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Persistent Differences in Horizontal Gradients in Phytoplankton Concentration Maintained by Surf Zone Hydrodynamics

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Abstract Surf zones, regions of breaking waves, are at the interface between the shore and coastal ocean. Surf zone hydrodynamics may affect delivery of phytoplankton subsidies to the intertidal zone. Over a month of daily sampling at an intermediate surf zone with bathymetric rip currents and a reflective surf zone, we measured surf zone hydrodynamics and compared concentrations of coastal phytoplankton taxa in the surf zones to concentrations offshore. At the intermediate surf zone, ~80% of the variability in the concentration of coastal phytoplankton taxa within the surf zone was explained by their variation offshore; however, concentrations were much higher and lower than those offshore in samples from a bathymetric rip current and over the adjacent shoal, respectively. Hydrodynamics at this intermediate surf zone did not hinder the delivery of coastal phytoplankton to the surf zone, but the bathymetric rip current system appeared to redistribute

phytoplankton concentrating them within eddies. At the reflective shore, we sampled surf zones at a beach and two adjacent rocky intertidal sites. Concentrations of typical coastal phytoplankton taxa were usually an order of magnitude or more lower than those offshore, even when offshore samples were collected just 20 m beyond the breakers. The phytoplankton assemblages inside and outside the surf zone often appeared to be disconnected. Surf zone hydrodynamics at the steep, reflective shore coupled with low phytoplankton concentrations in near-surface water appeared to limit delivery of phytoplankton subsidies to the surf zone. Surf zone hydrodynamics may be a key factor in the alongshore variation in phytoplankton subsidies to coastal communities.

Keywords Dissipative · Reflective · Intermediate · Rip current · Benthic pelagic coupling · Beach morphodynamics

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Introduction

Surf zones, defined as regions of breaking waves, are at the interface between the shore and coastal ocean. They occur in a wide variety of forms with different hydrodynamics as determined by the interaction of breaking waves with variation in coastal morphology (Lippmann and Holman 1990; McLachlan and Brown 2006; Wright and Short 1984). Subsidies of food (phytoplankton and detritus) and larval settlers from the coastal ocean sustain intertidal communities. Intertidal organisms live within surf zones, and surf zone hydrodynamics may affect the delivery of subsidies (Morgan et al. 2016; Rilov et al. 2008; Shanks et al. 2016, 2010, 2017b, which, in turn, may affect the structure of intertidal communities. Here, we investigate the effect of variable surf zone hydrodynamics on the delivery of phytoplankton subsidies from the coastal ocean by comparing the concentration of

coastal phytoplankton within a more dissipative and reflective surf zone to the concentrations of these taxa on the inner shelf.

Beach morphodynamic systems range from dissipative to reflective (Wright and Short 1984; McLachlan and Brown 2006). A wide surf zone including alongshore bars and troughs, and a wide gradually sloping shore, which, if the shore is a beach, consists of fine-grain sand, characterizes more dissipative surf zones. Alongshore variable bars often characterize these surf zones with shallow shoals separating deeper bathymetric rip channels. Within these surf zones, breaking waves and changes in pressure gradients as waves cross the surf zone induce aperiodic pulses that eject material from the surf zone via rip currents within the bathymetric rip channels (Bowen 1969a, b). The momentum that drives the offshore jets results in a corresponding mass balance of water back into the surf zone over the shoals (Brown et al. 2015; Reniers et al. 2010); this system of currents generates eddies in the surf (Fig. 1).

More reflective surf zones are characterized by narrow surf zones (often characterized as swash zones), steep slopes, and if the shore is a beach, coarse-grain sand (McLachlan and Brown 2006; Wright 1995). Here, *more* is used because a purely reflective shore would be a vertical wall. Beach slope determines which wave frequencies are reflected within the surf zone, with increased reflection at steeper slopes; a vertical wall reflects waves at all periods, whereas a steep shore will reflect long-period and dissipate short-period waves. Rocky shores are usually steep and, hence, more reflective shores; however, rocky shores associated with more dissipative surf zones are not uncommon. It is hypothesized that at reflective surf zones, the steepness of the shore limits the width of the surf zone inhibiting the formation of bathymetric rip currents. On topographically complex shores, alongshore variability in topography can contribute to the formation of rip currents. In this sort of topographic setting, where alongshore currents within a surf zone encounter an obstruction (e.g., breakwaters, groynes, points), they are turned seaward forming a rip (Castelle and Coco 2013). Transient rips are also present within reflective surf zones where they appear as transient turbulent eddies (Hally-Rosendahl et al. 2014; Suanda and Feddersen 2015). Often the latter, two types of rip currents are intermittent, forming only under the appropriate hydrodynamic conditions.

We investigated how surf zone hydrodynamics at an intermediate and a more reflective shore affected the ingress of coastal phytoplankton taxa into the surf zone from the inner shelf. We hypothesized that the hydrodynamics at intermediate beaches due to the relatively rapid exchange of water between the inner shelf and surf zone by bathymetric rip currents would lead to a tight linkage between the assemblage of phytoplankton on the inner shelf and in the surf zone. In contrast, we hypothesized that hydrodynamics of more reflective surf zones, due to the absence or rarity of bathymetric rip currents,

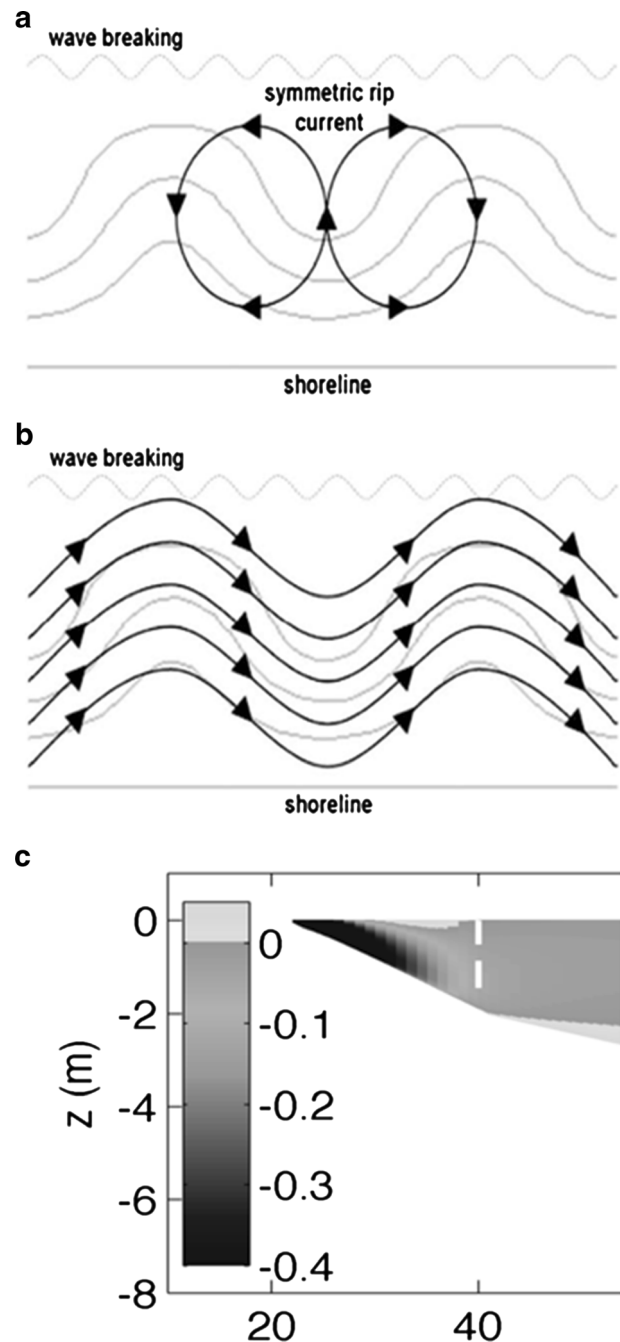


Fig. 1 Schematic diagrams of flow at **a** a dissipative surf zone with wave crests parallel to shore generating bathymetric rip currents within the surf zone. *Arrows* indicate the eddy generated by the rip current flow system. **b** A dissipative surf zone with wave crests at an angle to the shore, generating an alongshore current within the surf zone and suppressing the formation of bathymetric rip currents. **c** Mean modeled cross-shore Eulerian flow (positive onshore) at a beach similar to CRSB using a 1D profile model (Reniers et al. 2004) that included Stokes drift. The cross-shore flow is driven by normally incident waves. The *vertical dashed line* indicates the other edge of the surf zone, where waves start breaking. The undertow generated by the breaking waves within the surf zone is clearly visible (negative values) as is onshore flow near the surface at the outer edge of the surf zone (positive values at the surface). The near-bed streaming is visible as positive values near the *bottom* extending across the model domain. Figure redrawn from Shanks et al. (2015a, b)

limit exchange of surf zone with offshore water and this, in turn, would limit benthic/pelagic coupling of the intertidal zone with the coastal ocean (Shanks et al. 2010).

We tested these hypotheses by extensive daily biological and physical oceanographic sampling of an intermediate (Sand City, California) and reflective (Carmel River State Beach, California) surf zone and the waters just seaward (<200 m) of the surf zones. We compare results of phytoplankton sampling at these two different surf zones. Surf zone diatom taxa, diatom taxa adapted to life in surf zones (Garver 1979; Talbot and Bate 1987a), were absent or very rare in the samples. The only surf zone specialist observed during the study (*Asterionellopsis* spp.) was only present in Sand City samples where it made up only a small percentage (<1%) of the total phytoplankton present in surf zone. The study focuses on the concentration of typical coastal phytoplankton taxa in the surf zone (e.g., *Pseudo-nitzschia* spp., non-surf zone taxa of *Chaetoceros* spp.), subsidies from the coastal ocean to the shore.

Site Descriptions

We extensively sampled the hydrodynamics and biology of two sample sites, Sand City, a more dissipative surf zone, and Carmel River State Beach (CRSB), a reflective surf zone. The physical oceanographic and biological results from this work have appeared in several publications (Brown 2014; Brown et al. 2015; MacMahan et al. 2009, 2006; Morgan et al. 2016; Reniers et al. 2009, 2010; Shanks et al. 2016, 2014, 2015b). In this section, we summarize the physical oceanographic field experiments as background for the work presented in this paper, comparisons of the phytoplankton communities in and adjacent to these two surf zones.

