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Surfzone hydrodynamics as a key determinant of spatial variation in rocky intertidal communities

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Larvae of intertidal species develop at sea and must return to adult habitats to replenish populations. Similarly, nutrients, detritus and plankton provide important subsidies spurring growth and reproduction of macroalgae and filter-feeding invertebrates that form the foundation of intertidal communities. Together, these factors determine the density and intensity of interactions among community members. We hypothesized that spatial variation in surfzone hydrodynamics affects the delivery of plankton subsidies. We compared entire zooplankton communities inside and outside the surf zone daily while monitoring physical conditions for one month each at two shores with different surfzone characteristics. Opposite cross-shore distributions of larvae and other zooplankters occurred at the two sites: zooplankton was much more abundant inside the mildly sloping dissipative surf zone (DSZ) with rip currents and was more abundant outside the steep reflective surf zone (RSZ). Biophysical numerical simulations demonstrated that zooplankters were concentrated in rip channels of the DSZ and were mostly unable to enter the RSZ, indicating the hydrodynamic processes behind the observed spatial variation of zooplankters in the surf zone. Differences in the concentration of larvae and other zooplankters between the inner shelf and surf zone may be an underappreciated, key determinant of spatial variation in inshore communities.

1. Introduction

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 rocky intertidal communities where many concepts in marine ecology have been developed [1–4]. These subsidies ultimately must be transported into surf zones to reach intertidal communities. Spatial variation in surfzone hydrodynamics has long been recognized to affect transport of plankton and sediments to beaches [5,6], but has received little attention for rocky shores. Recently, alongshore variation in surfzone hydrodynamics was proposed to affect the recruitment of larvae to rocky intertidal populations in time and space, thereby affecting the intensity of postsettlement interactions among members of intertidal communities [7,8]. If so, spatial variation in surfzone hydrodynamics also may affect the concentration of entire plankton communities that provide food subsidies for suspension-feeding invertebrates, including foundation species that form habitat for many other species [3,4].



Figure 1. (a) The locations of study sites at Sand City beach and Carmel River State Beach (CRSB) from Google maps. Photos of the (b) more DSZ at Sand City and (c) the more RSZ at Carmel River State Beach.

We previously demonstrated that the densities of barnacle and limpet recruits were greater onshore of dissipative than reflective surf zones [8]. Wave energy dissipates gradually as waves break on gently shoaling shores resulting in progressive waves and wide surf zones [5], whereas it is reflected back on steep shores resulting in standing waves and narrow energetic surf zones [6] that may limit the delivery of larvae into the surf zone. Densities of new recruits on rocks were orders of magnitude higher at five reflective than five dissipative surf zones along the west coast of the USA, potentially affecting the intensity of postsettlement interactions among members of intertidal communities [8]. Investigations of surfzone hydrodynamics have focused on sandy beaches, because they are far more tractable than at rocky shores. However, the observed hydrodynamics should generally apply to rocky shores with similar slopes, which are widespread along this coast, including long stretches of rocky shore, cobble fields and rocks within beaches.

The goal of the present investigation was to conduct intensive interdisciplinary studies to determine whether spatial variation in surfzone hydrodynamics affects the entry of zooplankton assemblages into the surf zones with differing hydrodynamics. We hypothesized that zooplankters would be more abundant outside than inside reflective surf zones relative to dissipative and intermediate surf zones, thereby regulating larval recruitment and food subsidies to inshore communities. Further, holoplankton (permanent members of the plankton) and meroplankton (larvae of benthic adults) may respond differently to surfzone hydrodynamics. Holoplankters may avoid entering the surfzone where they would be exposed to benthic predators in shallow water and stranding on the shore, whereas larvae recruiting to intertidal and shallow water communities need to enter the surf zone to reach benthic settlement sites.

We tested these hypotheses by comparing entire zooplankton assemblages inside and outside of a gently sloping, wide, more-dissipative surf zone (DSZ) and a steep, narrow, more reflective surf zone (RSZ) daily for one month each near Monterey, CA, USA (figure 1). Because it is exceedingly challenging to track the transport pathways of zooplankton entering the surf zone directly, we conducted numerical simulations for both surf zones using the measured bathymetry and monthly averaged wave and wind forcing to calculate the fluid flow and wave velocities. Transport pathways were revealed by seeding the models with particles offshore and subsequently computing the Lagrangian particle trajectories [9]. The particles simulated larvae that were competent to settle, swimming downward [10,11] and sinking in response to turbulence from breaking waves [12,13].

