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Surf zones regulate larval supply and zooplankton subsidies to nearshore communities

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Abstract

Surf zone hydrodynamics vary along shorelines potentially affecting the delivery of larvae and zooplankton subsidies to intertidal communities, and, hence, the intensity of postsettlement interactions, growth and reproduction of filter-feeding foundation species and planktivorous fishes. We investigated the ability of zooplankton assemblages to enter the wide surf zone of the rip-channeled, more dissipative beach at Sand City, California, and the narrow surf zone of the steep reflective beach at nearby Carmel River State Beach. Every day for a month, we surveyed zooplankton inside and outside the surf zone and concomitant larval settlement of the dominant invertebrate onshore at each site in this upwelling regime. At the more dissipative surf zone, all zooplankters were far more concentrated inside than outside the surf zone. Many taxa increased in the surf zone and the predominant invertebrate on beaches, *Emerita analoga*, settled abundantly when prevailing northwesterly winds relaxed and waves were small. At the reflective surf zone, concentrations of zooplankters of most taxa were far greater outside than inside the surf zone, and many taxa increased in the surf zone when waves were small. Twice as many taxa were positively correlated inside and outside the surf zone at the dissipative than the reflective surf zone, indicating that zooplankters were more freely exchanged although behavior also played a role. Thus, spatial and temporal variation in surf zone hydrodynamics may regulate subsidies of zooplankton food and larval recruits to nearshore communities with potential cascading effects on community dynamics and structure.

Variation in larval supply and subsidies of nutrients and plankton can have a profound effect on coastal communities. Variation in larval supply affects the density of settlers and the intensity of postsettlement interactions (Morgan 2001; Underwood and Keough 2001), and variation in food in the form of phytoplankton and zooplankton affects growth and reproduction of filter-feeding invertebrates forming the foundation of intertidal communities (Bustamante et al. 1996; Menge et al. 1997, 2003). Larvae and planktonic food must cross from the inner shelf through the surf zone to reach intertidal communities. The characteristics of surf zones vary considerably along coastlines as determined by the interaction of breaking waves with variation in coastal

morphology (Wright and Short 1984; McLachlan and Brown 2006), potentially affecting the supply of larvae and food subsidies to intertidal communities.

At one end of the spectrum, dissipative beaches are characterized by 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 grain sand (Fig. 1A; Thornton and Guza 1983). Larvae and plankton may be transported into the surf zone by onshore winds and waves near the surface by Stokes drift (Fig. 2; Tilburg 2003; Fewings et al. 2008; Lentz et al. 2008). They also may be transported into the surf zone by wave-driven near-bed transport, called benthic streaming (Fig. 2), whereby a wave boundary layer is generated by the dissipation of energy near the bottom and flow forms in the direction of wave propagation (Longuet-Higgins 1953). The velocity of benthic
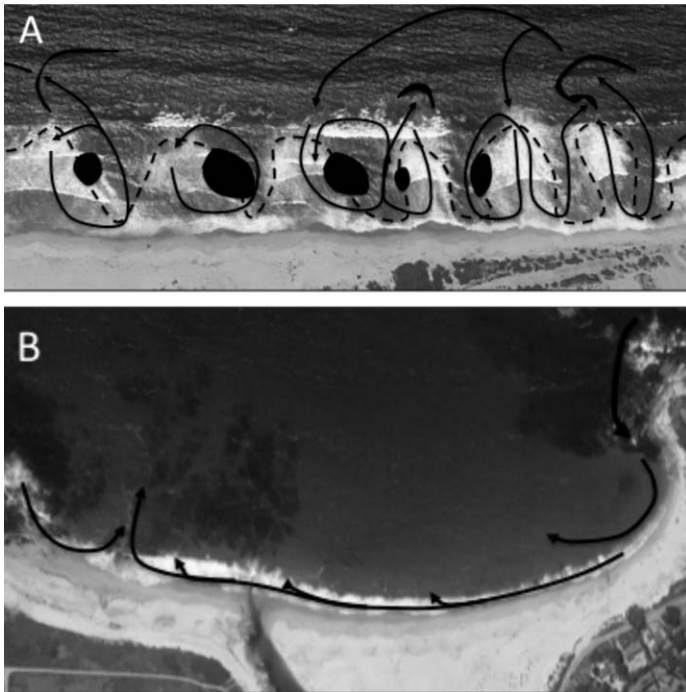
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Fig. 1. Bathymetric rip current recirculation pattern at the (**A**) dissipative Sand City beach and (**B**) recirculation pattern at the reflective Carmel River State Beach (lower panel) generated by topographic alongshore currents. Arrows represent currents, spots represent the core of rip current eddies and dashed line outlines alternating the bathymetry of rip current channels and shoals separating the rip currents.

streaming increases toward the surf zone as shoaling waves grow larger. When waves break, streaming is suppressed by compensatory return flow throughout most of the water column, called undertow, and material is deposited in this convergence zone (Reniers et al. 2013). Subsequent breaking waves then mix this material back into the water column and transport it into the surf zone (Reniers et al. 2013).

At the other end of the spectrum, steep reflective beaches are characterized by lower wave energy that is reflected back as waves surge onshore resulting in standing waves, narrow energetic surf zones and narrow beaches consisting of coarse grain sand (Fig. 1B; Battjes 1974; Elgar et al. 1994). Most beaches are intermediate, falling along the spectrum between dissipative and reflective beach types. Some rocky shores also are reflective.

Without rip currents, surface waves drive offshore Eulerian flows in the upper water column that may reduce the onshore transport of material into the surf zone from the inner shelf (Lentz et al. 2008; Ohlmann et al. 2012). In the presence of rip currents, the exchange between the inner shelf and surf zone is increased (Smith and Largier 1995; MacMahan et al. 2010; Brown et al. 2015), because water episodically exiting the surf zone in rip currents is balanced by water flowing into the surf zone over shoals alongside rip channels (Fig. 1A; Reniers et al. 2009, 2010). Within the surf

zone, water entering over the shoals, diverges along the beach face, enters the rip channel where the current deflects at the edge of the surf zone and subsequently returns over the shoals, creating a quasi-steady recirculation pattern (MacMahan et al. 2009). The quasi-steady rip current recirculation can concentrate fine sediments, detritus, and plankton (McLachlan and Hesp 1984; Nakane et al. 2013; Fujimura et al. 2014). Rip currents strengthen with increasing wave height and low tides (MacMahan et al. 2005). Rip currents are absent at reflective beaches, and thus the delivery of larvae and plankton subsidies into the surf zone by onshore wind, Stokes drift and benthic streaming may be limited.

Buoyancy or behavior of plankters interacts with physical processes, potentially affecting transport into surf zones (Fig. 2). Plankton near the surface may be transported into the surf zone via the sea breeze during the daytime (Jacinto and Cruz 2008) or via Stokes drift in large shoaling waves that are refracted toward shore (Morgan et al. 2009*a*; McPhee-Shaw et al. 2011). Plankton near the bottom may be transported together with sediment through the surf zone by benthic streaming (Lentz et al. 2008; Navarrete et al. 2015; Shanks et al. 2015). Benthic streaming may deliver heavy zooplankters that passively sink to the bottom following mixing by large waves (Navarrete et al. 2015) or swim to the bottom in response to turbulence (Fuchs and DiBacco 2011; Roy et al. 2012; Fuchs et al. 2013). In contrast, lighter or weakly swimming zooplankton and detritus would take longer to reach the bottom and may be transported onshore by benthic streaming following mixing by less turbulent small waves (Shanks et al. 2015).

We began determining the importance of surf zone characteristics to onshore transport by contrasting larval recruitment to populations of barnacles and limpets on rocks at dissipative and reflective shores along the west coast of the U.S.A. (Shanks et al. 2010). Recruitment and population densities were much higher at shores associated with dissipative than reflective surf zones, indicating that surf zone hydrodynamics may play a major role in determining larval supply to intertidal communities. Recent studies have shown that many larvae of intertidal and shallow-water species complete development within a few kilometers from shore, in the coastal boundary layer of reduced flow, along this coast and in other upwelling and non-upwelling regimes (Shanks and Shearman 2009; Fisher et al. 2014; Morgan 2014). Crossing the surf zone is the final step in recruiting to adult intertidal habitats.

