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The effect of an invasive foundation species on diversity is due to increased habitat availability

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ABSTRACT

Both foundation species and introduced species have exceptional influence on community diversity and structure, though they have historically been thought to have opposite effects. However, when introduced species can provide novel habitat within a community, their benefit to the community as a foundation species may outweigh their cost as an invader. The magnitude or direction of species interactions can depend on the environment, thus the net effect of introduced foundation species can vary across different environmental factors. A settlement tile experiment was conducted on the fouling communities of California harbors to determine whether the effects of a widespread invasive bryozoan, *Watersipora subtorquata*, vary between two locations in its California range, Alamitos Bay and Bodega Harbor. Treatments with live and dead colonies and two sizes of blank tiles were used to evaluate the effects of colony structure and available bare substrate on both mobile and sessile species in the community. Though mobile invertebrate communities in each location across treatments were not significantly dissimilar to each other, communities on large tiles were significantly dissimilar to other communities in each location. Mobile species richness was greatest on live colony and small tiles in Bodega, but greatest on dead colony and large tiles in Alamitos. Both the diversity and community structure of sessile invertebrates across treatments differed significantly between regions. Diversity was greatest on dead colony tiles in Alamitos, where communities were more dissimilar across treatments, but was greatest on live *W. subtorquata* tiles in Bodega where communities were less dissimilar across treatments. These results highlight the potential for *W. subtorquata* to have location-dependent net effects on the community throughout its invasive range as a foundation species.

1. Introduction

While antagonistic species interactions such as predation and competition are important factors that affect community structure and diversity, positive interactions between species (i.e., facilitation) have an underappreciated and often overlooked influence on community dynamics (Bruno et al., 2003; Rodriguez, 2006; Stachowicz, 2001). Examining the effects of facilitative species (e.g., keystone species, foundation species) is important for understanding the net effect of a single species on its community. Foundation species create structural habitat and facilitate community diversity and ecosystem function (Dayton and Hessler, 1972; Stachowicz and Byrnes, 2006). For example, corals (Holbrook et al., 2008), over story trees (Angelini and Silliman, 2014; Rohr et al., 2009), and kelp forests (Graham, 2004; Hughes, 2010), each increase structural habitat complexity, an important factor implicated in explaining the high biodiversity of these systems. Though they can dominate the landscape (Bruno et al., 2003; Stachowicz, 2001), foundation species have a net positive effect on species diversity by providing habitat for other species.

Introduced species can exhibit similar community-wide effects to foundation species as they expand their range. However, they often decrease species diversity (Burgiel and Muir, 2010), either directly via competition or predation, or indirectly by alteration of the physical or biotic environment (Bax et al., 2003; Sorte et al., 2010). In some cases, introduced species may also serve as foundation species and have net positive effects on the other species in the community (Jones et al., 1946; Rodriguez, 2006). Introduced foundation species can influence community composition, abundance, and diversity if they provide a novel or superior resource to the native community (Crooks, 2002; Parker et al., 1999). In marine fouling communities in tropical and temperate systems, native and non-native tunicates, mussels, bryozoans, and other sessile invertebrates create habitat complexity and structural heterogeneity through their growth on the substratum (e.g., docks, pier pilings, ship hulls). In fouling communities, limited

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settlement substrate promotes a colonization-competition tradeoff in life history traits of fouling community members (Edwards and Stachowicz, 2010), but introduced foundation species may alleviate such constraints by providing novel habitat that can have cascading indirect effects on composition and diversity (Crooks, 2002). As such, fouling communities provide an interesting opportunity to understand how introduced species can alter native community composition and diversity through facilitative and inhibitive effects, and whether the net effect on the community is positive due to novel habitat provision.

Interestingly, the net effect of the introduced habitat-provider on diversity is sometimes undetectable (Bouma et al., 2009; Hedge and Kriwoken, 2000) because the novel or superior habitat provided facilitates some species, while inhibiting others, or is functionally redundant to other habitat providers present. In any case, the effects of introduced species that provide novel habitat within a community can have cascading direct and indirect effects on composition and diversity such that the resulting net effect may be positive (Crooks, 2002; Parker et al., 1999; Simberloff, 1995). For example, *Zostera japonica*—a widely-introduced east Asian seagrass along the western North American coast—is associated with higher invertebrate abundance and facilitation of species diversity as its shoot density and morphology create greater structural complexity relative to the native congener, *Zostera marina* (Knight et al., 2015; Posey, 1988). The net positive effect on the community diversity was the result of facilitative effects for some fauna and reductions in others through both direct and indirect effects on the community composition and habitat factors (i.e., sediment size, chemical composition) (Posey, 1988). This study within seagrass communities highlights the importance of examining changes of different taxonomic groups and composition, rather than just overall diversity or richness.