2. Material and methods

The DSZ at Sand City ($36^{\circ}36'57''$ N, $121^{\circ}51'15''$) is mildly sloping with alternating rip currents and shoals along a wide surf zone. Large waves break on an offshore bar that is located approximately 100 m offshore, resulting in an increased exchange of water. By contrast, the RSZ at Carmel River State Park ($36^{\circ}32'18''$ N, $121^{\circ}55'43''$) is narrow and steep without rip currents or offshore bars. The surf zone is narrow (approx. 10 m) and water exchange between the surf zone and offshore is reduced.

Zooplankton in the DSZ was collected from 15 June through 15 July 2010, and it was collected at the RSZ from 19 June to 15 July 2011. Three replicate samples were collected outside the surf zone from a small boat by vertically hauling a plankton net (200 μ m mesh) that was equipped with a flowmeter from the bottom to the surface of the water column three times, filtering about 2 m³ of water per sample. These offshore samples were collected at the 5–10 m isobath during light winds in the morning.

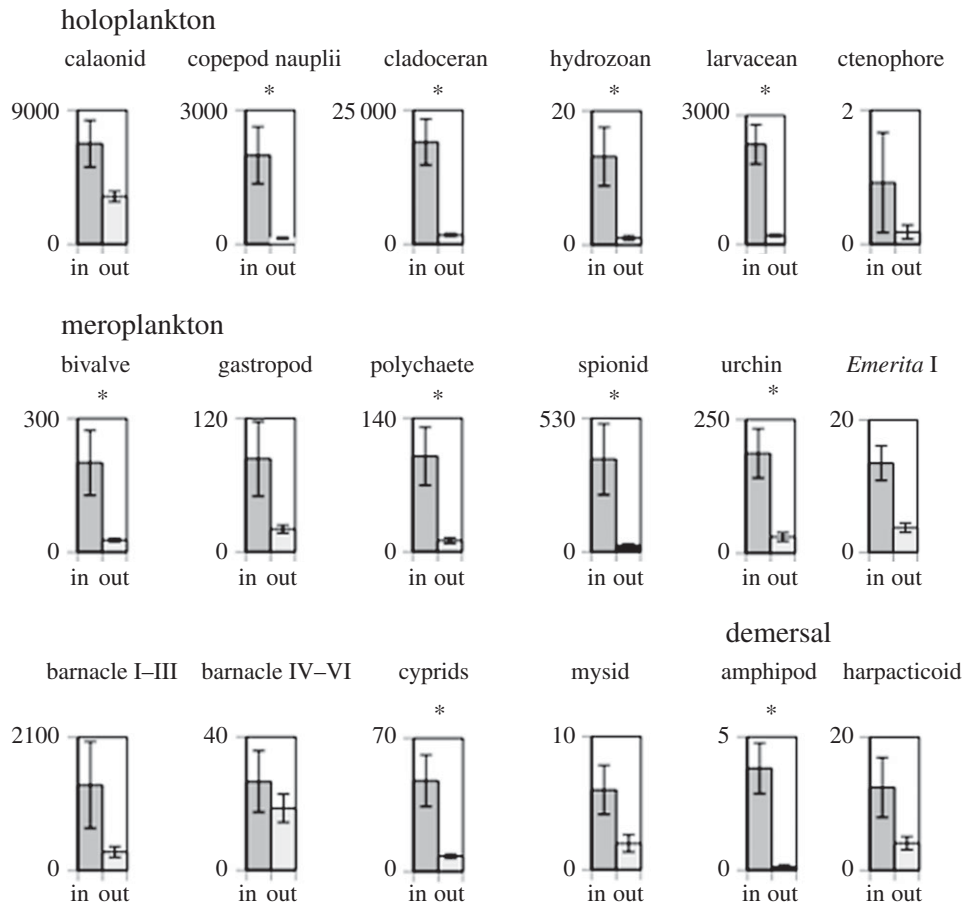


Figure 2. Concentrations of zooplankters ($\text{m}^{-3} \pm \text{s.e.}$) inside and outside the surf zone at the more DSZ, at Sand City, CA, USA. Asterisks indicate significant differences of t -tests: $*p < 0.05$. Significance levels were adjusted with a Bonferroni correction.

