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# Planktonic Subsidies to Surf-Zone and Intertidal Communities

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## Keywords

surf zone, zooplankton, phytoplankton, hydrodynamics, subsidies, larval recruitment, communities

## Abstract

Plankton are transported onshore, providing subsidies of food and new recruits to surf-zone and intertidal communities. The transport of plankton to the surf zone is influenced by wind, wave, and tidal forcing, and whether they enter the surf zone depends on alongshore variation in surf-zone hydrodynamics caused by the interaction of breaking waves with coastal morphology. Areas with gently sloping shores and wide surf zones typically have orders-of-magnitude-higher concentrations of plankton in the surf zone and dense larval settlement in intertidal communities because of the presence of bathymetric rip currents, which are absent in areas with steep shores and narrow surf zones. These striking differences in subsidies have profound consequences; areas with greater subsidies support more productive surf-zone communities and possibly more productive rocky intertidal communities. Recognition of the importance of spatial subsidies for rocky community dynamics has recently advanced ecological theory, and incorporating surf-zone hydrodynamics would be an especially fruitful line of investigation.

# 1. INTRODUCTION

Alongshore variation in ocean conditions affects the delivery of planktonic and larval subsidies to shore, with profound consequences for the dynamics and structure of surf-zone, rocky, and beach communities (Menge et al. 1997a, 2003; Morgan et al. 2016; Shanks et al. 2017a). Variation in phytoplankton, zooplankton, and detritus subsidies affects the growth and reproduction of the sedentary and sessile filter-feeding invertebrates that form the foundation of these communities (Menge et al. 1997a, Leslie et al. 2005) and, together with variation in larval supply, affects the density of settlers and the intensity of postsettlement interactions (Morgan 2001, Underwood & Keough 2001). Intense density-dependent interactions leading to high mortality occur where planktonic food and larval subsidies abound, and weaker interactions and lower postsettlement mortality occur where these subsidies are sparse (Menge & Sutherland 1987, Morgan 2001, Menge et al. 2003).

Multiple mechanisms may transport larvae, other zooplankton, and phytoplankton toward shore, including upwelling relaxation events, onshore winds, large waves, tidally generated internal waves, and shoreward-flowing bottom waters during upwelling (Shanks 1995, 2006; Pineda 1999; Morgan et al. 2009a,b; Drake et al. 2013). Once plankton are on the inner shelf, the degree to which they enter the surf zone may depend largely on spatial variation in surf-zone hydrodynamics, which is determined by the interaction of breaking waves with variation in coastal morphology, ranging along a spectrum from dissipative to reflective (Wright & Short 1984, McLachlan & Brown 2006) (**Figure 1**).

The goal of this review is to increase awareness of the importance of surf-zone hydrodynamics for plankton concentrations and the densities, growth, and reproduction of residents of surf-zone and intertidal communities. We first review physical processes that lead to exchange between the surf zone and the inner shelf. We then evaluate existing evidence for the effect of surf-zone hydrodynamics on plankton concentrations and the consequences for surf-zone and intertidal communities. We conclude by discussing future directions for this avenue of research.

**Subsidy:** plankton, detritus, and nutrients from the water column that sustain benthic communities

**Surf zone:** the region between the shoreline and the onset of depth-limited wave breaking

**Upwelling:** a process in which alongshore wind and Earth's rotation force surface water offshore, resulting in a compensatory onshore flow of cold, nutrient-rich bottom water that is forced to the surface upon reaching shore

**Relaxation:** weakening of upwelling-favorable winds

**Inner shelf:** a region seaward of wave breaking where the surface and bottom boundary layers interact

**Dissipative surf zone:** a surf zone with high wave energy that dissipates gradually as waves break on alongshore bars and gently shoaling beaches, resulting in progressive waves, wide surf zones, and fine-grained sand

# 2. PHYSICAL PROCESSES INDUCING EXCHANGE

The exchange of water between the surf zone and the inner shelf is induced by a complex circulation with high variability in fluid velocity, temperature, and potentially salinity at a wide range of temporal and spatial scales, which are presently not well understood. This interaction zone affects the transport of material such as biota, pollutants, and sediments. The three-dimensional inner-shelf circulations are influenced by wind, wave, and tidal (both surface and internal tides) forcing, with the relative importance of each depending on the water depth (Lentz 1994, Lentz et al. 1999, Cudaback et al. 2005, Fewings et al. 2008, Kirincich et al. 2009). Inside the surf zone, current dynamics are driven predominantly by breaking surface gravity waves and depend largely on surf-zone bathymetry and morphology classification (**Figure 1**). Because current dynamics differ substantially between the surf zone and the inner shelf, mechanisms for cross-shore transport also differ. Lentz & Fewings (2012) provided an overview of wind- and wave-driven inner-shelf processes. Here, we focus on recent developments that have improved understanding of the transport processes at the boundary between the surf zone and inner shelf (out a few surf-zone widths, on the order of 500 m). These processes include wave-driven Stokes drift, wave streaming, rip currents, and internal waves, all of which induce transport of subsidies.

## 2.1. Cross-Shore Exchange Caused by Vertical Structure (Stokes Drift, Undertow, and Streaming)

The flows driving exchange between the surf zone and inner shelf can occur over depth, and therefore the vertical structure of the flows is important in transporting plankton subsidies onshore

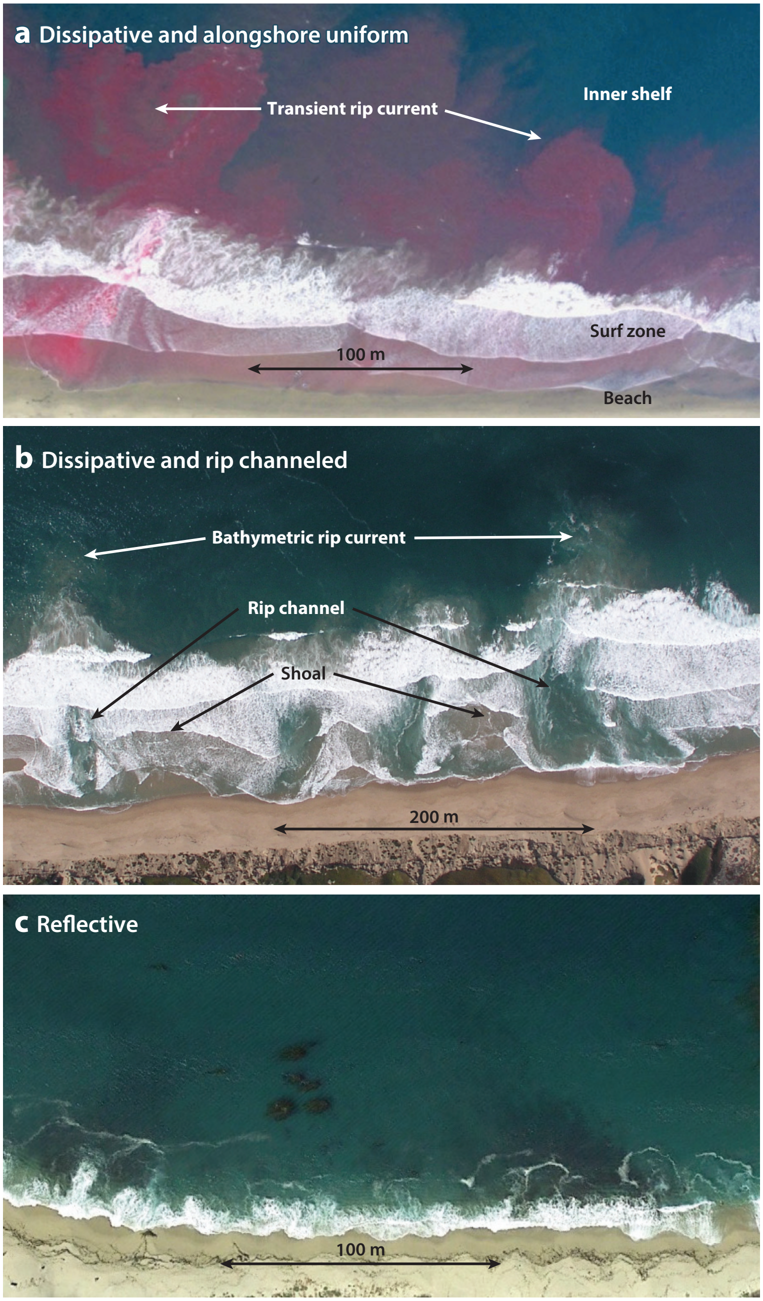


**Figure 1**

Aerial photographs of three different surf-zone morphodynamic types: (*a*) dissipative and alongshore uniform, (*b*) dissipative and rip channeled, and (*c*) reflective. The beach, surf zone, and inner shelf are labeled in panel *a* but are also visible in panels *b* and *c*. Panel *a* has an 8-m-wide surf zone shown during a Rhodamine WT dye release (Hally-Rosendahl et al. 2014), highlighting transient-rip-current ejection events. Panel *b* depicts a 150-m-wide surf zone, rip channels and shoals, and bathymetric rip currents. In panel *c*, the surf zone is narrow (less than 20 m wide) and the beach is very steep.