Because introduced species can settle successfully in environments with different abiotic (e.g., temperature, precipitation, salinity) and biotic (e.g., competition, facilitation) conditions, there is potential for their interactions with other species in the community to differ throughout their introduced range. Introduced species with ranges that span across environmental gradients can exhibit differences in growth rates (Arendt, 1997; Weis et al., 2000) and other traits that may be important to establishment and spread (Dmitriew, 2011; Li et al., 2014; Stinchcombe et al., 2010). These differences in introduced species traits are likely to translate to varying effects throughout their introduced range as they interact with different environments and communities, though few studies incorporate such spatial variation. A meta-analysis of 68 bivalve studies found that bivalve ecosystem engineers have an overall positive effect on both species richness and abundance, because they increase structural complexity, but their effect size was dependent on both bivalve traits and environmental context (Bateman and Bishop, 2017). For example, oysters facilitated a greater abundance of invertebrates than mussels or pinnids that were less structurally complex (Bateman and Bishop, 2017). While communities were generally more responsive to the structural heterogeneity of the bivalve, the magnitude and direction of effects also differed among tidal elevation, latitude, and habitat (Bateman and Bishop, 2017). As such, the environmental differences throughout an invasive species' range can have implications for the interaction strengths both among community members and between an invader and the native species.

The focal species of this study was a widespread introduced colonial bryozoan, *Watersipora subtorquata complex* (d'Orbigny, 1852, Fofonoff et al., 2018). Partly due to its adaptability to different environments and heavy metals present in anti-fouling paints (Floerl et al., 2004), *W. subtorquata* has successfully invaded California, Hawaii, Australia, New Zealand, Europe, and South Africa (Vieira et al., 2014). It was introduced from the Western Atlantic to Southern California in 1963 (Cohen and Carlton, 1995; Cohen, 2005), and has since spread along the coast, providing an interesting opportunity to examine its effects on communities in the different environmental contexts of its California range. *W. subtorquata* has been considered a foundation species because the foliose morphology colony serves as habitat for small ($\leq$2 cm) invertebrates (Sellheim et al., 2009; Stachowicz et al., 2007), while the encrusting morphology serves as a non-toxic settlement surface for fouling invertebrates (Floerl et al., 2004). The upright, foliose colonies facilitate polychaete worm diversity (Sellheim et al., 2009), and may serve to increase the diversity of other mobile organisms that can utilize the novel habitat they provide.

In this study, we used a manipulative field experiment to ask the following questions: 1) What is the net effect of an introduced colonial bryozoan, *W. subtorquata*, on the associated mobile and sessile invertebrate community diversity, abundance, and composition? 2) Does the net effect of *W. subtorquata* vary between locations within its introduced range? This experiment tested the hypothesis that *W. subtorquata* would have a net positive effect on diversity and therefore affect community structure due to its structural complexity. Additionally, since traits can differ across regions, which can lead to spatial variation in interactions with community members, the experiment also tested the hypothesis that the community-level effects of *W. subtorquata* would differ between locations in its introduced range.

2. Materials and methods

2.1. Study system

This field experiment was conducted in marinas within two protected bays—Bodega Harbor, CA (38°19′21.0“N) and Alamitos Bay, CA (33°44’58.4”N)—in the northern and southern sea surface temperature regimes of California (8–15 °C and 13–23 °C, respectively; noaa.gov). The fouling communities in these harbor environments comprised tunicates, bryozoans, sponges, bivalves, and hydrozoans, which dominate the artificial substrata of the marina docks (Scott and terHorst, 2019). All species experience seasonal variation in recruitment (Edwards and Stachowicz, 2011, 2012; pers. obs.), with the highest annual recruitment occurring during late spring/early summer. The experiment was conducted from April to August 2016 during the peak settlement of sessile fouling invertebrates (Sellheim et al., 2009). Temperature was monitored as part of a different study from December 2015 to November 2016 using Onset pendant HOBO loggers (UA-002-64) at 1 m depth in both locations, and the median temperature during the period of this study in Bodega Harbor was 14.6 °C. Temperature data is not available for Alamitos Bay during this time due to loss of equipment, but NOAA buoys show the median temperature during the period of the study at 16.2 °C. While other habitat-providers exist within the communities in both harbors (e.g. *Ciona intestinalis* [Chordata] and *Mytilus californianus* [Mollusca]), the present study focused on *Watersipora subtorquata,* an encrusting cheilostome bryozoan that grows morphologically complex colonies composed of many individuals called zooids (Vieira et al., 2014). The morphology of colonies ranges from flat and encrusting (Davis and Marshall, 2014; Floerl et al., 2004) to upright and foliose (Sellheim et al., 2009; pers. obs.), which may provide novel habitat for some of the mobile and sessile invertebrate species in the community. As *W. subtorquata* can influence both mobile and sessile species in the community (Sellheim et al., 2009), but each group is typically quantified in different ways, this study analyzed the two communities separately. Mobile and sessile invertebrates can differ in life history strategies and habitat or substrate preferences, so separating the analyses of mobile and sessile species allowed for more comprehensive exploration of community effects.