Samples inside the surf zone at RSZ were collected using a pump system during high tides while the intake was submerged. The intake of the hose (6 cm diameter) was attached to pipes that were embedded in the sand, and a gas powered pump sampled about 240 l of water per min filtering 1.2 m^3 of water per sample (three replicate samples) through a $200 \mu\text{m}$ mesh plankton net. Large waves at Sand City precluded installing a pump system during the first half of the study, and instead, a plankton net was deployed in rip currents during low tides using the flow of the rip current to provide the volumetric sample. A tethered swimmer released the net, which was held taught by a rope in the rip current. Plankton nets were $200 \mu\text{m}$ mesh and 0.25 m^2 mouth diameter. Pervasive differences in zooplankton were not owing to different sampling techniques inside the surf zone at the two study sites, because the same patterns were obtained using a pump during the second half of the study at the DSZ (data not shown).

Meroplankters were identified to species and developmental stage when possible, and holoplankters were identified to broad taxonomic levels. Detritus also was counted. To test the hypothesis that spatial variation in surfzone hydrodynamics affects the entry of zooplankton assemblages into the surf zones with different hydrodynamics, concentrations of each taxon of zooplankter collected inside and outside the surf zone at each study site were analysed by t -tests following a log-transformation to meet assumptions of the test.

Surfzone bathymetry was surveyed by walking with a GPS and personal watercraft equipped with a GPS-echosounder. *In situ* velocities and heights, periods and directions of waves were obtained from an array of acoustic Doppler current profilers, which were deployed inside and outside of the RSZ (3–7 m depth) and DSZ (13–20 m depth) sites.

Measured physical data were incorporated into a biophysical model validation that was based on work by Fujimura [9]. The

numerical simulation software package Delft3D provided three-dimensional hydrodynamic flow simulations of the near shore. Modelled physical parameters were incorporated into an individual-based model, including swimming by competent larvae. Virtual larvae were released hourly for 48 h and were initially distributed 410 m offshore at the DSZ site (602 larvae released) and 350 m offshore of the RSZ site (637 larvae released). Simulated larvae swam downward at $-10^{-3} \text{ m s}^{-1}$ until they encountered high turbulence (energy dissipation rate more than $10^{-5} \text{ m}^2 \text{ s}^{-3}$) in the surf zone, where their downward swimming increased to $-10^{-2} \text{ m s}^{-1}$, based on the responses of larvae to turbulence in the laboratory [12,13]. We did not include rollers from breaking waves, which could increase onshore larval transport and wave reflection, which could limit onshore transport.

3. Results

All members of the zooplankton assemblage were more abundant inside the more DSZ (figure 2), whereas they were more abundant outside the more RSZ (figure 3). At the DSZ, 15 of 18 zooplankton taxa counted were significantly more abundant inside the surf zone and the remaining three taxa tended to be more abundant there. Taxa included holoplankters, meroplankters and demersal zooplankters (adults of small benthic species that temporarily swim into the water column; figure 2). Furthermore, half of the 18 types of zooplankters were one to two orders of magnitude more concentrated inside than outside the surf zone at the DSZ (figure 2). A similar zooplankton assemblage occurred at the RSZ, but in stark contrast to the DSZ, all holoplankton and

