THE FACILITATIVE ROLE OF AN INTRODUCED BRYOZOAN (*WATERSIPORA* SPP.): STRUCTURING FOULING COMMUNITY ASSEMBLAGES WITHIN HUMBOLDT BAY

HUMBOLDT STATE UNIVERSITY

By

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We certify that we have read this study and that it conforms to acceptable standards of scholarly presentation. This study is fully acceptable, in scope and quality, as a thesis for the degree of Master of Science.

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ABSTRACT

THE FACILITATIVE ROLE OF AN INTRODUCED BRYOZOAN (*WATERSIPORA* SPP.): STRUCTURING FOULING COMMUNITY ASSEMBLAGES WITHIN HUMBOLDT BAY

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Studying the impacts on a community following the introduction of an exotic species is of increasing importance in the field of marine science. Recent investigations of marine biological invasion have primarily focused on studying the negative interactions resulting from species introductions. However, there is growing interest and need to include the influence of positive interactions when investigating the organization of recently invaded communities. Facilitation often occurs when a sessile species modifies the physical structure of a community by creating habitat that benefits others. Following recent introductions along the California coastline, the cheilostome bryozoan, *Watersipora* spp., has been shown to impact marine communities both through positive and negative interactions. Initially *Watersipora* may dominate a community by out-competing other sessile organisms for occupancy of primary substrate. However, as colonies collide and begin growing upward, they develop into a three dimensional structure that appears to serve as a new habitat utilized by other species for settlement and refuge.

In order to investigate the role of *Watersipora* spp. within the fouling community of Humboldt Bay, CA, experimental panels were deployed at Eureka Public Marina. Of the 20

panels, ten were initially seeded with *Watersipora* recruits, while the other ten were left blank (as controls). By monitoring experimental fouling panels for recruit survival, changes in percent cover, and final species diversity, it was determined that the presence of *Watersipora* spp. greatly alters the Humboldt Bay fouling community following its introduction. Initially, during the first two months of deployment, *Watersipora's* presence decreased the survivorship of new recruits that settled nearby. During the following months, rapid colony growth and competition by *Watersipora* reduced the percent cover of dominant sessile invertebrates (especially tunicates), by decreasing the establishment and successful growth of neighboring individuals and colonies. However, while *Watersipora* has the ability to outcompete sessile invertebrates for primary substrate, it also provides a complex three dimensional structure that can be utilized as habitat. After eight months of community development, experimental panels were destructively sampled to account for differences in final species diversity between treatments. Sampling revealed that the presence of *Watersipora* ultimately lead to the establishment of a more species diverse community. This increase in diversity was primarily due to the complex habitat modification provided by *Watersipora* that was not present on control panels.

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INTRODUCTION

Due to the continuing spread of exotic species, studying their impacts on community development is of increasing importance in the field of marine science (Wonham and Carlton 2005). Recent investigations of marine biological invasion have primarily focused on the identification of negative impacts to resident communities following the introduction of a non-native species (Hayes and Sliwa 2003; Agius 2007; Blum et al. 2007; Osman and Whitlatch 2007). When a new species is introduced into a marine system, a successional shift may occur in the community due to biotic interactions such as competition (Casas et al., 2004) and predation (Grosholz and Ruiz 1996). If the newly introduced species exhibits very strong competitive properties, it may dominate limited settlement substrate and push out previous residents of the community (Barnes and Dick 2000).

Studying the negative consequences of species introductions has been a major focus for this field of research. However, there is growing interest and need to include the influence of positive interactions when investigating the organization of recently invaded communities (Bruno et al. 2003). Facilitation can occur in multiple ways, including cases where a sessile species modifies the physical structure of a community by creating habitat that benefits others (Crooks 2002; Clarr et al. 2011). Recent studies of rocky intertidal habitats have found that certain species of corals, macroalgae, ascidians, and mussels play important roles in structuring these communities (Crooks 2002; Castilla et al. 2004; Altieri et al. 2007). These species act as "ecosystem engineers" or "foundation species", providing habitat that can be utilized by others for attachment and refuge from desiccation, wave action, and predation in these often hostile environments (Altieri et al. 2007). While environmental conditions may be stressful enough in

certain cases that facilitation is required for survival, it is less apparent what factors may drive the positive interactions observed within the subtidal fouling communities of protected bays and estuaries (Soniat et al. 2004; Thomsen and McGlathery 2005 and 2006; Dubois et al. 2006). Perhaps the pressures of competition and predation have a great enough impact in fouling communities, as observed in other marine communities where space is often a limiting factor (Stachowicz and Hay 1999), that species begin relying on each other for refuge from such stressors.

Following recent introductions along the California coastline, multiple species of the cheilostome bryozoan, *Watersipora* spp. (Mackie 2006), have been shown to impact marine communities both through positive and negative interactions (Stachowicz and Byrnes 2006; Needles 2007; Sellheim et al. 2010). Initially *Watersipora* has the ability to dominate a community by growing rapidly in an encrusting plate form, out-competing other sessile organisms for occupancy of primary substrate (Needles 2007). Similarly, another species of encrusting bryozoan, *Schizoporella errata*, has been shown to inhibit successful recruitment and growth of neighboring invertebrates (Sutherland 1978). Due to these strong competitive properties, *Watersipora* has the ability to greatly modify community composition and has been shown to dominate as much as 86% of primary substrata in some fouling communities (Needles 2007).

However, once available substrate becomes limited, *Watersipora* spp. may begin to take on a positive role in the community. As the leading edges of each colony collide, they begin growing upward, developing into a three dimensional form. This structure, potentially created by many colonies, appears to serve as a new habitat that is utilized by other species for

settlement and refuge (Sellheim et al. 2010). While invertebrate larvae avoid settling on certain species of tunicates and bryozoans (Osman and Whitlatch 1995 a,b), the surface of *Watersipora* appears to serve as a suitable secondary substrate for recruitment and growth. Larvae of some invertebrate species have even been shown to prefer settling on resident adults that provide structurally complex habitat over neighboring available substrate (Dean 1981; Bruno et al. 2003; Clarr et al. 2011). *Watersipora* could therefore have an overall beneficial impact on these communities by providing more habitat than it uses up (Stachowicz and Byrnes 2006; Sellheim et al 2010), leading to an overall increase in species diversity despite overgrowth competition with neighbors.

Determining the underlying cause by which *Watersipora* spp. increases species diversity within a fouling community is of particular interest. Physical structures, such as the upright folds provided by *Watersipora*'s colony, have been shown to disrupt water flow in a local hydrodynamic regime, allowing larvae to more easily settle and metamorphose (Soniat et al. 2004; Koehl 2007). It may also be possible that secondary recruitment on *Watersipora* is due to an attraction to some biological cue that is being recognized by larvae of neighboring species within the community. Previous studies suggest that the larvae of certain invertebrates have the ability to recognize cues from con-specific adults, signaling them towards a suitable zone for settlement (Gerbauer et al. 2002). Perhaps the larvae of certain species may have come to recognize cues from *Watersipora* as a suitable location for recruitment.

Facilitation within fouling communities may also be driven by factors other than physical and chemical properties. Perhaps biotic and abiotic pressures on the surrounding community cause stress on neighboring invertebrates, leading them to recruit and grow within colonies of *Watersipora*. For example, in a study directed at the facilitative properties of *Watersipora*,

colonies acted as a nontoxic refuge on ship hulls coated in antifouling paints and allowed for the settlement of species that could otherwise not tolerate such toxins (Floerl et al. 2004). This work found that secondary recruitment to the surface of *Watersipora* colonies was five to six times more common in the presence of toxic surfaces than in control treatments where toxins were absent. These findings suggest that it may be more likely for *Watersipora* to act as a foundation species when neighboring conditions are less favorable for settlement. Perhaps larval settlement on *Watersipora,* which has been observed in marine fouling communities, is a result of the surrounding pressures of competition and predation. If space is very limited and predators are abundant, invertebrate species could potentially escape these factors by recruiting to and living within colonies of *Watersipora*.