Intermediate Surf Zone: Sand City, California

In June and July 2010, we conducted an extensive field experiment on the hydrodynamics and biology of the surf zone and the inner shelf on a rip-channeled beach at Sand City (36.615760° N, 121.85485° W) at the southern end of Monterey Bay, California. Bathymetry surveys were performed with a GPS-equipped personal watercraft (MacMahan et al. 2001). Offshore waves were measured with an upward-looking acoustic Doppler current profiler (ADCP) deployed in ~11 m water depth, which measured co-located pressure and velocity data (Fig. 2). Hourly root-mean-square (rms) wave height, H_{rms} , in the sea-swell frequency band ($0.04 < f < 0.25$ Hz) was computed by transforming the measured pressure spectrum to sea surface elevation using linear wave theory (Guza and Thornton 1980). Long-term shoreline orientation, Monterey Bay headlands, and the Monterey Canyon result in nearly normally incident waves resulting in persistent rip channels throughout most of the year (Thornton

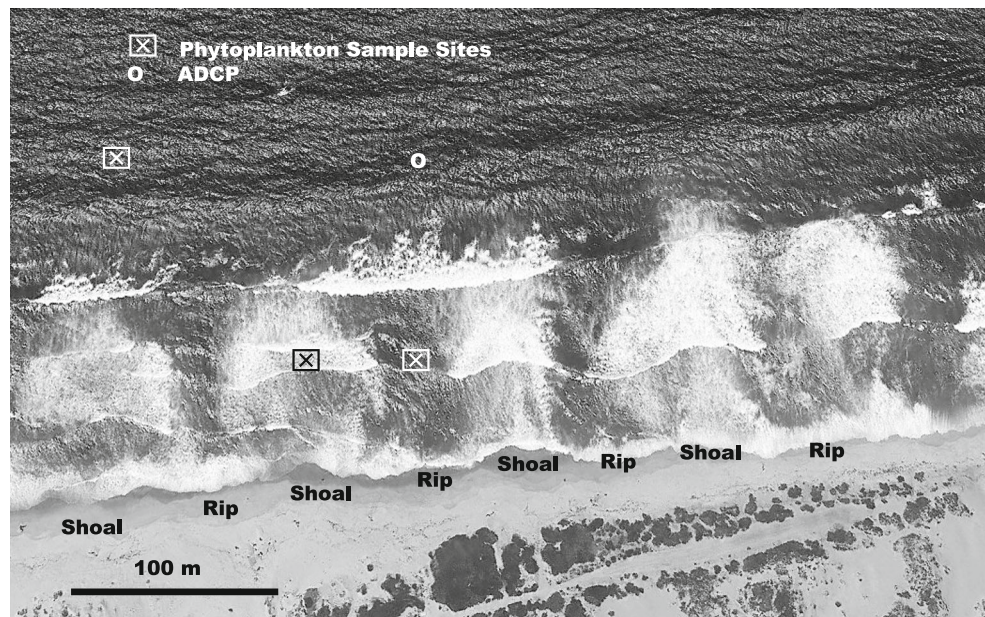
et al. 2007); rip currents were present throughout this experiment. Winds and tides were obtained from the NOAA Monterey tidal station. Surf zone hydrodynamics and cross-shore exchange at this site have been well described (Brown et al. 2015; Fujimura 2015; MacMahan et al. 2005, 2010b; Reniers et al. 2009, 2010).

The surf zone at the Sand City study site is an intermediate rip-channeled beach (MacMahan et al. 2005). The beach is characterized by repeating cusps at the edge of the surf, and within the surf zone, there are alternating bathymetric rip currents associated with deeper channels separated by shallower shoals (Fig. 1). The foreshore is relatively steep (1/10 slope) with straight and parallel contours, flattening inshore (1/100 slope), with quasi-periodic, O (125 m), incised rip channels and continuing with a 1/20 offshore slope and straight and parallel contours seaward of the breaker zone (MacMahan et al. 2005) (Figs. 2 and 4). Feeder channels near the shoreline converge with the incised rip channels. Drifter studies indicated that wave-driven flow over the shoals was landward, and these waters fed into channels at the edge of the surf zone and, from there, into the rip channels where the rip current flowed offshore (Brown et al. 2015; MacMahan et al. 2010a, b; Reniers et al. 2009). Water in rip currents jetted offshore and past the breaker line where it mixed with water on the inner shelf before returning to the surf zone over the shoals (Brown et al. 2015). Hence, the rip current system generated eddies that extended from about 100 m seaward of the breaker line back into and across the surf zone (Fig. 1) (MacMahan et al. 2010a). On average, around 20% of surface drifters released in the surf zone were expelled per hour, but most of these were ultimately returned to the surf zone by the onshore flow over the shoals (MacMahan et al. 2010a, b; Reniers et al. 2009). Surface drifters that returned to the surf zone generally became concentrated within the core of the eddy generated by the rip current system (MacMahan et al. 2010a, b; Brown et al. 2015; Reniers et al. 2010). Thus, the rip current system effectively exchanged water in the surf zone with water seaward of the surf zone while, at the same time, generally retaining and concentrating buoyant drifters (Brown et al. 2015; Reniers et al. 2009).

Reflective Surf Zone: Carmel River State Beach, California

In June and July 2011, we investigated nearshore processes contributing to mass transport and cross-shore exchange on a steep, highly reflective beach at Carmel River State Beach (36.53789° N, 121.928886° W, CRSB). Rocky intertidal zones flank the northern and southern ends of this crescent-shaped pocket beach (Fig. 3). The morphology and hydrodynamics of the study site have previously been described (Shanks et al. 2015a) and are summarized here.

Fig. 2 Study site at Sand City, California. The surf zone is intermediate characterized by rip currents with deep channels separated by shallow shoals (location of rips and shoals are indicated). Phytoplankton samples were collected in the surf zone at the bathymetric rip current and shoals labeled with an *X*. Offshore phytoplankton samples were collected just outside the surf zone at the offshore site indicated with an *X*. The *open circle* indicates the location of the ADCP used to measure waves. Image modified from a Google Earth photograph



The beach profile consists of a 1:8 subaerial beach slope, 1:3 subaqueous beach step, and 1:19 subaqueous beach profile (Fig. 4). Offshore waves and currents were measured with a cross-shore array of four bottom-mounted, upward-looking ADCPs and pressure sensors (Fig. 3), sampled at 1 Hz. At the ADCP mooring 125 m offshore, there were Conductivity, Temperature and Depths (CTDs) mounted at 3 and 10 m depth, which recorded temperature and salinity also at 1 Hz. To observe the vertical structure of the cross-shore and alongshore currents associated with the surf zone, a vertical array of six electromagnetic current meters (EMCMs) spaced at 0.2-m intervals was deployed in 0.4 m water relative to mean sea level (MSL), and they sampled at 16 Hz for 5 days (yeardays 169 to 173). Hourly, depth-averaged currents were computed from the ADCPs and EMCM array measurements to evaluate the mean currents inside and outside the surf zone. Depending on tidal elevation and wave energy, the EMCMs were located inside and outside the region of active wave breaking. A local wave breaking criterion of $H_{rms}/h \geq 0.42$ (Thornton and Guza 1982) was used to determine when the EMCMs were inside the surf zone, which was typically during low tides. Throughout the experiment, waves approached the site obliquely from the northwest, resulting in a predominantly southerly alongshore current within the surf zone (Fujimura et al. 2013).

There were no subaqueous bars, terraces, or periodic, smaller-scale alongshore features to induce 2D horizontal flow, such as bathymetric rip currents, that could contribute to the exchange of surf zone with offshore water, at more dissipative surf zones; however, transient rip currents were likely present and contributed to the movement of dye out of the surf zone. There were two routes whereby water and material from the inner shelf entered the surf

zone: (1) nearshore water entered the surf zone at the northern end of the beach via an alongshore current within the surf zone and (2) surface water was exchanged by diffusion due to turbulence from breaking waves. There is a large-scale curvature to the shoreline, which supported an alongshore current that typically flowed south while decreasing in magnitude. Offshore flux from the surf zone at the southern end of the beach compensated for slowing of the alongshore current. To conserve mass, there is a hypothesized onshore flux into the surf zone at the northern end of the beach. The onshore flow that initiates the alongshore current was just north of the study domain; hence, we do not have measurements from within this flow. This onshore flux appeared to be associated with wave breaking on the northern rocks, which likely drove near-surface onshore flow. The bubble streak that extends from the rocks to the shoreline in Fig. 3 is likely associated with this flow. As water within the alongshore current flowed downstream in the surf zone, the amount of coastal phytoplankton present within the alongshore flow should vary with the rate at which water within the surf zone is exchanged with offshore water and, given the results from the dye study, this exchange should vary with the speed of the wave-driven alongshore flow. At this reflective shore with a very narrow surf zone (Shanks et al. 2015a, b), flow was offshore throughout most of the water column (undertow) and landward near the surface due to breaking waves, but this current regime was only present within the surf zone (Fig. 1). Dye studies and daily observations indicated that bathymetric rip currents were not present; however, transient rips may have been present but were brief enough that they were not observed. The large-

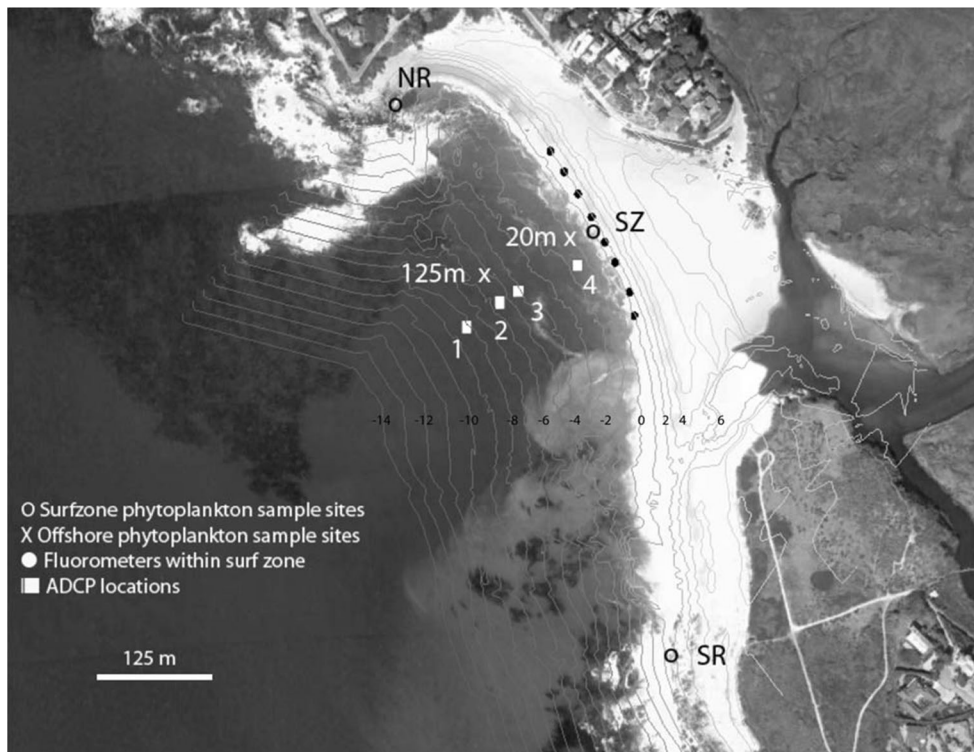
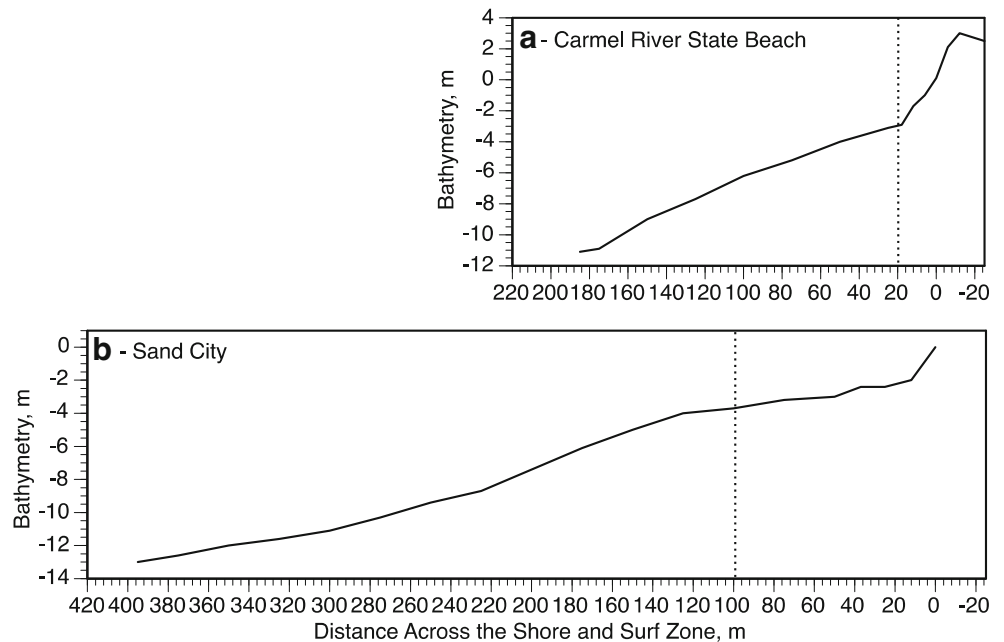