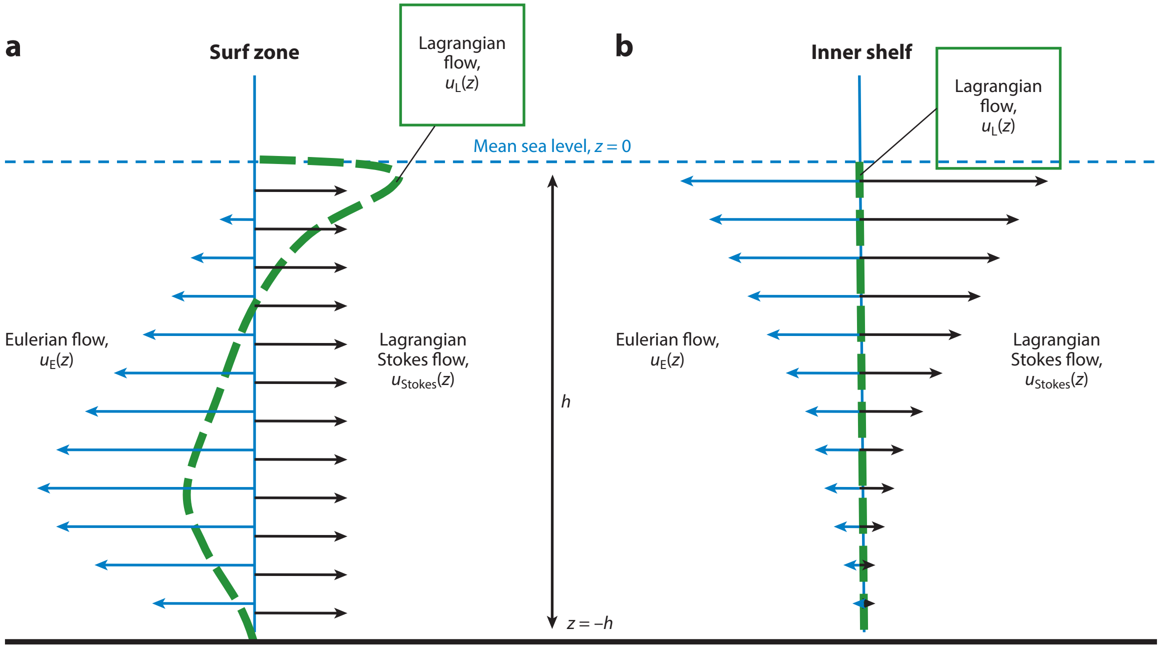


Figure 2

Wave and background flow description of an alongshore homogeneous beach in the Eulerian and Lagrangian frame of reference for (*a*) typical surf-zone behavior and (*b*) typical inner-shelf behavior, as observed in the field and described in the literature. The blue dashed line represents the mean sea level, the black solid line at the bottom represents the seabed, and the green dashed lines represent $u_L(z)$.

(**Figure 2*a***). Within the surf zone, onshore wave-driven flow (Stokes drift) is largely locally balanced by an offshore-directed, parabolic velocity profile below (**Figure 2*a***), referred to as undertow (Ursell 1950, Haines & Sallenger 1994, Reniers et al. 2004). The undertow velocity profile results in a vertical imbalance between the offshore Eulerian velocity [$u_E(z)$] and the onshore Stokes drift velocity [$u_{Stokes}(z)$] (**Figure 2*a***). Note that the Lagrangian velocity [$u_L(z)$, the sum of the Eulerian and Stokes velocities] represents the velocity that transports material, such as larvae and detritus. Outside the surf zone, on an alongshore uniform inner shelf, the offshore wave-driven Eulerian $u_E(z)$ can be in balance with $u_{Stokes}(z)$, resulting in zero $u_L(z)$ over depth on long timescales (many days) for weak winds and unstratified conditions (Lentz et al. 2008) (**Figure 2*b***). However, observations show that $u_L(z)$ is not zero for strong winds or stratified conditions (Lentz et al. 2008).

**Reflective surf zone:** a surf zone with steep shores and less wave energy that is reflected as waves surge onshore, resulting in standing waves, narrow and energetic surf zones, and narrow beaches of coarse-grained sand; rock benches also are reflective

**Internal tide:** a propagating gravity wave within a stratified fluid at tidal periods, often formed by the barotropic tide passing bathymetry that deflects isopycnals

With winds, the inner-shelf $u_L(z)$ is nonzero, resulting in cross-shore exchange (Fewings et al. 2008, Fujimura et al. 2013). Surface transport is in the direction of the wind at and near the surface, with a flow reversal occurring at greater depths, ensuring that the depth-integrated cross-shore transport is zero. The inclusion of wind stress modifies the vertical current profile by either enhancing or reducing the wave-driven transport. The vertical imbalance within the surf zone and the potential vertical balance outside the surf zone raise questions about the transition of the surf zone to inner-shelf $u_L(z)$ and material transport, particularly for weak winds.

At water depths less than approximately half the wavelength, surface waves start to feel the seabed and wave energy is dissipated by bed friction, resulting in a thin (on the order of centimeters) wave boundary layer. Within this layer, the horizontal and vertical orbital velocities are no longer 90° out of phase, resulting in a horizontal wave Reynolds stress acting on the water, forcing a persistent near-bed flow in the direction of wave propagation known as streaming (Longuet-Higgins 1953), with velocities on the order of centimeters per second. Enhanced wave nonlinearity with shoaling can reduce the streaming velocity (Trowbridge & Madsen 1984). Streaming commences tens to hundreds of meters offshore, depending on the wave field and bottom slope. Streaming velocity increases as waves shoal. Where waves start breaking, onshore streaming is suppressed by undertow, resulting in a convergence zone of bed material just outside the surf zone (Reniers et al. 2004). The combined mechanisms create a wave-averaged depth-dependent near-bed flow that increases from deeper water toward the shoaling zone, then slowly decreases within the shoaling zone as the wave nonlinearity increases and is fully reversed within the surf zone. This is expected to result in a convergence zone for benthic material at the outer edge of the surf zone.

**Stokes drift:** wave-driven transport

**Bathymetric rip current (BRC):** a rip current generated by alongshore variations in surf-zone sandbar morphology and the resulting breaking-wave variations and offshore controls

**Transient rip current (TRC):** intermittent surf-zone eddy ejection caused by random incident waves on alongshore uniform coasts

## 2.2. Rip-Current-Driven Exchange

Rip currents eject surf-zone water onto the inner shelf (Shepard et al. 1941) and are an important conduit for material transport between the two areas. Rip currents are divided into two categories: bathymetric rip currents (BRCs) and transient rip currents (TRCs). BRCs and TRCs can extend multiple surf-zone widths offshore, ejecting surf-zone water onto the inner shelf and providing an important conduit for material transport between the surf zone and inner shelf. Any natural beach has both a random wave field that drives TRCs and some alongshore bathymetric variation that drives BRCs. Thus, all rip currents can be considered to be some component of TRCs and BRCs (e.g., Reniers et al. 2009, 2010). We summarize recent results for TRCs and BRCs below; however, much work remains to understand the forcing and feedbacks between bathymetry, waves, stratification, and rip currents (both TRCs and BRCs).

**2.2.1. Transient-rip-current-driven exchange.** Many coastlines are essentially alongshore uniform, where the shoreline and the offshore bathymetry contours are straight over a long distance (a few kilometers). On alongshore uniform coasts, TRCs form because wave breaking of random directionally spread waves generates surf-zone eddies (e.g., Peregrine 1998, Johnson & Pattiaratchi 2006, Spydell & Feddersen 2009, Clark et al. 2012, Feddersen 2014). These eddies evolve and coalesce, leading to eddy ejection from the surf zone to the inner shelf, known as TRCs. Dye tracer exchange between the surf zone and inner shelf is dominated by TRCs in both observations (Hally-Rosendahl et al. 2014, 2015) (**Figure 1*a***) and models (Suanda & Feddersen 2015, Hally-Rosendahl & Feddersen 2016). Thus, they are also likely the dominant exchange mechanism for planktonic subsidies. TRCs are readily visible in infrared images of the surf zone (Marmorino et al. 2013) and in dye tracer images (Clark et al. 2014). TRCs have alongshore length scales of 10–100 m (Hally-Rosendahl et al. 2014, 2015). Suanda & Feddersen (2015) found that, on alongshore uniform planar beaches, the modeled exchange flow induced by TRCs is self-similar and can be parameterized by incident wave conditions. In addition, they found that the surf-zone flushing time (timescale for particles to leave the surf zone) is a strong function of the wave directional spread (the range of incident wave angles). In dye tracer studies, tracer was observed up to three surf-zone widths offshore after 3–4 h (Hally-Rosendahl et al. 2015). In unstratified conditions, TRC-induced exchange was larger than Stokes drift–induced exchange out to two to five surf-zone widths offshore.