2.2. Field experiment

To determine whether *W. subtorquata* can act as a foundation species at two locations in California, a field experiment was conducted using colonies attached to sanded grey polyvinyl chloride (PVC) tiles. The four treatments for this experiment were: small (100 cm^2) tiles with no *W. subtorquata* colonies, small tiles with live *W. subtorquata* colonies,

small tiles with dead *W. subtorquata* colonies, and large (400 cm^2) tiles with no *W. subtorquata* colonies. Small tiles with no colony attached served as a control for the presence of *W. subtorquata*, whereas large tiles with no colonies served as a control for the amount of additional available substrate for settlement and growth; both empty small and large tiles started with 100% bare settlement space. The treatment with dead *W. subtorquata* colonies served as a biotic control to separate the effect of increased habitat availability and structural complexity from any potential biotic effects of live zooids within the colony. Replicates of each of these treatments were placed in both Bodega Harbor and Alamitos Bay (n = 20 per treatment per harbor).

To prepare the treatments with *W. subtorquata*, 40 colonies of similar volume were collected from docks at Long Beach Marine Institute in Alamitos Bay and Spud Point Marina in Bodega Harbor. The colonies collected represented the natural sizes of *W. subtorquata* colonies encountered in each harbor. For the dead *W. subtorquata* colony treatment, 20 of the collected colonies were submerged in freshwater for several hours to kill colony zooids while preserving the structural integrity of the colony. The remaining 20 colonies were used for the live colony treatment, and were kept in a recirculating seawater tank for the same length of time. Both live and dead colonies were then attached to tiles using a hot glue gun, leaving approximately 50% of the tile bare.

Two replicates from each of the four treatments were secured to PVC racks (n = 10 racks per harbor), all of which were submerged facing down, approximately three meters apart from each other on the docks at 1 m depth. The downward orientation of the rack was chosen to minimize sedimentation on the tiles during the experiment, and to mimic the natural upside-down orientation of invertebrate growth on docks and ships (pers. obs.; but see Miller and Etter, 2008). After the experiment, all tiles were collected and brought back to the lab for processing. To preserve mobile species settled on *W. subtorquata* and on the PVC tiles, a plastic bag was placed around each tile and they were removed from the rack while submerged. All bags were put in coolers and transported to the nearest laboratory—Bodega Marine Laboratory in Bodega Harbor or California State University in Northridge.

Mobile invertebrates on each treatment were collected by rinsing tiles and the water in the bag over a 0.5 mm sieve. Samples were fixed in 10% buffered formalin for 24 h, then transferred to 70% ethanol in glass jars for preservation. After the removal of mobile invertebrates, each tile was photographed to quantify the sessile invertebrate community. Photos were analyzed using Coral Point Count with Excel extensions software (CPCe), which overlaid 100 randomly-stratified points (5 rows × 5 columns × 4 points/grid square) onto each image to determine diversity (Shannon-Wiener diversity index, H'), richness, and percent cover (Kohler and Gill, 2006). The stratified random method reduces the clumping of randomly-distributed points by dividing the bordered area into rows and columns and populating each cell with an equal amount of randomly distributed points (Kohler and Gill, 2006). Each point in the photo was assigned to the species that it covered, a list of which was generated by identifying all organisms to the lowest possible taxonomic level (usually to genus) using a taxonomic key (Carlton, 2008) and voucher specimens collected from the field. The same key was also used to identify all mobile invertebrates. Some of the genera identified may contain more than one species, thus the calculations of diversity are for taxonomic diversity, rather than species diversity, and likely underestimate diversity.