While recent studies suggest positive effects on community development following the introduction of *Watersipora* spp., (Stachowicz and Byrnes 2006; Needles 2007; Sellheim et al. 2010), this study focused on investigating the succession of events which drive this shift in the community to occur. In order to determine the timing during community development which leads to facilitation by *Watersipora*, experimental fouling panels were deployed to observe the succession of communities where *Watersipora* were initially introduced. While studies with short temporal scales have provided some insight into the impact of *Watersipora*, longer duration field experiments may account for seasonal variation that could otherwise be overlooked. This study was carried out for eight months to gain a better understanding of the community changes that occur while *Watersipora* colonies naturally grow into their three dimensional form. The intention was to investigate the system across a larger temporal scale to understand the initial impact of introducing *Watersipora*, as well as document changes to community succession that occur over time.

By conducting a manipulative field experiment, three questions were investigated regarding *Watersipora's* impact on the fouling community of Humboldt Bay: (1) Does *Watersipora* affect the survivorship of newly settled recruits on or near its colony? (2) Does *Watersipora* affect the percent cover of dominant sessile invertebrates establishing colonies over the course of succession (during an eight month period)? (3) Does *Watersipora* lead to an increase in species diversity at the end of eight months of community development? Monitoring experimental fouling panels for recruit survival, changes in percent cover, and final species diversity, revealed that *Watersipora* greatly alters a community following its introduction. Initially, *Watersipora* decreases survival and growth of resident tunicates that otherwise dominate space and limit secondary recruitment. Ultimately, however, colonies of *Watersipora* provide a complex three dimensional habitat, leading to the establishment of a more species diverse community after eight months of community development.

METHODS

Field Location

This study was conducted within the temperate subtidal fouling community existing below the docks at Eureka Public Marina (EPM) in Humboldt Bay, CA (40º 48' 07.94" N and 124º 10' 45.03" W) (Figure 1). The site was chosen as an ideal location due to the observed abundance of *Watersipora* spp. (Mackie 2006) colonies attached to the docks, lower sediment levels compared to other sites, and ease of access for deployment of field experiments. Perhaps due to its historic and current uses as a port for shipping of lumber products as well as commercial fishing, Humboldt Bay has a high prevalence of exotic species within fouling communities. These introduced species have been shown to account for up to 35 percent of species richness found in photographed fouling communities at nearby Woodley Island Marina in Humboldt Bay (Boyle et al. 2007). These environmental and historical factors make EPM an ideal location for studying the effects of an introduced species within a community that exhibits a high prevalence of exotic species.

Experimental Design and Treatments

In order to investigate the influence of *Watersipora* spp. within the Humboldt Bay fouling community, 20 experimental panels were deployed at EPM. Fouling panels (15 x 10 x 0.65 cm) were constructed of black ABS (Acrylonitrile Butadiene Styrene) plastic, which is known to be a suitable substrate for marine invertebrates. Of these 20 experimental panels, ten were seeded with *Watersipora* recruits, while the other ten were left blank as controls. Prior to field deployment, panels were prepared for each treatment within flow through seawater aquaria

at the Humboldt State University Telonicher Marine Laboratory (TML) in Trinidad, CA. First, adult colonies of *Watersipora* were collected from EPM in Humboldt Bay on September 1, 2008 and transported in seawater to TML where they were placed into a tank lined with ABS fouling panels. Colonies were then triggered to release larvae by first blocking off supply of light for two days, then flooding the tank with light on day three. Control panels were also placed in empty flow through aquaria, for the same duration as treatment panels, to ensure even accumulation of biofilms that may have occurred while in the laboratory. Panels were examined by microscope to determine that successful settlement and metamorphosis of *Watersipora* had occurred.

Immediately following successful metamorphosis, the 20 experimental panels were transported in seawater to EPM on September 5, 2008. They were mounted, using stainless steel carriage bolts and wing nuts, to an L-shaped rack constructed of 1" polyvinyl chloride (PVC) pipe (Figure 2). The rack was then attached to the dock using stainless steel gate latches, so that the surfaces containing fouling panels were oriented horizontally below the dock, submerged 1 meter below the surface of the water, and facing downward. Communities were allowed to develop on the panels for a duration of 8 months (September 2008-May 2009), and were pulled up monthly to be digitally photographed using a Canon Powershot SD750 7.1 mega-pixel camera.

Recruitment and Survival

The digital photographs taken from October 2008 through December 2008 were utilized to track the initial treatment effects of *Watersipora* on the subsequent larval settlement and survivorship of invertebrate species that recruited on these panels in the field. The total number

of recruits for all species that had settled during the first month of deployment (September 2008 – October 2008) was recorded for each panel. The difference in recruitment across treatments was then examined by conducting a one way ANOVA for total number of recruits. Next, the survival of established and new recruits was investigated for the following two months (October 2008 - December 2008). By using photographs to track the presence of individual recruits each month, the proportion that had survived since the previous sampling date could be determined. Survivorship was investigated for the total number of recruits between each treatment, in addition to analyzing recruit survival within each phylum of marine invertebrates separately. A repeated measures ANOVA was carried out (R version 2.13), to determine whether monthly survival of new recruits differed between *Watersipora* and control treatments within the initial three months of community development. The survival analysis was not carried out for the months following December 2008, as colonies began to collide and overgrow one another, making it difficult to differentiate between individuals.

Community Analysis via Percent Cover

To determine whether the initial presence of *Watersipora* may have an effect on the subsequent establishment and growth of individual species over time, the percent cover of species that dominated primary space (*Bugula neritina, Bugula californica, Watersipora* spp.*, Botrylloides violacious, Botryllus sp, Distaplia occidentalis, Didemnum sp., Ciona intestinalis, Corella inflata, and Molgula manhattensis*) was calculated from monthly photographs (January 2009 through May 2009). Each photograph was analyzed by using Image J software to trace individual colonies and determine the total percent cover of each species. An individual repeated measures ANOVA was then carried out for each species to determine whether there was a difference between treatments in the percent cover of dominant species within this five month

period. All data for percent cover were square root transformed to meet assumptions of normality. The first three months of panel photographs (utilized for analysis of recruitment) were not included in the percent cover analysis because colonies of *Watersipora* and other species in these early photographs had not yet come into contact with each other. The goal of this analysis was to determine whether competition between *Watersipora* and other dominant species played a role in the composition of these experimental communities.

Species Diversity via Destructive Sampling

In May 2009, experimental fouling panels were collected and sampled to determine whether initially introduced *Watersipora* spp. led to differences in the abundance of mobile and sessile invertebrates within these communities. Following eight months of community development below the docks at Eureka Public Marina, panels were removed from the PVC rack and transported in individual seawater containers to Telonicher Marine Laboratory in Trinidad. Once brought to TML, panels were each held in a separate flow through aquarium during the four days of data collection. Panels were rinsed through a screen to collect small invertebrates, and the community on each panel was teased apart with fine forceps, placing individual species into separate glass dishes containing seawater. Each invertebrate was identified to species level, or the highest taxonomic group possible, using dichotomous keys (Carlton 2007). The abundance of individual species was counted and recorded separately for each of the 20 panels. An individual one way ANOVA was run for each species to determine whether their abundance differed according to treatment at the end of the experiment. In addition, a Shannon Wiener Diversity Index was calculated for each panel, and differences in diversity were determined by conducting a one way ANOVA between treatments.

