006) describe the total depletion of nitrate and silicate and maximal concentrations of phytoplankton when upwelling-favorable winds are followed by periods of relaxed winds. These phytoplankton blooms are dominated by chlorophyll in the >5- μm phytoplankton size fraction and typically found in the nearshore region characterized by poleward flow and shallow stratification during relaxation events (Roughan et al., 2006 and Fig. 4). Similar events are observed in time-series of nitrate and chlorophyll fluorescence at the central mooring D090 (e.g., Kaplan and Largier, 2006; Vander Woude et al., 2006). This large-celled phytoplankton community was dominated by diatoms (Lassiter et al., 2006), important players in coastal new production and carbon cycling. During maximum chlorophyll concentrations in 2000–2002, the diatoms were primarily from a *Chaetoceros* complex—representing a diatom functional group that is well adapted to the high-nutrient, turbulent conditions typical of wind-driven coastal upwelling regions.

Nitrate levels, monitored shipboard and on the central mooring, control primary production (Wilkerson et al., 2006). A significant vertical flux of nitrate can be accounted for through the observed surface divergence within the mooring array (Dever et al., 2006). While silicate is also an important nutrient, silicate depletion never preceded that of nitrate during WEST. Discrete measurements of iron and aluminum (indicative of terrestrial inputs) collected during 2003 were not sufficient to determine if iron limitation occurs in this region (Kudela et al., 2006). In contrast to these other nutrients, ammonium does appear to have an important and direct influence through inhibition of nitrate uptake, even at low levels of ammonium (Dugdale et al., 2006).

Dugdale et al. (2006) find that during stronger winds later in the 2001 cruise, new production was less than the theoretical maximum and ascribe this to turbulence and strong advective loss. Rapid export of upwelled waters from the shelf is evident in HF radar data (Kaplan and Largier, 2006), but higher levels of detrital and inorganic materials are also observed over the shelf during strong upwelling winds in 2001 and 2002 (Kudela et al., 2006). Combined with increased depth of the mixed layer during strong winds (Dever et al., 2006), phytoplankton have reduced light exposure during strong winds.

In the idealized MLC model of biological production (Botsford et al., 2003, 2006), the

importance of relaxation events is apparent, specifically when event time scales match plankton response time scales. While upwelling indices based on volume upwelled (e.g., Bakun upwelling index) provide a reasonable index of intra-annual variability in productivity, these indices are misleading when comparing shelf productivity between years as a result of neglecting advective losses during strong winds (Botsford et al., 2006). While the MLC model represents export simply, the time scales are consistent with observed export trajectories from surface drifters and quasi-Lagrangian tracks calculated from surface HF radar data (Kaplan and Largier, 2006), as well as with 3-dimensional model trajectories (Kuebel-Cervantes and Allen, 2006). In strong winds shelf transit times may be 5 days or less, whereas in moderate upwelling winds shelf transit times can be up to 10 days—allowing ample time for full development of diatom blooms over the shelf.

4.4. Zooplankton populations

Results of distribution, abundance and composition of copepods and euphausiids are presented in Papastephanou et al. (2006) and Dorman et al. (2005), respectively. The copepod assemblage was dominated by *Oithona* spp., *Acartia* spp. and *Pseudocalanus* spp. The cross-shelf distribution of copepods generally shifted offshore during upwelling and onshore during relaxation events, although some variability between species occurred. Further, abundance of all copepod life stages generally exhibited a negative correlation with cross-shelf transport, indicating lower abundances during and immediately after active upwelling. Copepod nauplii respond positively to wind events followed by prolonged relaxation, but with a change in abundance that is too great to be due to local in situ growth and reproduction alone (Papastephanou et al., 2006). This observation is consistent with the advection of new nauplii-rich water masses into the WEST region after a few days of relaxation (Fig. 4).

In the MLC model (Botsford et al., 2003, 2006) zooplankton are assumed to have no migratory behavior, in which case optimal conditions for secondary production are achieved for variability in wind forcing on time scales comparable to those of the organisms, but much longer than observed wind variability. This model result argues that, in reality, longer-lived zooplankton populations counter the potential advective loss of shelf productivity

through ontogenetic behavior (e.g., Peterson et al., 1979) or diel vertical migration behavior (Wroblewski 1982; Peterson 1998).