To determine whether treatments caused differences in diversity or abundance of mobile or sessile organisms, the fixed factors of treatment, location, and the treatment*location interaction were tested against each response variable in linear mixed-effect models (using lmer in the lme4 package; Bates et al., 2015) in R (version 3.1.2). Rack was included as a random factor. Additionally, lsmeans (Lenth, 2016) and multcompView were used to calculate the least squared means for each model and Tukey post-hoc comparisons between groups.

Response variables included invertebrate abundance per tile (i.e., number of individuals for the mobile community and percent cover for the sessile community), taxonomic richness per tile, and Shannon-Wiener diversity per tile. For each response variable, the model fit with and without the block (rack) effect was compared using Akaike Information Criterion (AIC) to determine the best-fit model. Mobile species abundances were log-transformed to improve normality for the model. All other response variables met assumptions of parametric tests.

To compare dissimilarities in mobile invertebrate community composition across treatments between locations, mobile invertebrate counts were square-root transformed and used to construct a Bray-Curtis dissimilarity matrix. Then, a permutational analysis of variance (PERMANOVA) was performed on this dissimilarity matrix using the adonis function from the vegan package (Oksanen et al., 2015) in R (version 3.1.2), including rack nested within location. For post-hoc analyses of community dissimilarities between treatments, a pairwise adonis function with a Bonferroni p-value adjustment was used to account for multiple comparisons between treatments. Similarity percentage (SIMPER) analysis was used to determine the relative contribution of mobile species to the community differences across treatments and between locations. Multivariate analyses were conducted as above for sessile invertebrates, this time constructing the Bray-Curtis matrix from square-root transformed species percent cover across treatments and between locations. All graphics were produced in R (version 3.1.2) using ggplot2 (Wickham, 2009) and psych (Revelle, 2016).

3. Results

3.1. Mobile community

Across locations and treatments, 47 mobile invertebrate taxa were identified—21 to species, and 26 to genus (Supplementary Table S1). The most common taxa were crustaceans, gastropods, molluscs, and polychaetes (Supplementary Table S1). Treatment and location had a significant interactive effect on mobile invertebrate species richness ($F_{3,144}$ = 2.78, p = .043). In Bodega, all treatments had similar richness. In Alamitos, however, the large tiles exhibited significantly greater richness than dead and large tiles in Bodega (Fig. 1A). There was, however, no significant interactive effect of location and treatment on the abundance of mobile invertebrates ($F_{3,128}$ = 1.73, p = .16), but mobile abundance did differ significantly across tile treatments ($F_{3,125}$ = 60.51, p < .0001). Large tiles had significantly greater mobile invertebrate abundance than all other treatments in both Alamitos Bay and Bodega Harbor (Fig. 1B). There was no significant interactive effect of location and treatment on the diversity of mobile invertebrates. Diversity was not significantly different across treatments ($F_{3,144}$ = 0.31, p = .82), but Bodega Harbor communities on dead *W. subtorquata* tiles had significantly greater diversity than Alamitos Bay communities on large tiles (F1,144 = 21.23, p < .0001; Fig. 1C).

Though there was no interactive effect of location and treatment on community dissimilarity ($F_{3,144}$ = 1.32, G = 0.016, p = .12), mobile communities were significantly different between locations ($F_{1,150}$ = 48.86, G = 0.25, p < .001) and among treatments ($F_{3,148}$ = 10.12, G = 0.17, p < .001). Pairwise comparisons among treatments revealed that large tile communities were significantly dissimilar to other treatments (Table 1). Four arthropod taxa, *Ampelisca* spp., *Tanais* spp., *Caprella* spp., and *Idotea* spp., contributed the highest towards community dissimilarity among all treatments, but especially between all treatments and the large tile treatment replicates, where they were found in greatest abundance.

3.2. Sessile community

Thirty-one sessile invertebrate taxa were identified, 26 of which were identified to species, and five to genus (Supplementary Table S2); 12 taxa were found in both locations. Tunicates, bryozoans, sponges,