RESULTS

Recruitment and Survival

Recruit analysis revealed a treatment effect on the survival of individual settlers during the first three months of deployment (October 2008-December 2008). Photographs taken during the first month of recruitment (October 2008) revealed no difference in the number of invertebrate larvae settling on each of the two treatments (F = 0.0009, df =1,18, P-value = 0.976, one way ANOVA, Figure 3). On average, 140.8 individuals, of all species combined, recruited to control panels during the first month of deployment, while 140.3 total recruits (not including *Watersipora* recruits that were added experimentally) were counted on panels seeded with *Watersipora*. However, while initial recruitment was essentially the same, the presence of *Watersipora* reduced the survival of recruits substantially. Following individual recruits each month revealed a significantly lower survivorship on panels seeded with *Watersipora* relative to controls (F = 23.31, df =1,18, P-value < 0.0001, repeated measures ANOVA, Figure 4). On average, invertebrates settling on treatment panels had only 64.1% survivorship while 75.6 % survival was observed on control panels. Much of this reduction in survival was due to the lower survival of solitary and colonial tunicate species on the *Watersipora* treated panels (F = 38.86, df = 1,18, P-value < 0.0001, Figure 4). An average of only 57.3 % of ascidian recruits survived each month on panels treated with *Watersipora*, versus 73.9 % survival on controls.

Community Analysis via Percent Cover

By tracking changes in the percent cover (January 2009 - May 2009) of dominant invertebrates, a between treatment effect was determined. During the three months following

deployment, *Watersipora* had covered an average of 43.86 % of available space on treatment panels, compared to only 3.53 % on control panels ($F = 171.26$, df = 1,18, $P < 0.0001$, repeated measures ANOVA, Figure 5). Another species of bryozoan (*Bugula californica*) was marginally more abundant on treatment panels as well ($F = 3.51$, df = 1,18, $P = 0.077$, Figure 5). Finally, panels treated with *Watersipora* had significantly more cover of the colonial tunicate *Botryllus* when compared to controls (5.27 % and 0.98 % respectively) ($F= 28.88$, df = 1,18, $P < 0.0001$).

During the same five month period, the majority of space on control panels was dominated by species of solitary and colonial tunicates. *Didemnum* sp. covered 22.52 % of control panels while only 6.33 % cover was observed on treatment panels ($F=12.18$, df = 1,18, $P = 0$ .003, repeated measures ANOVA, Figure 5). Similarly, *Corella inflata* dominated an average of 25.67 % on controls versus the 8.72 % cover of treatments ($F= 8.58$, df = 1,18, $P = 0.009$, repeated measures ANOVA, Figure 5). Lastly, the bare panel surfaces remained significantly higher on control panels ($F = 48.84$, df = 1,18, $P < 0.0001$). Controls had on average 15.82 % bare space, while *Watersipora* panels maintained only 4.19 % bare space.

Species Diversity via Destructive Sampling

Destructive sampling revealed a significant increase in species diversity on panels initially treated with *Watersipora* ($F = 15.108$, df = 1,16, $P = 0.0013$, one way ANOVA). On average, the Shannon Wiener Diversity Index was 2.217 on *Watersipora* panels versus 1.707 on controls. This difference was largely due to a greater number of sessile and mobile invertebrates living in, around, and under the canopy layer that was accounted for in the percent cover analysis. By destructively sampling each panel separately, a greater number of several invertebrate species were found living on panels treated with *Watersipora* spp. These species

were often small and found living within the three dimensional colony structure provided by *Watersipora.* Two panels were lost during the experiment leaving a final sample size of n=9 control panels and n=9 *Watersipora* panels.

Six species of polychaete worms were significantly or marginally more abundant in the communities that developed on *Watersipora* treatment panels: *Polycirrus* sp.*, Neoamphitrite robusta, Myxicola infundibulum, Eudistylia vancouveri, Eudistylia polymorpha,* and *Halosydna brevisetosa*. On average, tube dwelling polychates were more abundant on panels that were initially seeded with *Watersipora*. There were 8.67 individuals of the worm *Polycirrus* sp. (which occupy muddy tubes) present on treatment panels versus only 1.56 that were observed on controls (F= 31.45, df= 1,16, $P < 0.0001$, one way ANOVA, Figure 6). Similarly, an average of 1.67 individuals of the muddy tube dweller *Neoamphitrite robusta* were found on treatment panels versus 0.56 on controls (F= 4.00, df= 1,16, P= 0.063, one way ANOVA, Figure 6). The worm *Myxicola infundibulum*, which lives inside a mucous tube which it secretes, was also more abundant on *Watersipora* panels with an average of 3.11 individuals present per panel compared to 1.56 observed on control panels (F= 5.26, df= 1,16, P= 0.036, one way ANOVA, Figure 6). The "feather duster" worms *Eudistylia vancouveri* and *Eudistylia polymorpha* were also found in significantly greater numbers on panels initially seeded with *Watersipora*. On average 2.44 individuals of *Eudistylia vancouveri* were observed on treatment panels compared to only 0.78 on controls (F= 5.29, df= 1,16, P=0.035, one way ANOVA, Figure 6). Similarly a mean of 5.67 *Eudistylia polymorpha* individuals were counted on *Watersipora* treated panels versus the 2.56 present on controls (F= 10.52, df= 1,16, P= 0.005, one way ANOVA, Figure 6). Aside from tube dwelling polychaetes, the mobile scale worm *Halosydna brevisetosa* was observed in significantly greater numbers on *Watersipora* treatment panels as well, with an average of 4.67

individuals compared to the 2.44 on control panels (F= 8.04, df= 1,16, P= 0.012, one way ANOVA, Figure 6).

In addition to polychaetes, two other species of mobile invertebrates were found in greater numbers on *Watersipora* treated panels. As the three dimensional colonies of *Watersipora* were pulled apart during sampling, juvenile *Cancer magister* (approximately 1cm in diameter) were found living within the folds and crevices of each colony. There were, on average, 6.22 individual crabs per *Watersipora* treatment panel versus the 1.33 observed on controls (F=51.29, df= 1,16, $P < 0.0001$, one way ANOVA, Figure 7). Similarly, the very common nudibranch, *Hermissenda crassicornis,* was found in greater abundance on treatment panels, with an average of 4.56 individuals present versus an average of 2.89 on control panels (F= 3.5, d.f.= 1,16, P = 0.079, one way ANOVA, Figure 7).

In contrast to the species mentioned above, which were found in greater numbers on *Watersipora* treatment panels, two species of solitary tunicates were observed to be significantly less abundant on panels treated with *Watersipora.* These two species of solitary tunicates form large aggregations when present and were observed to dominate space during the percent cover analysis. The larger of the two species, *Corella inflata*, had on average 26.00 individuals on control panels, while only 14.22 individuals were recorded on *Watersipora* treated panels (F = 13.356, df = 1,16, P = 0.002, one way ANOVA, Figure 7). Similarly, for the smaller tunicate *Molgula manhattensis*, an average of 108.33 individuals were observed on control panels and 64.33 were found present on panels treated with *Watersipora* (F = 8.646, df = 1,16, P = 0.0096, one way ANOVA, Figure 7).