In addition to studies of zooplankton distribution, abundance and composition, the grazing impact of mesozooplankton ($>200\ \mu\text{m}$) was measured directly through gut fluorescence studies on all five WEST cruises (Slaughter et al., 2006). Grazing impact of mesozooplankton varied inter-annually and seasonally, being highest during a prolonged period of relaxation in June 2000 (100% of phytoplankton standing crop consumed in less than a day). Typically, mesozooplankton grazing is much less during upwelling periods (25–38% per day), which are characterized by stronger winds, greater offshore transport and lower chlorophyll concentration. During most sampling periods, larger mesozooplankton ($>500\ \mu\text{m}$) contributed proportionally more to grazing impact than smaller (200–500 μm) mesozooplankton. These direct observations of grazing rate are key inputs for models of phytoplankton systems (e.g., Botsford et al., 2003, 2006; Spitz et al., 2005).

5. Discussion

The WEST program has yielded new insights into the temporal and spatial structure of wind-driven upwelling and the response of plankton communities. Inherent time scales in wind variability and topography-induced spatial structures in winds and currents are evident in the conditions observed off Bodega. These spatial and temporal structures are key to structuring the distribution and efficiency of primary and secondary production. Specifically, the paradox posed at the start of WEST is readily explained by recognizing the spatial or temporal separation of nutrient enrichment (through vertical fluxes) from maximal bloom development (in the absence of vertical and horizontal mixing). Temporal separation is provided by alternating pulses of upwelling and relaxation, while spatial separation can be provided by alternating regions of upwelling at headlands and retention in bays. The themes of upwelling-and-relaxation and cape-and-bay are at the heart of these and ongoing WEST analyses. Key elements of these themes addressed in WEST include:

- The spatial structure in winds and wind stress off northern California has been effectively modeled and small-scale curl has been observed directly

through an array of moorings. Further, the spatial structure in wind is seen to produce similar spatial structure in Ekman transport, resulting in upwelling extending well offshore due to wind-stress curl off Bodega.

- The spatial structure in surface currents observed off northern California reflects spatial patterns in wind forcing and the effect of headlands. Currents nearshore off Bodega are subject to wind forcing that is much weaker than offshore, and along-shelf transport is predominantly poleward during the upwelling season. Strong currents farther offshore are consistent with strong wind forcing and the presence of an upwelling jet originating at the Point Arena upwelling center. This jet appears to bifurcate north of Bodega, with the inner jet over the shelf inshore of Cordell Bank weakening during relaxation periods and a more persistent outer jet over the slope or farther seaward. Both of these features appear to be deflected offshore by interaction with Pt. Reyes.
- The spatial structure in the age of upwelled waters includes nearshore locations in which aged waters are observed during upwelling events. In particular, nearshore waters immediately downstream and upstream of Pt. Reyes are warmer and higher in chlorophyll, indicating that these areas may retain phytoplankton and zooplankton over the shelf during upwelling events.
- The temporal structure in wind forcing presents a series of discrete upwelling events interrupted by short periods in which winds are weak. Physical responses to relaxation occur as the wind relaxes (i.e. weakening upwelling winds), but these transitions are quick (less than a day), and by the time water properties and plankton levels show significant change the winds are weak. For this reason, and the importance of these calm periods to coastal ecology, “relaxation” has come to indicate a time of weak rather than weakening winds (as the word is typically used in physical systems).
- The temporal structure in nutrient and phytoplankton levels closely follows the cycle in wind forcing, with high levels of nitrate during active upwelling followed by blooms when winds relax for a few days or more. Prolonged relaxations lead to an import of water and plankton from the Gulf of Farallones.
- Zooplankton population responses lag these events even further, with observations indicating

a generally negative correlation between abundance and winds, but with modeling clearly demonstrating that upwelling/relaxation cycles are necessary to sustain secondary production.

- The net productivity of each upwelling event depends on the length of relaxation following well-developed upwelling. But productivity also is affected by the strength of the upwelling winds. Negative feedback from very strong winds leads to excessive off-shelf loss, increased turbidity and deep mixing, as well as elevated levels of ammonium that suppress nitrate uptake.
- When upwelling/relaxation events occur on time scales similar to those of phytoplankton blooms (several days), coastal waters are dominated by diatom blooms. During prolonged periods of upwelling, however, the bio-optical character of these coastal waters is increasingly influenced by detritus, with a shift towards phytoplankton offshore.

In summary, these studies off northern California point to the importance of properly resolving the critical temporal and spatial structure of wind forcing, currents, and water properties if one is to understand the role of wind-driven transport in the productivity and distributions of coastal plankton communities. The WEST study region and period is expected to represent temporal and spatial patterns and processes that are typical of other coastal upwelling regions in California and worldwide. Future work should delve deeper into specific physical and ecological processes, but also seek to develop comparative studies that can show the generality of these results for coastal upwelling systems.

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