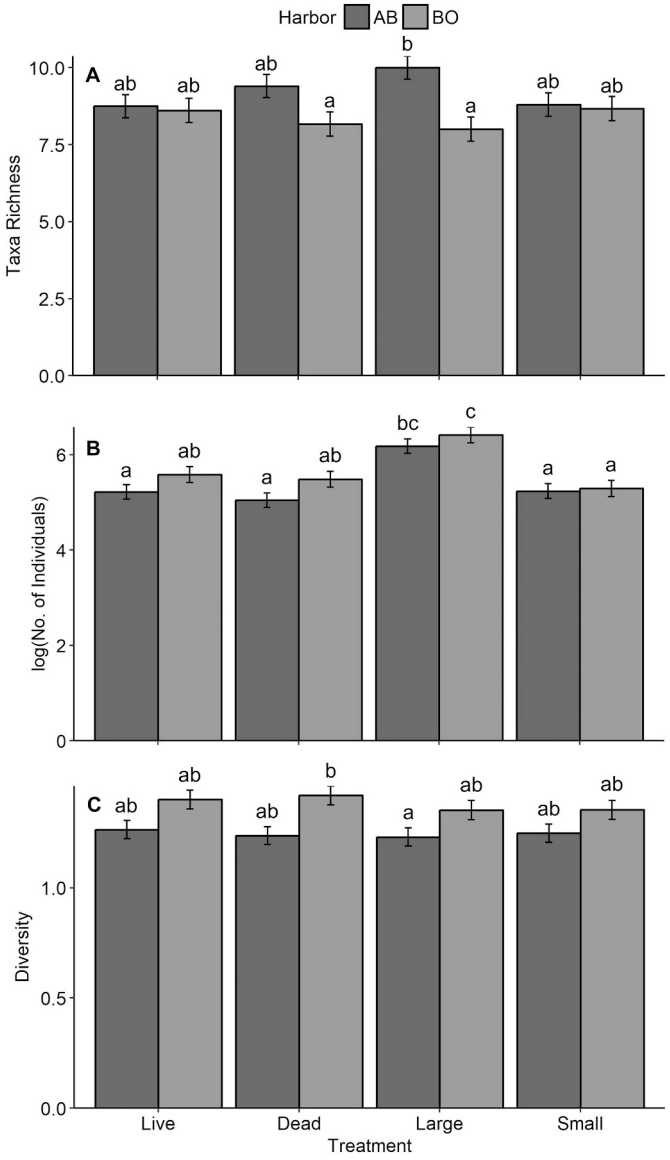

Fig. 1. Mean (± SE) A) richness, B) number of individuals, and C) diversity of mobile invertebrates. Data were analyzed using linear mixed-effects models. Letters above each bar indicate significantly different means (Tukey's HSD, $p < .05$).

Table 1
Pairwise PERMANOVA comparisons of mobile invertebrate community dissimilarity (R statistic) across treatments, environments (Alamitos Bay and Bodega Harbor) are pooled. A Bonferroni *p*-value adjustment (adj *p)* was used to account for multiple comparisons between treatments, and $p < .05$ for significant community dissimilarity shown in **bold**.

Pairwise Comparison	R statistic	adj *p*
Live *Watersipora,* Dead *Watersipora*	0.011	1.00
Live *Watersipora*, Large tile	0.19	**0.006**
Live *Watersipora,* Small tile	0.0095	1.00
Dead *Watersipora,* Large tile	0.25	**0.006**
Dead *Watersipora*, Small tile	0.0075	1.00
Large tile, Small tile	0.19	**0.006**

polychaetes, and molluscs comprised the communities and are representative of natural communities found in both locations (Scott and terHorst, 2019). Bryozoans and tunicates were the most represented taxonomic groups (occurring in > 50% of treatment replicates per

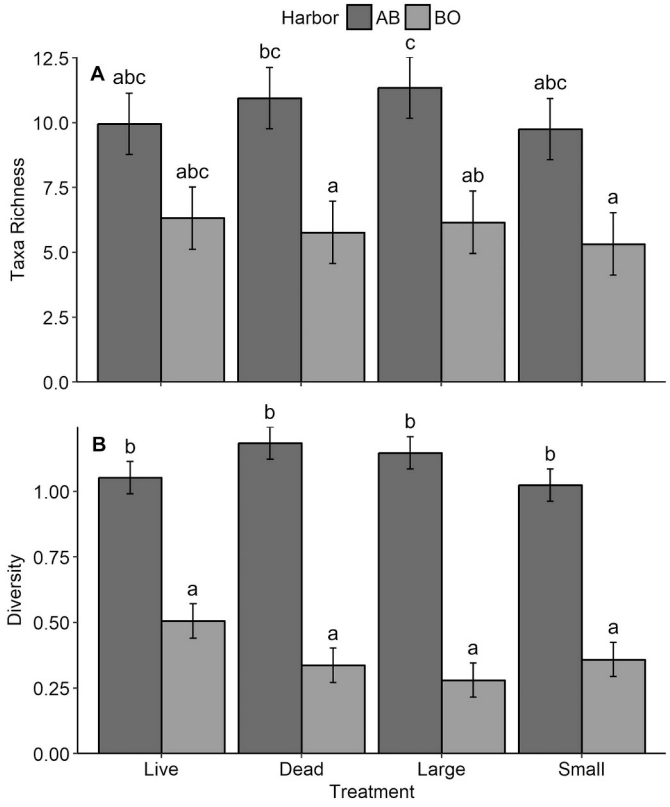

Fig. 2. Mean (± SE) A) richness and B) diversity of sessile invertebrates. Data were analyzed using linear mixed-effects models. Letters above each bar indicate significantly different means (Tukey's HSD, $p < .05$).

