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Testing the intermittent upwelling hypothesis: reply

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We evaluated the Intermittent Upwelling Hypothesis (IUH) in Shanks and Morgan (2018), henceforth S&M. We presented five expectations, which must be true if the hypothesis is correct. We tested each of these expectations against available published results and, as part of this analysis, we reanalyzed data from Broitman et al. (2008). We concluded that available data do not support any of the five expectations and, hence, the IUH was not supported. Menge and Menge (2019, henceforth M&M2) dispute our conclusions, and here we respond to their comments.

A detailed description of the IUH was presented in Menge and Menge (2013), henceforth M&M, and was reiterated in M&M2. M&M argued that the IUH can explain both the effect of the pelagic environment on coastal rocky shore communities by varying subsidies of larval settlers and phytoplankton food for filter feeders and the subsequent structure and function of those communities (e.g., competition, predation, and community structure) due to variation in subsidies.

Because in S&M we limited our comments to the pelagic aspect of the hypothesis, M&M2 concluded that we accepted that the structure and function of rocky shore communities varies with intermittent upwelling. We did not address the expectations of community structure and function because, as Dr. Menge and co-authors have repeatedly pointed out, the structure and function of rocky shore communities is largely regulated by bottom-up subsidies; subsidies of larvae set the composition and density of a community and subsidies of phytoplankton from the coastal ocean control the relative importance of filter feeders vs. herbivores within a community (Menge et al. 1997, 1999, Menge 2000). We do not dispute

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bottom-up regulation of community structure and function, but what S&M demonstrated was that variation in bottom-up regulation, subsidies, is not due to intermittent upwelling.

M&M2 stated that “As originally proposed, the IUH stopped short of identifying the dominant mechanism delivering subsidies to the shore.” Later they stated that the “IUH made predictions about rocky shore ecosystems, not about pelagic larval dynamics.” We find these statements surprising. The beginning of the formulation of the IUH was presented in Roughgarden et al. (1988), wherein they clearly hypothesized that larvae are advected much farther from shore by upwelling currents in regions of strong, persistent upwelling than regions of weak, intermittent upwelling leading to higher larval “wastage” and lower larval supply and settlement where upwelling was strong and persistent. They later proposed that, in regions of strong upwelling, larvae accumulating offshore at the upwelling front can be transported back to shore during infrequent downwelling/relaxation (Farrell et al. 1991, Roughgarden et al. 1991), an idea also presented in Woodson et al. (2012). These are clear mechanistic expectations that appeared at the origin of the IUH and have carried through to the present. Indeed, M&M2 stated that the “mechanisms underlying these dynamics could include conveyor belt-like cross-shelf flows induced by upwelling... or relaxation/downwelling” at which point they cited Roughgarden et al. (1988). The IUH clearly has from its inception presented a mechanism based on the relative strength and persistence of upwelling and downwelling for the delivery of subsidies to the shore. In S&M, we argued that this mechanism is not supported by available data.

IMPORTANCE OF SCALE

Scale is important. The scale of the studies we cited has been grossly understated by M&M2 and our conclusions are not compromised by limited coverage. For example, there have been 41 daily time series collected between 1983 to the present, 15 tracked barnacle settlement and 26 monitored the daily abundance of crab and shrimp post-larvae (Appendix S1: Table S1). These studies were conducted under a wide range of coastal hydrographic conditions and surfzone hydrodynamics, e.g., weak upwelling system, weak upwelling/persistent downwelling intermittent upwelling, and strong persistent upwelling system of central and northern California. In none of these studies did daily barnacle settlement cross-correlate with downwelling/relaxation events, instead, there was a strong relationship between settlement and the fortnightly tidal cycle suggesting shoreward transport by the internal tides. In only one of the studies of daily larval abundance (Mace and Morgan 2006) was abundance significantly correlated to downwelling/relaxation events. In two studies (Appendix S1: Table S1), larval abundance was

actually higher during upwelling events and in the remainder abundance varied significantly with the spring/ neap tidal cycle suggesting onshore transport by internal waves and bores.

