Comment

Testing the intermittent upwelling hypothesis: comment

Bruce A. Menge [ID][1,3] and Duncan N. L. Menge [ID][2]

Introduction

The impact of recruitment of marine organisms on populations and communities has bedeviled fisheries scientists and ecologists for decades. The problem is that most marine species have complex life cycles, with adults living in a separate habitat (e.g., benthic) from that of juveniles (e.g., pelagic). Pineda (1994, 2000) modeled the complexity of the problem by depicting larval movement shoreward as passing through a series of filters, each depleting larval density and yielding a small fraction of settlers and recruits. He suggested that determinants of larval supply are the larval pool and physical and larval transport processes; of settlement are microhydrodynamics, behavior, and substrate availability; and of recruitment are local biotic interactions and disturbance, including environmental stress (Fig. 2 in Pineda 2000). Many have engaged in the quest to quantify these steps, but typically have focused on a few steps at most of the entire process. For example, some (e.g., larval biologists) study the factors underlying larval transport to the adult habitat while others (e.g., intertidal ecologists) investigate the events occurring from settlement or recruitment to adulthood, attempting to assess their importance in determining the final products of this process, population density, and community structure. More recently, each of these groups has sought to gain more insight by extending their purview either shoreward or seaward (Woodson et al. 2012, Menge and Menge 2013, Menge et al. 2015, Pfaff et al. 2015, Shanks et al. 2017, Morgan et al. 2018). For example, Pfaff et al. (2015) used coordinated studies of coastal physical oceanography

(upwelling currents, temperature, swell, winds), larval sampling, and settlement collectors onshore. They showed that upwelling/downwelling delivered larvae to within 1–2 km of shore, and that subsequent delivery to rocky shores was via a combination of swell or wave action, tidal flux, and sea breezes. Mussel larval delivery to the inner shelf occurred via upwelling in a bay but by downwelling at a headland, and at both sites intertidal settlement was associated with surface waves. Barnacle larval delivery to the inner shelf occurred during relaxation/downwelling at both sites, and intertidal settlement coincided with spring tides (i.e., likely delivery by internal tidal bores).

Toward an integrated model of community dynamics

The intermittent upwelling hypothesis (IUH; Menge and Menge 2013; hereafter M&M 2013) focused on how large-scale oceanic conditions influence the end result of pre- and post-settlement processes. The IUH hypothesized that "rates of ecological subsidies (bottom-up effects and recruitment), prey responses, and species interactions [in rocky shore ecosystems] vary with upwelling regime." Specifically, ecological subsidies, organismal performance, and species interactions on rocky shore ecosystems should be maximal with "intermittent" upwelling (IU), and minimal with either persistent upwelling (PU) or persistent downwelling (PD). IU occurs when upwelling and downwelling processes alternate on a scale of a week or two (e.g., Fig. 3A in M&M 2013). We suggested mechanisms underlying these dynamics could include conveyor belt-like cross-shelf flows induced by upwelling (when surface waters flow offshore and bottom currents flow onshore) or relaxation/downwelling (the reverse) (e.g., Roughgarden et al. 1988, Botsford et al. 2006, Woodson et al. 2012). Hypothetically, seaward surface flow during upwelling could move nutrients, phytoplankton, and larvae offshore, while shoreward flow during relaxation/downwelling could bring them back onshore. Pulsed ecological subsidies (nutrients, phytoplankton, and larvae) would result, leading in turn to higher recruitment and growth of sessile invertebrates. Persistent offshore flow (PU) would remove subsidies from the coastal ecosystem, while persistent onshore flow (PD) would suppress nutrient pulses from depth that fuel phytoplankton growth and feed larvae. Hence, PU and PD should lead to low subsidies. The IUH predicted unimodal relationships between upwelling and multiple ecological processes, and monotonic increases in processes with increasing intermittency of upwelling, in rocky shore communities (Fig. 3 in M&M 2013).

To test the IUH, we used data on ecological subsidies, mussel growth, and species interactions from repeated

measurements and field experiments at 16 to 45 sites over 10+ years. These data resulted from studies in Oregon, California, and the South Island of New Zealand (SINZ). Sites spanned the full range of upwelling regimes, from PD (SINZ east coast) to IU (SINZ west coast, Oregon coast) to PU (California coast). The NOAA-derived Bakun upwelling index[4] (average of monthly averages from 1995 to 2005) was our independent variable. From the Bakun index, we also created an index of upwelling intermittency to test if response variables increased monotonically with intermittency. Further details can be found in M&M (2013).