DISCUSSION

The results of this study suggest an overall facilitative role of *Watersipora* spp. when recently introduced into a subtidal fouling community. While strong competitive properties of *Watersipora* allow it to overgrow neighbors and decrease recruit survivorship of other species, its colony also serves a positive function as it grows into a complex structure that provides habitat. This study highlights the importance of investigating the many impacts of species introductions at different phases of succession rather than simply looking for those that are negative or most obvious. Many marine ecosystems offer a home to hundreds of interacting species which often play complex roles within a community (Altieri et al 2007). To fully understand how an introduced species functions within these marine communities, it is important to take into account the influence of both positive and negative interactions when investigating these communities. (Sutherland 1978; Grosholz and Ruiz 1996; Barnes and Dick 2000; Casas et al. 2004; Castilla et al. 2004; Crooks 2002; Floerl et al. 2004; Needles 2006; Aqius 2007; Blum et al, 2007;Osman and Whitlatch 2007; Sellheim et al. 2010;) .

Colonial *Watersipora* spp. serves as an ideal organism for studying the very different roles that an introduced sessile invertebrate may have within a community. A recent study of *Watersipora* within the fouling community of Bodega Bay, CA (Sellheim et al. 2010) found similar results to those which I observed in Humboldt Bay. However, Sellheim's study differed in that adult colonies of *Watersipora* were affixed to settlement panels as opposed to recruiting larvae to panel surfaces to observe natural growth and the effect of their presence throughout initial and late stages of succession. It was during the earliest stages of succession that I observed major differences in community development that led to the succession of very

different fouling communities. By experimentally introducing *Watersipora* recruits in greater abundance than it was observed occurring naturally at the Eureka Public Marina study site, I was able to magnify the effects of its introduction on this particular subtidal fouling community within Humboldt Bay.

When *Watersipora* recruits in great numbers, as I simulated experimentally, its rapidly growing colonies quickly dominate available substrate. While initial recruitment of other species to each of the experimental treatment surfaces was essentially the same, the survivorship of these recruits differed over time. Panels that were seeded with *Watersipora* spp. displayed 11.5 % lower survivorship than neighboring control panels (Figure 4). Even more strikingly, by grouping species taxonomically, solitary and colonial tunicates showed an even greater decrease in survivorship when compared to controls. On average tunicates had 16.6 % lower survivorship during the first three months when *Watersipora* was initially introduced (Figure 4). Previous studies of *Watersipora*, while bringing insight to its role as a habitat forming species (Needles 2007; Sellheim et al. 2010; Stachowicz and Byrnes 2006), may have overlooked this important impact on the sessile invertebrates that were initially outcompeted by *Watersipora.* This initial lower survivorship of recruits on *Watersipora* panels suggests that, even in the earliest stages of community development, *Watersipora* colonies have a significant impact on the resident fouling community.

Experimental communities remained at Eureka Public Marina for eight months following deployment so that it could be determined whether the initial differences in survival between treatments affected community development over time. The differences in survival that were observed during the first months of the experiment led to the establishment of two very different

fouling communities. The set of control panels, which had higher survivorship of ascidians early on, developed into communities dominated by solitary and colonial tunicates (*Corella inflata, Molgula manhattensis*, *Botrylloides violaceus, Didemnum sp.,* and *Distaplia occidentalis*). These species grew very rapidly and at times consumed nearly 100 percent of the available substrate on control panels. The two most abundant ascidians, *Didemnum sp.* and *Corella inflata*, together covered an average of 48.19 % of control panels versus the 15.05 % that was observed when *Watersipora* was present (Figure 5). Similarly, Sellheim et al. (2010) found that solitary and colonial tunicates settling on *Watersipora* treatments did not appear to grow as quickly as when recruiting to bare panel surfaces. Introducing *Watersipora* spp. initially appeared to limit the growth of resident ascidian species that may have previously dominated the subtidal fouling community within Humboldt Bay.

After eight months of community development, the panels which had been seeded with *Watersipora* spp. held a surprisingly greater abundance of numerous species leading to an overall increase in species diversity. As colonies of *Watersipora* grew and collided with one another (after approximately three months), they began forming an upright and structurally complex habitat. As with the Sellheim et al. (2010) study in Bodega Bay, this study revealed that many species within the Humboldt Bay fouling community were found in greater numbers when habitat forming *Watersipora* was present. This increase in abundance was especially evident for mobile and sessile polychaete worms that were found living on and within the habitat provided by *Watersipora*. Sellheim et al. (2010) suggests that this increase in polychaete abundance is due to sediment accumulating within the folds of *Watersipora'*s colony. This sedimentary habitat can then be utilized by polychaetes to form the muddy tubes which they reside in. Sellheim et al. (2010) also agrees that *Watersipora* provides mobile invertebrates with habitat

and refuge from predators. This could explain the increased abundance of juvenile dungeness crabs (*Cancer magister*), a commercially important species to Humboldt County, which also appear to utilize the structure provided by introduced *Watersipora*.

This work suggests that succession within a Humboldt Bay fouling community, following the introduction of *Watersipora* spp., led to an overall increase in species diversity. *Watersipora* initially decreased survival of ascidians, gaining control of primary substrate, but eventually served as a structurally complex habitat that was utilized by other invertebrates for attachment and refuge. These effects led to the succession of a fouling community that can support a greater abundance of many species. The alternative community, observed on control panels where *Watersipora* had not been introduced, was dominated by rapidly growing tunicates that did not appear to provide a comparable habitat. Certain species of tunicates have antimicrobial qualities that deter bacterial communities from colonizing their surfaces (Findlay and Smith, 1995). Perhaps these antifouling chemicals, present in the tissues of ascidians, are a major factor in limiting the successful recruitment of other species within fouling communities.

Studies such as this one are important for understanding the ecology of marine systems, especially those that have been highly invaded. Little is known about the potential impacts that introduced species may have on resident endemic communities. In past years, this field of research has primarily focused on identifying negative impacts to a community following the introduction of a new species. While *Watersipora* spp. initially interacts negatively with neighboring species, decreasing survivorship via competition, it serves a positive function as well. This study highlights the importance of studying both positive and negative interactions of non-native species, which in this case leads to dramatic changes in the community structure and an increase in species diversity.

Figure 1: Location of study site at Eureka Public Marina in Northern Humboldt Bay, CA. (40º 48'07.94" N and 124º 10' 45.03" W).

