

Nearshore chlorophyll-a events and wave-driven transport

Erika E. McPhee-Shaw,¹ Karina J. Nielsen,² John L. Largier,³ and Bruce A. Menge⁴

Received 10 October 2010; revised 6 December 2010; accepted 15 December 2010; published 21 January 2011.

[1] Continuous records of temperature and chlorophyll-*a* [chl-*a*] fluorescence were used to characterize phytoplankton variability at two shallow intertidal stations on the northern California coast. Chl-*a* records from spring and summer 2007 and 2008 were characterized by distinct peaks persisting for 1.5 to five days. These peaks represent bloom events, which often coincided between the two sites even though they are separated by ~150 km. Blooms did not appear to be directly forced by individual upwelling episodes. While some events were associated with reversals of upwelling-favorable winds, there was a stronger relationship between chl-*a* peaks and peaks in surface swell height. This relationship was dominant in spring and early summer, but no longer evident by July. We suggest that these nearshore chl-*a* peaks are an accumulation of phytoplankton caused by convergence of onshore wave transport against the impermeable coastal boundary. Scaling arguments show this mechanism to be consistent with observed chl-*a* increase rates. This mechanism has not been previously considered as a forcing for blooms at rocky coasts, and it may have significant implications for understanding coastal productivity, larval dispersal, and nearshore water quality. **Citation:** McPhee-Shaw, E. E., K. J. Nielsen, J. L. Largier, and B. A. Menge (2011), Nearshore chlorophyll-a events and wave-driven transport, *Geophys. Res. Lett.*, 38, L02604, doi:10.1029/2010GL045810.

1. Introduction

[2] Understanding chl-*a* variability in shallow intertidal environments is extremely important: phytoplankton are the base of the food chain for filter feeders, and bloom events may be directly linked to shellfish toxicity and other effects on higher trophic levels. Coastal upwelling along the west coast of North America in the California Current Ecosystem drives high regional primary productivity and productive fisheries. However, a direct connection between discrete, intraseasonal upwelling events and phytoplankton blooms at similar time scales is far from clear, and individual bloom events can be markedly decoupled from upwelling [Wieters *et al.*, 2003]. A pattern of locally maximum chl-*a* confined to a relatively thin band near the coast has been documented in many locations [Wieters *et al.*, 2003; Kim *et al.*,

2009] yet questions remain concerning the causes and variability of this band. Twice-weekly samples from the southern California inner shelf demonstrated that this near-coast feature was consistently amplified compared to chl-*a* offshore on the shelf, but unrelated to upwelling (cold temperatures) or offshore winds [Kim *et al.*, 2009]. Intertidal recruitment of mussel larvae has been shown to vary dramatically from larval numbers outside of the surfzone, implying important dynamics between the inner shelf and the coastline that we do not yet understand [Rilov *et al.*, 2008; Shanks *et al.*, 2010].

[3] The event scale of blooms is similar to the synoptic, or “weather band,” scale that characterizes a good portion of coastal dynamics in a system that is fundamentally forced by wind. Dynamics in this category include upwelling/relaxation cycles, coastal eddies, surface swell, and even rainfall. It is reasonable to hypothesize that high chl-*a* events persisting several days are related to such dynamics, and indeed continental shelf studies have pointed out links between retentive circulation patterns and convergence of plankton [e.g., Roughan *et al.*, 2005; Ryan *et al.*, 2008]. While recent work (A. J. Lucas *et al.*, The green ribbon: Multi-scale physical control of phytoplankton productivity and community structure over a narrow continental shelf, submitted to *Limnology and Oceanography*, 2010) shows that internal wave mixing may account for the observed nearshore chlorophyll maximum in southern California and other locations characterized by shallow stratification, an alternative mechanism must be found to explain nearshore maxima in unstratified waters such as those off northern California. We observed a correspondence between many chl-*a* blooms and energetic surface swell events, and suggest convergence of wave-driven transport causing phytoplankton accumulation at the coastal boundary as an additional, previously unconsidered, mechanism forcing nearshore phytoplankton blooms.