As predicted by the IUH, all nine ecological processes varied unimodally with upwelling regime, explaining between 27% (competition rate) and 71% (effect of predation on prey colonization) of the variance (adjusted R^2). Relationships to the intermittency index were more variable, being unimodal in some cases, and monotonically increasing in others.

A critique

Shanks and Morgan (2018; hereafter S&M 2018) critiqued the IUH, listing five predictions that they said "must hold" for the IUH to be true: (1) Larvae should inhabit the surface layer during upwelling. (2) Larvae should occur farther offshore during upwelling than during relaxation or downwelling. (3) Settlement should be lower during upwelling than relaxation/downwelling. (4) Settlement and recruitment should be lower in areas of PU vs IU. (5) Phytoplankton subsidies should be highest with IU.

They reviewed their own larval and settlement work and reanalyzed some published recruitment data, concluding that the five predictions were unsupported: (1) Larvae of many intertidal taxa occur deeper where currents flow shoreward during upwelling. (2) Larvae could remain within several kilometers of shore during upwelling and downwelling. (3) Daily barnacle and crab settlement were not higher during relaxation or downwelling events, but in their data varied with tidal cycles, suggesting onshore larval transport by internal tides. (4) Barnacle recruitment did not vary with upwelling, but varied with desiccation potential, and with surf zone hydrodynamics (hereafter SZH). (5) Phytoplankton subsidies also varied with SZH rather than upwelling.

S&M 2018 concluded that SZH (including tidal bores, and for which they used surf zone widths [SZW] obtained from Google Earth as a proxy) was the primary factor delivering subsidies to rocky intertidal communities. They also suggested that our methods for assessing barnacle recruitment were flawed and thus our data could not be used to test the IUH. Here, we evaluate these claims and propose an integrated conceptual

[4] http://www.pfeg.noaa.gov/products/las/docs/global_upwell.html

model that links larval transport mechanisms to onshore community dynamics.

As originally proposed, the IUH stopped short of identifying the dominant mechanism delivering subsidies to the shore, largely because (see Discussion in M&M 2013) many candidate mechanisms were feasible but their relative impacts had not yet been assessed (but see Woodson et al. 2012, Pfaff et al. 2015). Importantly, such mechanisms can affect transport of phytoplankton (food for larvae, settlers, and recruits) as well as larvae, joining larval transport as another upwelling-related process that could explain the results (Appendix S1: Fig. S1). That is, survival and growth of settlers are dependent on food availability (Emlet and Sadro 2006), so high recruitment can result from high food availability.

Below, we (1) consider if their critique actually addresses the predictions of the IUH, (2) suggest that differences in spatial and temporal scales of their vs. our research is a key disconnect, (3) identify factual and logical errors underlying their arguments about stress effects on recruitment, noting that potential desiccation effects likely are opposite to those argued by S&M (2018), and (4) present analyses using our barnacle and mussel recruitment data that do not support the idea of SZW as a primary determinant of recruitment.

Our response

Complete understanding of coastal ecosystem dynamics clearly requires understanding mechanisms transporting subsidies to the shore. However, the IUH made predictions about rocky shore ecosystems, not about pelagic larval dynamics (see Fig. 3 and related text in M&M 2013). As such, our data are consistent with the IUH; regardless of underlying mechanisms, subsidies and interactions were all high in IU regimes, and low in PD and PU regimes. Notably, similar results were obtained in Chile, another upwelling-dominated coastal ecosystem (Navarrete et al. 2005). Further, S&M 2018 did not challenge the other eight results supporting the IUH. We thus argue that the issue is more narrowly focused than the "invalidation" of the IUH. The real question is what mechanisms underlie recruit densities on rocky shores?