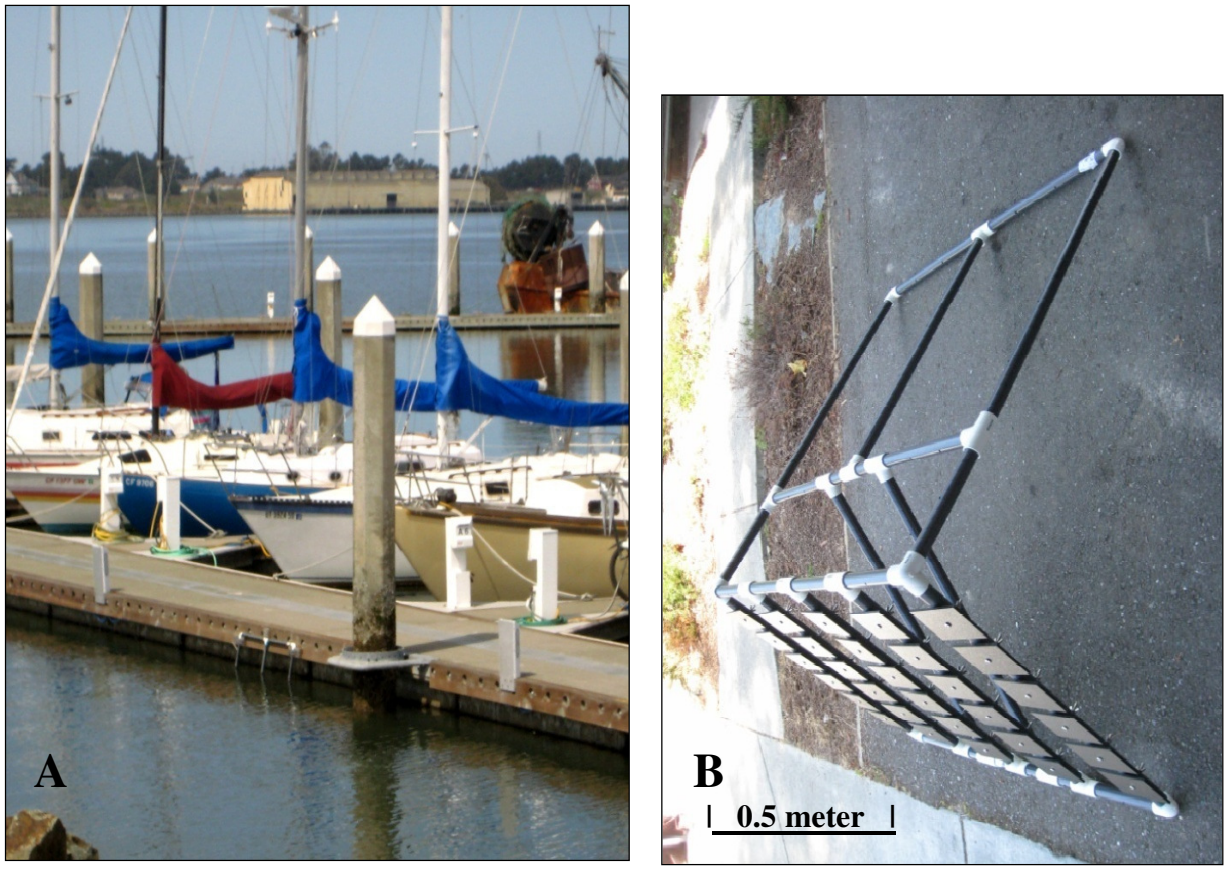

Figure 2: (A) Site at Eureka Public Marina where experimental panels were deployed. PVC rack is attached to the side of the dock directly to the left of the piling in view. (B) Rack design for experimental fouling communities. L-shaped rack constructed of schedule 80 PVC pipe. 30 ABS plastic panels attached with stainless steel carriage bolts and wing nuts.

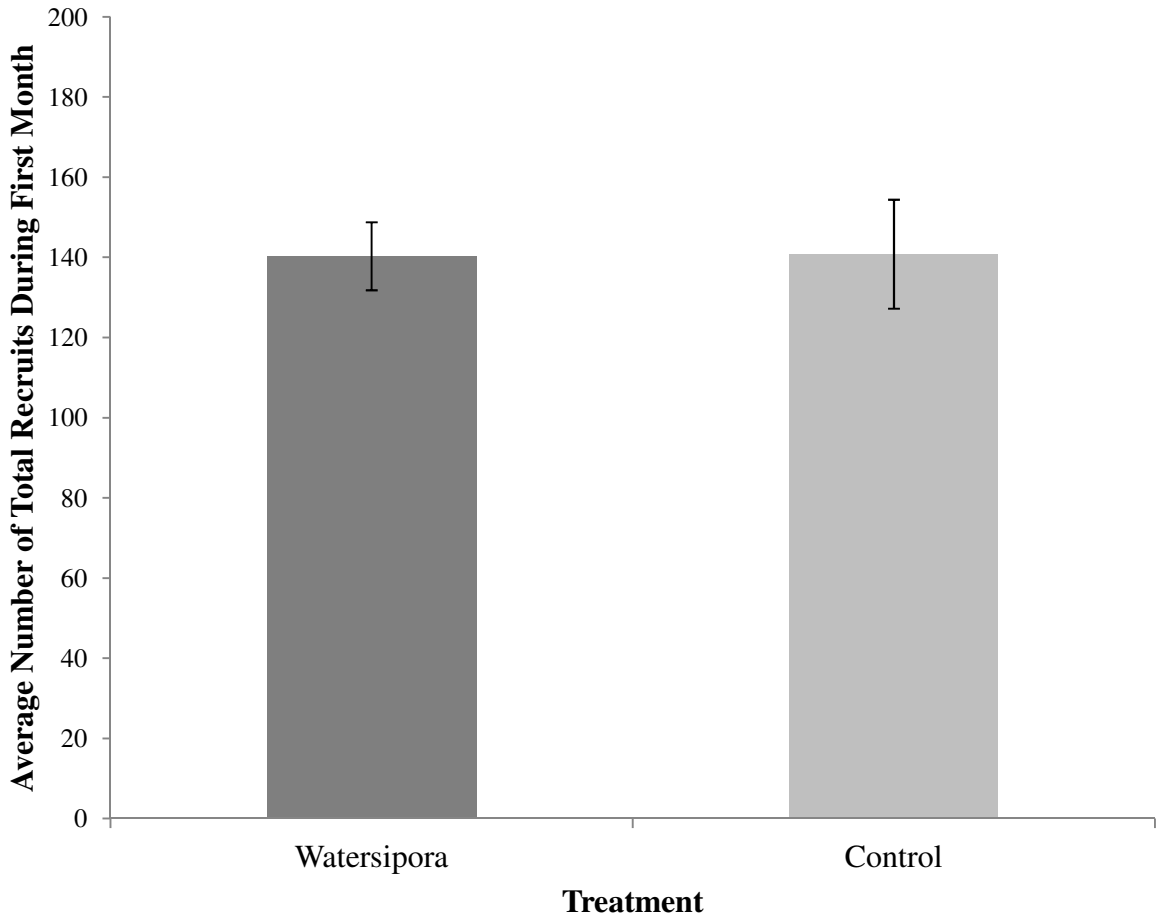

Figure 3: Average number of total recruits, for all species observed on experimental ABS panels during the first month of deployment (October 2008) at Eureka Public Marina (F = 0.0009, d.f.=1,18, P-value = 0.976; one way ANOVA). Dark grey represents recruitment to panels initially seeded with *Watersipora* spp., while light grey represents recruitment to control panels without *Watersipora* (±SE).