In this study, we investigated processes that may affect transport of plankton and settlement of larvae into different types of surf zones. We conducted intensive interdisciplinary studies near Monterey, California, U.S.A. in a more dissipative surf zone with rip currents and a more reflective surf zone. We determined (1) the extent to which zooplankton is exchanged between offshore waters and the surf zone, (2) processes that may facilitate transport of meroplankters
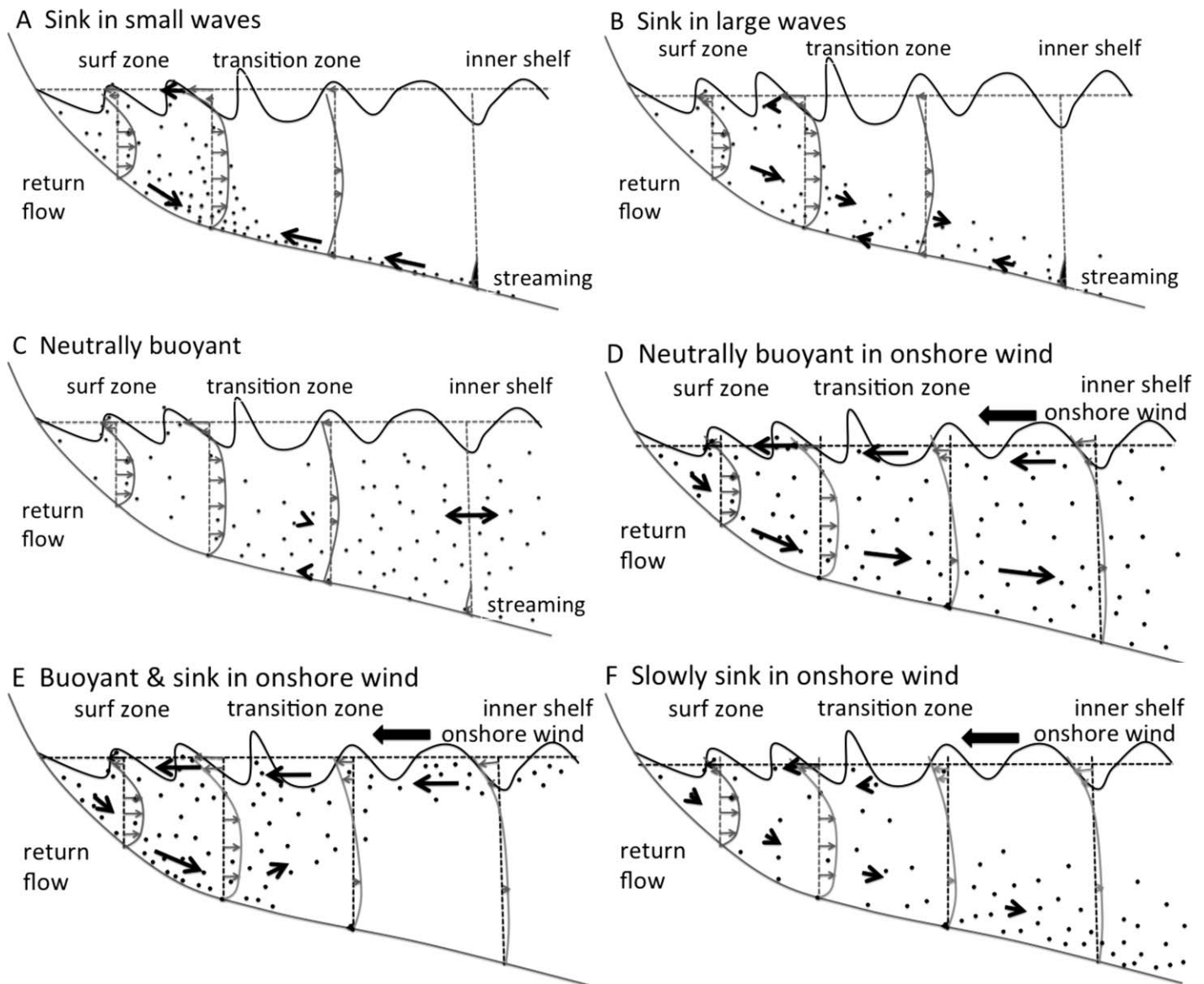
Fig. 2. Proposed cross-shore transport mechanisms at the reflective Carmel Beach River State Beach. (**A**) Streaming is effective while waves are small because sinking plankton stays close to the bed where shoreward velocities are high. (**B**) Streaming is less effective when large waves suspend sinking plankton out of the streaming zone, reducing the influx of plankton from offshore. (**C**) If plankters 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, flow will be 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 that sink after they encounter increased turbulence in the surf zone when wind is onshore. (**F**) Exchange of slowly sinking plankton is minimal between the inner shelf and surf zone while winds are onshore; the exchange rate depends on sinking velocity. Arrows represent transport of plankton (dots).

(temporary residents of the plankton) and holoplankters (permanent residents of the plankton) into the surf zone and (3) settlement at the two types of beaches. We compared entire zooplankton assemblages inside and outside the surf zone and larval settlement by the predominant macroinvertebrate inhabiting beaches, the mole crab *Emerita analoga*, daily for 1 month at each location while monitoring hydrodynamics from offshore waters through the surf zone to shore. We hypothesized that zooplankters of diverse taxa would more likely be exchanged across the more dissipative surf zone increasing the supply of larvae and planktonic food to nearshore communities. Thus, comparing the concentrations of diverse taxa in a plankton assemblage will indicate whether surf zone hydrodynamics affect the ability of all zooplankters to enter and remain in the surf zone and larvae to settle onshore or whether potential differences in
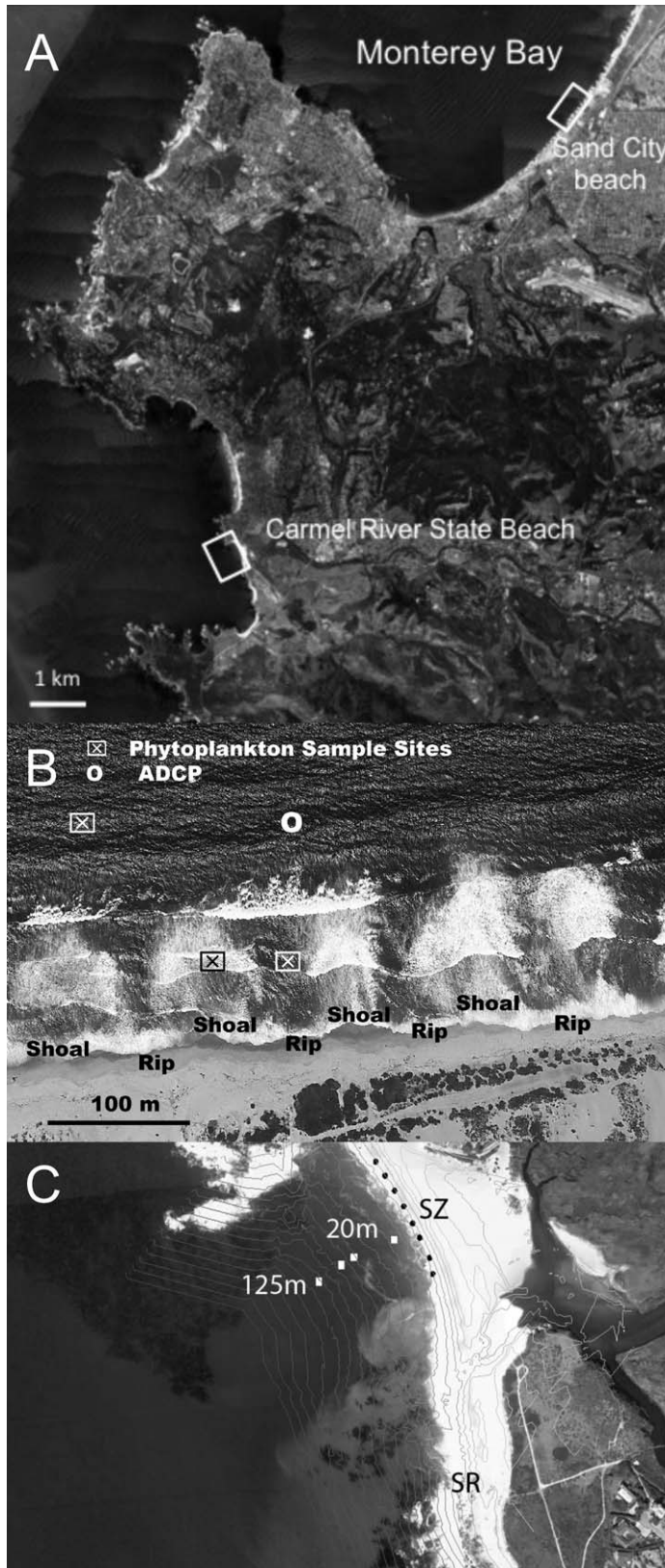
behavioral-physical processes among taxa affect transport across the surf zone to shore.

We distinguished among several mechanisms that may transport larvae and other zooplankters to the surf zone. Prevailing equatorward winds together with Coriolis acceleration drive near-surface waters offshore (Ekman transport), lowering sea level at the coast and forcing upwelling of cold bottom waters nearshore (Huyer 1983, 2005). When prevailing winds relax (weaken), surface water may flow back toward shore and poleward nearshore. If upwelling relaxation transports zooplankters to the surf zone, then concentrations of zooplankters should increase when prevailing upwelling-favorable winds weaken. If wind forcing and Stokes drift transport zooplankton into the surf zone, then zooplankton in the upper water column should increase in the surf zone during onshore winds and large waves. In contrast, zooplankton that sink or swim downward may be transported onshore by benthic streaming during calm conditions.

Methods

We conducted the study at a more dissipative surf zone and a more reflective surf zone on opposite sides of the Monterey Peninsula (Fig. 3). The more dissipative surf zone was located at Sand City, California (36° 36′56″ N; 121° 51′17″). The slope offshore of this broad beach is 1/20 before steepening to 1/10 slope with straight, parallel contours and then flattening inshore to 1/100 slope with rip channels and eddies that extend about 100 m seaward of breakers to shore (MacMahan et al. 2010; Brown et al. 2015). About 20% of surface drifters released in the Sand City surf zone were expelled per hour and those re-entering the surf zone were concentrated by eddies generated by the system of rip currents (Reniers et al. 2009, 2013; MacMahan et al. 2010). Most surface-drifters exported from the surf zone, eventually re-entered the surf zone over the shoals between rip channels (Brown et al. 2015).