Importance of scale.—In our view, spatiotemporal scales and the scope of the ideas are key issues underlying differences between S&M 2018 and M&M 2013. We contrasted dynamics occurring on spatial scales of ~100's of km within three oceanographic regimes: PU, IU, and PD. Our data were from multiple replicate sites embedded within each of these regimes. Observational data were long-term, spanning >10 yr, and we used site-specific temporal averages for each factor. Species interaction data were averages across repeated 2- to 3-year-long experiments. Consistent with the IUH, unimodal

patterns of effect strength occurred along a down-welling–upwelling gradient (see Figs. 4–6 in M&M 2013). Unsurprisingly, about 50% of the variance in ecological dynamics remained unexplained. Potential causes of this variation discussed (M&M 2013, pp. 301–304: *Sources of Variability*) included temperature, coastal geomorphology, physical disturbance, propagule biology (e.g., larval behavior), and tidal change (internal bores). We concluded that "upwelling-related processes do not explain all of the variance observed, and factors typically operating at shorter time scales and smaller spatial scales are . . . also . . . important."

By contrast, although the spatial scale of the 2017 study (Shanks et al. 2017) was the entire US west coast, their studies were mostly shorter-term, based on 1–2 yr of samples. Since our data often reveal dramatic interannual differences in subsidies, this difference may be important. For example, S&M's first two predictions (see above) deal with larval location based on point-in-time samples: Larvae were typically within several kilometers of shore and often at midwater depths rather than in surface or bottom layers (e.g., Shanks and Brink 2005, Morgan et al. 2009). Prediction 3, that daily settlement should correlate to upwelling event scales (i.e., days), may not reflect large-scale and long-term average inputs. However, while details of the "mixed layer conveyor" model (Roughgarden et al. 1988, Botsford et al. 2006) may be inaccurate, to complete their pelagic life stage, larvae have to move from 5 to 6 km offshore to the inner shelf to have the potential to settle on rocky shores (Pineda 1994, 2000). Prior studies (Shanks et al. 2000, Shanks and Brink 2005, Woodson et al. 2012, Pfaff et al. 2015) suggest that upwelling regime processes (e.g., shoreward relaxation of upwelling fronts) may be an important mechanism in this shoreward larval movement. Once larvae arrive within a few hundred meters of shore, they must penetrate what has been termed the "semi-permeable" surf zone (e.g., Rilov et al. 2008). We argue that it is at this point that processes such as those investigated by Shanks, Morgan, Pineda, and others come into play.

Thermal stress and desiccation.—S&M's (2018) dismissal of the IUH is partly based on the claim that data from Saf-T-Walk ® (STW)-coated PVC recruitment plates (e.g., Broitman et al. 2008) are unreliable. In a ~60-d study (21 May to 4 August) in 2007 at one site, Shanks (2009) observed high cyprid mortality under exposure to solar radiation, which he extrapolated to infer that all data obtained with STW were flawed. One of us (Menge et al. 2010) has addressed this criticism before. Although if realized, this problem could only affect only one (barnacle recruitment) of the nine response variables we presented in 2013 (S&M 2018 expressed no reservations about the methods we used for the other eight measurements), the insistence that STW-based data are invalid clearly needs further discussion.

The benefits and flaws of STW-based estimates of barnacle recruitment are well-known; they provide a uniform surface that removes substratum texture heterogeneity as a source of recruitment variation, but usually (but not always; see Scrosati and Ellrich 2018) yield higher recruit densities than occur on rock (e.g., Menge et al. 2010). As Shanks (2009) demonstrated, under sunny conditions, they can heat up more than does rock and the resulting thermal stress can kill cyprids. However, as detailed below, (1) low tides occur progressively earlier in the day from spring through summer and (2) occur progressively earlier southward. Thus, environmental stress during low tides likely decreases from spring through summer and southward.

First, on the US west coast, spring and summer lower low tides (S&S-LLTs) occur in early mornings. Due to lunar cycles, exposure to desiccating conditions declines because good S&S-LLTs (i.e., ≤0 m) occur progressively earlier in the morning. Using 2017 tides in Oregon, for the 16 April LLT series, LLT time on the first (last) day was 07:24 = 00:54 h after sunrise (13:39 = 07:21 h after sunrise) (Appendix S1: Fig. S2, Appendix S2: Table S1). On 7 August, the first (last) tide was 03:28 = 2:42 h before sunrise (09:52 = 03:34 h after sunrise). Thus, by July and August, most LLTs occur in the dark or shortly after sunrise. Hence, each tide series, stressful conditions are likely limited to the later LLTs in May and June, the months Shanks (2009) did his study. Further, in Oregon, the annual barnacle settlement/recruitment window is long, spanning 9 months (~270 d) from February to December, and peaks from August to October (Menge et al. 2011)—clearly later in the season than Shanks' (2009) study. Hence, high cyprid mortality during May–June, even if an annual event, likely has little bearing on cumulative annual barnacle recruitment.