2. Methods

[4] Temperature and fluorescence were measured every 15 minutes at two sites on the northern California coast between May and late August of 2007 and 2008. Instruments were affixed to rocky intertidal benches, away from tide pools, just above mean lower low water (MLLW) and fully exposed to nearshore waters at both locations. The first site was at Bodega Marine Laboratory, facing west/southwest on Bodega Head at 38.3187°N, 123.0742°W (henceforth BML) and the second at a west-facing site, Kibesillah Hill (henceforth KH), at 39.5999°N, 123.7889°W, approximately 20 km northwest of Fort Bragg (Figure 1). Both sites are located on a stretch of rocky coastline exposed to the open ocean and are not sheltered by a local headland or embayment.

[5] Temperature was measured with Onset Temperature TidBit v2 Data Loggers (accuracy 0.2°C, time constant 5 minutes). Fluorescence was measured with a WET Labs

¹Moss Landing Marine Laboratories, San Jose State University, Moss Landing, California, USA.

²Department of Biology, Sonoma State University, Rohnert Park, California, USA.

³Bodega Marine Laboratory, University of California, Davis, Bodega Bay, California, USA.

⁴Department of Zoology, Oregon State University, Corvallis, Oregon, USA.

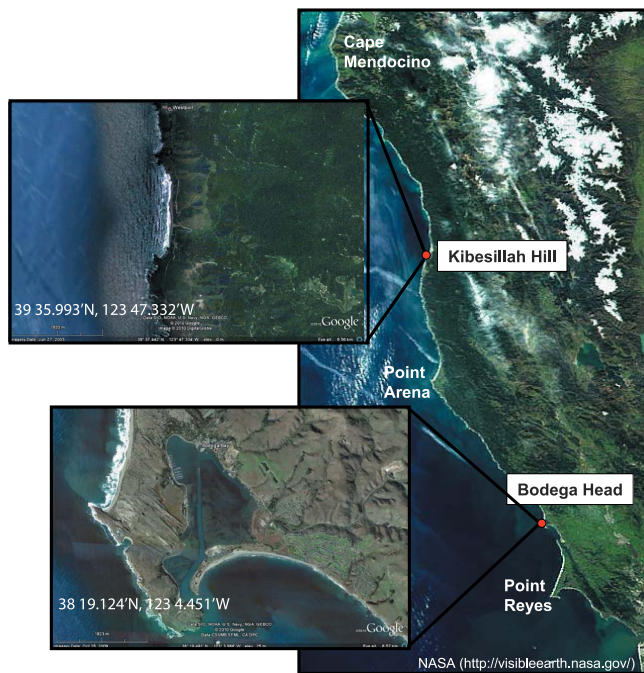


Figure 1. Map of study sites.

ECO fluorometer (Ex/Em: 470/695 nm). Raw fluorescence was calibrated to in situ chl-*a* ($\mu\text{g/L}$) (a proxy for phytoplankton biomass) from extracted chl-*a* (extraction methods described by *Wiersma et al.* [2003]) collected in 3 replicate sample bottles every 2 weeks during deployment periods. The fluorometer window was cleaned bi-monthly to prevent biofouling. Chl-*a* records were de-spiked and statistical outliers (>2 SD from the mean for the time series) were removed. Records corresponding to a tide height <1 m above the fluorometer height were removed. Instruments at both sites were deployed ~ 0.5 m above MLLW, yielding data coverage over typically 60% of each day, leaving ample data for characterizing events with time scales of days. Intertidal temperature was slightly warmer than, but very well correlated with, temperature measured at 4-m depth at a mooring 1.2 km offshore of Bodega Head during summer 2007. A least-squares fit between mooring and BML intertidal temperature for 01 June to 15 September 2007 gives $T_{\text{intertidal}} = 0.899 \cdot T_{\text{mooring}} + 0.471$, with $R^2 = 0.73$. No improvement was obtained by accounting for time of solar day or limiting to higher tides. The high correlation, and the close visual match between offshore and intertidal temperature (Figure 2a, red and black lines) demonstrate that intertidal temperatures were strongly controlled by the same mechanisms that control temperature on the shelf, and that these shallow records can be used to characterize oceanic conditions. Hourly wind speed and direction and significant wave height and direction were obtained from National Data Buoy Center (NDBC) buoys 46014 (near Point Arena, 39.1958°N 123.9694°W), 46013 (near Bodega Bay, 38.2419°N 123.3006°W), and NDBC 46042 (near Monterey Bay, 36.7886°N 122.4042°W).