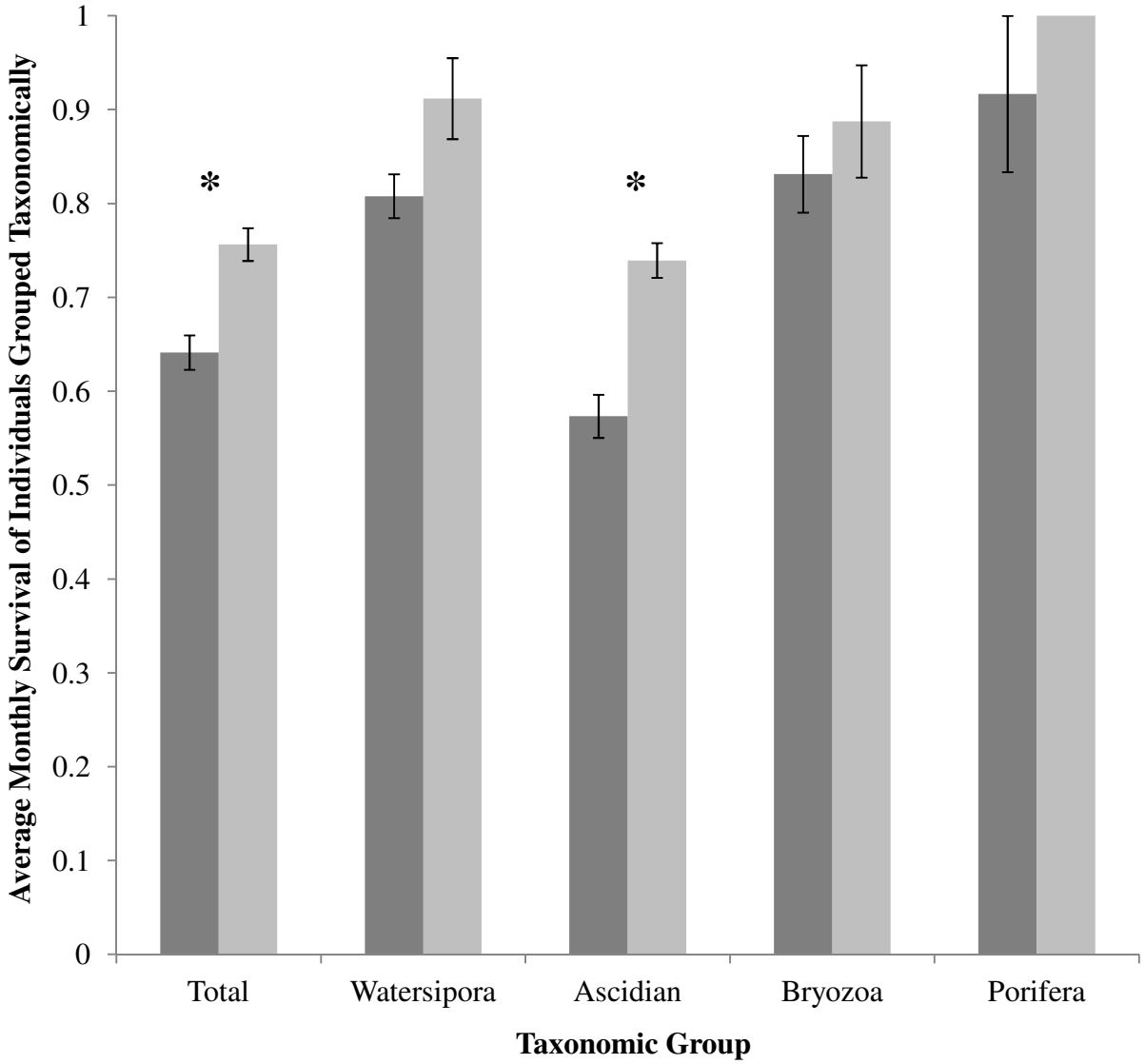

Figure 4: Average monthly survival of individually tracked recruits observed during the first three months (October 2008-December 2008) of deployment in the field. Total recruit survival (F = 23.31, df=1,18, P-value < 0.001, repeated measures ANOVA) and Ascidian survival (F = 38.86, df = 1,18, P-value < 0.001; repeated measures ANOVA) were significantly different between treatments. Dark grey bars represent panels seeded with *Watersipora* spp. while light grey represents controls. Mean ± SE.

Table 1: Summary of results for each Repeated Measures ANOVA: testing for differences in the percent cover of sessile invertebrates between *Watersipora* treatment panels and control panels. Each row represents results for the individual analysis carried out for each species between treatments within the months of December 2008 to May 2009. Bonferroni correction for multiple comparisons, $\alpha = 0.005$

Species Present	**df**	**SS**	**MS**	**F**	**P-value**
Bugula neritina	1,18	0.319	0.31871	0.07	0.790
Bugula californica	1,18	4.789	4.789	3.51	0.077
Watersipora spp.	1,18	661.66	661.66	171.26	<0.0001
Botrylloides violaceus	1,18	2.615	2.615	1.12	0.304
Botryllus sp.	1,18	48.726	48.726	28.88	<0.0001
Distaplia sp.	1,18	0.359	0.3595	0.72	0.407
Didemnum sp.	1,18	125.13	125.135	12.18	0.003
Corella inflata	1,18	104.15	104.15	8.58	0.009
Ciona intestinalis	1,18	2.592	2.592	0.08	0.783
Molgula manhattensis	1,18	1.346	1.346	0.38	0.545
bare panel	1,18	93.957	93.957	48.84	<0.0001

Table 2: Summary of results for the Treatment|Month interaction (Repeated Measures ANOVA): testing for differences in the percent cover of sessile invertebrates between *Watersipora* treatment panels and control panels within five months (December 2008 to May 2009). Each row represents results for the individual analysis carried out for each species. Bonferroni correction, $\alpha = 0.005$.

Species Present	**df**	**SS**	**MS**	**F**	**P-value**
Bugula neritina	4,18	0.950	0.237	0.71	0.585
Bugula californica	4,18	3.204	0.801	1.89	0.122
Watersipora spp.	4,18	8.602	2.150	5.78	<0.0001
Botrylloides violaceus	4,18	12.785	3.196	7.18	<0.0001
Botryllus sp.	4,18	28.583	7.146	12.09	<0.0001
Distaplia sp.	4,18	0.569	0.142	0.45	0.770
Didemnum sp.	4,18	29.909	7.477	4.88	0.002
Corella inflata	4,18	17.420	4.355	6.27	<0.0001
Ciona intestinalis	4,18	2.959	0.734	2.04	0.097
Molgula manhattensis	4,18	9.882	2.471	3.59	0.010
bare panel	4,18	3.695	0.924	1.61	0.181