In evaluating the potential effect of surfzone hydrodynamics on subsidies of larvae and planktonic food, we surveyed barnacle and limpet populations from northern California into central Oregon (Shanks et al. 2010), and in our follow-up study, we surveyed barnacle populations at 40 sites from San Diego to northern Washington (Shanks et al. 2017a). We also cited our two-month long time series of daily concentrations of zooplankton and phytoplankton within and seaward of a reflective and dissipative surf zone (Morgan et al. 2016, Shanks et al. 2016, 2017b, Morgan et al. 2017a,b) as well as phytoplankton concentrations in surf zones around Cape Arago, Oregon, sites with a wide range of surfzone widths that were sampled during two years (Shanks et al. 2017c, Salant and Shanks 2018). In addition, we reanalyzed the extensive data set on barnacle and mussel recruitment presented by Broitman et al. (2008) and surfzone phytoplankton abundance in Bracken et al. (2012). In all our surf zone work and our reanalysis of published work, the results have been consistent; subsidies of larval settlers and zooplankton and phytoplankton food are higher within more dissipative than reflective surf zones.

M&M2 characterized the studies testing two of the key predictions of the pelagic side of the IUH, e.g., whether larvae inhabit the surface Ekman layer or not and are they distributed further offshore during upwelling than downwelling, as “point-in-time samples,” suggesting that the results are snapshots of limited utility. Essentially, all ship-based plankton sampling, including the CalCOFI samples used by Roughgarden et al. (1988) to generate the initial IUH, is of limited duration, point-in-time samples. Many larval surveys have, however, been conducted by multiple investigators in time and space (Appendix S1: Table S2). The results from these studies have been quite consistent, demonstrating reliable interspecific differences in the vertical distribution of larvae and the distances they are found from shore. We collected extensive data from a site of weak upwelling (Duck, North Carolina, USA), in the intermittent upwelling off Southern Oregon, and multiple locations for many years in the persistent, strong upwelling off northern California including the jet off a major headland (Point Reyes), and the strongest upwelling center on the West Coast (Point Arena). Other investigators have obtained similar results in the weak upwelling off southern California (Tapia and Pineda 2007) as well as in other upwelling regimes, including the Iberian Peninsula and Chile. One might be tempted to discount the work off Duck because upwelling is weak there, but no matter the site and hydrodynamics, wind-driven, cross-shelf currents in the surface Ekman layer are always faster, generally at least 10× faster, than the swimming speed of nearly all larvae. Hence, the predictions of the IUH should hold even outside the four major

eastern boundary current wind-driven upwelling systems. Thus, these pelagic studies spanned a large range of upwelling conditions and the results are quite consistent. Larvae of many organisms that live in the intertidal or shallow subtidal as adults tend to avoid the surface Ekman layer and are found close to shore, generally within several kilometers of shore despite upwelling and downwelling cross-shelf currents (the conveyor belt of currents) while other species reliably occur at species-specific distances farther from shore regardless of upwelling conditions (Shanks and Brink 2005, Morgan et al. 2009, 2018, Shanks and Shearman 2009).

Clearly the conclusions presented in S&M are not weakened due to a lack of scale.

THERMAL STRESS AND DESICCATION

In a pair of papers (Shanks 2009a,b), Shanks investigated why studies of barnacle recruitment suggested that recruitment varied with the intensity of upwelling while daily settlement studies did not. He replicated the methods of previous recruitment studies and used Safety-Walk tape (3M Corporation, Maplewood, Minnesota, USA) on PVC plates as the settlement surface. To his surprise, he discovered that these plates heated very rapidly in the sun, reaching temperatures lethal to cyprids (e.g., >50°C) within as little as 10 min. These results called into question the use of Safety-Walk plates as recruitment surfaces for barnacles. Recruitment on a plate would be equal to settlement minus natural mortality plus mortality due to unnatural overheating of the Safety-Walk plate while in the sun. The longer plates are deployed before counting the number of recruits, the more likely that they would be exposed to direct sunlight that would heat the plates to lethal temperatures. Safety-Walk plates typically have been checked monthly in most recruitment studies cited to support the IUH (Connolly et al. 2001, Menge et al. 2003, Broitman et al. 2008) during which time there is a high probability that results will be affected by repeated heating events.