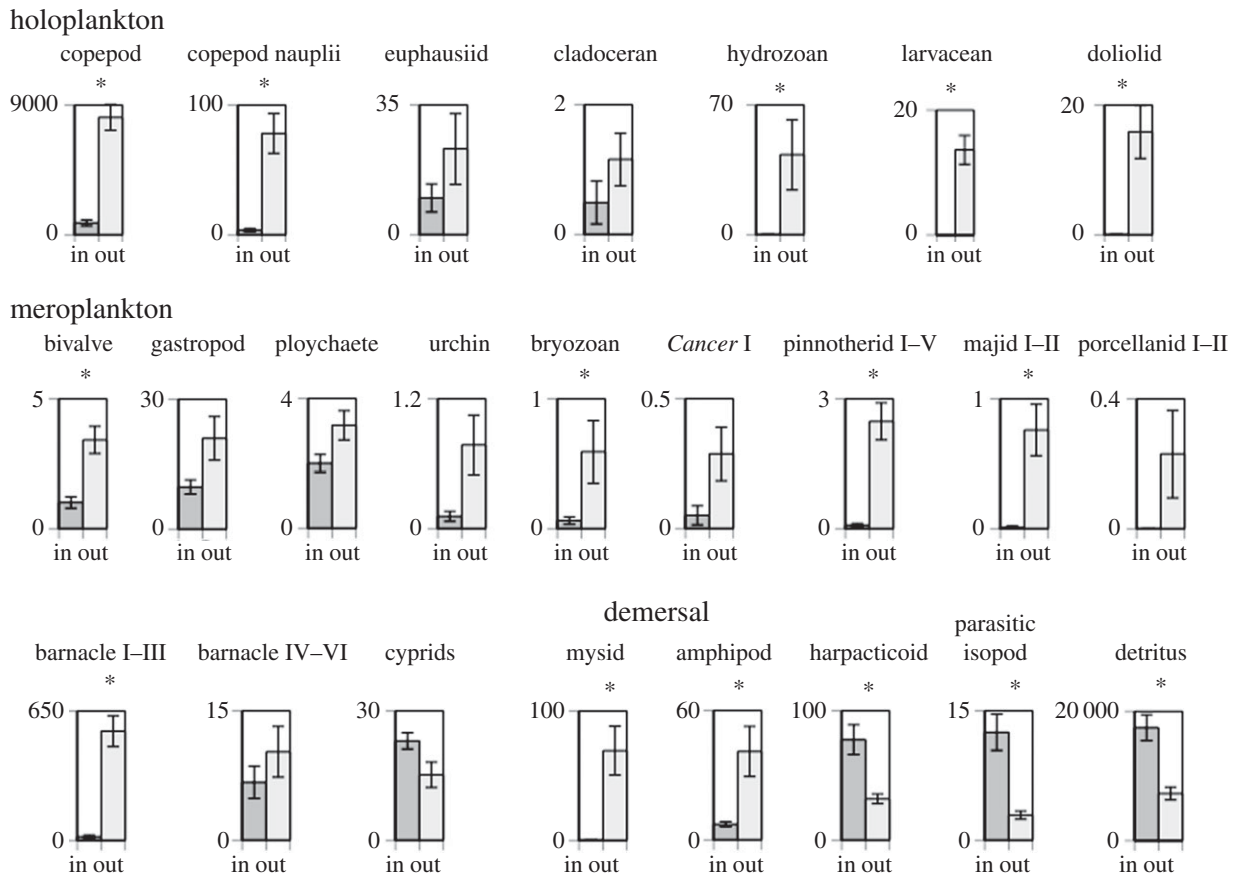


Figure 3. Concentrations of zooplankters ($m^{-3} \pm s.e.$) inside and outside the surf zone at the more RSZ, at Carmel River State Beach, CA, USA. Asterisks indicate significant differences of *t*-tests: $*p < 0.05$. Significance levels were adjusted with a Bonferroni correction.

meroplankton taxa were more abundant outside the surf zone (figure 3). However, only early stage larvae of barnacles were more abundant outside the surf zone, whereas the post-larval stage (cyprid) was more abundant inside the surf zone on about half the days, reflecting an ontogenetic shift in the delivery of barnacles to the surf zone. Furthermore, two of the four taxa of demersal zooplankters (mysid, amphipod) were more abundant outside the surf zone, and the other two demersal taxa (harpacticoid, parasitic isopod) were more abundant inside the surf zone. Hence, the few taxa that were more abundant in the surf zone (cyprids, harpacticoid, parasitic isopod) frequented bottom waters together with passively sinking detritus (figure 3), indicating that they might enter the surf zone near the bottom while the rest of the assemblage occurring higher in the water column might not.

The numerical simulations revealed that competent larvae at the DSZ entered the surf zone over shoals and were concentrated in rip channels in a system of alternating shoals and rip channels (figure 4). These onshore flows compensated for water that was transported seaward from the surf zone by the rip currents creating a strong recirculation. Once inside the surf zone, simulated larvae and other bottom dwellers exited the surf zone in rip currents and were transported shoreward again within these recirculation cells, thereby concentrating larvae in the surf zone.

Far fewer simulated competent larvae entered the surf zone at the RSZ in the absence of recirculation cells generated by rip currents owing to strong return flow from waves breaking on the beach called undertow (figure 4). Instead, simulated zooplankters mostly were transported alongshore outside the surf zone in prevailing equatorward flow,

where they were concentrated in eddies formed by the complex beach morphology.

4. Discussion

We found a strikingly pervasive pattern in the densities of zooplankton assemblages inside and outside the two surf zones, with zooplankters being much more concentrated inside the DSZ than the RSZ. These community-wide patterns were consistent with hydrodynamically driven numerical model simulations of larval concentrations, suggesting that surfzone hydrodynamics are the mechanism underlying the observed patterns.