The development of a new model that couples a TRC-generating surf-zone model and an ocean circulation model that includes stratification (Kumar & Feddersen 2017a) has enabled the study of the interaction of TRCs and stratification on the inner shelf. **Figure 3** shows an example model

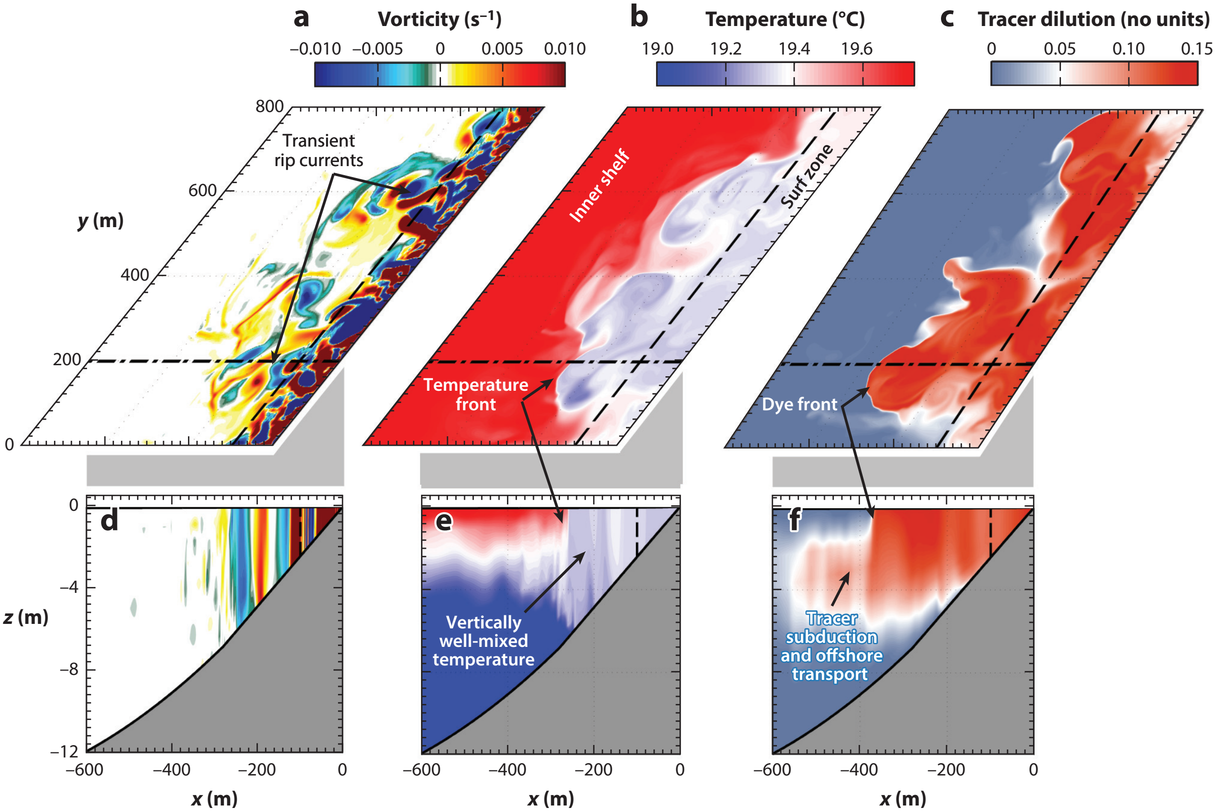


**Figure 3**

(*a–c*) Snapshots of near-surface vertical vorticity (panel *a*), temperature (panel *b*), and normalized tracer concentration (panel *c*) versus cross-shore (*x*) and alongshore (*y*) coordinates at 6 h after surf-zone dye release. The surf zone (onshore from the *dashed line*) has a width of 100 m, and the region offshore is the inner shelf. (*d–f*) Snapshots of cross-shelf transects of vertical vorticity (panel *d*), temperature (panel *e*), and normalized tracer concentration (panel *f*) versus cross-shore (*x*) and vertical (*z*) coordinates at $y = 200$ m (*dash-dotted lines* in panels *a–c*). Transient rip currents, surface temperature and dye fronts, a region with vertically well-mixed temperature, and the tracer subduction and offshore transport are highlighted. Adapted from Kumar & Feddersen (2017c) under the Creative Commons 4.0 Attribution-NonCommerical-NoDerivatives license (**https://creativecommons.org/licenses/by-nc-nd/4.0**).

simulation with a surf-zone-released tracer representative of early-stage larvae. In this example, with a significant wave height of approximately 1 m and initial stratification of 0.25 m °C$^{-1}$, TRCs ejected onto the initially stratified inner shelf leave a strong offshore eddy (vorticity) field (**Figure 3*a***) and break down the stratification two to three surf-zone widths offshore (**Figure 3*e***); farther offshore, the inner shelf is still stratified, with a strong meandering surface temperature front. TRC export also results in patchy tracer to within ~300 m from shore, with sharp surface tracer fronts (**Figure 3*c***). Farther offshore, isotherms slope in the cross-shelf direction, inducing an offshore along-shelf geostrophic velocity (Kumar & Feddersen 2017b). Tracer is subducted under this TRC-induced front and transported offshore in a subsurface layer 2–5 m below the surface between two isotherms. This offshore transport represents a previously unconsidered offshore transport pathway that, for typical conditions for Southern California, can transport across-shelf 1.2 km per day (Kumar & Feddersen 2017c). The pathway requires both TRCs and stratification. TRCs are ubiquitous on all wave-exposed coasts (both reflective and dissipative), and the inner shelf is often stratified. Thus, this offshore transport pathway may be an important mechanism for export of early-stage invertebrate larvae from the surf zone and across the inner shelf.

**2.2.2. Bathymetric-rip-current-driven exchange.** Many shorelines exhibit alongshore variability, and owing to continuity, these alongshore variations induce mean cross-shore flows. At headlands, canyons, or rip-channeled beaches, these flows can lead to strong BRCs that induce rapid exchange between the surf zone and inner shelf. On rip-channeled beaches, the offshore-directed rip currents are located at the deeper channels incised through the sandbars when wave breaking occurs (**Figures 1*b*** and **4*a***). These alongshore variations in wave-breaking-induced alongshore gradients in wave momentum fluxes and pressure describe the well-known rip-current circulation (Bowen 1969, Haller et al. 2002). MacMahan et al. (2006) and Dalrymple et al. (2011) have provided more detailed reviews of BRC generation and observations.

BRC circulation patterns can trap surface material within the surf zone (Talbot & Bate 1987, MacMahan et al. 2010) (**Figure 5*a***) as the surf-zone circulation moves material toward the center of an eddy (McLachlan & Hesp 1984, MacMahan et al. 2010, Fujimura et al. 2014) (**Figures 4*a*** and **5*a***). In a study by MacMahan et al. (2010), on the order of 20% of surface drifters exited the surf zone, a result that was relatively similar for several rip-channeled beaches throughout the world. Reniers et al. (2010) successfully modeled the observed surf-zone drifter exits and showed how they were related to the surf-zone width, wave height, and wave period (**Figure 4*b***). Castelle et al. (2014) numerically explored the bathymetric controls and found that the ratio of rip-channel spacing to surf-zone width was an important parameter in controlling rip-current exchange. On embayed (pocket) beaches with obliquely incident waves, BRCs also led to strong exchange offshore of the embayment (Castelle & Coco 2013). For mildly curving coasts, gradual cross-shore exchange between the surf zone and inner shelf can also be induced (**Figures 1*c*** and **5*b***). The details of BRCs and the cross-shelf exchange they induce can be affected by subtle bathymetric variations (Castelle et al. 2014).

To gain further insight into BRC exchange seaward of the surf zone, Brown et al. (2015) deployed drifters outside the surf zone (**Figure 4*c***). BRCs removed material from the surf zone, but as this material exited, new material entered, which can be explained by continuity (**Figure 4*c*,*d***). The BRC circulation patterns outside the surf zone were actually important for bringing material back into the surf zone (Brown et al. 2015) and were larger than the estimated Stokes drift (**Figure 4*d***), similar to TRCs. The cross-shelf exchange extended a few surf-zone widths offshore (**Figure 4*c***), representing the outer boundary for surf-zone-generated exchange, as for TRCs.

## 3. BEHAVIORAL PROCESSES

Zooplankton behaviorally mediate transport by physical processes, facilitating transport across the shelf and into the surf zone. They undertake migrations between adult and larval habitats that range from retention near adult habitats to cross-shelf migrations by regulating depth in a sheared water column, where surface and bottom currents flow at different rates or directions (Peterson 1998, Queiroga & Blanton 2005, Morgan 2014). The extent of these migrations is regulated by depth preferences and vertical migrations that are timed exogenously or endogenously by diel and tidal cycles over planktonic development. Depth regulation is cued primarily by gravity, hydrostatic pressure, and light and secondarily by temperature, salinity, and turbulence (Queiroga & Blanton 2005, Epifanio & Cohen 2016, Morgan 2017). Depth regulation may also facilitate cross-shelf transport to surf zones via internal waves, Stokes drift, downwelling (by upward swimming), and upwelling (by downward swimming) (Shanks 1995, Shanks & Brink 2005, Morgan et al. 2009a). In addition, late-stage larvae and postlarvae navigate to suitable settlement sites using hierarchies