Fig. 3 Carmel River State Beach, California. Phytoplankton samples were collected within the sandy beach surf zone (*O* labeled SZ), 20 and 125 m seaward of the surf zone (*X*s labeled 20 and 125 m) and within the surf zone adjacent to the rocks north and south of the beach (*O*s labeled NR and SR). The *squares* indicate the locations of the ADCP moorings. ADCPs at 1–3 measured currents, and that at 4 measured waves. Also located at 4 were CTDs positioned at 10 and 3 m depth. An EMCM was

located close to the pump intake within the surf zone (near the *O* labeled SZ). The *black circles* indicate locations of fluorometers within the surf zone used during dye studies (Brown et al., in revision). The *white arrow* at the northern edge of the beach indicates the bubble streaks associated with onshore flow that feeds into an alongshore current within the surf zone. *Contour lines* are in meters measured from MLW. Modified from a Google Earth image

Fig. 4 Contour plots of bathymetry at **a** Carmel River State Beach and **b** Sand City. The *vertical dotted lines* indicate the approximate location of the outer edge of the breakers, and 0 distance is the approximate edge of the beach. Figures redrawn from Fujimura et al. (2013)



scale circulation and water exchange of this surf zone depend on local topography, variable bathymetry, and wave breaking characteristics of the impinging wave field.

Methods

Phytoplankton Sampling and Analysis

Intermediate Surf Zone: Sand City, California

We sampled phytoplankton at the intermediate surf zone daily from 15 June to 15 July 2010. We collected samples within the surf zone at low tide when it was safer to put a swimmer in the water to collect samples and, from a boat, about 50 m seaward of the breaker line (water depth ~4.5 m, Irrabarren no. ~1.6 with an average surf zone width of 90 m) in the morning before the sea breeze strengthened, making work from a small boat difficult. Initial sampling within the surf zone was limited to samples collected within a bathymetric rip current, but we later sampled daily (6 to 15 July) over the shoal just south of this rip current (Fig. 2). We assumed that turbulence mixed phytoplankton vertically within the surf zone. Within the surf zone, swimmers collected three replicate 1-L water samples from ~1 m depth within the rip and over the shoals. On July 13, 14, and 15, the rip channel and shoal waters were sampled hourly from morning low tide to the next high tide. Offshore samples were collected a bit south of the sampled shoal and rip current (Fig. 2). Offshore, the phytoplankton may have been stratified vertically. Here, we sampled the entire water column by hauling a 25- μm -mesh plankton net from the bottom to the surface. We took three replicate tows, which filtered approximately 400 L of water. To describe the vertical structure of the water column at the offshore sample site during the time series, we used a CTD to sample temperature and salinity vs. depth. Phytoplankton samples were preserved in acidic Lugol's solution. In the laboratory, phytoplankton samples were concentrated on a 25- μm -mesh sieve and cells were identified to genus and counted on Sedgwick Rafter slides (Sournia 1978). Nearly all of the phytoplankters in the surf zone were coastal taxa, typical surf zone diatom taxa were rare making up <1% of the surf zone phytoplankton community, and coastal phytoplankton taxa are the focus of this study.

If surf zone hydrodynamics does not limit the delivery of coastal phytoplankton to the surf zone, we hypothesized that concentrations of coastal phytoplankton taxa in the surf zone and on the inner shelf would be the same. To test this hypothesis, we calculated correlation coefficients between the log-transformed concentrations of phytoplankton in the two habitats. In addition, we calculated the correlation coefficients from regressions of wave height (independent variable) and the concentration of phytoplankton in the surf zone (dependent variable).

In order to compare concentrations in the surf zone as a whole to offshore, we first estimated the total abundance of phytoplankton within the surf zone, e.g., the abundance in the sampled rip channel plus that over the shoal, before making comparisons with the abundance offshore. The width of the surf zone was determined from historical Google Earth images of the Sand City surf zone. The bathymetry of the rip and shoal was taken from data reported in Fujimura et al. (2014). The alongshore extent (width) of the rip and shoal portions of the surf zone were taken from data presented in three papers (Brown et al. 2015; Fujimura et al. 2014; Reniers et al. 2010) and from measurements taken from historical Google Earth images. The cross-sectional shape of the surf zone was assumed to be a right triangle fitting the observed bathymetry out to the width of the surf zone. This area was multiplied by the width of rip and shoal as measured from the papers and Google Earth images. The volume of water in each section of the surf zone was multiplied by the respective daily average concentrations of phytoplankton (all cells) in those habitats, and values were summed; this provided estimates of the total abundance of phytoplankton in the surf zone. This estimate of total abundance of phytoplankton in the sampled section of surf zone sampled (e.g., the total abundance within the sampled bathymetric rip current and adjacent shoal) was regressed against the abundance of phytoplankton in an equal volume of water offshore. This calculation is sensitive to the assumed configuration of each habitat; hence, we used a range of values to estimate the surf zone abundance of phytoplankton.

Surf zone diatoms produce mucus, which trap bubbles forming foam. The foam is trapped in the rip current eddy system concentrating and maintaining the cells in the surf zone (Garver and Lewin 1981; Talbot and Bate 1987a, b). We determined whether phytoplankton was present and concentrated in foam. Tethered swimmers, by scooping foam into a jar, sampled foam within the surf zone. A small amount of water beneath the foam was also sampled, and we did not separate this water from the sample. Foam samples were allowed to collapse back into water and were processed like the other phytoplankton samples. Concentrations of phytoplankton in foam samples (no./L) were compared to concentrations in the water column collected in the rip current and offshore and regressed (dependent variable) against wave height (independent variable).

Reflective Surf Zone: Carmel River State Beach, California

Phytoplankton samples were collected daily from 6 June through 15 July 2011. Surf zone samples were collected at the sandy beach and two rocky intertidal sites at either end of the beach (Fig. 3). We sampled phytoplankton 125 m from shore (10 m water depth), and during the last 18 days (starting 28 June) of the time series, we also sampled within 20 m of shore (3 m water depth), about 5 to 10 m outside the breaker

line (Irrabarren no. ~ 1.5) (Fig. 3). At the sandy beach surf zone site, phytoplankton was collected with a pump system. A 6-cm-dia. hose was attached to pipes that were jetted into the sand; the hose extended into the surf zone. A gas-powered pump sampled about 240 L of water per min, and three replicate 1-L phytoplankton samples were collected within 1 h of high tide each day. Depending on wave height, samples were collected within the breakers or just a few meters seaward. At the two rocky intertidal sites, three replicate 1-L samples were collected around low tide with a well bailer that was cast into the surf with a fishing pole. Well bailers are designed to sample water from a well. The well bailer consisted of a plastic cylinder with a stopper and a small hole at one end to let air out of the cylinder and a ball valve at the other end. When filling, the ball valve opens allowing water to enter, but when the tube is full, the valve closes. At the two offshore sites, three replicate 1-L phytoplankton samples were collected from a kayak in the morning when winds were light. Samples were collected approximately in the middle of the water column at the 20 and 125 m station (~ 1.5 and 5 m depth, respectively). The stainless steel well bailer was lowered on a line to depth. A second line was used to open a spring-loaded valve. The valve was held open several seconds until the bailer was filled. Phytoplankton samples were preserved and processed following the methods described above for the Sand City experiment. Temperature and salinity data from the CTDs associated with the ADCP at 125 m offshore were used to describe the vertical structure of the water column.

Starting on 27 June, we had access to an in situ fluorometer used to measure vertical profiles of chlorophyll *a* (Chl *a*). Vertical profiles of Chl *a* concentration were made daily at the same time and stations as the sampling for phytoplankton cells. We also attempted to collect data with the fluorometer within the surf zone, but the signal was contaminated with suspended sand and bubbles; the data were unusable. From these profiles, we calculated the average water column concentration of Chl *a*, the concentration of Chl *a* at the sample depth at which phytoplankton cell samples were taken, and the Chl *a* concentration near the surface (<0.5 m depth; on some dates, there were no data from this shallow). Using a *t* test, we compared the average concentration of Chl *a* at the 125- and 20-m offshore stations, the average concentration at each station to the concentration at the sample depth at which phytoplankton cells were sampled at that station, and the average concentration within the water column at the 20-m offshore station to the concentration in the near-surface waters. We calculated the correlation coefficient for the relationship between the Chl *a* concentration in the near-surface waters at the 20-m station with the concentration of phytoplankton cells (all cells) in the beach surf zone.

We compared the concentration of phytoplankton from samples collected by the different methods. These phytoplankton samples were preserved and processed as described

above for Sand City. We found no significant difference in the concentration of phytoplankton in pump samples and those collected by hand by submerging and filling a jar in the surf zone (paired *t* test, $t = 0.597$, $df = 5$, $P > 0.5$), nor did we find significant differences in the concentration of phytoplankton as determined from the jar samples and those collected by the two different types of well bailers (jar vs. stainless steel (SS) well bailer, $t = 0.422$, $n = 5$, $P = 0.684$; jar vs. plastic well bailer, $t = 0.928$, $n = 5$, $P = 0.380$; plastic vs. SS well bailer, $t = 0.259$, $n = 5$, $P = 0.802$).