3. Observations

[6] Water temperature, wind vectors, and significant wave height squared, H_{sig}^2 (proportional to wave energy), are shown

with chl-*a* records at both stations in Figure 2. Background chl-*a* levels were typically 5 to $10 \mu\text{g L}^{-1}$, punctuated by peaks where chl-*a* was elevated to between 20 and 30 , and sometimes $>50 \mu\text{g L}^{-1}$ (Figures 2d, 2e, 2i, and 2j). Individual peaks, marked with letters, were defined by rapid chl-*a* increases to more than one standard deviation ($\sim 8 \mu\text{g L}^{-1}$) above levels of the previous few days and remaining elevated for a period of at least one day. Some peaks lasted just over a day, most were 1.5 to 3 days duration, but the longest bloom persisted up to 6 days. Chl-*a* variance increased in July relative to May and early June, particularly at the BML site in 2008, making it difficult to distinguish bloom events from rapid, within-day chl-*a* fluctuations during the late summer.

[7] Winds were predominantly upwelling-favorable (south/southeastward) throughout the study (Figures 2b and 2g) and the water temperatures remained cold, between 8 and 12°C , until at least mid-July in both years, reflecting the strong seasonal signal of coastal upwelling. There was no relationship between individual bloom events and distinct cold events that might indicate growth spurred by a pulse of newly upwelled nutrients. Temperature varied at time scales quite different from the scales of chl-*a* variability. Various instances of water temperature falling and rising from maxima to minima and back were gradual, typically taking about 10 to 12 days, in contrast to the more abrupt rise and fall of chl-*a* within several days. Although unrelated to cold temperatures in a day-to-day sense, most of the blooms in our study were observed during upwelling conditions and relatively steady upwelling winds. Upwelling winds were punctuated by brief relaxation events (wind weakening or reversing for 2 days or less). Several bloom events appeared associated with wind relaxation, e.g., the 01 to 02-July inception of a long-lived bloom at BML (event k, Figure 2e) and a shorter bloom at KH (event f, Figure 2d) following a brief relaxation on 29 June 2007 and weak winds for several days. Also, event d in 2007 and events c, m, h, and p in 2008, either coincided with or immediately followed significant wind reversals. Seven of 28 total blooms identified coincided with wind relaxation, while 21 (75%) coincided with upwelling conditions, suggesting blooms were not associated with wind relaxations, but possibly with upwelling favorable winds ($\chi^2 = 5.19$, $df = 1$, $p = 0.0227$).

[8] Of the oceanographic parameters investigated, surface swell energy showed the strongest relationship to chl-*a* events. In 2007, events a, b, c, d, e, h, i, j, k, and l coincided with relative peaks in H_{sig}^2 . In 2008, chl-*a* events a, b, c, d, f, g, i, j, k, l, m, n, and p co-occurred with peaks in surface wave height. Although wave direction is not shown, almost all of the bloom events occurred during northwest swell (300° to 320°) typical for spring and summer in this region. The initial rise of chl-*a* consistently followed the initial rise of H_{sig}^2 with a lag of typically 5 to 8 (but ranging from 0 to 21) hours. With few exceptions, the wave-related bloom events were limited to May and June. The wave-to-chl-*a* association seemed to disappear in the late summer. Of the 28 bloom events identified, 23 (82%) were associated with elevated waves, and a test of independence between peaks in H_{sig}^2 and blooms provides supporting evidence for association at the event-to-event level ($\chi^2 = 14.26$, $df = 1$, $p = 0.0002$). However, there were wave events without corresponding nearshore blooms, and although the rise of H_{sig}^2 and chl-*a* were often surprisingly simultaneous, magnitude did not