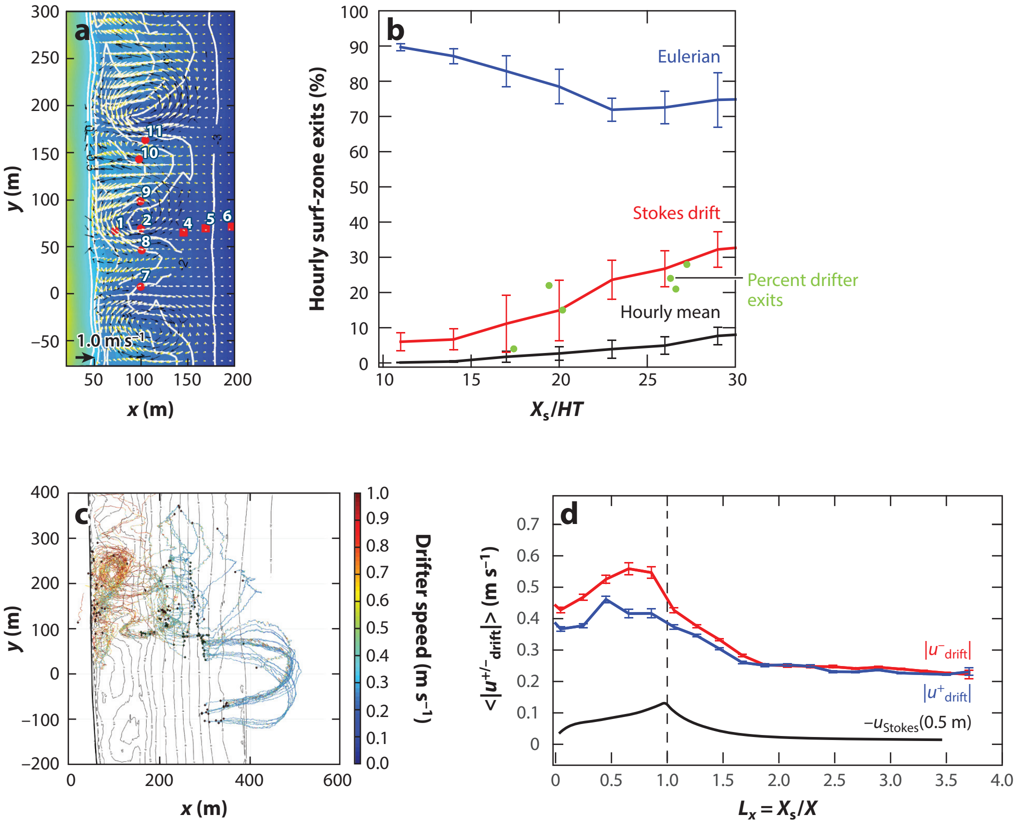


**Figure 4**

(*a*) Mean surface velocity vectors (with velocity scale shown in the *lower left corner*) from a surf-zone drifter deployment during the Rip Current Experiment (RCEX) for the surface drifters (*black arrows*), Eulerian model computations (*white arrows*), and Eulerian computations, including the Stokes drift (*yellow arrows*). The red circles and squares indicate the positions of the instruments. The bathymetry with bottom contours (*white lines*) in meters is included as a reference. (*b*) Model-estimated percentages of hourly surf-zone exits versus the drifter exit parameter (ratio of surf-zone width, $X_s$, to wave height, $H$, and wave period, $T$). The exits were calculated with Eulerian computations, including Stokes drift (*red line*), Eulerian (*blue line*), and hourly mean (*black line*) velocities ±1 standard deviation (*vertical bars*) from RCEX. The green dots show the observations of the percentage of drifter exits during RCEX for different deployment days. (*c*) RCEX drifter positions and speed. The color of the line represents the speed, indicating the locally contained cross-shore exchange drifter pattern. Bathymetry contours are shown in the background in black, the shoreline is shown as a thick black line, and the approximate surf-zone boundary, $X_s$, is shown as a dashed gray line. Green circles show drifter release locations, and red circles show drifter retrieval locations. (*d*) Mean drifter cross-shore velocity magnitude as a function of normalized cross-shore distance from the shoreline relative to surf-zone width ($L_x = X_s/X$). Shoreward drifter velocities are shown in red, seaward drifter velocities are shown in blue, and 95% confidence intervals are shown as vertical bars. The black line represents the theoretical estimate of Stokes drift averaged over the upper 0.5 m of the water column, $u_{\text{Stokes}}(0.5\text{ m})$, which corresponds to the depth of the surface drifters.

of acoustic, chemical, visual, and celestial cues that are effective at different distances (Kingsford et al. 2002, Leis et al. 2011).

Zooplankton may even be able to distinguish among hydrodynamic environments and alter behaviors by detecting differences in turbulence from shear and acceleration from waves (Fuchs & Gerbi 2016). Surf zones are most readily distinguishable based on accelerations from large shoaling waves and intense turbulence from breaking waves. These strong signals distinguish the surf zone in sheltered coastal habitats (where high shears from stratified and tidal currents along the benthic

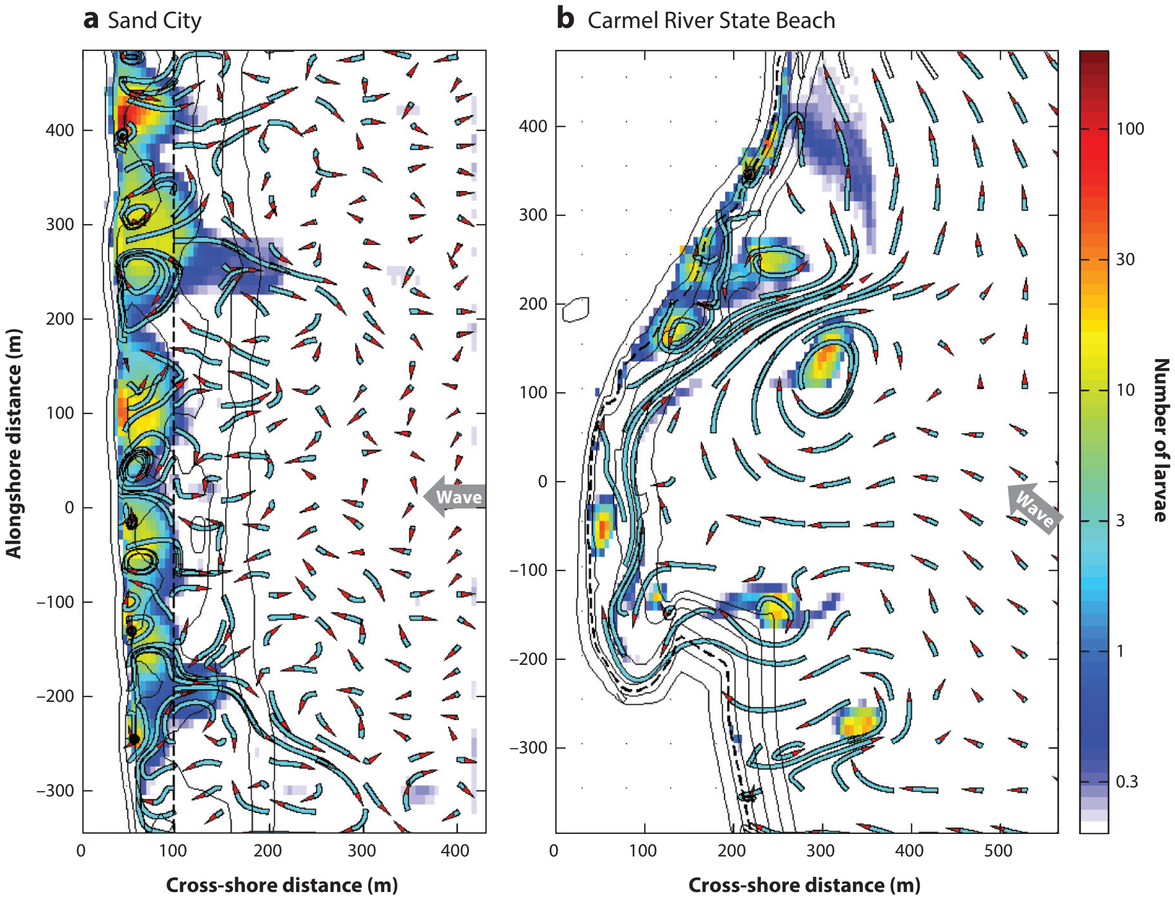


**Figure 5**

Modeled trajectories of depth-averaged Lagrangian velocities with an integration interval of 30 min in calm, light winds at (*a*) the more dissipative surf zone at the Sand City beach near Monterey, California, where the root mean square wave height was 0.54 m and the peak wave period was 8.75 s, and (*b*) the more reflective surf zone at Carmel River State Beach near Monterey, California, where the root mean square wave height was 0.4 m and the peak wave period was 9.45 s. The red tips indicate the direction of the velocity, the overlay color shows the time- and depth-averaged number of competent larvae obtained from the model, and the dashed line indicates the approximate edge of the surf zone. Bottom contour lines from 0 m (shoreline) to 5 m at 1-m increments are also shown. Adapted from Morgan et al. (2016).

boundary layer can occur with low accelerations from small waves) from the continental shelf (where moderate accelerations from moderate waves can occur with small shears). Shear is likely sensed as fluid deformation by external mechanoreceptors, such as antennae, or as rotation from vorticities by internal gravity detectors, such as statocysts, whereas the pressure gradient force from waves could be felt as a change in speed by accelerometers (Budelmann 1988). Mechanoreceptors or gravity detectors may be sufficient to identify surf zones as having high shear, but also using an accelerometer to sense pressure gradients from moderate waves could more definitively distinguish surf zones from inner-shelf habitats (Fuchs & Gerbi 2016). This potential ability to distinguish the surf zone from the inner shelf in other habitats might keep holoplankton from entering the surf zone, where high densities of predators occur, and might facilitate entry into the surf zone by larvae of intertidal and surf-zone species that developed farther from shore (Morgan et al. 2016).

**Holoplankton:** zooplankton that are permanent members of the plankton

# 4. TRANSPORT OF SUBSIDIES IN SURF ZONES

## 4.1. Transport of Subsidies to the Inner Shelf

**Upwelling front:** a front formed between the convergence of cold offshore water and warm surface water pushed offshore during wind-driven upwelling

The shoreward transport of larvae and phytoplankton blooms across the continental shelf to the shore is at least a two-step process: First they must be transported from offshore onto the inner shelf adjacent to the surf zone, and then they must enter the surf zone. Mechanisms of cross-shelf transport have been reviewed previously (Shanks 1995, Lentz & Fewings 2012). Briefly, phytoplankton often bloom, and zooplankton aggregate at upwelling fronts. The plankton are transported shoreward, sometimes reaching the inner shelf during prolonged relaxation or downwelling events (Shkedy & Roughgarden 1997, Adams et al. 2006). Plankton in surface waters can also be transported shoreward by onshore winds, often caused by the land and sea breeze system (Shanks 1995, Jacinto & Cruz 2008). Internal waves and bores can transport both phytoplankton (Ryan et al. 2005, Shanks et al. 2015) and larvae (Pineda 1999, Ladah et al. 2005, Shanks 2006, Shanks et al. 2014, MacTavish et al. 2016) from offshore to the inner shelf and outer edge of surf zones.