As part of the S&M critique of the IUH, we reanalyzed data from Broitman et al. (2008), who used Safety-Walk plates to monitor barnacle recruitment. Because of the potential deleterious effects of solar heating on recruitment when these plates are used, we tested the effect of solar radiation and heating on recruitment. M&M2 suggested that our analysis is flawed because we did not include the effect of the timing of low tide on thermal stress (Helmuth et al. 2000). This criticism is irrelevant and not correct. It is irrelevant because Safety-Walk plates heat up so rapidly in the sun that overheating can occur during any daytime low tide rather than just long low-low tides in the afternoon. Helmuth et al. argued that thermal stress depends on both the duration of exposure and the time of day the exposure during low tide occurs; thermal stress will be more severe where extreme low tides tend to occur during hotter times of the day. For adult organisms living on natural substrate, Helmuth et al. is undoubtedly correct, but

for cyprids on a Safety-Walk plate that can heat to $>50^{\circ}\text{C}$ in as little as 10 min in the sun, the timing of the extreme low tide is irrelevant; whenever a plate is exposed to the sun, even briefly, it can reach temperatures lethal to cyprids. For example, Shanks (2009b) observed complete mortality of a cohort of recently settled cyprids during an early morning low tide. The plates were exposed by the falling tide at 04:00, the sun rose at 05:30, plates were exposed to direct sunlight at about 07:00, $>50\%$ of the cyprids were already desiccated and dead at 07:20 when the plates were first inspected, and all cyprids were dead two hours later. Throughout the summer that these observations were made (Shanks 2009b), surface temperatures on the Safety-Walk plates under a variety of weather conditions (full sun to overcast) were consistently higher than on tile plates or rock, and cyprid mortality was consistently much higher on the Safety-Walk plates than on rock or tile. For example, in full sun and partly cloudy conditions, cyprid mortality in the daily counts of Safety-Walk plates were 100% and 80%, respectively, while mortality on adjacent tiles was $<5\%$. The timing of extreme low tides has little effect on the lethality of Safety-Walk plates.

The criticism is also not correct. To address this perceived problem put forward in M&M2, we used two measures of solar heating: average solar radiation levels on land at the study sites (the shoreline at low tide is exposed to the same solar radiation as the adjacent land) and average maximum low tide temperature (S&M) using the Robomussel temperature data from Helmuth et al. (2016), which provides a measure of low tide temperature extremes. Thus, we did include in our analysis a measure of temperature during low tide and its effect on recruitment.

Before we could determine the effects of upwelling/downwelling or surfzone hydrodynamics on recruitment in the Broitman et al. (2008) and our data, we first had to remove the potential effect of mortality due to solar heating on recruitment. We calculated regressions between our two measures of potential solar heating and recruitment of mussels and *Balanus* in the Broitman et al. (2008) data and the *Balanus* recruit density data in Shanks et al. (2017a). In the Broitman et al. (2008) data set, 60–70% of the variability in mussel and *Balanus* recruitment could be explained by the two measures of potential solar heating, whereas in the Shanks et al. data set, only 11–20% of the variability of new recruit density on rocks could be explained by solar heating.

Surprisingly, Safety-Walk plates are still being used to measure barnacle recruitment. Researchers doubting the veracity of the experiments presented by Shanks (2009b) should replicate the experiments.