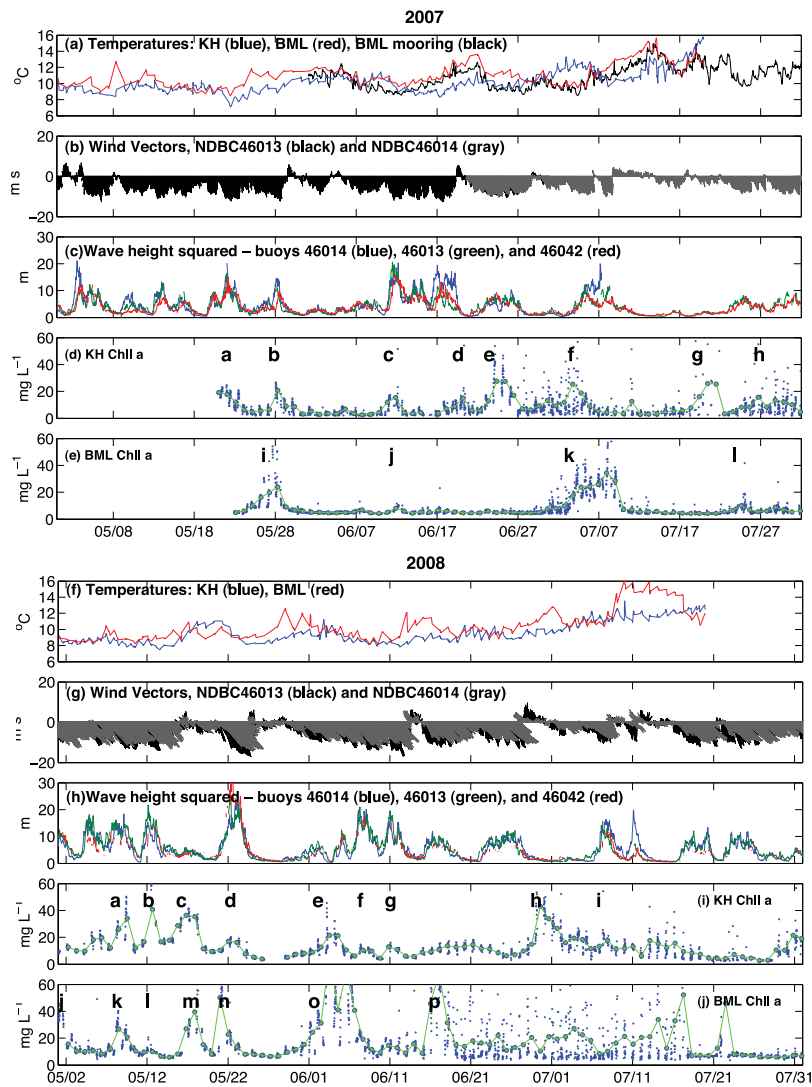


Figure 2. Records from 01 May to 31 July 2007. (a) Near-surface water temperatures at the KH intertidal site (blue), the BML intertidal site (red), and BML mooring offshore of the BML intertidal site (black). (b) Wind vectors from NDBC buoys 46013 (black) and 46014 (grey). A northward vector points upward, eastward is to the right. (c) Significant wave height squared (H_{sig}^2 , m^2) at NDBC buoys 46014 (blue), 46013 (green), and 46042 (red). Chl-*a* at (d) KH and (e) BML. Individual 15-minute records are plotted as small blue dots. The larger green dots are the 25-hour average chl-*a* centered around the highest tide of each day, which captures the greatest continuous span of in-water coverage. (f–j) Same as Figures 2a–2e for 01 May to 31 July 2008 (except no mooring temperature in 2008).