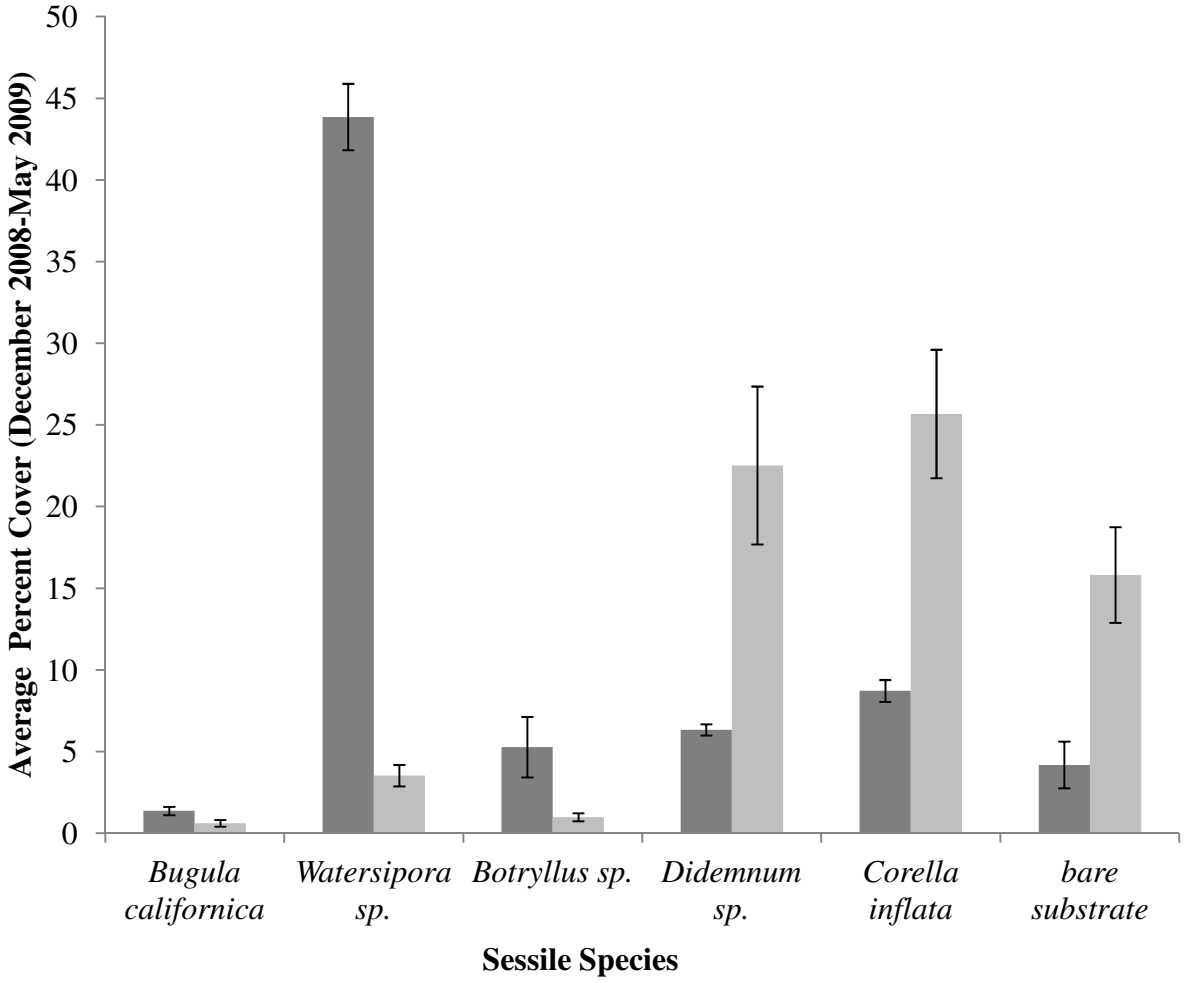

Figure 5: Differences in the percent cover between treatments of dominant sessile invertebrates within a five month period (December 2008- May 2009). (via repeated measures ANOVA): *Bugula californica* (F =3.51, df = 1,18, P = 0.077)*, Watersipora* spp. (F = 171.26, df = 1,18, P < 0.0001) *, Botryllus* sp. (F= 28.88, df = 1,18, P < 0.0001)*, Didemnum* sp. (F=12.18, df = 1,18, P < 0 .003,) *, Corella inflata* (F=8.58, df = 1,18, P = 0.009)*,* and bare panel surface (F = 48.84, df = 1,18, P < 0.0001). Dark grey represents panels seeded with *Watersipora* spp. while light grey represents controls panels. Mean ± SE. Bonferroni correction, $\alpha = 0.005$.

Table 3: Average number of individuals for all species observed and identified during destructive sampling of experimental fouling panels (May 2009). The column labeled "Wat" represents panels initially seeded with *Watersipora* recruits, while "Con" represents individuals found present on control panels. "N" = a species that is native to Humboldt Bay, while "E" = exotic species.

Species Present		**Avg # per panel**		**Species Present**		**Avg # per panel**	
		Wat	**Con**			**Wat**	**Con**
Porifera				**Crustacea**			
Halichondria sp.	E	0.22	0.22	*Balanus* sp.	N	0.44	2.78
Leucosolenia		0.11	0.22	*Cancer magister*	N	6.22	1.33
Cnidaria				*Monocorophium uenoi*	E	0.33	1.78
Obelia dichotoma	E	0.22	0.11	*Caprella drepanochir*		1.22	2.22
Nemertea				*Caprella mutica*	E	21.78	30.00
Tubulanus polymorphus		0.22	0.44	**Bryozoa**			
Tubulanus sexlineatus		0.56	0.78	*Bugula neritina*	E	5.44	3.22
Polychaeta				*Bugula californica*	N	1.89	0.56
Eudistylia polymorpha	N	5.67	2.56	**Urochordata**			
Eudistylia vancouveri	N	2.44	0.78	*Botrylloides violaceus*	E	4.89	3.00
Eulalia quadrioculata		0.44	0.44	*Botryllus* sp.	E	1.67	0.11
Halosydna brevisetosa		4.67	3.00	*Corella inflata*		14.22	24.56
Nereis diversicolor		3.44	3.44	*Ciona intestinalis*	E	1.22	1.22
Neoamphitrite robusta		1.67	0.56	*Distaplia occidentalis*	E	2.78	3.11
Myxicola infundibulum	E	3.11	1.56	*Didemnum* sp.	E	1.33	1.78
Polycirrus sp.	E	7.67	0.89	*Molgula manhattensis*	E	64.33	99.11
Serpula vermicularis	E	0.22	0.00	*Styela clava*	E	0.11	0.22
Polyplacophora							
Mopalia hindsii		0.11	0.11				
Gastropoda							
Hermissenda crassicornis	N	4.56	2.89				
Janolus fuscus	N	0.11	0.00				
Triopha spp.		0.11	0.00				
Archidoris sp.		0.11	0.56				

Table 4: Summary of results for each one way ANOVA: testing for differences in the abundance of individual species (between *Watersipora* treatment panels and control panels) recorded during destructive sampling in May2009. Each row represents results for an individual ANOVA carried out for each species testing for differences between treatment groups. Bonferroni correction for multiple comparisons: $\alpha = 0.005$

Species Tested	**df**	**MS**	**SS**	**F**	**P-value**
Eudistylia polymorpha	1,16	43.556	43.556	10.524	0.0051
Eudistylia vancouveri	1,16	12.50	12.50	5.294	0.0352
Halosydna brevisetosa	1,16	22.222	22.222	8.040	0.0119
Neoamphitrite robusta	1,16	5.556	5.556	4.00	0.0627
Myxicola infundibulum	1,16	10.889	10.889	5.262	0.0357
Polycirrus sp.	1,16	10.335	10.335	31.447	< 0.0001
Cancer magister	1,16	107.556	107.556	51.285	< 0.0001
Hermissenda crassicornis	1,16	12.50	12.50	3.502	0.0797
Corella inflata	1,16	7.775	7.775	13.356	0.0021
Molgula manhattensis	1,16	23.599	23.599	8.646	0.0096