SURFZONE HYDRODYNAMICS

We begin by clarifying apparent misunderstandings of our surfzone work by M&M2. Our initial work (Shanks et al. 2010) tested the hypothesis that adult and recruit

densities of barnacles and limpets varied with surfzone hydrodynamics. Densities of recruits on boulders and rock platforms within sandy beaches were much higher and more dissipative than reflective shores. This led to the hypothesis that surfzone hydrodynamics limits or facilitates the delivery of subsidies to the shore. To test this hypothesis, we collaborated with surfzone oceanographers to intensively study a more reflective and more dissipative surf zone (Fujimura et al. 2013, 2014, Fujimura 2015, Shanks et al. 2015, Morgan et al. 2016, 2017a,b, Shanks et al. 2016, 2017b, 2015). We focused this work at two sandy shores because surfzone oceanographers have developed theory and effective techniques for sampling surf zones of sandy beaches but have not worked at rocky shores. However, whether a surf zone is more dissipative or reflective is largely due to the slope of the shore and is unaffected by the composition of the benthos (i.e., rock or sand); conclusions from this work should be generally applicable, though this remains to be tested. Subsidies of larval settlers and phytoplankton and zooplankton food were much lower in the more reflective than the more dissipative surf zone. In a subsequent study of barnacle population structure, we sampled 40 sites spanning a range of surfzone hydrodynamics and upwelling conditions (i.e., Southern California Bight with weak upwelling and more persistent downwelling, northern California with persistent upwelling, and Oregon and Washington with intermittent upwelling). Because we surveyed barnacle populations, all of this work was conducted on rocky shores, many of which were the rock platforms typically studied by intertidal ecologists (roughly 50% of the sites) while the rest were smaller stretches of rocky shore surrounded by sandy beaches. We have clearly studied the effects of surfzone hydrodynamics on subsidies to the shore under a wide range of conditions and within a large geographic setting.

Despite our data, M&M2 are skeptical that surfzone hydrodynamics, as indicated by surfzone width (SZW), could be used to explain variability in recruitment and subsidies to rocky shores. In M&M2, they conducted an independent assessment of the relationship between SZW and recruitment and phytoplankton concentration using their data and, reportedly, the same methods as we used in S&M and Shanks et al. (2017a). In actuality, they did not use the same methods. They stated that “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.” They did not state the spacing used, but given the scale at which surf zones can change along a shore, this approach will yield erroneous results. In several of our papers (Shanks et al. 2017a,c, Salant and Shanks 2018), we sampled closely spaced stations (as little as tens of meters separation) so the coastal oceanography beyond the surf zone should be homogeneous. If the surf zones at the two closely spaced sites were similar in width (similar hydrodynamics), there were no differences in the number of settlers, recruits, or phytoplankton concentration within in the surf zone. If,

however, the hydrodynamics were different, a wide compared to a narrow surf zone, then the density of recruits, the number of settlers, and the concentrations of phytoplankton within the surf zone were consistently higher at the wider surf zone. For example at Indian Beach, Oregon, sample sites separated by 220 m had surfzone widths of 47 and 152 m and *Balanus* density at the wider surf zone was almost 10× higher (Shanks et al. 2017a). In two other studies (Shanks et al. 2017c, Salant and Shanks 2018), two sample sites were only 30 m apart, yet the surf zone at one was more dissipative (mean SZW 250 m) and the other more reflective (mean SZW 19 m) and the phytoplankton concentrations in the surf zones differed by about a factor 10. We measured SZW immediately seaward of our sample sites (Shanks et al. 2017a,c, Salant and Shanks 2018), taking the average SZW at sites on either side of the sample site will produce erroneous results. Thus, it is to be expected that M&M2 did not find a relationship between SZW and their recruit and phytoplankton data.

CONCLUSION

We appreciate the opportunity to address the rebuttal to our evaluation of the IUH. The critique by M&M2 did not persuade us to modify any of the conclusions in S&M; the IUH is not supported by the available data.

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