Table 2
Pairwise PERMANOVA comparisons of sessile invertebrate community dissimilarity (R statistic) across treatments and harbor environments. A Bonferroni *p*-value adjustment (adj *p*) was used to account for multiple comparisons between environments and treatments, and $p < .05$ for significant community dissimilarity shown in **bold**.

Pairwise Comparison	R statistic	adj *p*
North: Bodega Harbor		
Live *Watersipora,* Dead *Watersipora*	0.073	0.64
Live *Watersipora*, Large tile	0.14	0.056
Live *Watersipora,* Small tile	0.083	0.448
Dead *Watersipora,* Large tile	0.036	1.00
Dead *Watersipora*, Small tile	0.043	1.00
Large tile, Small tile	0.10	0.224
South: Alamitos Bay		
Live *Watersipora,* Dead *Watersipora*	0.061	0.700
Live *Watersipora*, Large tile	0.17	**0.028**
Live *Watersipora,* Small tile	0.087	0.084
Dead *Watersipora,* Large tile	0.064	0.364
Dead *Watersipora*, Small tile	0.020	1.00
Large tile, Small tile	0.052	0.76

environment) across treatments in Bodega Harbor, while molluscs were the most common taxa across treatments in Alamitos Bay (Supplementary Table S2). There was no significant interactive effect between treatment and location on sessile invertebrate richness ($F_{3,128} = 1.37$, $p = .26$). However, sessile invertebrate richness did differ significantly between locations ($F_{1,1267} = 8.39$, $p = .0038$), with Alamitos Bay communities showing nearly a two-fold higher richness than Bodega Harbor (Fig. 2A). Treatment and location had significant interactive effects on the diversity of sessile invertebrates ($F_{3,144} = 2.89$, $p = .037$). Though not significantly different from other treatments, tiles with dead colonies tended to have the highest diversity in Alamitos

Bay, whereas tiles with live colonies tended to have the highest diversity in Bodega Harbor, (Fig. 2B).

Multivariate analyses revealed that sessile invertebrate communities were significantly dissimilar as a result of interactive effects of treatment and location ($F_{3,144}$ = 1.91, G = 0.021, p = .002). In Bodega, pairwise community comparisons revealed that communities across all treatments did not differ significantly (Table 2). In Alamitos Bay, however, the live colony and large tile treatments had significantly dissimilar communities. Communities on live tile treatments were more dissimilar than communities on large tile treatments. Live tiles included species such as *Bugula pacifica* and *Styela clava* that were either rare or not found on large tiles (Supplementary Table S2).

To evaluate the effect of large tile community data on the results, large tile data for both environments were removed from the PERMANOVA. As a result, there was no longer an interactive effect of treatment and harbor environment on sessile communities ($F_{2,108}$ = 1.3, R^2 = 0.013, p = .094). However, the main effects still produced dissimilar communities across the remaining treatments (i.e., live, dead, small tile; $F_{2,110}$ = 3.26, R^2 = 0.034, p < .001), and communities were significantly dissimilar between locations ($F_{1,110}$ = 77.24, R^2 = 0.40, p < .001). SIMPER analysis identified three tunicates—*Ciona intestinalis* (Linnaeus, 1767), *Ascidia ceratodes,* and *Diplosoma listerianum*—as the highest contributors to community dissimilarity among the three remaining treatments. Both *C. intestinalis* and *A. ceratodes* were found in greatest abundance on live replicates. In both experimental locations, *D. listerianum* was found less frequently on live or dead *W. subtorquata* replicates, but was found in the greatest abundance on live replicates. In Alamitos Bay, a demosponge, *Halichondria* sp. grew directly on *W. subtorquata* colonies, and was found in at least 70% of—and in twofold greater abundance on—live colony treatment replicates (Supplementary Table S2).