Circulation in the surf zone is driven by breaking waves and bathymetry. At the DSZ, simulated zooplankters were concentrated in the surf zone by recirculation in an alongshore system of alternating shoals and rip currents [14–16]. Simulated zooplankters were transported into the surf zone over shoals, and they were concentrated in deeper rip channels before some returned seaward in offshore flow episodically with the arrival of wave groups. Prior to our study, diatoms that were specifically adapted to remaining in surf zones throughout their life cycles were known to be concentrated in surf zones [17], but it is now apparent that all zooplankters as well as passive particles may accumulate by recirculation in surf zones of rip-channelled shores [18,19].

Water exchange at the RSZ was about half that of the mild sloping DSZ owing to the absence of rip currents, which together with strong undertow, limited entry of zooplankton into the surf zone [20]. The RSZ resembled a large swash

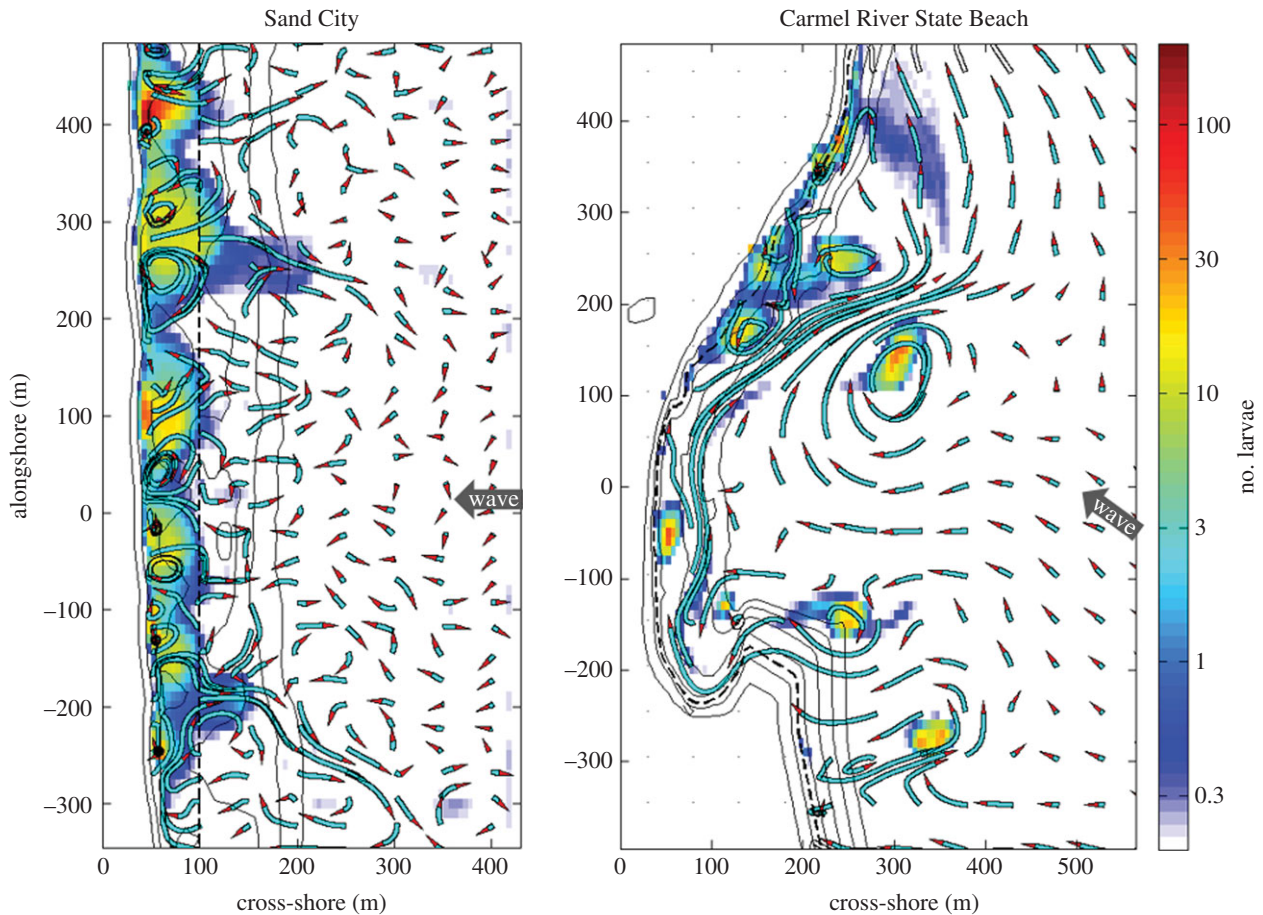


Figure 4. Modelled trajectories of depth-averaged Lagrangian velocities with an integration interval of 30 min in calm light winds at the more DSZ at Sand City beach where the root mean square wave height was 0.54 m and the peak wave period was 8.75 s and the more RSZ at Carmel River State Beach where the root mean square wave height was 0.4 m and the peak wave period was 9.45 s. Red tip indicates direction of the velocity. Overlay colour shows time and depth-averaged number of competent larvae obtained from the model. Approximate edge of the surf zone is indicated by a dashed line. Bottom contour lines from 0 m (shore line) to 5 m with 1 m increments are shown.