We tested whether surf zone hydrodynamics limits ingress of coastal phytoplankton into the surf zone. If water is freely exchanged between the surf zone and inner shelf, concentrations of phytoplankton in the two habitats should be similar and significantly correlated. We present data on the total phytoplankton abundance and the two most abundant offshore taxa, *Pseudo-nitzschia* spp. and *Chaetoceros* spp. We calculated percentages of phytoplankton at each of the surf zone sites relative to samples collected 125 and 20 m offshore.

We investigated whether the concentration of offshore phytoplankton within the surf zone varied with the speed of the wave-driven alongshore flow. We hypothesized that when the alongshore current was slower during periods of smaller waves, there would be more time for the exchange of surf zone water with offshore water, leading to higher concentrations of phytoplankton at the Beach site relative to the North Rocks site. We calculated the relative abundance of phytoplankton (total cells) at the Beach sample site relative to that at the North Rocks site (North Rocks concentration/Beach concentration), and this metric (dependent variables) was regressed against wave height (independent variable).

Results

Intermediate Surf Zone: Sand City, California

At the offshore sample site, there was little variation in salinity through the water column; during the nearly month of daily samples, salinity varied from about 33 to 34 (Fig. 5). Temperature was more variable, 11 to 15 °C, and, given the small variation in salinity, was the principal cause for variation in vertical structure. The maximum difference in temperature through the water column, about 3 °C, occurred around day 185. On most days, the temperature difference through the water column was ~ 1 °C or less.

Concentrations of coastal phytoplankton in rip current samples were significantly correlated with concentrations in offshore samples (Fig. 6). Concentrations in rip samples were, however, higher, often by a factor of 10, than offshore. Concentrations in shoal samples were also correlated with concentrations offshore, but concentrations were much lower than those from offshore and the rip current; concentrations were

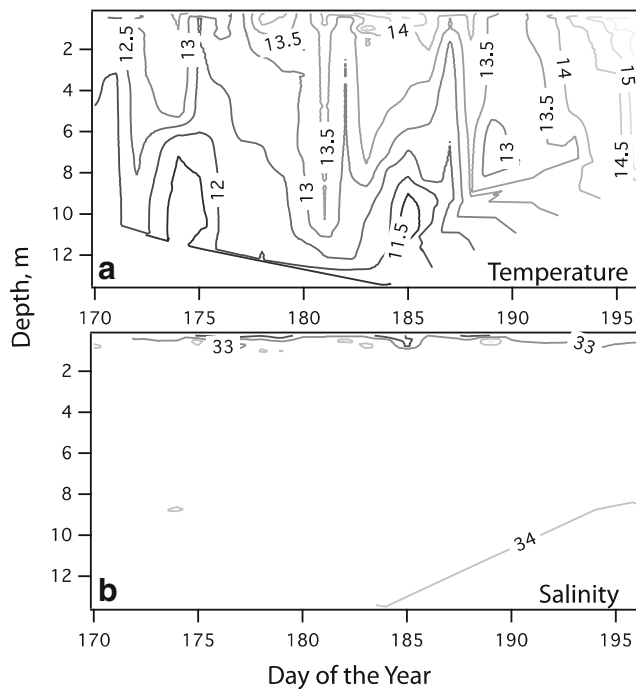


Fig. 5 Time series of contours of constant **a** temperature and **b** salinity. Data collected with a CTD just seaward of the Sand City, California, surf zone

~100 and 1000 times lower, respectively (Fig. 6). Concentrations in and out of the surf zone of *Asterionellopsis* spp., the only surf zone diatom taxon present, were not correlated. *Asterionellopsis* spp. was not common, accounting for <1%, on average, of the phytoplankton present in the surf zone.

Our sampling was at low tide, and this could have biased our observations, so we sampled phytoplankton hourly from low tide to high tide on 3 days. As the tide rose, there was essentially no change in the concentrations of phytoplankton in the rip current and over the shoals (see [Supplemental Data](#)).

Phytoplankton concentrations were significantly related to wave height (Fig. 7). Concentrations tended to peak between 0.5 and 1 m wave heights. The limited sampling over the shoals occurred when the wave height varied from 0.2 to 0.6 m, but over this range, concentrations in shoal waters exhibited a similar relationship to wave height as in rip currents.

Foam was present in rip currents but tended to be absent over the shoals. Phytoplankton was present in all foam samples with concentrations that varied by orders of magnitude from a high concentration of $>10^8$ cells/L to concentrations not different from those within the rip current (Fig. 8). These concentrations are likely underestimates of the true concentration in the foam as we invariably collected at least some water along with the foam, and it was not possible to separate the water from the foam in the field. There were no significant correlations between concentrations of phytoplankton in the

foam samples and those in the rip current and offshore. The concentration of phytoplankton within the foam samples was correlated to wave height (Fig. 9); concentrations tended to be higher when waves were smaller.

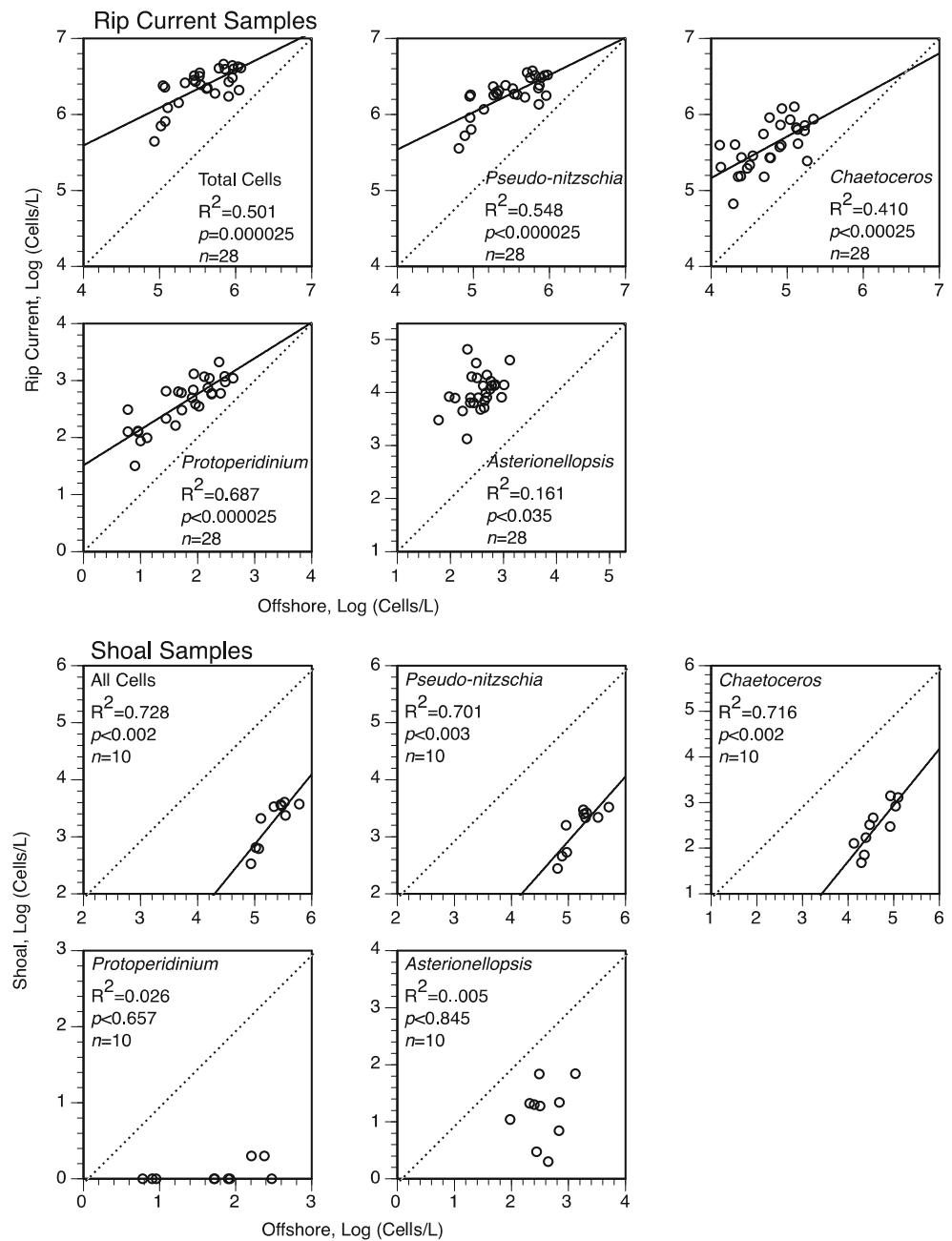
The very high concentrations of phytoplankton in rip currents suggest that phytoplankton abundance may be higher in the surf zone than offshore. Alternatively, currents in the surf zone may have redistributed phytoplankton such that concentrations were high in the rip and low over the shoals, but the overall abundance in the surf zone was similar to offshore. In the Google Earth images of the Sand City surf zone, surf zone width ranged from 47 to 119 m (ave. = 77 m, SD = 38 m, $n = 7$). For the calculations, we used surf zone widths of 50 and 100 m. Our estimate of overall abundance of phytoplankton in the surf zone was strongly correlated to the offshore abundance (Fig. 10) with >80% of the variability in surf zone phytoplankton abundance explained by that in the offshore waters. The estimated surf zone abundance was higher than that offshore. Surf zone abundance ranged from 1.3 to 4.3 times the abundance offshore (ave. = 2.5, SD = 4.3, $n = 10$). These significant correlations and those in Fig. 6 all indicate that the abundance of phytoplankton in the intermediate dissipative surf zone at Sand City varied directly with the abundance of phytoplankton on the inner shelf.

Reflective Surf Zone: Carmel River State Beach, California

At the mooring 125 m offshore, temperature ranged from about 13 to 9.5 °C (Fig. 11). There were three periods of maximum and minimum temperatures during the time series (around days 174, 181, and 190 and days 170, 178, and 184, respectively). The periods of warmer (cooler) temperatures were associated with downwelling (upwelling) favorable winds (Shanks et al. 2014). Bottom salinity remained a bit above 33.5 until day 188; after which, salinity tended to be below 33.5 (Fig. 11). Around days 181 and 194, there were sharp drops in salinity (33.5 decreasing to 31) at the bottom sensor. These events lasted several hours. Surface salinity was more variable (Fig. 11). Between days 170 and 186, salinity at the surface ranged from 32.5 to 33.5. After day 186, surface salinity declined with a daily salinity range from 32 to 32.5.