The reflective surf zone was located at Carmel River State Beach (CRSB), which is a crescent-shaped pocket beach located at the mouth of the Carmel River and the head of a submarine canyon (Fig. 3; 36° 32′18″ N; 121° 55′43″). The Carmel River ephemerally breached near the southern end of

Fig. 3. (**A**) Map of the two study sites near the Monterey Peninsula, California. (**B**) Sand City: zooplankton was collected within the dissipative surf zone in rip currents and shoals ∼ 100 m apart (X) and ∼ 125 m seaward of the surf zone along the 5-m isobath (Offshore site). One Acoustic Doppler Current Profiler (ADCP; square) was moored at 13 m depth to measure waves, and one ADCP was moored in 7 m of water to measure currents together with near-surface and near-bottom CTDs. (**C**) Carmel River State Beach: zooplankton was collected within the reflective surf zone (SZ) and ∼ 125 m seaward of the surf zone. An ADCP (square) was moored ∼ 125 m from shore in 12 m of water, and near surface and bottom CTDs were moored ∼ 150 m offshore (triangle). Maps were modified from Google Earth images.

Table 1. Mean (+SE) concentration (m^{-3}) and percentage of zooplankters collected from 18 June 2010 to 15 July 2010 at Sand City, California.

Taxon	Mean	SE	Percentage
Cladocerans	9243.97	2055.47	54.12
Calanoid copepods	3477.41	739.49	20.36
Larvaceans	1848.74	361.79	10.82
Copepod nauplii	935.29	293.30	5.48
Barnacle nauplii II–VI	909.42	310.73	5.33
Spionid late larvae	167.78	64.30	0.98
Urchin late larvae	104.02	24.64	0.61
Bivalve late larvae	90.91	33.44	0.53
Harpacticoid copepods	69.89	48.60	0.41
Gastropod late larvae	50.92	15.36	0.30
Other polychaete late larvae	46.55	14.13	0.27
Mysids	37.66	9.84	0.22
Cyprids	33.17	6.62	0.19
Hydrozoans	27.68	5.83	0.16
Amphipods	22.10	6.03	0.13
Emerita larvae I	8.35	1.70	0.05
Pinnotherid larvae I-PL	4.96	3.22	0.03
Cancer spp. larvae I	1.05	0.68	0.01
Majid larvae I-PL	0.57	0.14	0.00
Ctenophores	0.41	0.34	0.00
Porcellanid larvae I-PL	0.32	0.18	0.00
Grapsid larvae I-PL	0.21	0.09	0.00

the beach. Rocks occur at either end of the beach, and a kelp bed is situated offshore of the northern end of the beach. The steep beach profile consisted of a 1 : 8 beach slope, 1 : 3 submerged step, and 1 : 19 submerged profile farther from shore (Brown 2014). Waves broke close to shore resulting in a narrow energetic surf or swash (water runs up and down the beach with each wave) zone that was only ∼ 3 m wide when waves were small and ∼ 10 m wide when waves were large. Dye released in the surf zone initially mixed rapidly across the surf zone by turbulent diffusion from breaking waves, and it was slowly transported offshore while being advected equatorward in the prevailing alongshore current (Fig. 1B; Brown 2014).

We studied the sites during consecutive summers. We sampled the more dissipative surf zone from 18 June 2010 to 15 July 2010 and the reflective surf zone from 18 June 2011 to 15 July 2011. Wind velocity was obtained from the NOAA National Data Buoy Center 46042, which is located seaward of the mouth of Monterey Bay. We calculated daily average wind stress using standard equations and a constant drag coefficient (Pedlosky 1987). We monitored current velocity and waves continuously with Acoustic Doppler Current Profilers (ADCPs; Fig. 3). At the more dissipative surf zone, we deployed one ADCP at 13 m depth to measure waves and

another ADCP in 7 m of water to measure currents together with near-surface and near-bottom CTDs. At the reflective surf zone, we deployed one ADCP 12 m deep to measure waves, and we moored one ADCP 7 m deep to measure currents together with near-surface and near-bottom CTDs. The 2MHz Nortek ADCPs were moored 35 cm off the seabed. They sampled at 1 Hz with a bin size of 0.11 m at the more dissipative surf zone and 0.5 m at the reflective surf zone. Bins near the sea surface were removed while velocities within 0.5 m of the bottom were not measured. Wave height and period were computed hourly.

We collected three replicate samples of zooplankton daily in the surf zone (Fig. 3). At the more dissipative surf zone, we sampled zooplankton daily in rip currents throughout the study and from adjacent shoals for 11 d. Large waves precluded installing a plankton pump system during the first half of the sampling period, so we sampled using a plankton net equipped with a flowmeter during low tide. A tethered swimmer released the net, which was held taught in the rip current by a rope to a person onshore. Over the shoals, swimmers held the net into the oncoming waves. At the reflective surf zone, a gas-powered centrifugal pump sampled about 240 L of seawater per min (1.2 m^3 per sample) during high tide from the surf zone through a plankton net that was immersed in a bucket. The hose (6-cm diam) was attached to pipes that were implanted in the sand, and the intake of the hose was positioned midway into the surf zone.

At both sites, we towed a plankton net vertically throughout the entire water column seaward of the surf zone from a small boat in the morning while winds were calm. Samples were collected about 125 m from shore. The net was equipped with a flowmeter to determine the volume of water filtered, which averaged 2 m^3 per tow. All plankton nets deployed during this study had a 25-cm diameter mouth and 200-μm mesh.

Zooplankton samples were preserved in buffered formaldehyde and rinsed before processing. Subsamples were taken by adding water to the sample until it weighed 200 g (200 mL), thoroughly mixing it and taking an aliquot with a Stempel pipette. Aliquots were counted serially until about 200 of the common organisms were counted. Using dissecting microscopes, meroplankters were identified to species and developmental stage when possible, and holoplankters were identified to broad taxonomic levels.