Second, recruitment bias due to artificially high thermal stress on plates would strengthen, not weaken our conclusions. The IUH was tested using cross-site comparisons, so our conclusions regarding barnacle recruitment could be invalidated by contrary cross-site temperature trends, not thermal effects at any given site. Although S&M 2018 argue that this is the case, latitudinally, recruitment actually varies positively, not inversely with solar energy-induced desiccation stress. That is, because LLT timing is steadily earlier in the morning southward, many spring and summer low tides in the (e.g.,) Point Conception region are actually at night (Appendix S1: Fig. S2, Pt. Arguello). For example, all first LLTs in a tide series occurred before dawn at Pt. Arguello (between 1:29 and 3:49 h before sunrise), while those in Oregon occurred after sunrise. Thus, spring tides in Oregon (where recruitment is high) should be more stressful than those at Point Conception (where recruitment is low).

Third, S&M 2018 correlated recruitment data with average (terrestrial) solar radiation for a given latitude

rather than with actual LLT solar conditions on intertidal rocks. That is, logically, to underlie high recruit mortality, higher solar radiation southward must coincide with daytime LLTs. However, the opposite is the case. As noted above, most LLTs in southern California are predawn or early morning (Appendix S1: Fig. S2A, Appendix S2: Table S1), so solar radiation in the intertidal should be weaker than if tides occurred midday. Further, strongly upwelled regions typically have dense coastal fog, especially southward, cooling the coastal strip, thus likely keeping thermal stress low. Finally, Robomussel-derived data (see Helmuth et al. 2002) clearly overestimate, and are thus inappropriate measures of, rocky shore air temperatures. Mussel mimics are black, solar energy-absorbing, and estimate mussel body temperature, not air temperature. For example, at our Strawberry Hill study site from April through August 2009, overall mean ($\pm$ 1 SE, $n = 153$) and means of the highest 40 average daily Robomussel-recorded LLTs were 1.61 ± 0.11 °C and 2.31 ± 0.05°C higher, respectively, than recorded in situ by Onset TidBits®. Further, averages of the 15 highest single readings were 35.2°C for Robomussels vs. 29.9°C for TidBits. These considerations suggest that correlations shown by S&M (2018, see their Figs. 1B, 2D–F) have little bearing on realized barnacle recruitment.

To examine actual latitudinal gradients of LLT air temperature, we compared mid intertidal zones at study sites from Oregon (44.77° N) to southern California (34.45° N). LLT extremes were estimated as the average of the five highest daily air temperatures recorded. In contrast to S&M 2018's claims and consistent with prior reports (Helmuth et al. 2002), LLT air temperatures in the north, where recruitment is higher, are actually higher than to the south (Appendix S1: Figs. S2, S3). Thus, although solar radiation undeniably increases southward, rocky intertidal air temperatures during LLTs vary inversely to this trend, suggesting that thermal stress cannot explain the southward recruitment decline (Broitman et al. 2008, Woodson et al. 2012).

Surf zone hydrodynamics.—S&M (2018) reported that larval delivery and barnacle recruitment were higher on "dissipative" than on "reflective" beaches. Dissipative beaches are broad gently sloping beaches with shallow bottom slope
offshore, allowing waves to expend their energy and presumably carry particles (larvae, phytoplankton) across shore and deposit them on the beach. Reflective beaches are narrow steep beaches with steeper offshore slopes that reflect the energy of waves back seaward, presumably carrying particles back seaward. S&M (2018) suggested that as a result, larval delivery, recruitment, and phytoplankton abundance were higher on dissipative beaches, and that in all cases, upwelling had little to do with these patterns.

Besides sandy beaches, Shanks et al. (2017) studied sandy beaches with embedded rocks ($n = 18$) and rocky shores ($n = 22$). In an impressive investigation, they quantified barnacle settlement (spring and summer 2010) and recruitment (spring and summer 2011) to previously cleared rock surfaces. In 2012, they photographically surveyed barnacle densities at 40 sites along 2,000 km of coast to assess geographic adult and recruit abundance. Correlations between these data and SZWs measured using images from Google Earth were consistent with their argument that recruitment is higher at sites with wide surf zones.