Concentrations of the enumerated offshore phytoplankton taxa (six taxa) at 125 and 20 m offshore were correlated with each other with R^2 ranging from 0.67 to 0.59 ($P < 0.0002$, $n = 27$ in all cases). The average concentration of Chl *a* tended to be lower at the more inshore station, but the difference was not significant ($t = 1.7$, $P = 0.098$, $n = 17$). Cell concentrations offshore steadily increased by 1 to 2 orders of magnitude over the time series with several pulses in abundance (Shanks et al. 2014). The rapid onset and short duration of pulses indicated they were due to advection, likely upwelling relaxation events, rather than in situ phytoplankton growth (Shanks

Fig. 6 Log of the concentrations of phytoplankton (all cells; the most abundant taxa, e.g., *Pseudo-nitzschia* and *Chaetoceros*; all dinoflagellates; and the only surf zone diatom, *Asterionellopsis*) collected offshore plotted against the log of the concentrations in the bathymetric rip current (*upper set of graphs*) and over the shoal adjacent to the rip current (*lower set of graphs*) at Sand City, California. The *dotted lines* indicate one-to-one relationships between phytoplankton concentrations. The *solid lines* and statistical results indicate significant regressions between the variables. Where *solid lines* are absent, the regressions were not significant. Significance levels were modified with a Holm-Bonferroni correction



et al. 2014). Chl *a* concentrations offshore at the depths at which the phytoplankton cell samples were collected were not significantly different from the average concentrations of Chl *a* throughout the water column at each of these stations (125 m offshore, $t = -0.298$, $P = 0.767$, $n = 17$; 20 m offshore, $t = 0.61$, $P = 0.546$, $n = 17$), suggesting that the samples collected with the well bailers at mid depth of these shallow water columns adequately represented concentrations through the water column.

Concentrations within the Beach surf zone of offshore phytoplankton taxa were correlated with concentrations at the 125- and 20-m stations (all phytoplankton and two abundant representative taxa are presented in Figs. 12 and 13).

Concentrations of offshore taxa in the surf zones at the rocks north and south of the Beach site were not correlated with concentrations at 125 or 20 m offshore (Figs. 12 and 13). Concentrations of coastal phytoplankton taxa within all of the sampled surf zones were, however, 1 to 2 orders of magnitude lower than farther offshore (Figs. 12 and 13). Concentrations in the surf zone tended to be highest at the Beach and South Rocks sites and much lower at the North Rocks site. The low concentrations of coastal phytoplankton taxa in the surf zone were further indicated by the median percentages of offshore taxa at surf zone sites relative to offshore (e.g., offshore/surf zone concentrations). The median percentage of offshore taxa in the surf zone relative to the

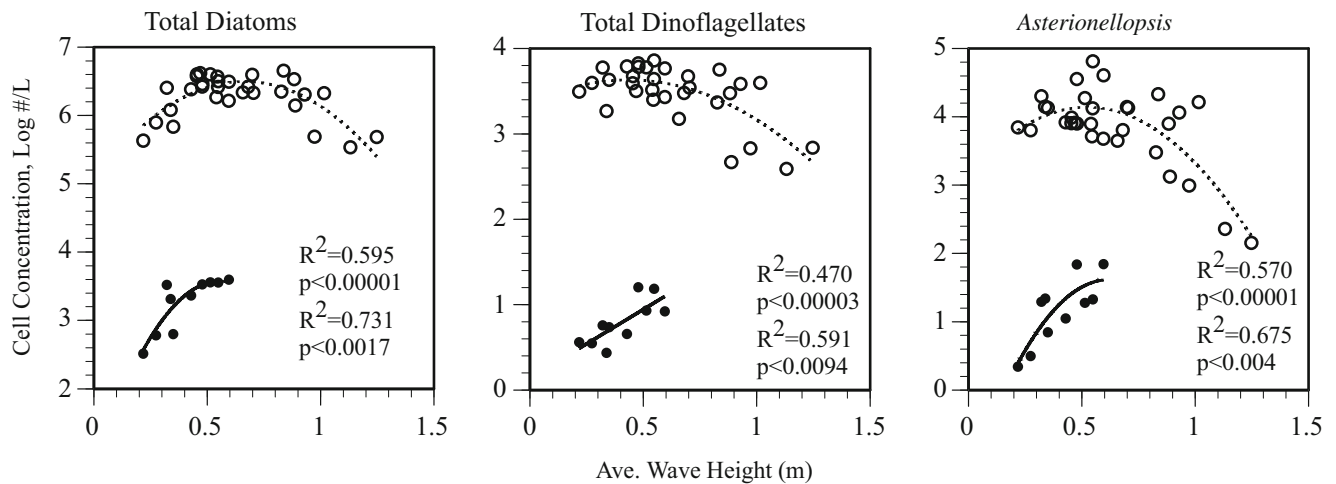


Fig. 7 Average wave height plotted against the log concentration of phytoplankton (total diatoms, total dinoflagellates, and *Asterionellopsis*) in rip currents (*open circles*) and over shoals separating the rip currents (*filled circles*) in the surf zone at Sand City. *Dotted lines* indicate

significant nonlinear regression between the variables. The results of the regressions are presented in each figure. Upper and lower values are for the rip current and shoal data, respectively. Significance levels were modified with a Holm-Bonferroni correction

125 and 20-m sites ranged from 16% (Beach) to 1% (North Rocks) and from 32% (Beach) to 4% (North Rocks), respectively. The abundance of coastal phytoplankton within the surf zones was consistently much lower than that in the offshore waters, even waters just tens of meters outside the breakers.

Concentrations of Chl *a* near the surface measured with the fluorometer at the most inshore station were significantly lower than those at the depth at which the phytoplankton samples were collected or the average concentration through the water column at this station (surface vs. sample depth, $t = 2.99$, $P = 0.006$, $n = 15$; surface vs. ave. concentration, $t = 2.98$, $P = 0.006$, $n = 15$). The concentration of Chl *a* near the surface was only 28% of the average concentration through the water column at the nearshore station. The Chl *a* concentration near the surface was significantly correlated to the log of the concentration of phytoplankton cells (all cells) in the beach surf zone ($R^2 = 0.404$, $n = 15$, $P < 0.0101$). Similar correlations using the average Chl *a* concentration from the water column and from the sample depth were not significant.

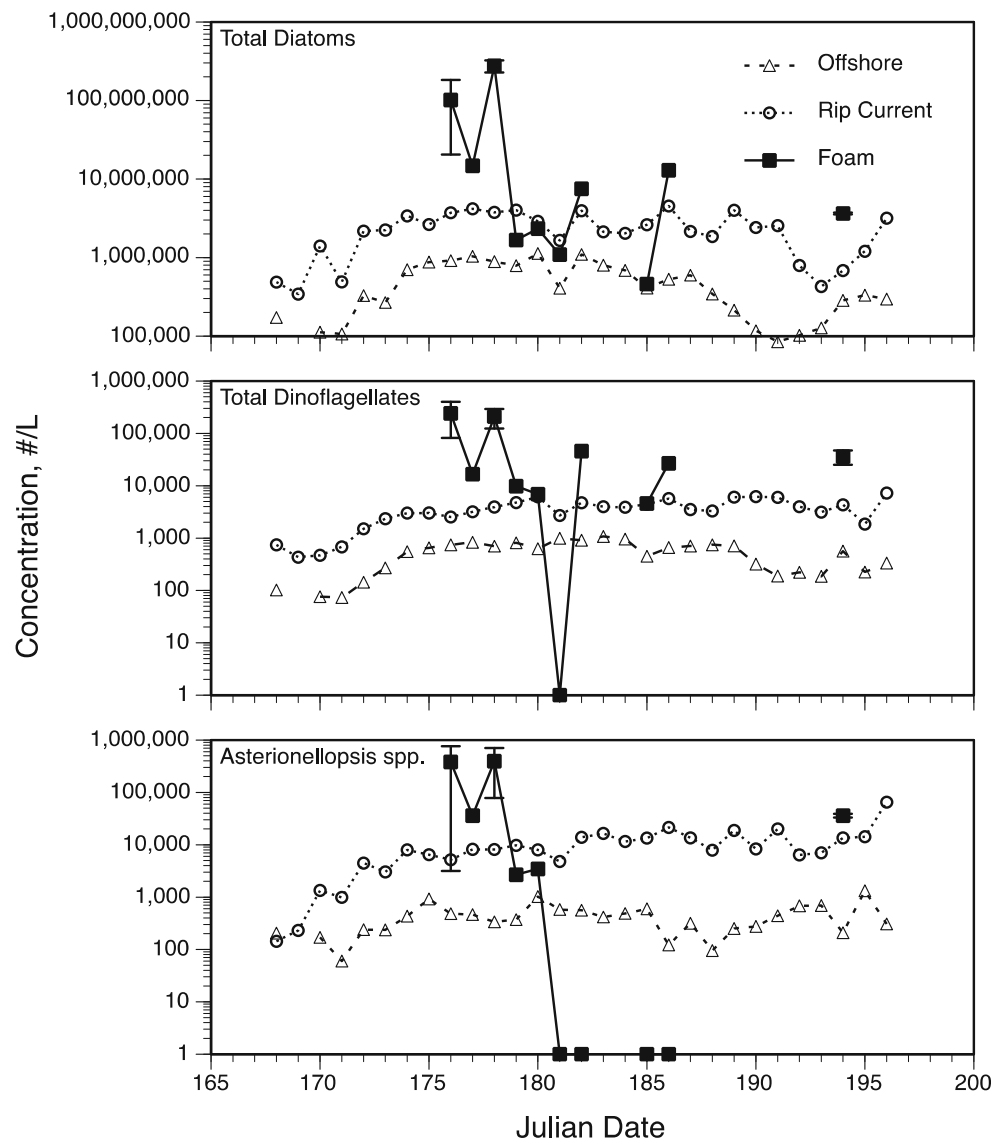
We found that, when compared to the North Rocks phytoplankton samples, the relative abundance of offshore phytoplankton present at the Beach site was highest when waves were smaller (Fig. 14), suggesting that the slower alongshore current generated by smaller waves provided more opportunity for the exchange of surf zone water with offshore water, leading to an increase in the concentration of offshore phytoplankton at the Beach site.

Discussion

Phytoplankton are not conservative tracers; they can be consumed and grow. At Carmel River State Beach, we observed

large differences in the concentration of coastal phytoplankton taxa within the surf zones relative to that just offshore on the inner shelf. Phytoplankton abundances in the three CRSB reflective surf zones sampled were often not correlated with concentrations offshore, and concentrations in each of the three sample surf zones were much lower than those offshore. Could the much lower concentrations of phytoplankton in the reflective surf zones be due to consumption by filter feeders? There were no filter feeders in the surf zone at the Beach site, which is typical of steep reflective sandy beach surf zones (McLachlan and Brown 2006), where energetic breaking waves prevent the establishment of a filter-feeder community. Hence, the low concentration could not be due to consumption. At the rocky shore sites at the north and south ends of the beach, there were benthic filter feeders. These were primarily mussels and barnacles; however, mussel beds were small and barnacles were at low density (195 and 16 individuals/100 cm² at North Rocks and South Rocks, respectively (Shanks et al. 2017a). Filter feeders can reduce the concentration of phytoplankton, but it requires very high densities of filter feeders to make an appreciable impact. For example, Petersen et al. (2008) looked at the reduction in Chl *a* as water passed through a raft of mussel (750 individuals/m³) in an aquaculture facility. Despite the very high abundance of filter feeders, Chl *a* concentration dropped, on average, by only 30% as water passed through the raft of mussels (transit time 24 min). At the North Rocks and South Rocks sites, surf zone phytoplankton concentrations were only a small fraction of those offshore (median 13 and 1% of offshore, respectively). Given the much lower density of filter feeders in these rocky shore communities than that in an aquaculture

Fig. 8 Comparison of phytoplankton concentrations (mean and SE) in foam samples (filled squares) to concentrations of phytoplankton collected within the water column of the rip current (open circles) and in waters just seaward of the surf zone (open triangle) at Sand City, California. Missing values indicate no data



facility, water would have to remain stationary over the rocky shores for hours before filter feeders could consume enough cells to obtain the observed surf zone concentrations of phytoplankton.