## 4.2. Phytoplankton: Surf-Zone Taxa

Historically, studies of phytoplankton in surf zones have focused primarily on surf-zone specialists, which have adapted to this habitat. The biomass and production of these taxa are higher in surf zones of dissipative bar-built beaches than just offshore, becoming extremely abundant under the right conditions (Campbell & Bate 1988, Kahn & Cahoon 2012). Nutrients are enriched by groundwater seepage in the surf zone, and currents generated by BRCs tend to retain phytoplankton in the surf zone, concentrating them within the eddy system and between the shore and offshore bars of intermediate and dissipative beaches (Campbell & Bate 1988, Kahn & Cahoon 2012).

Diatoms are the only phytoplankton that are adapted to the surf-zone habitat, and dinoflagellates and other flagellates are limited by the high turbulence of surf zones (Reynolds 2006). There are seven species of surf diatoms, which live in surf zones of high-energy intermediate and dissipative beaches and are absent at reflective beaches (Garver & Lewin 1981). They occur in South America, South Africa, India, Australia, New Zealand, the Iberian Peninsula, and the Pacific Northwest of the United States (Odebrecht et al. 2014). The main processes determining the distribution, biomass, and growth of surf diatoms are wave energy, beach slope and length, surf-zone circulation, and nitrogen availability. Peak concentrations occur when wind stress and wave energy are high during onshore winds and storms (Odebrecht et al. 2014). Nitrogen is replenished primarily by discharge of groundwater, especially after rains (Campbell & Bate 1988, Niencheski et al. 2007), as well as coastal upwelling (Lewin 1978).

As shoaling waves approach shore, high turbulence is generated, increasing the nutrient uptake, light exposure, and suspension of surf diatoms or resting spores from the sediment into the water column (Odebrecht et al. 2014). Some species of surf diatoms may produce a mucilaginous coat that adheres to air bubbles produced by breaking waves, causing them to accumulate in foam at the sea surface, where retention in BRC eddies is facilitated (Talbot & Bate 1987, Lewin et al. 1989, Talbot et al. 1990). Cells below the surface in the surf zone are transported onto the inner shelf with the rip-current flow and therefore are not concentrated in the surf zone; cells at the surface, by contrast, are carried into rip currents and transported beyond the breakers, tend to return to the surf zone via onshore flow over the shoals, and accumulate within the BRC eddy.

In species that produce a mucilaginous coat, particles adhere to a thicker coat produced in the afternoon until cells are deposited on the bottom (Talbot & Bate 1988a). However, a histochemical analysis indicated that the mucilage is probably not the feature that regulates the diel cycle, and other species without a mucilaginous coat also undertake diel vertical migrations (Lewin et al. 1989, Gayoso & Muglia 1991). Another species floats at the surface in both the daytime and nighttime (Lewin & Hruby 1973).

Alongshore currents advect surf diatoms from the ends of beaches longer than 4 km except when they are bounded by rocky headlands (Odebrecht et al. 2014). Surf diatoms that are washed from the surf zone beyond the breaker line during calm conditions may return when winds blow onshore (Du Preez & Bate 1992).

Because more reflective surf zones do not generate BRC systems, modeling studies suggest that surface drifters released in these surf zones tend to be transported offshore by TRCs without being returned to the surf zone (Suanda & Feddersen 2015, Hally-Rosendahl & Feddersen 2016, Kumar & Feddersen 2017c). Hence, surf diatoms attached to bubbles tend to be transported from the surf zone onto the inner shelf without returning, and populations of surf diatoms therefore do not occur in reflective surf zones.

## 4.3. Phytoplankton: Coastal Taxa

Intensive interdisciplinary studies have been conducted at an intermediate and a reflective beach near Monterey, California (Shanks et al. 2016, 2017b). At the intermediate beach, surf diatoms composed less than 1% of the phytoplankton in the surf zone, and the rest were typical coastal taxa. Concentrations of phytoplankton were far higher in the surf zone than offshore but still reflected the daily concentrations offshore (**Figure 6*d***). A BRC system caused the rapid exchange of water between the surf zone and the inner shelf but may have retained phytoplankton at the surface, similarly to drifter retention (Reniers et al. 2009, 2013; MacMahan et al. 2010; Brown et al. 2015). The BRC eddies appeared to redistribute and concentrate phytoplankton, leading to concentrations 100 times higher in the rip current than over the adjacent shoals (Shanks et al. 2017b). Filter feeders living under a rip-current eddy or at the head of a rip current, as the abundant mole crab *Emerita analoga* does (Shanks et al. 2016), will receive much higher concentrations of phytoplankton food than those living under shoals. Individuals associated with the rip current will likely grow more rapidly, have higher reproductive output, and concentrate more toxins from exposure to harmful algal species.

Although surf diatoms were uncommon at the intermediate beach, offshore phytoplankton species can also be caught by bubbles rising through the water column (Csordas & Wang 2004, Krichnavaruck et al. 2007) and often were highly concentrated ($>10^8$ cells $L^{-1}$) in surf-zone foam (Shanks et al. 2017b). Modeling suggests that coastal phytoplankton taxa floating at the surface in foam are concentrated in BRC eddies (Fujimura et al. 2014). The time phytoplankton spend at the surface may depend on the stability or longevity of the foam, resulting in higher concentrations in the eddies as the residence time of the foam increases. If the residence time within the surf zone is long, the higher growth rates of coastal phytoplankton in the surf zone might also contribute to greater abundances of phytoplankton there than offshore (Shanks et al. 2017b).

Although *Pseudo-nitzschia*, a genus of harmful algae, typically occurs offshore, particulate domoic acid produced by it was an order of magnitude higher in BRCs at dissipative beaches than just seaward of the surf zone (Trainer et al. 2010, Shanks et al. 2016). Particulate domoic acid was 1,000 times more concentrated in rip channels than in the shoals separating rip currents at the more dissipative beach near Monterey (Shanks et al. 2016). Consequently, concentrations of domoic acid in mole crabs from rip channels varied directly with the concentration of particulate domoic acid and *Pseudo-nitzschia* there rather than with the concentration of *Pseudo-nitzschia* offshore (Shanks et al. 2016). The amount of particulate domoic acid per *Pseudo-nitzschia* cell was

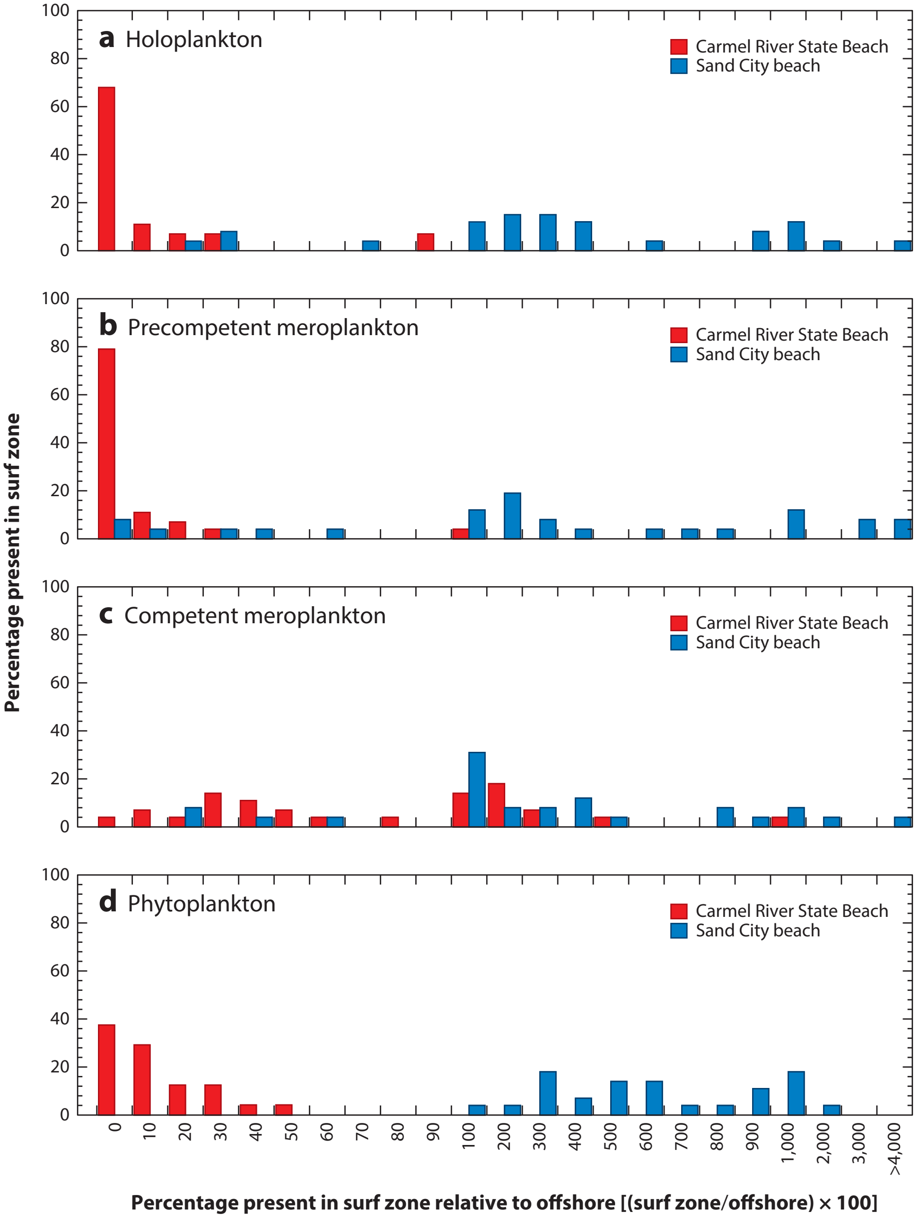


**Figure 6**

Percentages of offshore phytoplankton and zooplankton assemblages present in a reflective surf zone (Carmel River State Beach near Monterey, California; *red bars*) and a more dissipative surf zone with bathymetric rip currents (the Sand City beach near Monterey, California; *blue bars*): (*a*) holoplankton, (*b*) precompetent meroplankton, (*c*) meroplankton competent to settle, and (*d*) total phytoplankton. The median percentages were as follows for the reflective and intermediate locations, respectively: holoplankton, 4% and 389%; precompetent meroplankton, 2% and 276%; meroplankton competent to settle, 73% and 282%; and total phytoplankton, 14% and 668%.

also much higher in the surf zone than offshore, perhaps because stressful conditions in the surf zone stimulated the production of domoic acid.