4. Discussion

Watersipora subtorquata had different effects on mobile and sessile communities. Though no net positive effect of *W. subtorquata* on mobile communities was observed, live and dead *W. subtorquata* colonies had different effects on sessile diversity and composition, depending on location. For mobile species, increased habitat availability increased richness and altered community composition, yet an effect of increased structural complexity on diversity from the presence of *W. subtorquata* colonies was not observed. For sessile communities, either live or dead colonies tended to have the largest effect on diversity or composition, depending on location, but these treatments were most different from the large tile treatment. This suggests that the effect of *W. subtorquata* colonies was not driven by increased habitat availability.

4.1. Mobile community

Mobile community abundance and richness varied across treatments and locations, but the treatment effects were largely driven by the large tile treatment, rather than *W. subtorquata* presence, despite the additional structural complexity and available habitat spaces on *W. subtorquata* treatments relative to the small tile treatments. Such a finding contrasts results of similar studies, where treatments with *W. subtorquata* had the greatest species richness and diversity (Sellheim et al., 2009). In both locations, increased habitat availability appears to be the dominant driver of mobile community composition. Most mobile species require at least some structural habitat in order to remain on the tile. The large tile effect may be driven by the additional complexity of more settling sessile invertebrates on the greater amount of space. So, the effect of increased habitat availability is likely an indirect effect, which is mediated by the settlement of other sessile species besides *W. subtorquata*. Increased settlement space may have reduced competition among habitat-providing species, allowing for greater colonization. Both harbors had other habitat-providing species that increased habitat complexity—*Crisulipora occidentalis* (Bryozoa) and *Styela plicata* (Chordata) in Alamitos Bay, and *Ciona intestinalis* (Chordata) and *Ascidia ceratodes* (Chordata) in Bodega Harbor—and the tunicate species create few, large habitat spaces compared to the numerous, smaller crevices created by *W. subtorquata*. The dominance of *C. occidentalis* and *S. plicata* on large tiles may help explain differences in community composition between the large tile and other treatments, especially as the composition across treatments was significantly different independent of environment.

Tiles with live and dead *W. subtorquata* colonies also have increased habitat availability for mobile species to live in, but these treatments were not significantly different from the small tiles with initial *W. subtorquata* colonies. One reason for this lack of effect could be that *W. subtorquata* facilitated some species by providing habitat, but inhibited others, either by outcompeting habitat providing species, or through some more direct means (e.g., stolonal outgrowth on the zooid; Tzioumis, 1994), resulting in no net effect on diversity. However, *W. subtorquata* also did not have a significant effect on community composition, so this explanation seems unlikely.

W. subtorquata may be functionally redundant to other habitat providers. So, while *W. subtorquata* colonies were more structurally complex than the small and large tile treatments, the increased amount of refugia within the colonies was not enough to facilitate a greater abundance of organisms than the large tile treatment. When an introduced species is functionally similar to a habitat provider native to the community, differences in the abundance or biomass of native species may not be detectable (Rodriguez, 2006). The potential positive effects of *W. subtorquata* providing habitat for other species may be similar to those services provided by other species in the community already, though this study was unable to test the potential effects of removing these other habitat providers on community diversity and composition. Future studies on the relationship between refugia parameters (e.g., size, density, area) and diversity and community structure of mobile invertebrates would help determine which aspect of structural heterogeneity drives more of the variance in diversity.

4.2. Sessile community

The significant interaction between treatment and location reveals that different tile treatments had different effects on sessile diversity between locations. At Bodega Harbor, tiles with dead colonies tended to have the highest diversity, followed by large tiles, and then tiles with live colonies and small tiles. This rank order indicates that at Bodega, available space is an important determinant of diversity, as both dead colonies and large tiles had the greatest diversity. Competitive interactions between *W. subtorquata* and other sessile species may be important species interactions in these communities that decrease sessile species diversity (Claar et al., 2011; Stachowicz and Byrnes, 2006). An increase in habitat availability may alleviate the effects of competition.

At Alamitos Bay, tiles with live colonies tended to have higher diversity than the other treatments; the large tiles actually had the least diverse sessile communities at this location. Perhaps competitive interactions are less consequential in the communities of southern California where tiles across all treatments typically had greater percent bare space, relative to those communities further north where bare space is at a premium (pers. obs.). These tiles typically had more, smaller, individuals in comparison to the fewer, larger individuals, on tiles in Bodega, thus creating many patches of bare space.