Concentrations of typical offshore phytoplankton in the surf zone at Sand City were much higher in the bathymetric rip current and lower over the shoal than just seaward of the surf zone. Given the dynamic flow within this surf zone due to the rip current system, the difference in phytoplankton concentration between the shoal and the rip samples is most likely due to redistribution. Could the higher concentration of phytoplankton in the rip samples than those samples collected offshore be due to differential growth of phytoplankton within the surf zone? Net growth rates of phytoplankton cells are around 0.5 divisions per day with maximum growth rates around 1.5 divisions per day (Parson et al. 1984). We assume that the net division rates of phytoplankton on the inner shelf

are typical for phytoplankton (0.5 divisions per day) while phytoplankton within the surf zone are growing rapidly (1.5 divisions per day). Surf zones are shallow, so light levels are high and ground water seepage through the beach can fertilize surf zones (McLachlan and Brown 2006). We then used these division rates to calculate how long it would take for cell growth to generate the observed differences. Rip current phytoplankton concentrations were often 10 times higher than offshore. Given these assumed division rates, it would take about 2 days for rip current concentrations to increase 10 times the concentrations offshore. Water is not resident in surf zone rip currents for this long (Smith and Largier 1995; Talbot and Bate 1987a, b), and it seems unlikely that the high concentrations of phytoplankton observed in the rip currents were due simply to differential growth. Our estimates of the overall abundance of phytoplankton cells in the Sand City surf zone suggest that phytoplankton was, on average, 2.5 times more

abundant in the surf zone than offshore. Given the assumed difference in division rates offshore and in the surf zone, this difference in overall phytoplankton abundance could be achieved within a day. While this analysis is speculative and we did not collect the needed phytoplankton productivity data, it does suggest that at least some of the difference in cell concentrations in more dissipative surf zone may be due to growth within this habitat.

Studies of phytoplankton in surf zones fall into two general categories: investigations focused on the ecology and biology of surf zone-dependent species (Talbot et al. 1990) and investigations of subsidies of phytoplankton from the coastal ocean to communities of intertidal filter feeders (Bracken et al. 2012; Krenz et al. 2011; McPhee-Shaw et al. 2011; Menge et al. 1997a, b). Surf zone diatoms occur in more dissipative surf zones where they can attain very high concentrations and are absent from less dissipative or reflective surf zones (Garver and Lewin 1981). These diatoms produce mucus, which traps bubbles, floating the cells to the surface and maintains them there. More dissipative surf zones often have bathymetric rip currents, and this flow system produces persistent eddies within the surf zone (MacMahan et al. 2006). Foam with the attached diatom cells becomes trapped in the convergent eddies, which simultaneously concentrates the cells into patches and maintains them within the surf zone (Talbot et al. 1990). Surf zone diatoms were absent from CRSB and were only a tiny component of the phytoplankton community at Sand City.

The growth rate and reproductive output of intertidal filter feeders and the structure of intertidal communities vary with the amount of phytoplankton in the surf zone (Bracken et al. 2012; Leslie et al. 2005; Menge et al. 1997b; Phillips 2005,

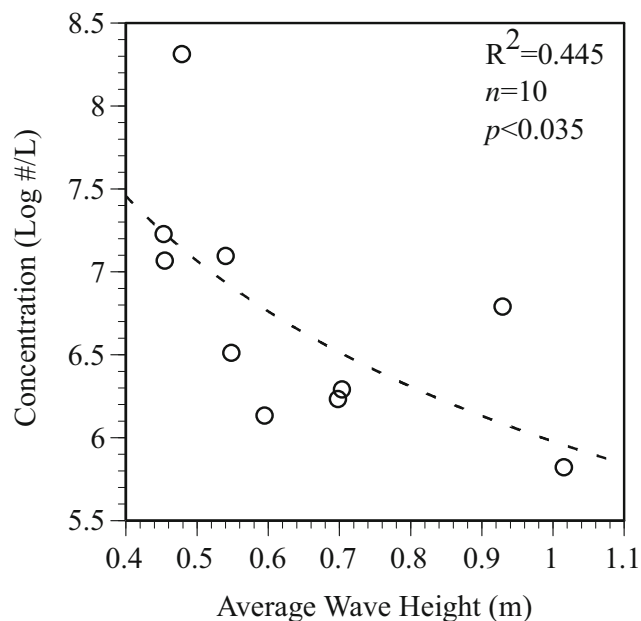


Fig. 9 Log of the concentration of phytoplankton (all taxa) in foam samples from Sand City, California, plotted against wave height

2007); hence, understanding the factors controlling phytoplankton concentrations in the waters over the intertidal zone is of great interest to ecologists. At more reflective shores, there are no surf zone-dependent phytoplankton species, and phytoplankton within these surf zones are subsidies from the coastal ocean. A number of studies have measured surf zone phytoplankton concentrations, usually as Chl *a*, by sampling water right against the shore at low tide (e.g., Bracken et al. 2012), methods essentially identical to those we used to sample the rocky shores at CRSB in this study. These studies have generally sampled a number of locations along the coast at widely spaced interval in time and space (e.g., Krenz et al. 2011), but none has simultaneously measured the concentrations of phytoplankton just offshore and within the surf zone as we did. In addition, none of these studies related variation in phytoplankton abundance next to shore to the surf zone type. Given the descriptions of the sample sites, it is likely that most sites had reflective surf zones. Comparisons of two sites in Oregon, Strawberry Hill and Boilers Bay, are an exception (Menge et al. 1997a, b). The rocky shore at Strawberry Hill consists of large rocky benches surrounded by sandy beaches with wide surf zones (average Google Earth surf zone width = 123 m, SD = 20 m, $n = 6$), Strawberry Hill is a more dissipative site. The surf zone associated with Boilers Bay is narrow and more reflective (average Google Earth surf zone width = 13 m, SD = 9 m, $n = 4$). There were no differences in the nutrients available for phytoplankton growth at the two sites, yet the concentrations of Chl *a* at

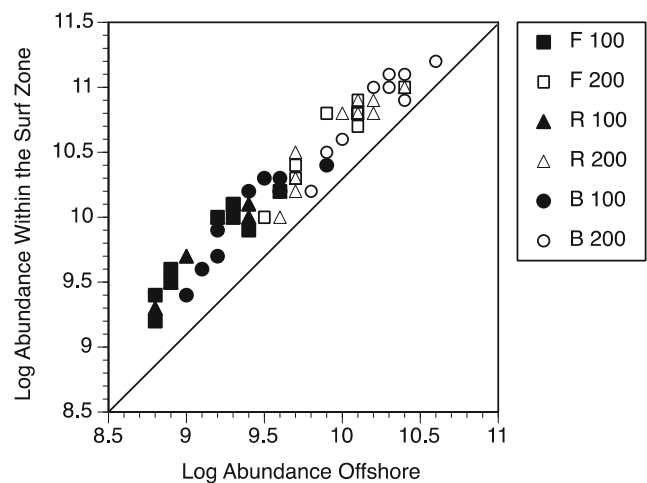
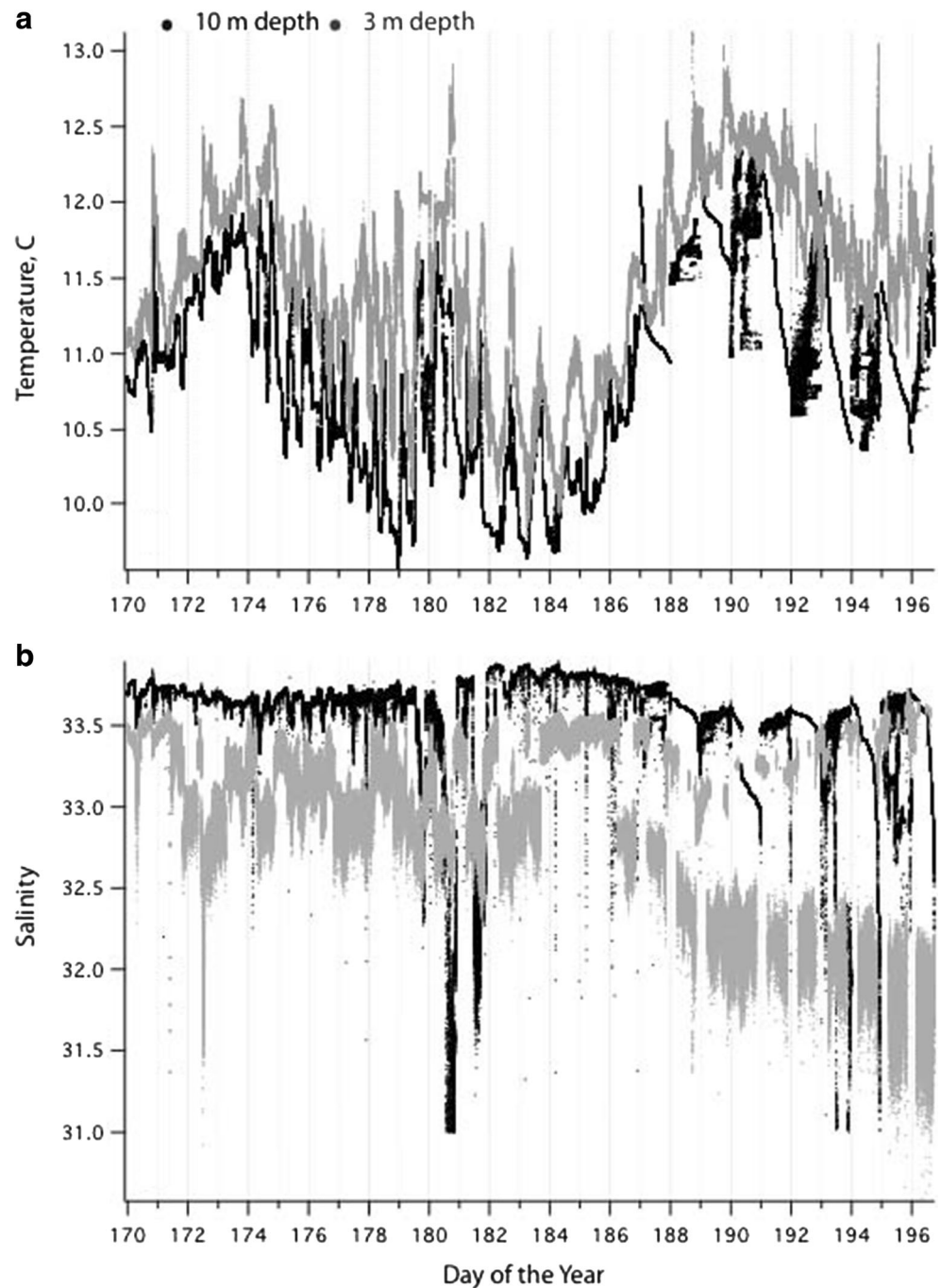