zone with water oscillating back and forth with each wave, and flow was offshore above the wave boundary layer with the bottom, resulting in little onshore transport of zooplankton into the surf zone. Zooplankton outside the surf zone were transported alongshore by the prevailing current, while onshore transport varied with the complex configuration of the shoreline.

When winds are light at both types of shores, currents stream landward near the bottom owing to wave stress, with benthic streaming increasing closer to shore as shoaling waves peak while currents are seaward throughout the rest of the water column [20–24]. Benthic streaming may increase entry of zooplankton into the surf zone at the RSZ, where only demersal taxa, including harpacticoid copepods, juvenile parasitic isopods seeking host shrimp and cyprids were more abundant inside than outside the surf zone. Streaming is suppressed by breaking waves at the seaward edge of the surf zone, but zooplankton, detritus and sediments near the bottom enter the surf zone by entrainment into breaking waves [25–27]. Although some species of cyprids have been reported to be more abundant near the sea surface [28–30], we previously demonstrated that cyprids of all species recruited almost entirely to the bottom of moorings just outside the surf zone over 5 years on this coast [31]. Hence, cyprids may descend near the bottom as they enter the surf zone regardless of their depth preferences, before they reach the surf zone in response to increased turbulence from shoaling waves, as do other zooplankters in

response to turbulence [12,13]. Benthic streaming also may deliver heavy zooplankters that passively sink to the bottom following mixing by large waves [27], whereas lighter zooplankton that do not swim downward would take longer to reach the bottom following mixing by small waves. The greater abundance of passively sinking detritus inside than outside the surf zone further indicates that streaming may transport zooplankton occupying the benthic boundary layer onshore [6,24]. Two other demersal taxa (mysids, amphipods) were not more concentrated in the surf zone, probably because they are stronger swimmers and spend more time above the benthic boundary layer than the other demersal taxa, especially at night [32].

Although zooplankters accumulated in the DSZ, they would not be expected to accumulate in the DSZ in the absence of rip currents owing to undertow limiting the onshore transport of zooplankton into the surf zone [33]. Thus, the abundance of zooplankton in the surf zone is expected to differ in the three types of surf zones. The abundance of zooplankton may be greatest in dissipative surf zones with rip currents, followed by dissipative surf zones without rip currents and least in reflective surf zones.

Although numerical simulations were based on light winds, our companion study demonstrated that simulated larvae also enter surf zones during windy conditions [34]. Simulated larvae near the surface were transported towards the surf zone by surface flow generated by wind stress and wave transport (Stokes drift). In the model, simulated larvae moved downward

in response to turbulence from breaking waves upon reaching the DSZ and were transported into the surf zone.

Our study demonstrates that the extent of subsidies of larvae and zooplankton to near-shore communities may be predictable depending on the bathymetry of the surf zone. The supply of larvae establishes the densities of communities, while the supply of zooplankton determines the food supply for growth and reproduction of filter-feeding foundation species of rocky shore communities [3,35,36]. In turn, these subsidies determine the intensity of top-down processes in communities [4,37]. Hence, surfzone hydrodynamics as well as near-shore productivity may determine the initial abundance of communities that are later modified by top-down processes, physiological stress and disturbance [1]. Our interdisciplinary comparative approach has demonstrated that spatial variation in surfzone hydrodynamics regulates the delivery of larvae and other zooplankters to shore, and our

companion study found similar patterns for phytoplankton [19], which has implications for the ecology, conservation and management of marine communities.

Data accessibility. All data are available through the National Science Foundation (<http://www.bco-dmo.org/person/506185>).

Authors' contributions. S.G.M. and A.L.S. conceived and designed the study and analysed biological data. All conducted the research. A.G.F. and A.J.H.M.R. conducted the numerical model and S.G.M. wrote the manuscript in collaboration with all.

Competing interests. We declare no competing interests.

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