co-vary. Especially intense waves did not necessarily mean the highest chl-*a* levels; for example despite energetic waves on 11 June 2007 (events c and j) chl-*a* peaks were relatively low compared to other events. Similarly, weak wave events were sometimes associated with relatively intense blooms.

4. Discussion

[9] Winds and waves stand out as the most likely drivers of phytoplankton variability in this system. While some chl-*a* events either co-occurred with or immediately followed a weakening or reversal of upwelling-favorable winds, there was a stronger correspondence between chl-*a* and waves. A majority of identified events coincided with elevated H_{sig}^2 events, while only 7 were associated with wind relaxation or weakening. Furthermore, five of these co-occurred with energetic waves, leaving only two events

associated with wind relaxation only. These results suggest that although upwelling and relaxation underwrite coastal phytoplankton growth, the building, peaking, and subsiding of nearshore chl-*a* often matches the building, peaking, and subsiding of nearshore wave energy. While we lack the necessary data to rule out influences from eddies, fronts and other convergent circulation patterns near the coast, to-date there is no evidence of these factors being important in this region (R. E. Fontana and J. L. Largier, personal communication, 2010). The lack of relationship to cold temperatures suggests that bloom events are not driven by pulses of upwelled nutrients. Further, we do not expect significant terrestrial nutrient input along this coast in May–June, where rainfall and stormwater is absent and groundwater flow and streamflow is very weak and mostly trapped within closed estuaries [Largier and Behrens, 2010].

[10] Wave transport is just one mechanism among many setting the stage for bloom events. However it is a mechanism that has been overlooked, and during the early upwelling season it appears to play a dominant role in setting the timing of 1.5- to 5-day chl-*a* intertidal events. The role of surface waves in promoting blooms has received little previous consideration. Although there have been previous studies of phytoplankton dynamics on sandy beaches [Campbell and Bate, 1997; McLachlan and Brown, 2006], to our knowledge this study is the first to report waves as a dominant forcing on reflective, rocky shorelines. How can surface swell events cause blooms? Wave resuspension could spur shelf-wide productivity via the introduction of benthic micro-nutrients [Chase *et al.*, 2007]. Or, wave erosion might inject benthic diatoms to the water column. However, benthic diatoms were not the dominant taxa observed during high or low chl-*a* periods in preliminary studies of the phytoplankton communities from these sites (K. J. Nielsen and A. Paquin, unpublished data). One possibility is that resuspended sediment dominates the signal, e.g., chl-*a* fluorescence measurements can be contaminated by stray light from co-located turbidity sensors [Omand *et al.*, 2009]. However, we avoided sensor interaction by measuring fluorescence only and, further, our check-samples show a close correspondence between fluorescence and chl-*a* ($R^2 = 0.78$), confirming that suspended sediments have little direct effect on our chl-*a* measurements. Finally, many wave events lacked a corresponding chl-*a* response, which would be unexpected if suspended sediment alone had dominated the fluorescence signal.