While the SZH mechanism is a sensible means for larval penetration of the semipermeable surf zone barrier (Rilov et al. 2008), we were skeptical that recruitment on rocky shores could be predicted by SZW. Rocky shores can be highly heterogeneous and rarely have the smooth planar surfaces seen on sandy beaches (including those with embedded rocks). Hence, different portions of rocky shores can be both reflective (i.e., are steep and waves reflect from them) and dissipative (i.e., waves shoal across broad rocky benches) (B. A. Menge, *personal observation*).

S&M (2018) used indirect methods to expand their previous analysis. They extracted recruitment data for *B. glandula* (and *Mytilus* spp.) from Broitman et al. (2008, see Figs. 2 and 3) by matching colors on a heat map of temporal patterns of recruitment to the associated logarithmic heat map scale. They correlated those values to daily solar radiation, maximum low tide temperature (from Robomussels), alongshore wind stress (their measure of upwelling), and SZW (Fig. 2 in S&M 2018), concluding that the results were consistent with their hypothesis.

With some modifications, we quantified SZW using the same method to conduct an independent assessment of the relationship between SZW and recruitment and phytoplankton (Chl-a). Because of the topographic heterogeneity of rocky shores, we took four evenly spaced measurements for each of our sites for each image rather than one. Although the great majority of images were from spring and summer, we also used images from fall when recruitment to our sites is highest. Although *Chthamalus* spp. recruitment was not considered by S&M (2018), Broitman et al. (2008) presented data on this species as well. Further, Woodson et al. (2012) found that *Chthamalus* spp. recruitment was associated with upwelling fronts colliding with the shore. We used data averaged across multiple years (up to 23) at sites ranging from 38 to 45° N latitude (Appendix S2: Table S2). Excepting a weak saturating nonlinear increase in Chl-a with increased SZW ($P = 0.043$), recruitment was unrelated to SZW (Appendix S1: Fig. S4, Appendix S2: Tables S3, S4) and varied only with latitude, along which upwelling increases southward.

With respect to barnacle recruitment, we are unsure why S&M's (2018) and our analyses differed. Possible

factors: (1) Our sampling per site per image was denser (four measurements vs. one) and focused on the portion of each site where our collectors were located. (2) All our sites were the most wave-exposed sites we could safely access, while based on images in the various papers of Shanks and Morgan, their sites were often in somewhat more sheltered locations where recruitment is typically lower. (3) We used long-term means of data vs. either 1 yr of data at a site or estimations from published heat maps. (4) S&M 2018 had a greater latitudinal range of sites, but a similar number of rocky sites, so our sampling was finer scale in space but shorter in extent. All of these possibilities could underlie the differences.

CONCLUSION

Despite conflicting results on the relation between SZW and recruitment, we believe that with many other factors, SZH likely plays a role in transporting larvae to intertidal rocks. Prior research shows that multiple processes, including upwelling/downwelling currents, internal waves, surface waves, benthic streaming, surf zone dynamics, and shoreward movement of upwelling fronts, are all involved in the complex process of transporting larvae through the multiple filters impeding their progress toward shore. Although Shanks and Morgan have contributed greatly to our understanding of larval transport mechanisms, we believe their critique is narrowly focused and rather than invalidating the IUH, serves to provide mechanistic insight helping to explain unexplained variance in community dynamics. We suggest a more profitable approach would be to develop and test a comprehensive model that links benthic ecology to the pelagic processes that underlie subsidy delivery to the coast.

A synthesis of Shanks, Morgan, Pineda, Rilov, Woodson, Pfaff, and others with ours might go as follows (Appendix S1: Fig. S1): Adult spawning produces larvae that migrate/are transported several km offshore where they develop and mature. Here, behavioral interactions with vertical currents can enable many species to prevent cross-shelf currents from moving them out of the system. Transport shoreward is driven by upwelling-related flows, probably interacting with behaviors that take advantage of such flows. These dynamics move larvae to the inner shelf (~500–1,000 m of shore), where waves, upwelling fronts, internal tides, sea breezes, benthic streaming, and in rocky areas, topographically driven complex microhydrodynamics interact to enable them to penetrate the surf zone and settle. As envisioned in the IUH, post-settlement processes, including delivery of phytoplankton, stress, physical and biological disturbance, competition, facilitation and predation, then interact to produce patterns of community structure. Research programs integrating these many stages would go far in solving the problem of the roles of oceanic conditions and site-scale processes in determining community structure and dynamics.

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Supporting Information