We determined when most zooplankters may enter the surf zone. Because winds and waves affect surf zone hydrodynamics, we correlated concentrations of the most abundant zooplankters in the surf zones with daily averages of alongshore and cross-shelf wind stress and root-mean square wave height to investigate potential transport processes at each site. To determine whether zooplankters were freely exchanged between the surf zone and adjacent waters, we correlated the concentrations of the most abundant zooplankters inside and outside the surf zone. If zooplankters are freely exchanged,
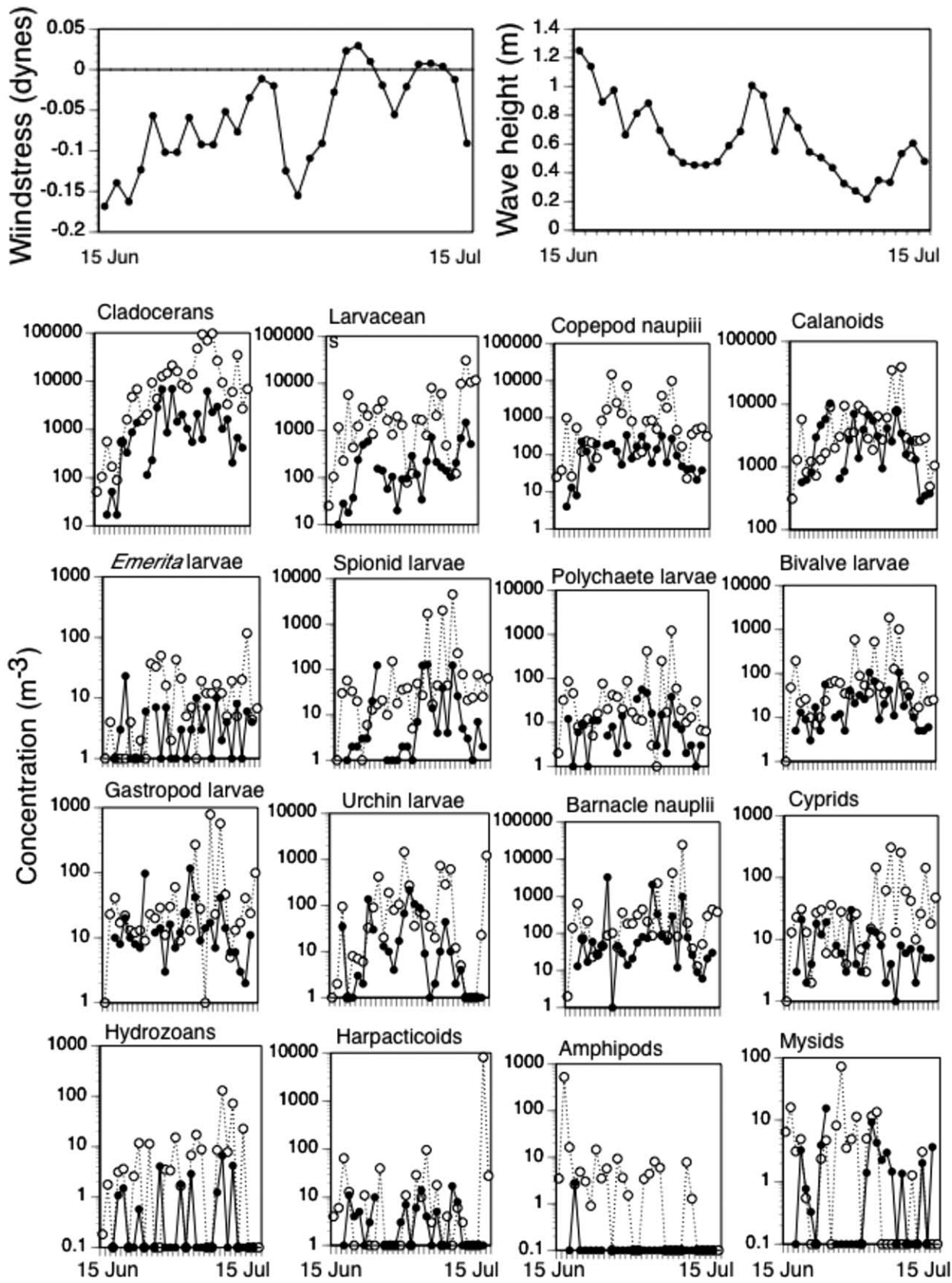
Fig. 4. Alongshore wind stress (dynes), root-mean square wave height (m) and mean concentrations (m^{-3}; $n = 3$) of the 16 most abundant zooplankters collected just outside the dissipative surf zone on the 125-m isobaths (filled circles) and inside the surf zone in rip currents (open circles) from 18 June 2010 to 15 July 2010 at Sand City, California. Negative wind stress values indicate northerly winds and positive values indicate southerly winds.
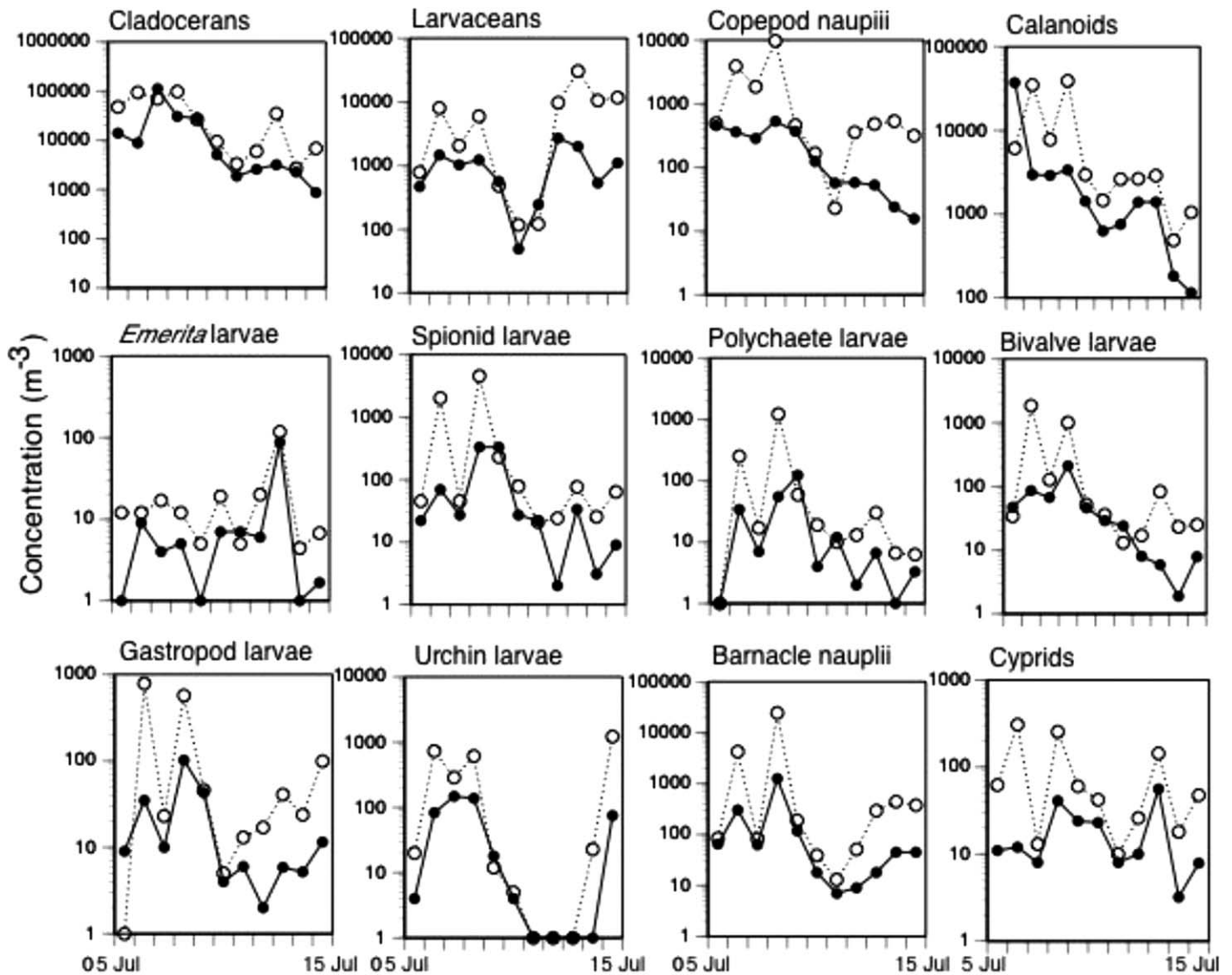
Fig. 5. Mean concentrations (*n* = 3) of the 12 most abundant zooplankters collected in three rip currents (open circles) and three adjacent shoals (filled circles) inside the dissipative surf zone from 05 July 2010 to 15 July 2010 at Sand City, California.

then concentrations inside and outside the surf zone should be similar and significantly correlated. However, if exchange between the surf zone and offshore water was limited by hydrodynamics or behavior, then concentrations of zooplankters should not be correlated and lower in the surf zone.

The ability of larvae to enter the surf zone should result in greater settlement. We investigated this by surveying daily larval settlement of the mole crab, *E. analoga*, following the methods of Schlacher et al. (2008). Ten cylindrical cores (10 cm diameter) were taken to a depth of 200 mm and placed in a mesh bag (1.5 mm mesh). Three replicate samples were taken per day. Samples were washed in the swash zone to remove sand. A series of sieves was used to sort mole crabs into size classes, and only colorless postlarvae were counted. After detrending data when necessary, we

cross-correlated the log-transformed number of settling mole crab postlarvae with wind stress and wave height to identify potential transport processes.

Results

More dissipative surf zone

We examined the 16 most abundant taxa, which composed 99.96% of the zooplankton collected at Sand City; cladocerans and calanoid copepods composed 74.5% of the zooplankton collected (Table 1). All larval stages of barnacles and several taxa of crabs (pinnotherids, porcellanids, majiids, and grapsids) were present in the samples, indicating that they completed development nearshore. In contrast, only first stage larvae of *E. analoga* and *Cancer* spp. were
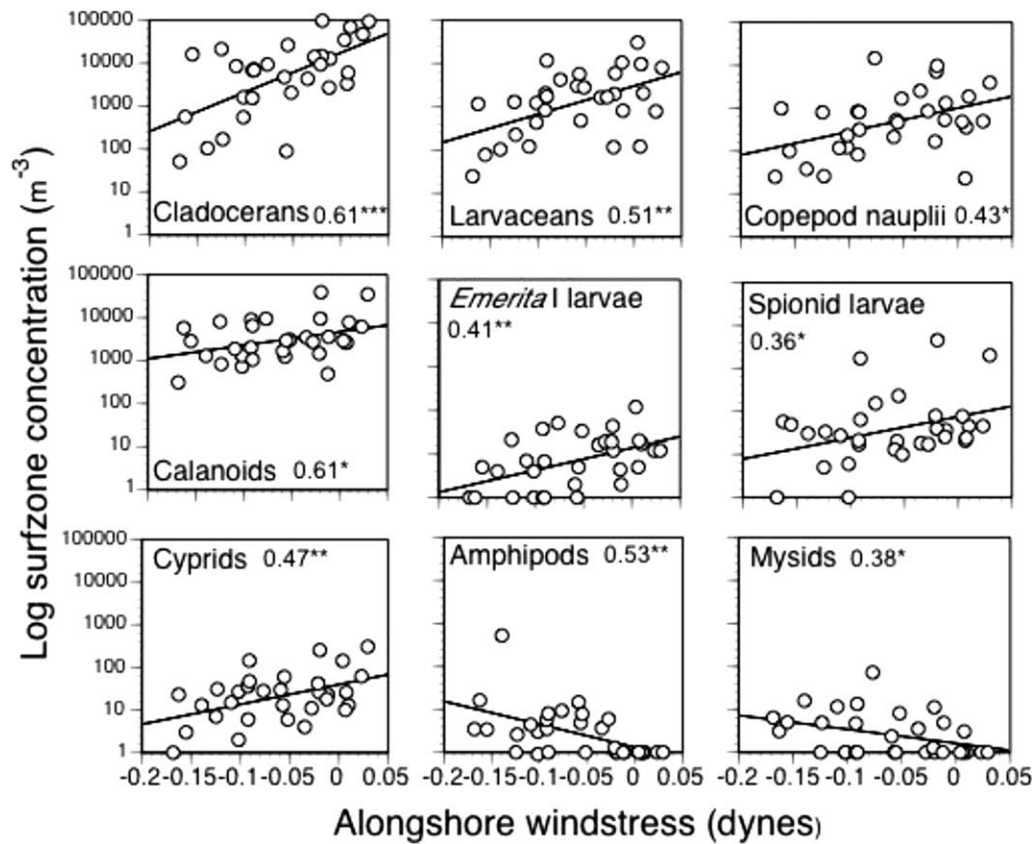
Fig. 6. Correlations of zooplankters inside the dissipative surf zone with alongshore wind stress (dynes) zone from 18 June 2010 to 15 July 2010 at Sand City, California. Negative wind stress indicates northerly and easterly winds, and positive wind stress indicates southerly and westerly winds. Solid lines indicate significant correlations (r): $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$.

present, indicating that they hatched nearshore and developed offshore. Only larvae that were ready to settle were present for urchins, gastropods, bivalves, spionids and other polychaetes, likely because early stages developed outside the surf zone.