[11] We suggest instead that wave-driven mass transport, or onshore surface Stokes drift, may be an important mechanism. Onshore wave-driven transport creates a convergent flux in nearshore waters, and resulting “blooms” would represent an accumulation of plankton rather than in-situ reproductive growth in the local population. The onshore component of wave-driven volume transport is given by $Q_w = \frac{gH_{sig}^2}{c} \cos(\theta_w)$, where g is gravitational acceleration, H_{sig} is the significant wave height, c is the wave phase speed, and θ_w is the wave direction relative to onshore [Fewings *et al.*, 2008; Longuet-Higgins, 1953]. The coast angle is fairly similar at both sites, and accounting for slight variations in incident wave direction did not improve the relationship between chl-*a* peaks and wave peaks. Direct measurements of wave transport are rare, but detailed field studies combined with models have found cross-shelf velocity over the inner shelf to be strongly correlated with wave forcing, with mean values of 1 to 1.5 cm s^{-1} [Fewings *et al.*, 2008], and closer to 5 to 6 cm s^{-1} during higher waves [Lentz *et al.*, 2008; Garcez Faria *et al.*, 2000], although transport is weakened under high vertical mixing [Lentz *et al.*, 2008]. We consider wave transport offshore of the surf zone where water depth $>2H_{sig}$ [Lentz *et al.*, 2008], or roughly 8 to 10-m depth based on NDBC significant wave heights. At this depth waves have not yet steepened enough to break and we can neglect effects of rollers and breakers [Garcez Faria *et al.*, 2000], yet water is shallow enough to assume Q_w is roughly independent of wave period. Using a range of onshore transport $u \sim [0.02 \text{ to } 0.06] \text{ m s}^{-1}$ to characterize wave-driven surface transport offshore of the surf zone, we can characterize the onshore transport of chl-*a* and assess its accumulation rate at the coastal boundary. A simple 2-D model for the rate of increase of chl-*a* due to a con-

vergence of chl-*a* flux between the inner shelf and the shore is $\frac{\partial C}{\partial t} \cong -\frac{(Q_{coast} - Q_{outside})}{L}$ (shoreward positive in the x -direction), where C is chlorophyll-*a* concentration and Q is chlorophyll-*a* flux. Q_{coast} is the flux through the coastal boundary, equal to zero, $Q_{outside}$ is the chl-*a* flux over the inner-shelf region, outside the nearshore zone of interest, and the length scale L is the distance between this region and the coast. If inner-shelf chl-*a* prior to the initiation of a wave event is chl- $a_{outside}$, we can estimate the shoreward flux as $Q_{outside} = u \cdot C_{outside}$. Using $C_{outside} = 5 \mu\text{g L}^{-1}$, based on observed background, between-peak chl-*a* values, and using the u range given above, $Q_{outside}$ scales as approximately 0.1 to 0.3 $\mu\text{g L}^{-1} \text{ m s}^{-1}$. We assume L to be roughly 500 m, a conservative offshore distance over which breaking waves recede to linear wave conditions [Garcez Faria *et al.*, 2000]. From these scales we estimate the chl-*a* accumulation rate at the coastal boundary to be $[2 \text{ to } 6] \times 10^{-4} \mu\text{g L}^{-1} \text{ s}^{-1}$. Note that “bloom” rates would be twice as fast if the initial concentration were 10 $\mu\text{g L}^{-1}$. With these estimated accumulation rates, near-shore chl-*a* would take approximately 7 to 21 hours to increase from 5 to 20 $\mu\text{g L}^{-1}$. These estimates bracket well the chl-*a* increase rates observed at our sites: a representative time scale for a bloom event to rise from 5 to 20 $\mu\text{g L}^{-1}$ was about 14 to 22 hours (too short to be explained by reproductive growth of a resident population, given typical generation times of order a day). The agreement between scaled predictions and observations suggests that convergent onshore wave transport is indeed a plausible mechanism for near-coast blooms, and a consistent explanation for the fairly immediate (<1 day) chl-*a* response to rising H_{sig} . This rapid response may also explain why chl-*a* usually peaked early in a wave event rather than near its end: concentrations near the coast could quickly (in a time shorter than the duration of the swell event) build to levels high enough for an offshore mixing loss to balance the onshore wave-driven flux.