By contrast, phytoplankton assemblages inside and outside the surf zone at the steep reflective shore near Monterey often appeared to be disconnected. Concentrations of typical coastal phytoplankton, including *Pseudo-nitzschia* spp., were usually lower by an order of magnitude or more in the surf zone than on the inner shelf, even just 20 m seaward of the breakers (Shanks et al. 2016, 2017b) (**Figure 6*d***). BRCs did not occur, and TRCs were not observed. BRCs may have been suppressed by waves impinging on the shore at an angle, thereby generating an alongshore current in the surf zone, as occurs at intermediate and dissipative beaches (Komar 1983, MacMahan et al. 2006). Without consistent rip currents, undertow likely slowed the exchange of water between the surf zone and offshore compared with the more dissipative shore.

The much lower concentrations of phytoplankton within the reflective surf zone were not due to consumption by filter feeders. Energetic breaking waves prevent the establishment of filter feeders at reflective beaches (McLachlan & Brown 2006), and no filter feeders were observed in the surf zone at the study site. Preliminary evidence indicated that the concentration of phytoplankton in surface water entering the surf zone with breaking waves was low, limiting delivery of phytoplankton subsidies to the surf zone.

Phytoplankton subsidies from the inner shelf to the intertidal zone were also at least an order of magnitude higher at surf zones that were closely spaced (median distance 1 km) and more dissipative than reflective, even though differences in the concentration of phytoplankton outside the surf zone should be small (Shanks et al. 2017c). Surf-zone width explained 60–90% of phytoplankton concentration variation, as at the pair of reflective and dissipative surf zones near Monterey (Shanks et al. 2017b).

## 4.4. Zooplankton

Like coastal phytoplankton, more coastal zooplankton occurred in dissipative surf zones, where BRC systems could redistribute and concentrate them (Morgan et al. 2016, 2017; Stull et al. 2016). Dominant taxa in the surf zone also occurred on the inner shelf, such as copepods, mysids, amphipods, chaetognaths, and fish larvae, whereas others likely originated in adjacent estuaries, such as decapod larvae and megalopae (Modde & Ross 1981, DeLancey 1989, Watt-Pringle & Strydom 2003, Defeo & McLachlan 2011, Morgan et al. 2016).

As with phytoplankton, opposite patterns in the relative concentrations of zooplankton inside and outside the surf zone were observed at the intermediate and reflective surf zones near Monterey (Morgan et al. 2016, 2017) (**Figure 6*a–c***). Zooplankton concentrations of all taxa were higher inside the more dissipative surf zone and outside the reflective surf zone (**Figure 6*a–c***). Zooplankton were also far more concentrated in rip channels than over adjacent shoals at the more dissipative surf zone. These patterns were evident despite the high diversity of zooplankton assemblages at each site. Thus, surf-zone hydrodynamics profoundly affected the exchange of zooplankton between the surf zone and offshore waters, resulting in different patterns of concentration for entire plankton assemblages in the intermediate surf zone than in the reflective surf zone.

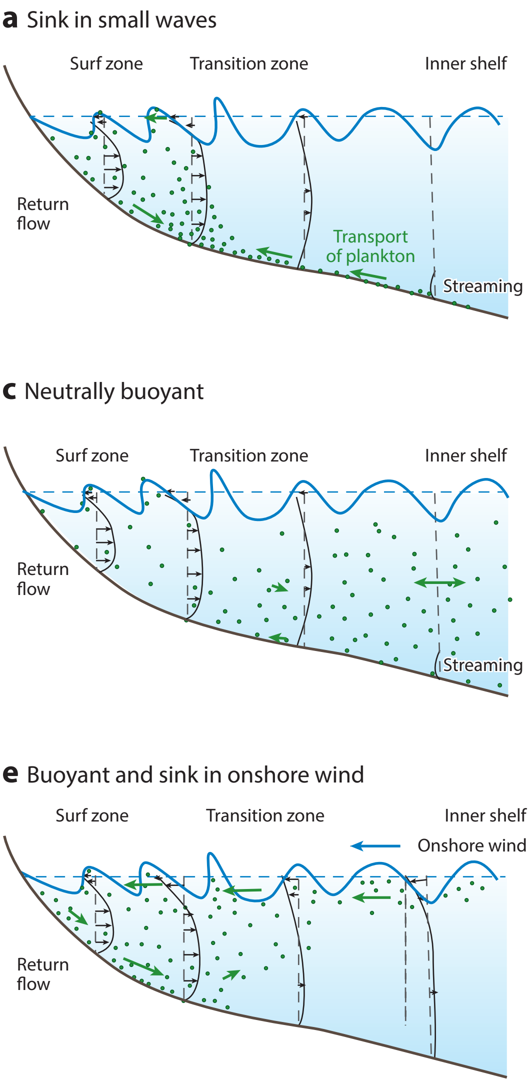
Unlike phytoplankton assemblages, the abundance of zooplankton inside and just outside the surf zone generally was not positively correlated at either the intermediate or reflective site near Monterey (Morgan et al. 2017). At the intermediate surf zone, less than half of the 16 most abundant zooplankton taxa were positively correlated inside and outside the surf zone. The lack of correlations might have occurred because zooplankton are better able to regulate depth rather than being passively distributed throughout the water column, which might alter the extent of accumulation in rip channels by recirculation cells. Zooplankton at the surface should be transported by wind and Stokes drift, and those at the bottom should be transported onshore by benthic streaming, whereas zooplankton distributed throughout the rest of the water column should be held away from the surf zone by undertow (**Figure 7**).

At the reflective surf zone near Monterey, several zooplankton taxa were positively correlated inside and outside the surf zone and were more abundant inside rather than outside the surf zone, unlike other members of the plankton assemblage (Morgan et al. 2017) (**Figure 6*a–c***). Harpacticoid copepods, juvenile parasitic bopyrid isopods, and barnacle postlarvae all likely occurred near the bottom, where benthic streaming facilitated their transport into the surf zone (**Figure 7**). Furthermore, passively sinking detritus was more abundant inside than outside the surf zone when waves were small, further suggesting that wave-induced streaming may transport zooplankton in the benthic boundary layer onshore (Shanks et al. 2015). Deposited material is resuspended by breaking waves at the shore break and transported into the surf zone (Reniers et al. 2013). During a lull in the waves, low-density bed material settles close to the narrow edge of the surf zone, and when the next set of large waves breaks farther offshore, these particles and zooplankton may be transported into the surf zone. During large-wave events, turbulence near the bottom is high, and low-density particles (detritus) and zooplankton are prevented from accumulating near the bottom. Because of their higher sinking rates, dense particles and organisms, such as late-stage mussel larvae, can accumulate in the boundary layer even when waves are large and may be transported shoreward by streaming (Navarrete et al. 2015). Many species descend in the water column late in development (Thorson 1964, Queiroga & Blanton 2005) and sink in response to turbulence (Fuchs & DiBacco 2011, Roy et al. 2012, Fuchs et al. 2013); therefore, benthic streaming may transport competent larvae near the surf zone onshore to adult habitats at both dissipative and reflective shores (**Figure 7**).

A three-dimensional hydrodynamic model based on measured physical data at the more dissipative and reflective beaches near Monterey and the swimming behavior of zooplankton (depth preferences and sinking in response to turbulence) demonstrated that behavior facilitated cross-shore zooplankton transport at both beaches in two ways (Fujimura et al. 2013, 2014; Morgan et al. 2016) (**Figure 5**). Benthic streaming transported simulated zooplankton in the bottom boundary layer onshore when winds were calm (**Figure 5*a***). Simulated zooplankton near the surface drifted to the surf zone in surface currents during onshore winds and sank upon reaching the turbulent surf zone, whereupon benthic streaming transported them shoreward (**Figure 7*e***). By contrast, undertow may prevent holoplankton and precompetent larvae between the near surface or near bottom from entering surf zones (**Figures 6*a*,*b*** and **7*c***). Simulated larvae released offshore were orders of magnitude more abundant at the more dissipative shore, where they were concentrated in rip channels by BRCs (**Figure 5**).

Settlement of cyprids on rocks in northern California and Oregon was orders of magnitude lower in reflective surf zones than at dissipative shores, where more efficient exchange of offshore and surf-zone water enables competent larvae to cross the surf zone (Shanks et al. 2010). Barnacle settlement on rocks was greatest during large-wave events at more dissipative shores (Shanks et al. 2010), consistent with modeled increasing exchange between the surf zone and inner shelf with wave height (Suanda & Feddersen 2015). Barnacle settlement was not related to wave height at the reflective shore near Monterey because undertow may impede the onshore transport of competent larvae (Shanks et al. 2014). Thus, larval subsidies from the inner shelf to the intertidal zone should be higher at shores adjacent to more dissipative surf zones than at those adjacent to more reflective ones, especially during large-wave events.