The most abundant zooplankters were frequently an order of magnitude or more abundant in rip channels of the surf zone than outside the surf zone (Fig. 4), and they typically were about one to two orders of magnitude more concentrated in rip channels than in the waters over the adjacent shoals (Fig. 5). Concentrations of these zooplankters in rip channels were most closely related to alongshore wind stress and root-mean square wave height. An extended period of northerly winds occurred at the outset of the study, and two brief southerly wind relaxation events occurred thereafter (Fig. 4). Two larger wave events occurred during the first half of the study, and waves were small near the end of the study after winds relaxed. Concentrations of seven taxa increased in the surf zone as wind stress from prevailing northerly winds decreased, including four holoplankters (cladocerans, larvaceans, copepod nauplii, calanoid copepods) and three meroplankters (first stage *E. analoga*, late stage spionid larvae, cyprids), while two demersal zooplankters (amphipods, mysids) decreased (Fig. 6).

The four holoplankters, another holoplankter (hydrozoans) and the three meroplankters also were more abundant in the surf zone when waves were small, whereas one of the two demersal zooplankters (amphipods) was more abundant in the surf zone when waves were large (Fig. 7). Concentrations of six zooplankters in rip channels were positively correlated with their concentrations outside the surf zone (cladocerans, late stage spionid, bivalve and urchin larvae, barnacle nauplii, hydrozoans), indicating that they were more freely exchanged across the surf zone than the other 10 taxa (Fig. 8). *E. analoga* larvae settled in high densities (mean 1342.3 m^{-2}) in four pulses that were cross-correlated with poleward ($r = -0.2425$ without a lag and $r = -0.3795$ with a 1-d lag), onshore ($r = -0.2552$ with a 1-d lag) flow and large waves ($r = 0.1957$ with a 1-d lag; Fig. 9).

Reflective surf zone

We examined the most abundant 16 taxa, which composed 99.9% of the zooplankton collected at Carmel River State Beach; calanoid copepods and early stage (I–III) of barnacle nauplii composed 74.4% of the zooplankton collected (Table 2). All larval stages of barnacles and several taxa of crabs (pinnotherids, porcellanids, majiids, and grapsids) were
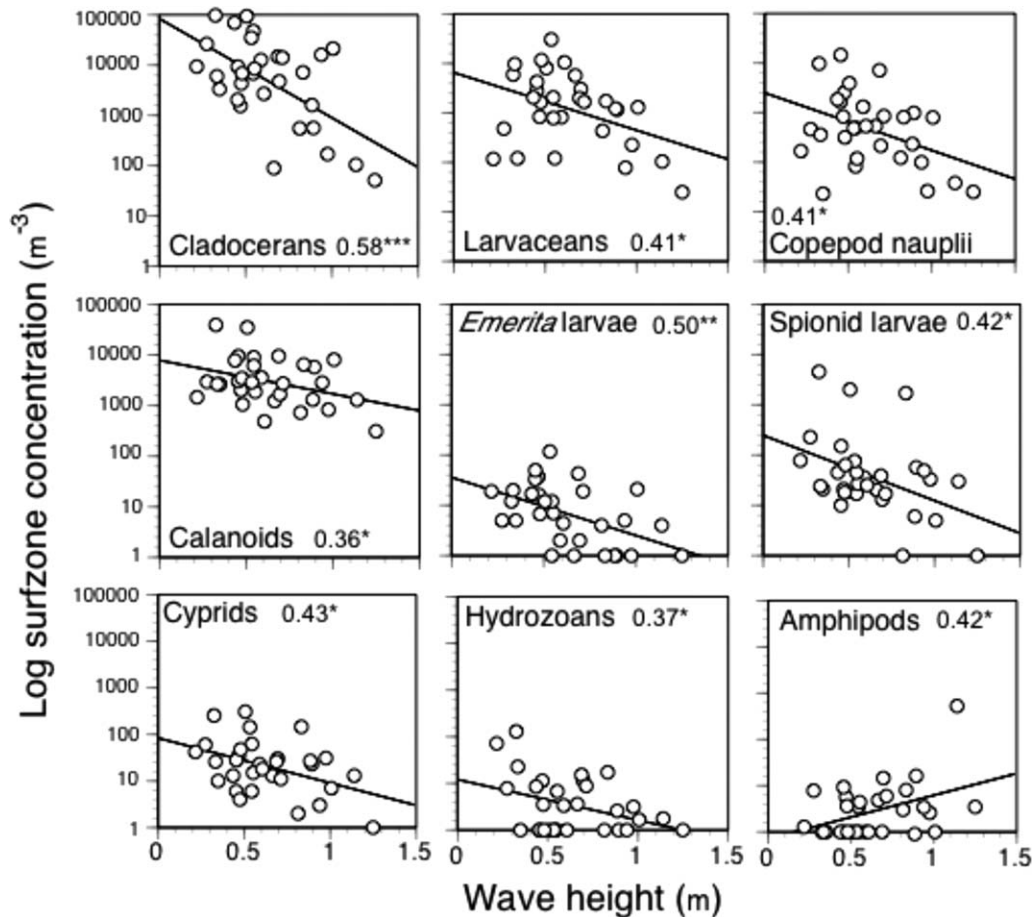
Fig. 7. Correlations of zooplankters inside the dissipative surf zone with root-mean square wave height (m) from 18 June 2010 to 15 July 2010 at Sand City, California. Solid lines indicate significant correlations (*r*): * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

present in the samples, indicating that they completed development nearshore. In contrast, only early stage larvae of *Cancer* spp. were collected, indicating that they hatched nearshore and developed offshore. As at the Sand City site, only larvae that were ready to settle were collected for urchins, gastropods, bivalves and polychaetes, because early stages develop outside the surf zone.

Throughout the study period, zooplankters typically were at least an order of magnitude more abundant outside than inside the surf zone (Fig. 10). Four taxa (hydrozoans, larvaceans, doliolids, and mysids) were sparse in the surf zone, and nine more taxa occurred there sporadically or in low concentrations. Only three of the 16 taxa (cyprids, harpacticoid copepods, juvenile bopyrid isopods) were more abundant inside the surf zone on some days. An ontogenetic shift occurred in barnacles: early stage nauplii were more abundant outside the surf zone, late-stage nauplii occurred in similar concentrations inside and outside the surf zone, and cyprids were most abundant inside the surf zone. Four species of cyprids composed 96% of those collected in the surf zone: *Balanus glandula* (57.1%), *Balanus*

crenatus (15.1%), *Pollicipes polymerus* (12.1%), and *Chthamalus dalli* (11.7%).

Of the 12 taxa that occurred in the surf zone, seven of them were significantly (calanoid copepods, late stage polychaete larvae, cyprids, harpacticoid copepods, juvenile bopyrid isopods) or marginally significantly ($p = 0.06$ for bivalve larvae and $p = 0.07$ for gastropod larvae) more abundant in the surf zone when waves were small (Fig. 11). Concentrations of only four taxa (calanoid copepods, late stage gastropod, polychaete, and barnacle larvae) were positively correlated inside and outside the surf zone (Fig. 12). Neither recruits nor adults of *E. analoga* were present at this beach.

Discussion

Opposite effects of surf zone hydrodynamics on plankton assemblages

Opposite patterns in the relative concentration of zooplankton inside and outside the surf zone occurred at the two types of beaches. Zooplankton concentrations were higher inside the more dissipative surf zone and higher outside the
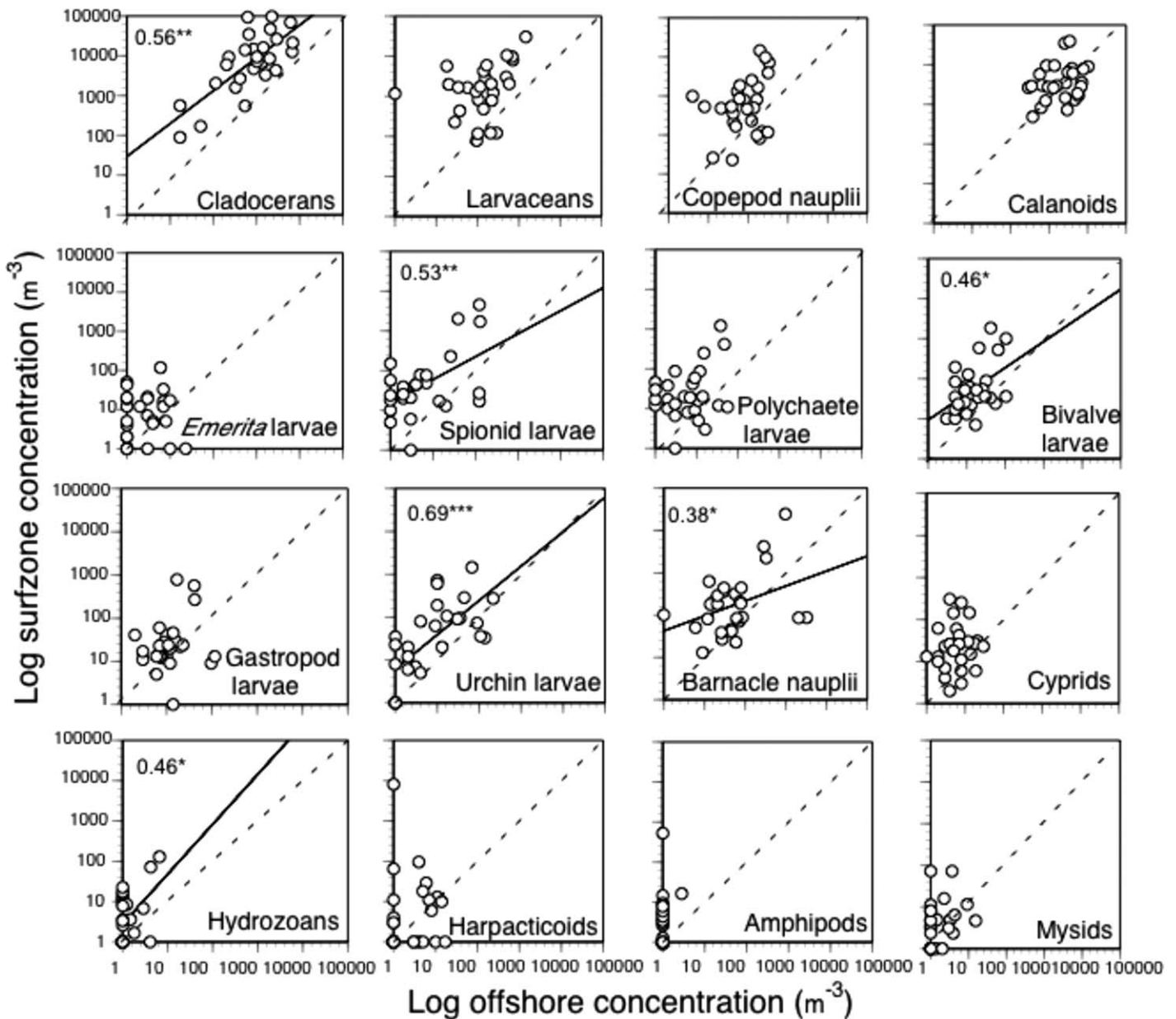
Fig. 8. Correlations of the 16 most abundant zooplankters collected inside and outside the dissipative surf zone from 18 June 2010 to 15 July 2010 at Sand City, California. Dashed lines indicate a one-to-one relationship. Solid lines indicate significant correlations (r): $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$.