Fig. 10 The log of the abundance of phytoplankton in the surf zone (i.e., the concentrations within the bathymetric rip current and over the shoals times the estimated volume of each habitat) compared to the log of the abundance in the water just offshore of the surf zone at Sand City, California. The *solid line* represents the one-to-one relationship between the two variables. For these calculations, surf zone width was assumed to be either 50 or 100 m (approximately the range of surf zone widths observed in historical Google Earth images of the site). The width of shoals and rips habitats was estimated from Fujimura (2015; A50 and A100), Brown (2014; B50 and B100), and Reniers et al. (2010; R50 and R100) and from historical Google Earth images (G50 and G100). The bathymetry of the surf zone was estimated from Fujimura (2015)

Fig. 11 Time series plots of **a** temperature and **b** salinity collected 125 m offshore at Carmel River State Beach. There were two CTDs: one at 10 m depth (*black dots*) and the other at 3 m depth (*gray dots*)

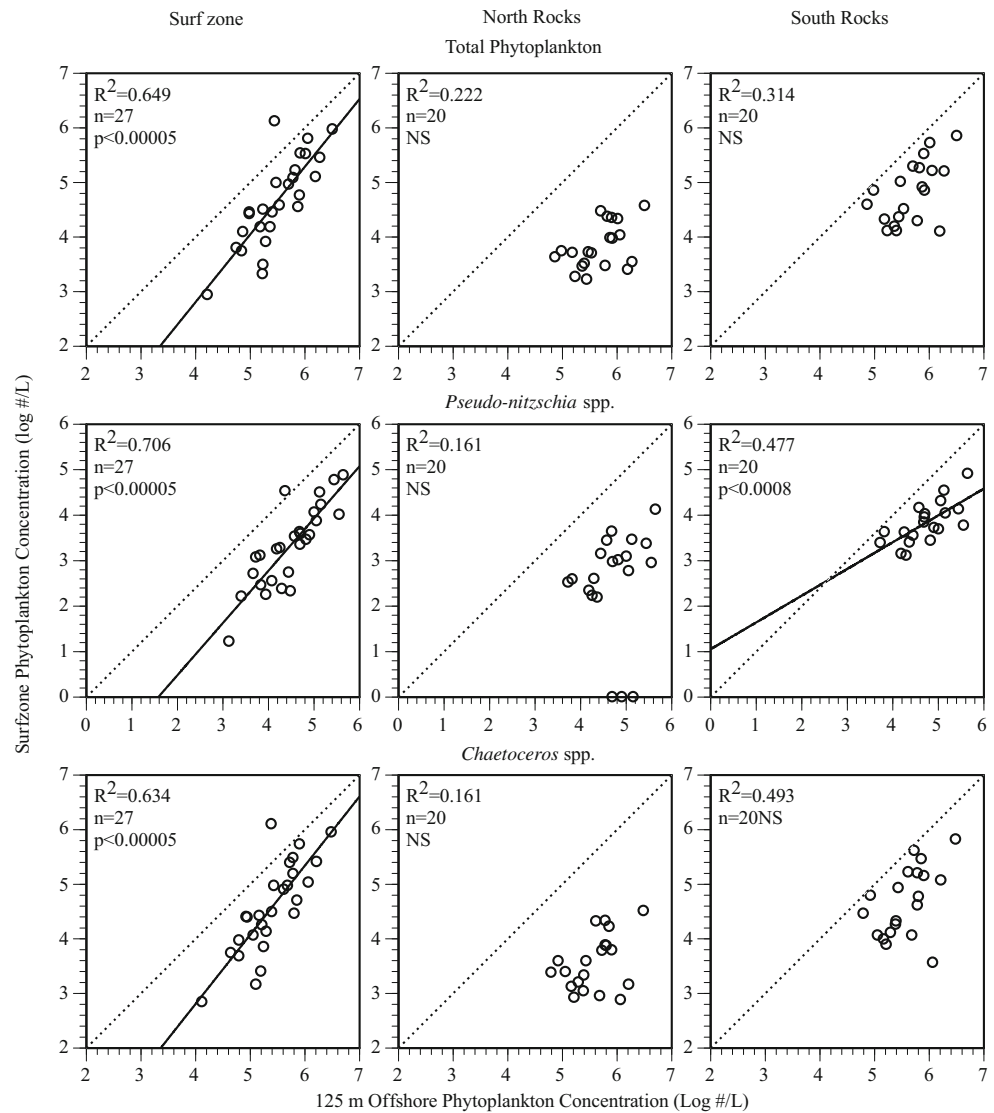


Strawberry Hill were consistently around an order magnitude higher than at Boilers Bay. Without concurrent measurements of offshore phytoplankton concentrations, comparing these results to those reported here must be tentative, but the results are consistent with our observations.

The major difference between the two surf zones was the absence of bathymetric rip currents at CRSB and their presence at Sand City. At the intermediate surf zone, water exited the surf zone as a jet flowing out to the sea in bathymetric rip currents and mixed with water on the inner shelf, and then

waves transported the water back into the surf zone over the shoals (MacMahan et al. 2010a, b). This rip current system was an effective mechanism for exchanging surf zone water with that beyond the breakers. Bathymetric rip currents are generally suppressed at intermediate and dissipative surf zones when waves impinging on the shore at an angle (e.g., wave crests not parallel to shore) generate alongshore currents in the surf zone (Komar 1983; MacMahan et al. 2006), and without rip currents, the exchange of water between the surf zone and offshore is also suppressed (Fig. 1). This can be

Fig. 12 Log of the concentration of phytoplankton collected 125 m offshore plotted with the log of the concentration of phytoplankton collected in the beach surf zone (left hand figures) and in the surf zone at the rocky shore just north (middle figures) and south (right hand figures) of the beach at Carmel River State Beach. Dotted lines indicate the one-to-one relationships between variables. Solid lines and statistical results are from linear regressions between the variables. Only significant regression lines are plotted. Significance levels were modified with a Holm-Bonferroni correction



clearly seen in Johnson and Pattiaratchi (2004); surf zone drifters were transported through the surf zone when bathymetric rip currents were present, but they remained in the surf zone and traveled alongshore when rip currents were absent and alongshore currents were present.

Phytoplankton concentrations were higher in the rip current samples, and this may be due to entrainment of phytoplankton cells within the rip current eddy system. Surf zone diatoms produce exudates that trap bubbles forming foam, floating the cells to the surface where they become concentrated within bathymetric rip current eddies (Talbot and Bate 1987b). Typical offshore phytoplankton taxa can also be caught by bubbles rising through the water column (Csordas and Wang 2004; Krichnavaruck et al. 2007; Schlichting 1972), and cells adhering to bubbles might also be concentrated in rip current eddies. We consistently found coastal phytoplankton taxa in foam sometimes at very high concentrations. We hypothesize

that phytoplankton attach to bubbles rising through the water column of the surf zone transporting them to the surface. Depending on the stability of the bubbles, attachment of phytoplankton to bubbles may occur at the surface for variable amounts of time, but while at the surface, they may, like buoyant current drifters and surf zone diatoms, become concentrated in rip current eddies. A model of the surf zone at Sand City demonstrated that buoyant particles can become concentrated in rip eddies (Fujimura et al. 2014).

Surf zone diatoms were not present in the surf zone at CRSB. They were present in the surf zone at Sand City, but they composed only a small fraction of the phytoplankton community. Surf zone diatoms are only present or abundant at more dissipative surf zones with bathymetric rip currents (Garver 1979; Garver and Lewin 1981). This is likely because rip current eddy systems concentrate cells attached to foam and floating at the surface (Talbot and Bate 1987b). In

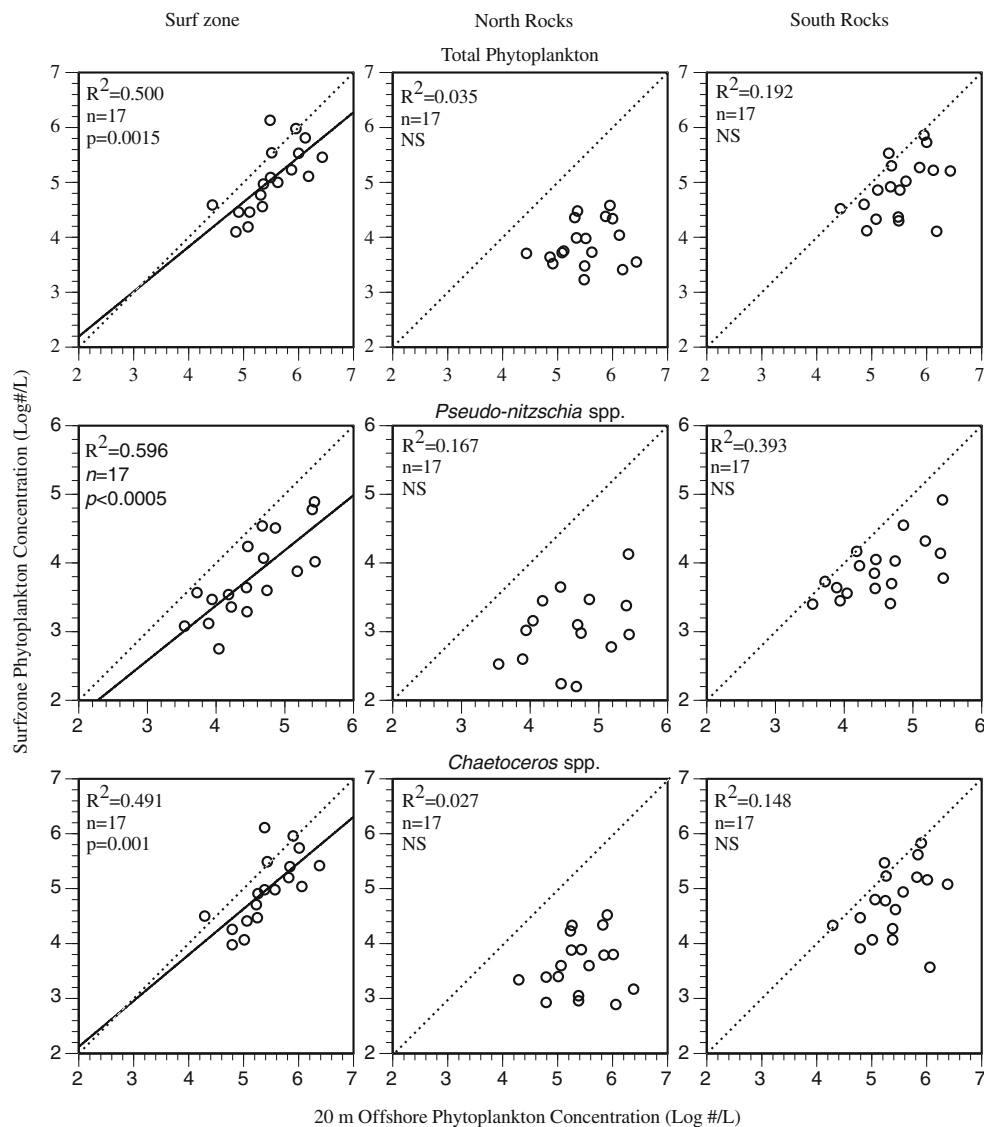


Fig. 13 Log of the concentration of phytoplankton collected 20 m offshore plotted with the log of the concentration of phytoplankton collected in the beach surf zone (left hand figures) and in the surf zone at the rocky shore just north (middle figures) and south (right hand figures) of the beach at Carmel River State Beach. Dotted lines indicate