A follow-up survey of 40 diverse rocky shores with different surf-zone types along the west coast of the United States revealed that barnacle recruitment was often more than an order of magnitude greater at dissipative shores than at intermediate shores with BRCs and was



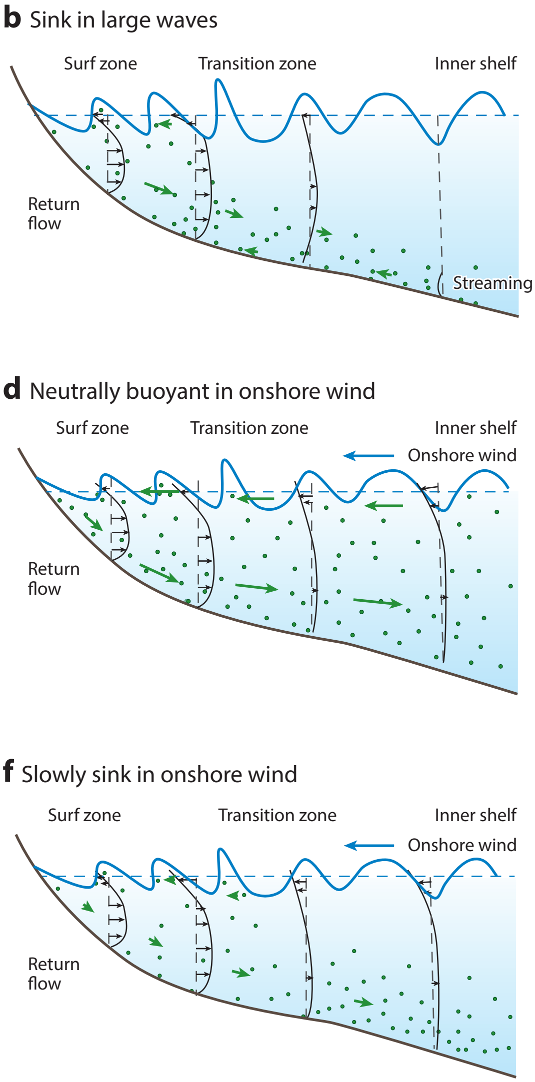
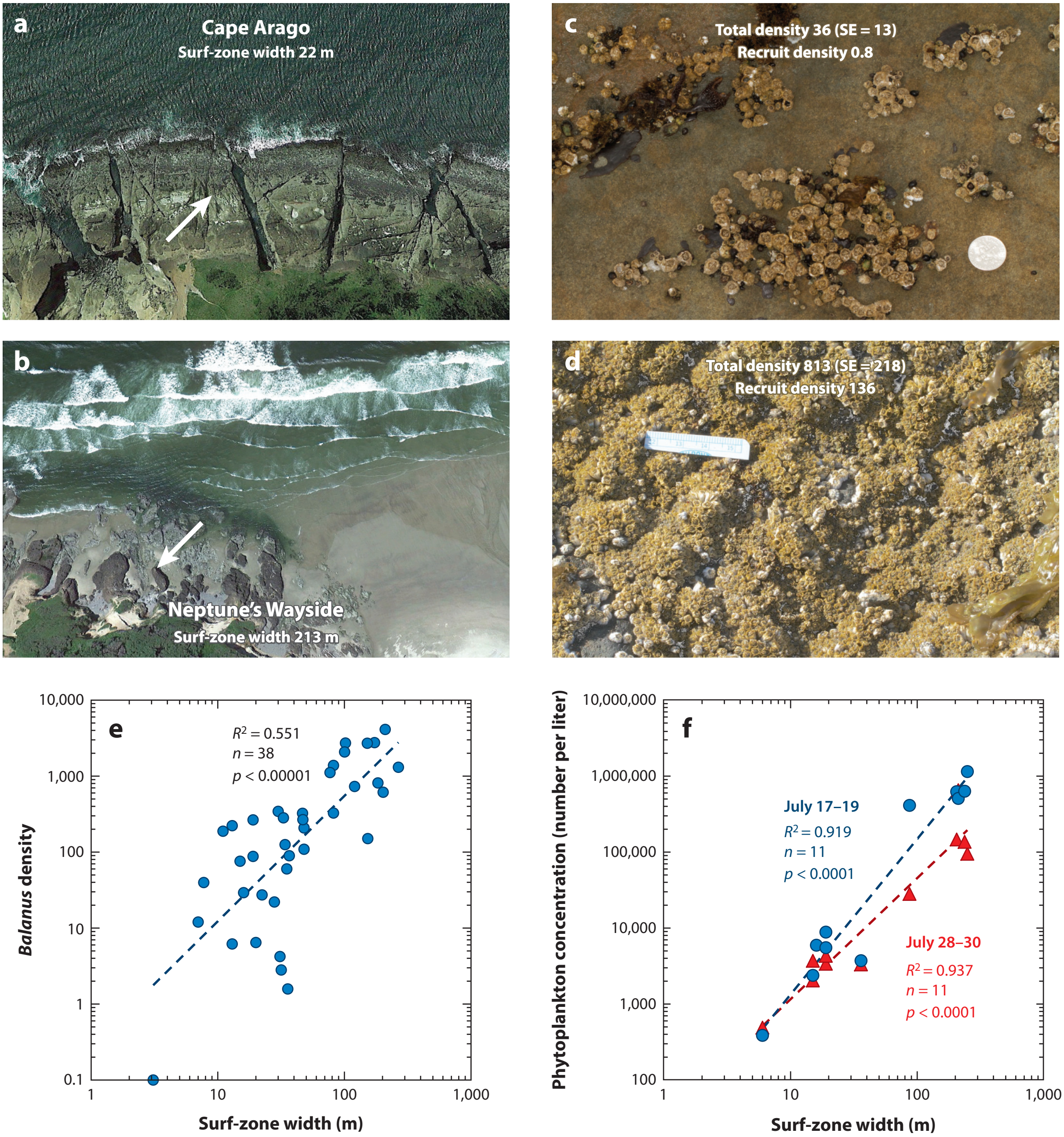


**Figure 7**

Proposed cross-shore transport mechanisms at Carmel River State Beach, a reflective beach near Monterey, California. (*a*) Streaming is effective when waves are small because sinking plankton stay close to the bed, where shoreward velocities are high. (*b*) Streaming is less effective when large waves suspend sinking plankton from the streaming zone, reducing the influx of plankton from offshore. (*c*) If plankton avoid or sink from the surface, then they are not carried into the surf zone by near-surface turbulent onshore transport and are held away from the surf zone by offshore undertow currents. (*d*) During onshore winds, the flow moves into the surf zone near the surface and offshore throughout the remainder of the water column within the surf zone. (*e*) Concentrations of buoyant plankton sink after they encounter increased turbulence in the surf zone when the wind is onshore. (*f*) Exchange of slowly sinking plankton is minimal between the inner shelf and surf zone when winds are onshore; the exchange rate depends on sinking velocity. Green arrows represent transport of plankton (*dots*). Adapted from Morgan et al. (2017).

lowest at reflective shores and one dissipative shore that lacked rip currents (Shanks et al. 2017a) (**Figure 8**). Barnacle settlement (monitored daily) and recruitment (tracked weekly) were also 10–100 times greater at more dissipative shores than at reflective shores, demonstrating that documented patterns from the latitudinal survey occurred for months at a subset of the study sites. Population density, settlement, and recruitment were much greater at more dissipative surf zones even when sites were less than 5 km apart. New recruits composed more of barnacle populations



and density-dependent effects were more common at dissipative shores than at reflective shores. Low densities of both adults and new recruits at reflective shores indicated that populations were limited by larval recruitment.

BRC systems appeared to be key in regulating recruitment along the west coast of the United States (Shanks et al. 2017a). Densities of new recruits were much greater at dissipative and intermediate surf zones with BRCs. For example, the density of new recruits was very low at the wide, more dissipative surf zone of Nesika Beach in Oregon because of an absence of BRCs, a result of an alongshore current in the surf zone that was generated by waves approaching the shore at a steep angle. BRC systems appeared to be critical to the free exchange of plankton between the inner shelf and surf zone because in the absence of those systems, undertow limits the delivery of plankton subsidies from the ocean to shore (Shanks et al. 2015, 2016; Morgan et al. 2016).

Barnacle densities, but not new recruits, were higher at more northern latitudes than at southern latitudes during the coast-wide survey (Shanks et al. 2017a). Previous longer-term studies found higher densities of both new recruits and adults at higher latitudes and attributed this pattern to weaker, less persistent upwelling north of Cape Blanco, Oregon (Connolly & Roughgarden 1998, Connolly et al. 2001, Broitman et al. 2008), although surf-zone hydrodynamics was not considered. This latitudinal pattern could also be due to higher solar radiation to the north than to the south of Cape Blanco, which increases the mortality of settlers and older intertidal organisms from desiccation and thermal stress as well as ultraviolet radiation damage. However, thermal hot spots caused by seasonal afternoon low tides are also important (Helmuth et al. 2002). Higher barnacle densities along the Oregon and Washington coast compared with the northern California coast might also result from chlorophyll *a* concentrations (indicating plankton abundance) that are several times higher there (Hickey & Banas 2008), which would provide more food for adults and larvae, increasing reproductive output or larval survival (Morgan 2001).