[12] Stokes drift is not unique to shallow waters, but is a ubiquitous feature of surface swell. It is the presence of the impermeable coastal boundary and the buoyancy of phytoplankton that causes the convergent flux and accumulation in this simple model. The coastal boundary requires that onshore and offshore mass transport must balance, yielding a mean vertical circulation (not unlike estuarine or frontal circulation). Buoyant phytoplankton “particles” are more likely to be in the near-surface waters that have a net onshore flow than in the offshore-tending deeper water, yielding the observed accumulation. Coastal phytoplankton are dominated by diatoms which are often seen close to the surface, and several taxa have been documented to have positive buoyancy during at least part of their growth cycle [Villareal, 1988, 1992; Acuña *et al.*, 2010]. However, phytoplankton buoyancy must be better understood before we can assess the effectiveness of the proposed mechanism. A number of wave events lacked corresponding intertidal blooms. This highlights the importance of better determining chl-*a* levels offshore of the near-coast zone (to properly quantify $Q_{outside}$) before calculating accumulation rates based on convergent wave transport, and reminds us that the dynamics determining phytoplankton levels on the shelf can be markedly de-coupled from dynamics at the shoreline.

[13] The proposed mechanism of convergent wave transport requires further study, but the connection between wave events and near-coast blooms has several implications that

challenge our understanding of coastal ecosystem variability. For example, we might predict the co-occurrence of blooms at sites separated by great distances, since swell events span immense scales along the coast. Our two study sites are ~150 km apart and, although not all events coincided between KH and BML, many did co-occur. A chi-square test rejected the null hypothesis that bloom events at the two sites are independent of each other ($\chi^2 = 7.09$, $df = 1$, $p < 0.0078$), which strongly suggests co-occurrence at the event-scale. Another important consideration is that different plankton taxa may respond differently to wave forcing, implying a changing response to the proposed mechanism as species assemblages shift in time. We speculate that the diminished relationship between waves and chl-*a* events in late summer may be caused by a seasonal shift in the buoyancy of the dominant species and thus in the ability of phytoplankton to respond to wave forcing. The role of buoyancy and species composition in setting the timing of interaction with transport mechanisms and blooms deserves further study.

[14] **Acknowledgments.** We thank N. Welschmeyer, M. Fewings, and S. Monismith for helpful conversation during the development of this paper. A. Miller and an anonymous reviewer kindly provided helpful reviews. Funding was provided by NSF grant OCE-0727611, CSU COAST, NOAA, and by the D&L Packard and the G&B Moore Foundations.