the one-to-one relationships between variables. Solid lines and statistical results are from linear regressions between the variables. Only significant regression lines are reported. Significance levels were modified with a Holm-Bonferroni correction

addition, when floating objects are ejected from a more dissipative surf zone, there is a good chance that the floating object, e.g., foam with attached diatoms, will be transported back into the surf zone (Castelle et al. 2014). Transient and topographic rip currents form at more reflective surf zones (Hally-Rosendahl and Feddersen 2016; Hally-Rosendahl et al. 2014), but they do not tend to set up persistent eddy systems and, perhaps more importantly, these rip currents tend to eject floating objects out of the surf zone with few returns (Castelle and Coco 2013). Hence, these rip currents would not concentrate cells attached to foam and would tend to eject them from the surf zone onto the inner shelf. Thus, the physics of transient and topographic rip currents coupled with the behavior

of surf diatoms, i.e., attachment to foam, prevent surf zone diatoms from becoming established at more reflective surf zones.

Sandy beaches associated with more dissipative surf zones are frequently very productive, supporting populations of bivalves and crustaceans (McLachlan and Brown 2006). At some shores, this high productivity is due to populations of surf zone diatoms. However, our results clearly indicate that, even without substantial populations of surf zone diatoms, dissipative surf zones can support populations of filter feeders due to high concentrations of typical coastal phytoplankton within the surf zone. However, phytoplankton subsidies to the benthic community in the surf zone at Sand City appear

to be unevenly distributed. Filter feeders living on shoals would receive a much lower ration of phytoplankton than those living under the rip current system; in our samples, their ration would be ~1000 times lower. Consequently, filter feeders under the rip current system should be better fed, grow faster, and be more fecund than those on shoals. However, filter feeders living in the rips are also exposed to higher concentrations of toxins from harmful algal species (Shanks et al. 2016). Thus, filter-feeding benthic organisms in surf zones with bathymetric rip currents may predictably receive different amounts of food and toxins when they reside under the rip current system rather than shoals.

Why were concentrations of phytoplankton so low in shoal samples? First, low concentrations may represent redistribution of phytoplankton within the surf zone due to the rip current system. Second, flow changes with depth outside of the surf zone, which can modify transport into the surf zone (Fujimura et al. 2014). Flow into the surf zone tends to be concentrated near the surface due to the action of breaking waves. Although we did not measure the vertical distribution of phytoplankton in the waters just seaward of the Sand City surf zone, if phytoplankton was less abundant near the surface (as we observed in Chl *a* profiles at CRSB), surface waters entering the surf zone may have contained low concentrations of phytoplankton. Hence, the concentration of phytoplankton over the shoals may represent the concentration of phytoplankton near the surface on the inner shelf rather than the average offshore concentration. Both of these mechanisms could be occurring.

Phytoplankton concentrations within a reflective surf zone, CRSB, were significantly lower, usually 10 times lower, than just seaward of the surf zone. While water within the surf zone

was exchanged with offshore water, the pattern of flow appears to limit onshore transport of offshore taxa. Modeling results suggest that at the northern end of the study area, water flows from offshore into the surf zone, feeding an alongshore current (Fujimura 2015). This onshore flow might transport coastal phytoplankton into the surf zone; however, the concentration of offshore phytoplankton taxa collected at the North Rocks was only a small percentage (median 1%) of that offshore. Therefore, the onshore flow, the source of the alongshore current, was not a source of offshore plankton. Furthermore, we measured daily settlement of barnacle cyprids to the North Rocks and only one settled over 38 days (Shanks et al. 2014). If the onshore current transported offshore plankton to the shore, we would expect cyprid settlement at this site to be high, and therefore once again, the onshore flow did not appear to be a source of plankton.

It is not clear why phytoplankton concentrations were so low in the water entering the alongshore current. As waters flowed shoreward to enter the alongshore current, phytoplankton and zooplankton may have been removed by consumers. Predation by fish in kelp beds can dramatically reduce the abundance of zooplankton as waters pass through a kelp bed (Gaines et al. 1985), and dense aggregations of filter feeders can reduce the concentration of phytoplankton (Kamermans 1993). Perhaps, the very low concentration of plankton entering the surf zone at CRSB as part of the alongshore current is a consequence of having first passed through a kelp bed.

Within the surf zone at CRSB, flow below the wave trough was offshore, consistent with the presence of substantial undertow, and it diminished at the seaward edge of the surf zone where waves break (Fig. 1). At the breaker line, surface flow was landward and was largely balanced by offshore undertow (Shanks et al. 2015a, b). The undertow and wave-driven onshore flow at the surface essentially stopped at the breaker line and do not exchange the water between the surf zone and inner shelf. Surface water is, however, exchanged across the breaker line by turbulence generated by breaking waves (Fig. 1), but it was not clear from our measurements how deep this turbulent exchange extended. If phytoplankton was distributed throughout the water column, cells close to the surface may enter the surf zone via the turbulence generated by wave breaking. Most Chl *a*, however, was found at the subsurface within the water column, and these cells would have been pushed away from the surf zone by offshore advective transport, the undertow, characteristic of this reflective surf zone. If, however, phytoplankton are evenly distributed throughout the water column, ultimately, the concentration of phytoplankton in the surf zone should resemble that offshore. Despite the exchange of water between the inner shelf and surf zone, the concentration of coastal phytoplankton taxa within the surf zone was far lower than that just offshore. We hypothesized that the near-surface concentration of phytoplankton was low, and it was due to this water and concentration of

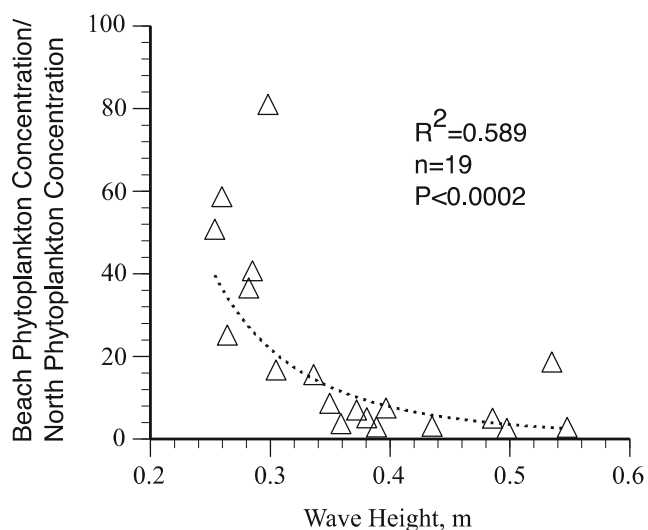


Fig. 14 The relative concentration of total phytoplankton between the Beach and North Rocks sites (Beach/North Rocks/surf zone), plotted with wave height. Dotted lines and statistical results are from regressions between the variables

phytoplankton that enters the surf zone (Shanks et al. 2016). Near-surface (<0.5 m depth) Chl *a* concentrations measured with the fluorometer just outside the surf zone were significantly lower than the average concentration in the water column and at the depth where we sampled phytoplankton cells. Hence, these results are consistent with this hypothesis. Phytoplankton may simply sink away from the surface, or motile taxa may swim away from the surface to avoid harmful light levels or in response to other vertical migration cues (Heaney and Eppley 1981), leading to the observed low surface concentrations of Chl *a*.

The changes in the concentration of phytoplankton in the alongshore current at CRSB clearly indicate that water and phytoplankton were being exchanged between the surf zone and inner shelf, but despite this exchange, phytoplankton concentrations within the surf zone remained very low. The weak connection between the surf zone and the offshore waters appeared to be driven by surf zone hydrodynamics, which, in turn, is primarily driven by the steep slope of the shore. Shores with similar morphology will likely display similar relationships between concentrations of phytoplankton offshore and within the surf zone. We sampled a number of surf zones along the West Coast with different hydrodynamics and found that the concentration of phytoplankton in more reflective surf zones was 1 to 2 orders of magnitude lower than that in more dissipative surf zones (Shanks et al. 2017b). We also found a similar association between the abundance of new barnacle recruits at reflective and dissipative surf zones; new recruits were 1 to 2 orders of magnitude lower in intertidal zones associated with more reflective than dissipative surf zones (Shanks et al. 2010, 2017a). Rocky shores are often steep and reflective, and like CRSB, subsidies of coastal phytoplankton and zooplankton to the intertidal zone may be lower than those at shores with more dissipative surf zones.

Most phytoplankton taxa have no means of locomotion; they can sink or rise slowly. Flagellated cells can swim, but slowly. Given the turbulence associated with surf zones, we initially hypothesized that phytoplankton cells would act as passive tracers of water movement, but this did not appear to be the case. Given the complex hydrodynamics of surf zones, even small changes in the vertical distribution of cells appear to be capable of generating large differences in the horizontal distribution of phytoplankton populations. Cells, likely sinking away from the ocean surface, lead to lower concentrations of phytoplankton cells very near the surface. This near-surface water is drawn into reflective surf zones by wave-generated turbulence so that phytoplankton concentrations in the surf zone are lower than average concentrations on the inner shelf. At the more dissipative surf zone, we hypothesize that cells trapped in foam become concentrated in the rip current eddy system, leading to a redistribution of cells within the surf zone and high cell concentrations within bathymetric rip current eddies.

In conclusion, we intensively investigated the biology and hydrodynamics of surf zones at a reflective and more dissipative shore. Our results should be generally applicable as the hydrodynamics of surf zones depend on the slope of the shore and the wave field rather than substrate type. At the intermediate surf zone, phytoplankton concentrations tracked abundance in the coastal ocean, but they were unevenly distributed within the surf zone, and concentrations were much higher in bathymetric rip currents than over shoals. At the reflective shore, phytoplankton concentrations were much lower within the surf zone than even just 20 m offshore, indicating that surf zone hydrodynamics limited the ingress of coastal phytoplankton into the surf zone. The hydrodynamic effect, due to the steep morphology of the shore, is likely characteristic of reflective surf zones including many rocky shores, and phytoplankton subsidies to steep rocky shores with reflective surf zones may be lower than at shores with more dissipative surf zones. Thus, surf zone hydrodynamics may play an important role in controlling subsidies from the inner shelf to the intertidal zone.

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