There are few examples of sessile invertebrates settling directly on *W. subtorquata* (Davis and Marshall, 2014; Sellheim et al., 2009), as the feeding zooids on the surface of the colony may make successful settlement and growth difficult. However, this study provides evidence of direct facilitation of settlement by other sessile species; a demosponge, *Halichondria* sp. grew directly on *W. subtorquata* colonies, and was found in over half of the live colony treatment replicates (Supplementary Table S2). *Halichondria* sp. has also been observed growing on the

surface of *W. subtorquata* in previous surveys (Scott and terHorst, 2019), and was found in almost twice the abundance on tiles with live *W. subtorquata* colonies than on tiles with dead colonies or empty space. Other studies have found that epizoic sponges help prevent predation on scallops by asteroid predators through camouflage and preventing attachment by the predator's tube feet (Pitcher and Butler, 1987). Additionally, a study in the Florida Keys found examples of epizoic symbioses between different orders of sponges, where the sponges were exclusively found growing together and not solitarily (Wilcox et al., 2002). Though the external sponge did not appear to negatively affect the ability of the internal sponge to filter water in that study, the relationship between the epizoic sponge and *W. subtorquata* in this study is unclear. Future studies on the symbiosis between epizoic sponges and *W. subtorquata* or a similar bryozoan species would help disentangle the nature of the relationship, and determine whether the sponge serves a benefit to the host through its growth or water filtration.

The idea that positive and negative effects of *W. subtorquata* offset one another is supported by the fact that this introduced species has effects on community composition, though this effect varies between locations. Bodega treatments had similar communities, while large tile and live *W. subtorquata* colony treatments differed significantly in their communities in Alamitos Bay; this may be explained by differences in species substratum preferences or growth and reproduction mechanisms. Three tunicates—*Ciona intestinalis, Ascidia ceratodes,* and *Diplosoma listerianum*—contributed the most to dissimilarity among treatments, when the large tile treatment was excluded. While *C. intestinalis* and *A. ceratodes* were found in at least 80% of replicates in the *W. subtorquata* and small tile treatments in Bodega Harbor, *D. listerianum* was encountered the least on tiles with live *W. subtorquata* colonies (Supplementary Table S2). Unlike the other two tunicates, *D. listerianum* is a colonial tunicate, which likely competed with the live *W. subtorquata* colonies for space. While growth of solitary tunicates depends on reproduction and recruitment to form aggregations on the substrate, the indeterminate growth of colonial tunicates allows them to continuously grow across the surface and occupy space (Jackson, 1977). *W. subtorquata* competes strongly for space with other colonial tunicates and encrusting bryozoans (Edwards and Stachowicz, 2012; Sellheim et al., 2009), and across both environments several species of tunicates and bryozoans were encountered less on *W. subtorquata* treatments (Supplementary Table S2).

5. Conclusions

This study highlights the importance of examining not only the competitive and other negative effects of introduced species on species richness and diversity, but also of understanding the extent to which their positive role as a foundation species alters community composition and diversity. *W. subtorquata* may facilitate some taxa while inhibiting others, making it more difficult to detect a net effect of this introduced species. It may also be difficult to detect any effect of *W. subtorquata* in these natural environments because they included other habitat providers, such as native and introduced tunicates and bryozoans, that may be functionally redundant to *W. subtorquata* (Rodriguez, 2006), making it an introduced species that has similar effects as species already present in the community. An experiment that excludes other sessile species and isolates *W. subtorquata* as the sole complex habitat available for mobile species would allow for more direct study of the effects of an introduced foundation species on the community.

Additionally, the effects of *W. subtorquata* on the community differed between locations, which means that the net effect of *W. subtorquata* can differ within its introduced range when accounting for both facilitative and competitive interactions. Introduced species have historically been considered pests in many systems, but more recent examples within the last 20 years are emerging, which indicate that introduced species can benefit the native flora and fauna as foundation species (Rodriguez, 2006). Although studies of introduced foundation species are useful for identifying potential benefits to the community, they are often spatially limited to a single location. Because trait differentiation allows introduced species to expand their distribution to wide environmental ranges with similar or dissimilar communities (Dmitriew, 2011; Li et al., 2014; Stinchcombe et al., 2010), it is vital to understand whether such expansion to different environments and communities translates to variation in the net effect on the community. Though this study found spatially-dependent community effects, the experiment was spatially limited and not representative of the full introduced range of *W. subtorquata*. Therefore, future studies of similar introduced species would benefit from considering a greater spatial range of environments to understand how the facilitative and inhibitive effects of introduced foundation species may variably affect communities across their range.

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Author contributions

ZRS designed and conducted the field experiment, completed data analysis, and wrote the manuscript. CPT assisted with the field experiment design and edited the manuscript.

Declaration of Competing Interest

The authors have no conflict of interest to report for this manuscript.

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