reflective surf zone, and these patterns were maintained every day with few exceptions. The patterns were evident despite diverse biological traits in zooplankton assemblages at each site, indicating that surf zone hydrodynamics profoundly affect the exchange of zooplankton between the surf zone and offshore waters. Moreover, the same patterns occurred in phytoplankton assemblages (Shanks et al. 2016, In press *c*), indicating that fundamental differences in surf zone hydrodynamics at the two types of beaches must be responsible for the different patterns cutting across entire plankton assemblages.

Processes transporting zooplankton into surf zones

We developed a three-dimensional hydrodynamic model based on our measured physical data and coupled it with an individual based model of swimming behavior of zooplankton to determine how zooplankton may be transported into surf zones (Fujimura et al. 2013, 2014). The model incorporated three key variables: depth preferences of zooplankton (positive or negative buoyancy), sinking or no sinking of zooplankton in response to turbulence and onshore wind or no wind with Stokes drift. After releasing simulated zooplankton well seaward of the surf zones of the more dissipative and reflective
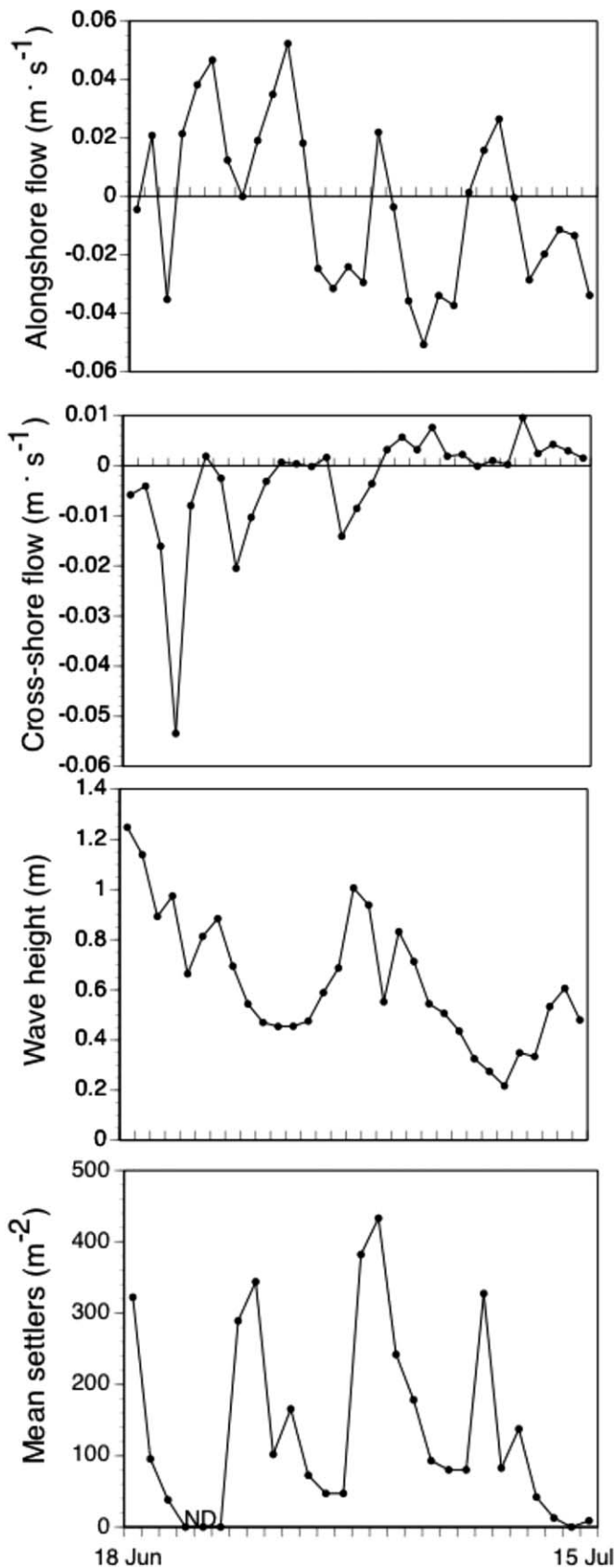
beaches, we found that behavior may facilitate transport of zooplankton across the surf zones of both types of beaches in two ways. In the model, when winds were calm, benthic streaming transported simulated zooplankton in the bottom boundary layer onshore (Fig. 2A). During onshore wind forcing, simulated larvae near the surface drifted to the surf zone in wind-driven surface currents, sank in the turbulent surf zone and were transported shoreward by streaming (Fig. 2E). In contrast, undertow may often keep precompetent larvae and holoplankters throughout most of the water column from entering hazardous surf zones (Fig. 2C).

The model showed that zooplankters were concentrated in the dissipative surf zone by recirculation formed by rip currents (Fig. 1A), alongshore currents and gravity waves (McMahan et al. 2010; Reniers et al. 2013; Brown et al. 2015), as previously found for plankton and detritus (Clutter 1967; McLachlan and Hesp 1984; Nakane et al. 2013). Dye and drifter studies were consistent with model results at the dissipative beach (Brown et al. 2015). Dye entered the surf zone over shoals during our study, exited episodically in rip currents following the arrival of wave groups, mixed with water outside the surf zone and re-entered the surf zone over shoals (Brown et al. 2015). Drifters released during our study accumulated in the recirculation cells with few lost to offshore waters due to the resulting rip current circulation patterns both inside and outside of the surf zone (MacMahan et al. 2010; Brown et al. 2015). Thus, all zooplankton taxa were more concentrated inside than outside the surf zone because they were continually concentrated in the surf zone by recirculation cells.

During our study, both zooplankton and phytoplankton (Shanks et al. 2016, In press *c*) were far more concentrated in rip channels than over adjacent shoals. Less than half of the 16 most abundant zooplankton taxa were positively correlated inside and outside the dissipative surf zone, likely because they regulate depth rather than being passively distributed throughout the water column, altering the extent of accumulation in rip channels by recirculation cells. We also suspect that entrainment in eddies and accumulation in rip channels of the phytoplankton assemblage may have been enhanced by cells attached to bubbles from breaking waves floating them into landward-flowing surface waters (Shanks et al. 2016, In press *c*), similar to diatom species residing entirely in surf zones (Talbot et al. 1990).

Recirculation formed by rip currents often does not occur at some beaches. Rip currents are suppressed in intermediate and dissipative surf zones when waves reach the shore at an angle generating alongshore currents, in which case plankton would not be concentrated in the surf zone (Komar

Fig. 9. Density of *E. analoga* settlers relative to alongshore and cross-shelf current velocity (m. s^{-1}) and root-mean square wave height (m) from 19 June 2010 to 15 July 2010 at Sand City, California. ND = no data.

Table 2. Mean (+SE) and percentage of zooplankters collected at Carmel River State Beach, California, from 18 June 2011 to 15 July 2011.