References

- Acuña, J. L., M. López-Alvarez, E. Nogueira, and F. González-Taboada (2010), Diatom flotation at the onset of the spring phytoplankton bloom: An *in situ* experiment, *Mar. Ecol. Prog. Ser.*, *400*, 115–125, doi:10.3354/meps08405.
- Campbell, E. E., and G. C. Bate (1997), Coastal features associated with diatom discoloration of surf zones, *Bot. Mar.*, *40*, 179–186, doi:10.1515/botm.1997.40.1-6.179.
- Chase, Z., P. G. Stratton, and B. Hales (2007), Iron links river runoff and shelf width to phytoplankton biomass along the U.S. West Coast, *Geophys. Res. Lett.*, *34*, L04607, doi:10.1029/2006GL028069.
- Fewings, M., S. J. Lentz, and J. Fredericks (2008), Observations of cross-shelf flow driven by cross-shelf winds on the inner continental shelf, *J. Phys. Oceanogr.*, *38*, 2358–2378, doi:10.1175/2008JPO3990.1.
- Garcez Faria, A. F., E. B. Thornton, T. C. Lippmann, and T. P. Stanton (2000), Undertow over a barred beach, *J. Geophys. Res.*, *105*, 16,999–17,010, doi:10.1029/2000JC900084.
- Kim, H.-J., A. J. Miller, J. McGowan, and M. L. Carter (2009), Coastal phytoplankton blooms in the Southern California Bight, *Prog. Oceanogr.*, *82*, 137–147, doi:10.1016/j.pocean.2009.05.002.
- Largier, J. L., and D. M. Behrens (2010), Hydrography of the Russian River Estuary, Summer–Fall 2009, report, 71 pp., Sonoma County Water Agency, Santa Rosa, Calif.
- Lentz, S. J., M. Fewings, P. Howd, J. Fredericks, and K. Hathaway (2008), Observations and a model of undertow over the inner continental shelf, *J. Phys. Oceanogr.*, *38*, 2341–2357, doi:10.1175/2008JPO3986.1.
- Longuet-Higgins, M. S. (1953), Mass transport in water waves, *Philos. Trans. R. Soc. London, Ser. A*, *245*, 535–581, doi:10.1098/rsta.1953.0006.
- McLachlan, A., and A. C. Brown (2006), *The Ecology of Sandy Shores*, 2nd ed., Academic, Amsterdam.
- Omand, M. M., F. Feddersen, D. B. Clark, P. J. S. Franks, J. J. Leichter, and R. T. Guza (2009), Influence of bubbles and sand on chlorophyll-*a* fluorescence measurements in the surfzone, *Limnol. Oceanogr. Methods*, *7*, 354–362.
- Rilov, G., S. E. Dudas, B. A. Menge, B. A. Grantham, J. Lubchenko, and D. R. Schiel (2008), The surf zone: A semi-permeable barrier to onshore recruitment of invertebrate larvae?, *J. Exp. Mar. Biol. Ecol.*, *361*, 59–74, doi:10.1016/j.jembe.2008.04.008.
- Roughan, M., A. J. Mace, J. L. Largier, S. G. Morgan, J. L. Fisher, and M. L. Carter (2005), Subsurface recirculation and larval retention in the lee of a small headland: A variation on the upwelling shadow theme, *J. Geophys. Res.*, *110*, C10027, doi:10.1029/2005JC002898.
- Ryan, J. P., J. F. R. Gower, S. A. King, W. P. Bissett, A. M. Fischer, R. M. Kudela, Z. Kolber, F. Mazzillo, E. V. Rienecker, and F. P. Chavez (2008), A coastal ocean extreme bloom incubator, *Geophys. Res. Lett.*, *35*, L12602, doi:10.1029/2008GL034081.
- Shanks, A. L., S. G. Morgan, J. MacMahan, and J. H. M. Reniers (2010), Surf zone physical and morphological regime as determinants of temporal and spatial variation in larval recruitment, *J. Exp. Mar. Biol. Ecol.*, *392*, 140–150, doi:10.1016/j.jembe.2010.04.018.
- Villareal, T. A. (1988), Positive buoyancy in the oceanic diatom *Rhizosolenia* *debyana* H. Peragallo, *Deep Sea Res., Part A*, *35*, 1037–1045, doi:10.1016/0198-0149(88)90075-1.
- Villareal, T. A. (1992), Buoyancy properties of the giant diatom *Ethmodiscus*, *J. Plankton Res.*, *14*, 459–463, doi:10.1093/plankt/14.3.459.
- Wieters, E. A., D. M. Kaplan, S. A. Navarrete, A. Sotomayor, J. Largier, K. J. Nielsen, and F. Véliz (2003), Alongshore and temporal variability in chlorophyll *a* concentration in Chilean nearshore waters, *Mar. Ecol. Prog. Ser.*, *249*, 93–105, doi:10.3354/meps249093.

J. L. Largier, Bodega Marine Laboratory, University of California, Davis, PO Box 247, Bodega Bay, CA 94923, USA.

E. E. McPhee-Shaw, Moss Landing Marine Laboratories, San Jose State University, 8272 Moss Landing Rd., Moss Landing, CA 95039, USA. (eshaw@mml.calstate.edu)

B. A. Menge, Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97331, USA.

K. J. Nielsen, Department of Biology, Sonoma State University, 1801 E. Cotati Ave., Rohnert Park, CA 94928, USA.