Newly released larvae and gametes may be rapidly transported from the surf zone by undertow, subducted on stratified inner shelves, and transported offshore (Kumar & Feddersen 2017a–c) (**Figure 3**). First-stage larvae of *E. analoga* were released into the surf zone at the intermediate beach near Monterey and dispersed offshore quickly enough that second-stage zoea were not collected (Morgan et al. 2009b), indicating that they had escaped the recirculation of the surf zone by the time they molted to the second larval stage (>1 week).

## 4.5. Effects on Communities

The high abundance of surf diatoms in intermediate and dissipative surf zones at beaches with BRCs results in exceptionally high levels of primary production that support invertebrates (Barros et al. 2001, McLachlan & Dorvlo 2005, Rodil et al. 2006, Dugan et al. 2010) and fishes (McLachlan

**Figure 8**

(*a*,*b*) Examples of rocky shores with a narrow, reflective surf zone (Cape Arago, Oregon; panel *a*) and a wide, more dissipative surf zone (Neptune's Wayside, Oregon; panel *b*). Arrows indicate the approximate locations at which the photographs in panels *c* and *d* were taken. (*c*,*d*) Photographs of barnacle populations at Cape Arago (panel *c*) and Neptune's Wayside (panel *d*). The total density (number per 100 cm$^2$) is the average of 5–10 photographs, with the standard error (SE) also shown; the recruit density was determined by multiplying the size frequency distributions (percentage of the population less than 1.5 mm in diameter) by the overall density. For scale, note the dime in panel *c* and the 3.5-cm rule in panel *d*. (*e*) Relationship between surf-zone width and the density (number per 100 cm$^2$) of *Balanus* sp. Samples were collected at 36 sites from San Diego, California, to central Washington state. Surf-zone width is the average of 3–10 Google Earth images. (*f*) Relationship between surf-zone width and the concentration of coastal phytoplankton species (typical surf diatoms were absent). Samples were collected during two three-day periods (July 17–19 and July 28–30) from closely spaced sites (median separation 1 km) around Cape Arago, Oregon. For details, see Shanks et al. (2017a).

& Hesp 1984, Layman 2000, Inoue et al. 2008, Manning et al. 2013). At many locations, more than 50% of the organic carbon can be dissolved organic carbon (Du Preez & Campbell 1996), although more than 50% of particulate organic matter was detritus at one location (Talbot & Bate 1988b). The high concentrations of surf diatoms, particulate organic matter, and detritus can sustain short and highly productive food webs in beach surf zones (Odebrecht et al. 2014). Filter-feeding benthic invertebrates, such as clams, polychaetes, and mole crabs, are the main consumers, with mysids and copepods playing important roles as pelagic consumers. These organisms collectively support secondary and tertiary consumers, such as fishes, birds, and even marine mammals (Garcia & Gianuca 1997, McLachlan & Brown 2006). More dissipative surf zones serve as nursery habitats for larval and juvenile fishes, which feed on the high concentrations of zooplankton (McLachlan & Hesp 1984, Watt-Pringle & Strydom 2003, Inoue et al. 2008), as well as for adult planktivores, such as anchovies and silversides (Modde & Ross 1981, DeLancey 1989, Du Preez et al. 1990). Surf diatoms also support interstitial meiofauna, which in turn provide dissolved inorganic nutrients to fuel primary production and the microbial loop in the water column (McGwynne 1991, McLachlan & Brown 2006). Much of the production of surf diatoms also enters the microbial loop that recycles nutrients (McGwynne 1991, McLachlan & Brown 2006). Surf diatoms can also be heavily deposited in the supratidal zone after storm events, feeding insects and ghost crabs (Garcia & Gianuca 1997).

Concentrations of zooplankton, dominated by copepods, mysids, and amphipods, differed among dissipative, intermediate, and reflective surf zones every month for two years in Japan, with the highest abundance of zooplankton occurring at dissipative beaches and the lowest occurring at reflective beaches (Nakane et al. 2013). These differences were attributed to the higher concentrations of phytoplankton and nanoplankton that serve as food for zooplankton as well as possible BRCs passively accumulating both phytoplankton and zooplankton at the dissipative beach. Concentrations of amphipods and mysids may also be lower in the harsh, coarse-grained sand of reflective surf zones because they cannot burrow into coarser sediments (Nel et al. 1999) or tolerate turbulent swashes (Defeo & McLachlan 2011). Zooplanktivorous fishes showed the same pattern as their prey, with the highest abundances of all species and the highest species richness occurring at the dissipative beach and the lowest occurring at the reflective beach each month (see also Romer 1990, Clark 1997, Layman 2000, Inui et al. 2010). Fishes were also smaller at the dissipative beach because they are weaker swimmers and prefer calmer conditions (Watt-Pringle & Strydom 2003). The abundance of piscivorous fishes was similar in all three types of surf zones, and previous studies have not been able to demonstrate that surf zones serve as refuges from fish predation (Baker & Sheaves 2007, Nakane et al. 2009).

The growth rates and reproductive output of intertidal filter feeders and the structure of rocky intertidal communities vary with the amount of phytoplankton in the surf zone (Menge et al. 1997b; Leslie et al. 2005; Phillips 2005, 2007; Bracken et al. 2012). Therefore, filter feeders in the rip channels of beaches should be better fed and more fecund and should grow faster than those on shoals, but they are also exposed to higher concentrations of toxins from harmful algal blooms (Shanks et al. 2016). Concentrations of domoic acid were much higher at intermediate and dissipative beaches with rip currents than at reflective beaches, and they were far higher in rip channels than in adjacent shoals just meters away (Shanks et al. 2016). Both ecological and public health monitoring programs should focus on sampling sentinel species, such as razor clams and mole crabs, during low tide from rip currents in dissipative and intermediate surf zones (Altwein et al. 1995, Ferdin et al. 2002). By contrast, mussels living on rocky, more reflective shores are usually not contaminated by domoic acid (Scholin et al. 2000, Ferdin et al. 2002).

Surf-zone hydrodynamics has not been considered when determining subsidies of phytoplankton to rocky shore communities. Differences in chlorophyll *a* at two sites in seminal studies conducted on rocky shore communities in Oregon might be due to differences in surf-zone hydrodynamics (Menge et al. 1997a,b). The rocky shore at Strawberry Hill consists of large rocky benches surrounded by sandy beaches with a wide surf zone and appears to be more dissipative than Boiler Bay, which has a narrow surf zone (Shanks et al. 2017c). Chlorophyll *a* concentrations at Strawberry Hill were consistently approximately an order of magnitude higher than those at Boiler Bay.

A study by Shanks et al. (2010) found that surf-zone hydrodynamics had opposite effects on macroalgae and barnacles. In the later coast-wide survey, higher densities and percent cover of macroalgae occurred at sites with narrower surf zones, with densities and percent cover approaching zero at sites with surf zones wider than approximately 50 m (Shanks et al. 2017a). The planktonic duration of spores of many taxa of macroalgae is far shorter (hours to days) than that of barnacle larvae (weeks), so the hydrodynamics of reflective surf zones might have maintained algal propagules close to shore, contributing to the observed higher density of macroalgae. Alternatively, barnacles might have outcompeted macroalgae for space at dissipative shores where cyprids settled abundantly, because the percent cover of the macroalgae was very low, whereas that of the barnacles approached 100%.

## FUTURE ISSUES

1. Much of ecological theory of intertidal communities has been developed from research on rock benches, but little is known about surf-zone dynamics in this challenging environment. Rock benches are typically steep and highly reflective, and therefore larval and food subsidies to intertidal communities may often be low.
2. The higher settlement and recruitment rates of barnacles at more dissipative shores compared with reflective shores should result in stronger postsettlement interactions and density-dependent effects at more dissipative shores, but does surf-zone hydrodynamics similarly affect the delivery, settlement, and postsettlement interactions of other taxa?
3. Are macroalgae more abundant at reflective shores than at dissipative shores because of the slower exchange of water and retention of spores with short development times at reflective shores, or because of competition for space with barnacles and other abundant invertebrate settlers at dissipative shores?
4. Low concentrations of phytoplankton and zooplankton at one reflective surf zone were proposed to be due to their low concentrations in surface water that is transported into the surf zone by turbulence from breaking waves, but is this generally the case? Does avoidance of surface waters contribute to this pattern for zooplankton?
5. How do alongshore currents affect the delivery of subsidies to shore? Is surface water transported into the surf zone by wave turbulence and the source of water feeding alongshore currents typically low in plankton concentrations, as proposed for the reflective surf zone near Monterey? What is the residence time of water in the surf zone when alongshore currents are present?
6. How do rip currents affect cross-shore exchange of plankton subsidies? The interaction of transient rip currents and bathymetric rip currents with other processes, such as wind and diurnal heating and vertical variation in stratification, may be important in cross-shelf exchange, becoming inactive only when strong winds break down stratification.

7. Hydrodynamics models and time series of larval abundance and settlement indicate that benthic streaming may deliver larvae onshore, but actual measurements of the process are needed. Is benthic streaming affected by the sharp step into deeper water at the seaward edge of many rock intertidal benches? Do late-stage larvae of many species descend in the water column as an adaptation for exploiting onshore transport by benthic streaming? Are filter-feeding benthic animals more abundant in areas where benthic streaming is present?
8. A comprehensive field experiment that combines intensive measurements coupled with modeling approaches is needed to determine how plankton are transported from the inner shelf into the surf zone and onshore. Field observations might include flow, temperature, turbulence, and concentrations of planktonic species throughout the water column, extending alongshore to several surf-zone widths offshore at dissipative and reflective shores, including rocky shores. This experiment would establish the contributions of surface gravity and internal waves, Stokes drift, transient rip currents, bathymetric rip currents, and benthic streaming in transporting plankton subsides onshore.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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