Taxon	Mean	SE	Percentage
Calanoid copepods	499.74	60.09	47.40
Barnacle nauplii I–III	284.31	44.19	26.96
Harpacticoid copepods	54.81	6.30	5.20
Copepod nauplii	40.88	8.22	3.88
Mysids	34.81	9.80	3.30
Amphipods	24.16	5.98	2.29
Hydrozoan medusa	21.59	5.57	2.05
Cyprids	19.13	2.37	1.81
Euphausiid larvae	16.97	5.38	1.61
Gastropod late larvae	15.37	2.69	1.46
Barnacle nauplii IV–VI	8.49	1.74	0.81
Doliolids	7.95	2.14	0.75
Bopyrid isopod juveniles	7.72	1.14	0.73
Larvaceans	6.81	1.27	0.65
Polychaete late larvae	2.77	0.49	0.26
Bivalve late larvae	2.22	0.30	0.21
Insects	1.81	0.28	0.17
Pinnotherid zoeae I–III	1.03	0.20	0.10
Cladocerans	0.83	0.26	0.08
Urchin late larvae	0.44	0.14	0.04
Majid zoeae I–II	0.38	0.10	0.04
Cyphonotes larvae	0.33	0.12	0.03
Pinnotherid zoeae IV–V	0.25	0.08	0.02
Cancer zoeae I–III	0.17	0.06	0.02
Porcellanid zoeae I–II	0.12	0.07	0.01
Majid megalopae	0.11	0.03	0.01
Pinnotherid megalopae	0.05	0.04	<0.01
Grapsid zoeae I–III	0.04	0.02	<0.01
Grapsid megalopae	0.02	0.01	<0.01
Grapsid zoeae IV–V	0.01	0.01	<0.01

1998; Ohlmann et al. 2012). Rip currents also were absent at our reflective beach (Fig. 1B), and consequently, neither zooplankton nor phytoplankton (Shanks et al. 2016, In press *c*) was concentrated in the surf zone. The absence of rip currents, the reflective nature of the narrow energetic surf zone and weaker undertow resulted in an exchange rate of surf zone water that was consistent with dissipative beaches when alongshore currents were present (Brown 2014). In a coastwide survey of 40 sites, recruitment was greater at dissipative than intermediate shores with rip currents and least at reflective shores and one dissipative shore that lacked rip currents (Shanks et al. in press *b*).

Although concentrations of only some zooplankton taxa inside the surf zone were correlated with those outside at the more dissipative beach, most phytoplankton showed positive correlations at this beach (Shanks et al. 2016, in press *a*). This was not the case at the reflective beach where

neither zooplankton nor phytoplankton taxa was correlated inside and outside the surf zone, revealing differences in water exchange across the surf zone at these sites (Shanks et al. 2016, In press *c*).

At the reflective surf zone, some zooplankton taxa were positively correlated inside and outside the surf zone, likely because they occur near the bottom where benthic streaming facilitates onshore transport (Fig. 2A). Several taxa that are known to frequent bottom waters were on some days more abundant inside rather than outside the surf zone, unlike other members of the plankton assemblage. Harpacticoid copepods are demersal, and juvenile parasitic bopyrid isopods might occupy bottom waters while searching for benthic shrimp hosts and cyprids also commonly occur in the lower water column. Although *B. glandula* and *C. dalli* have been reported to be more abundant in the upper water column as they approach shore (Grosberg 1982; Morgan et al. 2009*a*; Morgan and Fisher 2010), we previously demonstrated that cyprids of all species recruited almost entirely to the bottom of moorings just outside the surf zone over 5 yr (Mace and Morgan 2006; Morgan et al. 2009*a*). Hence, cyprids may descend near the bottom as they enter the surf zone regardless of their depth preferences before they reach the surf zone. Although we did not determine the vertical distributions of zooplankters in the present study, passively sinking detritus also was more abundant inside than outside the surf zone when waves were small further suggesting that streaming may transport zooplankton occupying the benthic boundary layer onshore (Shanks et al. 2015). Benthic streaming may commonly transport competent larvae near the surf zone to adult habitats on shore, because many species descend in the water column late in development (Thorson 1964; Queiroga and Blanton 2005) and sink in response to turbulence (Fuchs and DiBacco 2011; Roy et al. 2012; Fuchs et al. 2013).

Seven of the dominant taxa increased in the reflective surf zone when waves were small, regardless of wind direction. All but one of these taxa (calanoid copepods) were competent larvae or benthic zooplankters raising the possibility that transport into the surf zone by benthic streaming may have occurred when reduced turbulent mixing by small waves enabled zooplankters to spend more time near the bottom (Fig. 2A; Shanks et al. 2015).

Seven of the 16 dominant taxa were most concentrated in the dissipative surf zone when the prevailing northwesterly winds weakened and waves diminished. These zooplankters would have been transported poleward alongshore from just to the south of the study site rather than across the shelf, because zooplankton concentrations increased in the surf zone as soon as winds relaxed rather than taking longer to cross the shelf from the upwelling front from offshore to onshore (Roughgarden et al. 1988; Wing et al. 2003).

Postlarvae of *E. analoga* recruited to the dissipative beach during wind relaxation events the day after the onset of onshore winds and large waves, consistent with one of the
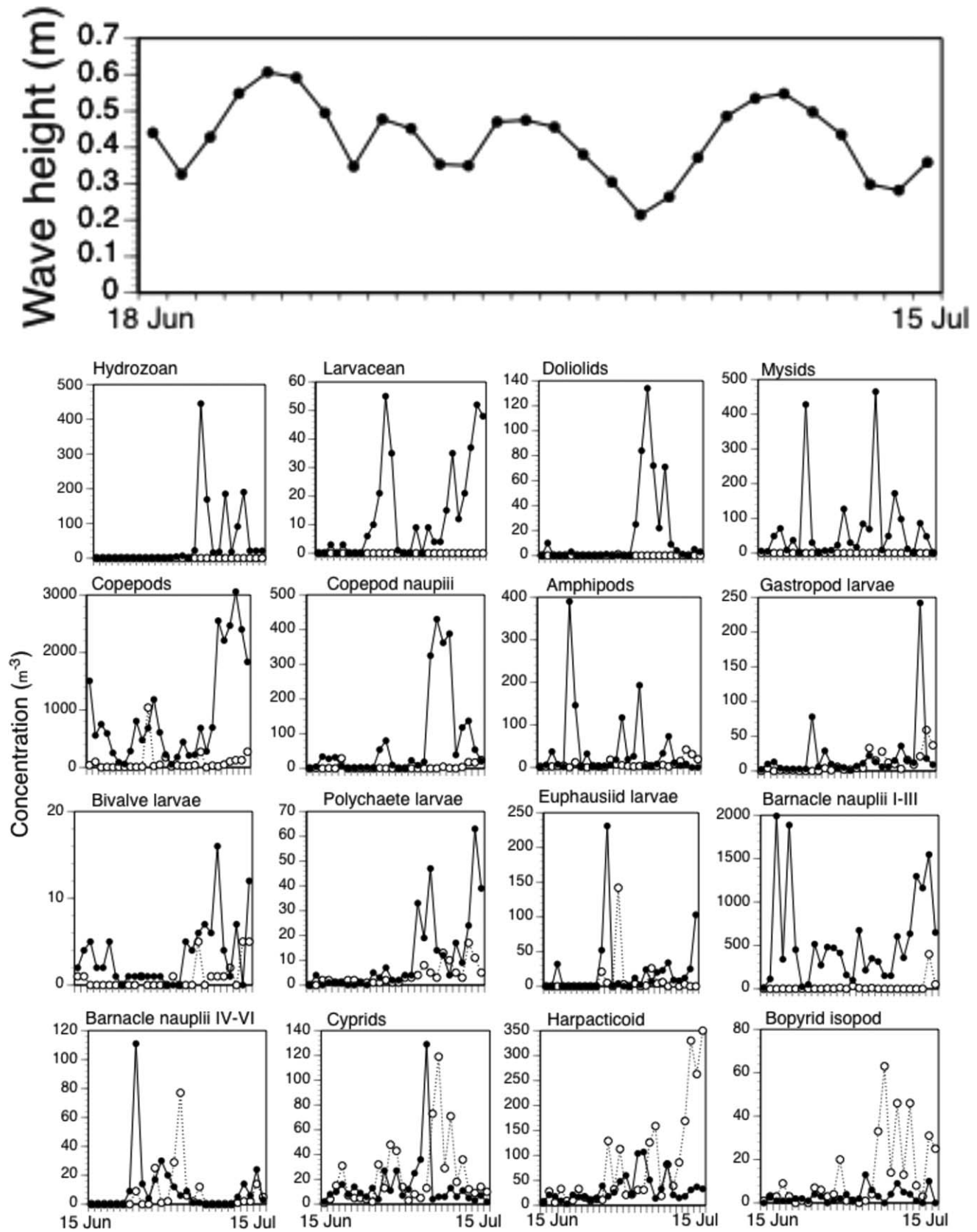
Fig. 10. Wave height (m) and mean concentrations (m^{-3}; $n = 3$) of the 16 most abundant zooplankters collected just outside the surf zone (filled circles) and inside the reflective surf zone (open circles) from 18 June 2011 to 15 July 2011 at Carmel River State Beach, California.
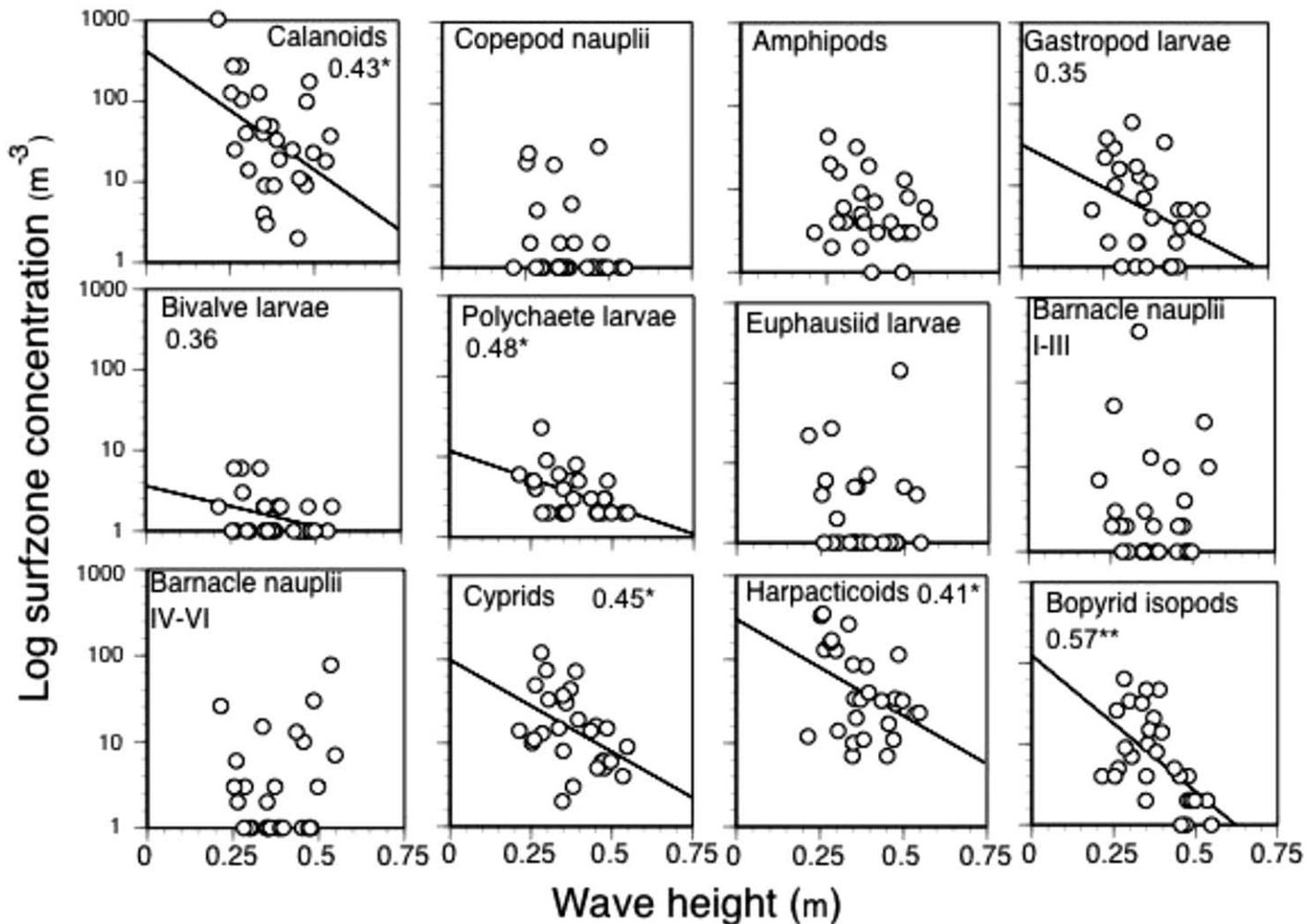
Fig. 11. Correlations of zooplankters inside the reflective surf zone with wave height (m) from 18 June 2011 to 15 July 2011 at Carmel River State Beach, California. Solid lines indicate significant correlations (r): $* = p < 0.05$, $** = p < 0.01$. Correlations for gastropod and bivalve larvae were marginally nonsignificant.

modeled mechanisms of larval transport (Fujimura et al. 2013, 2014). Neither first stage *E. analoga* larvae nor settlers were collected at the reflective beach where inhospitable coarse shifting sands may preclude this species from burrowing. First stage *E. analoga* larvae were released into the surf zone at the dissipative surf zone and dispersed far offshore (Morgan et al. 2009c), indicating that they escaped recirculation of the surf zone within the time it took them to molt to the second larval stage (> 1 week).

Implications for subsidies to coastal communities

Alongshore variation in ocean conditions affects the delivery of nutrients, planktonic food, and larvae to shore with profound consequences for the dynamics and structure of surf zone and intertidal communities. Much of this variation may be due to the strength and persistence of prevailing upwelling-favorable winds interacting in the configuration of the shoreline, including headlands and bays (Roughgarden et al. 1988;

Graham et al. 1992; Drake et al. 2015). Larval behavior may mediate the extent of alongshore and cross-shelf transport with multiple mechanisms delivering competent larvae to shore, including wind relaxation events, onshore winds, large waves and internal waves in surface waters and shoreward-flowing bottom waters during upwelling (Shanks 1995; Morgan et al. 2009a; Drake et al. 2013). Larvae and other zooplankters may enter the surf zone in near-surface onshore wind-driven currents, Stokes drift and internal waves, whereas those near the bottom may be transported shoreward by benthic streaming (Fujimura et al. 2014; Shanks et al. 2014; Navarrete et al. 2015). Larval settlement and planktonic food may be greater on dissipative than reflective shores, and they may be greatest on dissipative and intermediate shores where rip currents increase exchange of water outside and inside the surf zone (Shanks et al. in press b). In turn, the subsidies of larvae and food determine the intensity of top-down processes in communities (Menge et al. 1997, 2003). Hence, surf zone
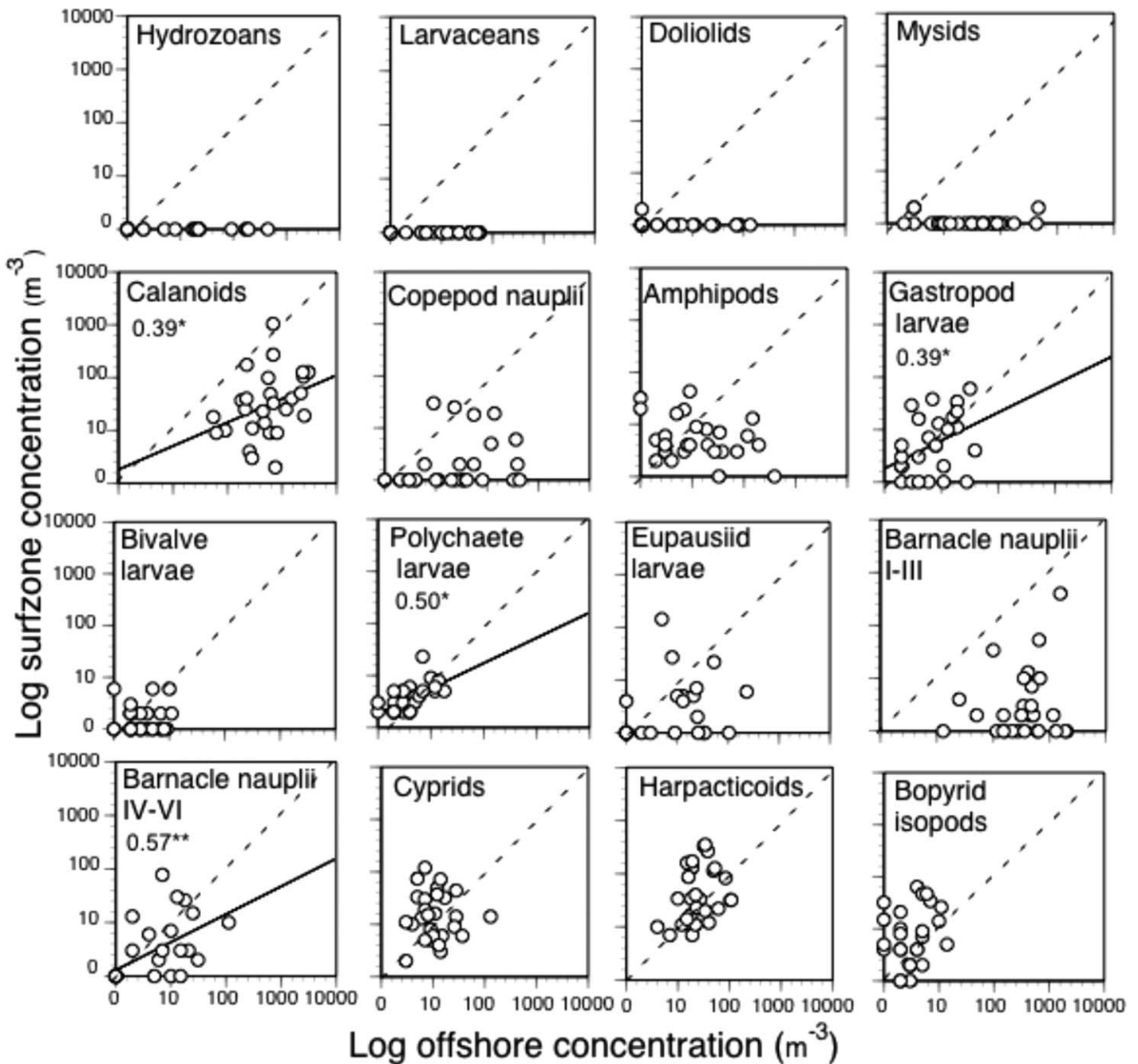
Fig. 12. Correlations of the 16 most abundant zooplankters collected inside and outside (100 m offshore) the reflective surf zone from 18 June 2011 to 15 July 2011 at Carmel River State Beach, California. Dashed lines indicate a one-to-one relationship. Solid lines indicate significant correlations (*r*): * = $p < 0.05$, ** = $p < 0.01$.

hydrodynamics as well as nearshore productivity may determine the initial abundance of communities that are later modified by top-down processes, physiological stress and disturbance (Menge and Sutherland 1987).

Our surveys of larval recruitment along the west coast of the U.S.A. indicated that spatial variation in surf zone hydrodynamics is a key determinant of the supply of larvae and food for benthic filter-feeders (Shanks et al. 2010, in press *b*).

The most recent survey included rock benches as well as rocks embedded in beaches, which commonly occur along the West Coast. Many rock benches are steep and highly reflective, so larval subsidies to these intertidal communities was low. The next step is to conduct intensive interdisciplinary studies of subsidies of food and larvae to rock benches where much of ecological theory of the intertidal communities has been developed.

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Conflict of Interest

None declared.