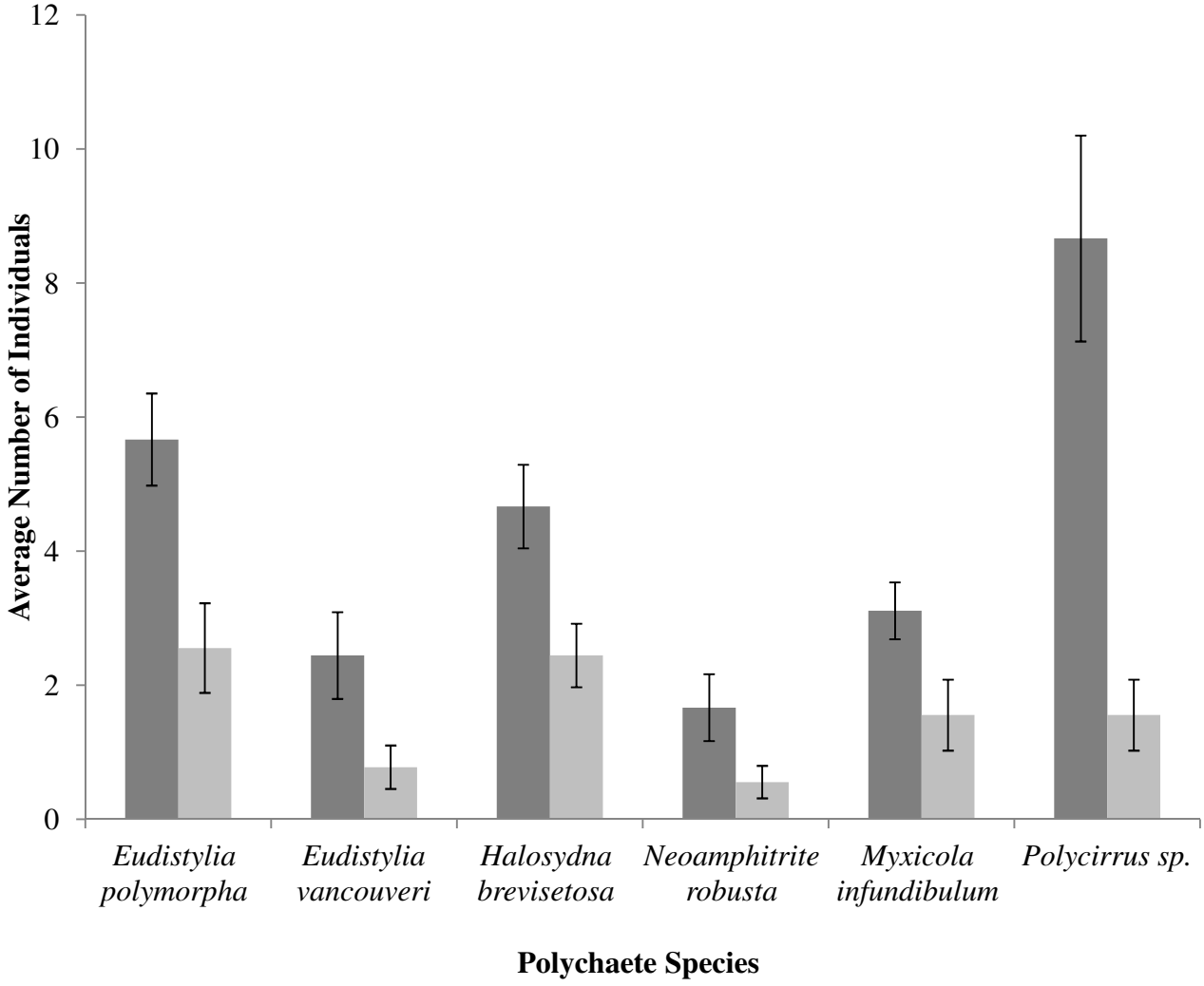

Figure 6: Species of mobile and sessile polychaetes that were found to be significantly more abundant at the end of the experiment on panels treated with *Watersipora,* via one way ANOVA: *Eudistylia polymorpha (F*= 10.52, df= 1,16*, P*= 0.005) *, Eudistylia vancouveri (F*= 5.29, df= 1,16*,P*=0.035)*, Halosydna brevisetosa (F*= 8.04, df= 1,16, *P*= 0.012)*, Neoamphitrite robusta (F*= 4, df= 1,16, *P*= 0.062)*, Myxicola infundibulum (F*= 5.26, df= 1,16*, P*= 0.036)*, Polycirrus* sp. *(F*= 19.14, df= 1,16*, P*= 0.0005). Dark grey represents panels seeded with *Watersipora* spp. while light grey represents control panels. Error bars represent ± SE. Bonferroni correction α = 0.005.

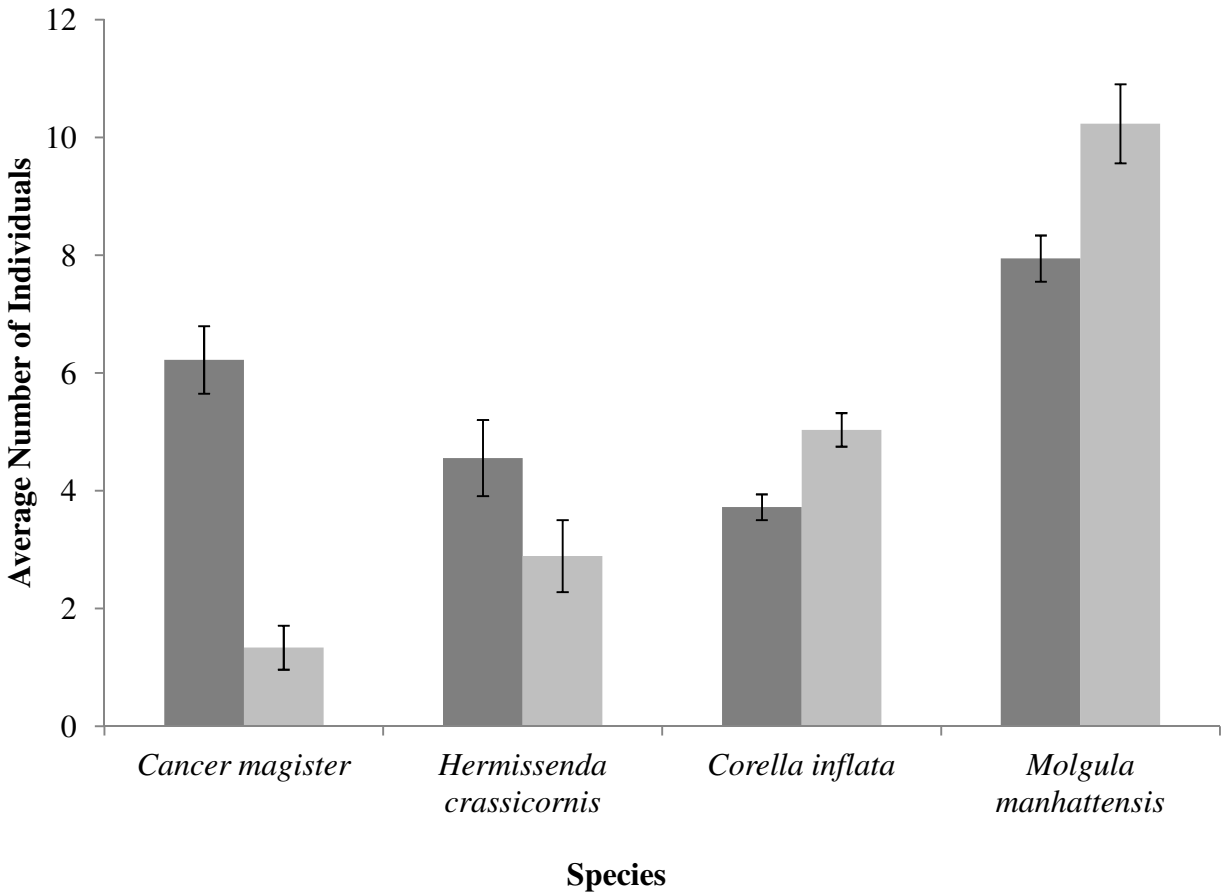

Figure 7: Average number of four additional invertebrates found to be significantly different (individual one way ANOVA's) following destructive sampling of panels at the end of 8 months in the field (May 2009). Two mobile species were found in greater abundance on panels initially treated with *Watersipora*: the crab *Cancer magister* (F=51.29, df= 1,16, $P < 0.0001$) and the nudibranch *Hermissenda crassicornis* ((F= 3.5, df= 1,16, P = 0 079). Two species of tunicates, however were found in significantly lower numbers on *Watersipora* treated panels: *Corella inflata* (F = 13.356, df = 1,16, P = 0.002) and *Molgula manhattensis* (F = 8.646, df = 1,16, P = 0.0096). Dark grey represents panels seeded with *Watersipora* spp. while light grey represents control panels. Error bars represent ± SE. Bonferroni correction $\alpha = 0.005$.

Table 5: Results for each repeated measures ANOVA to determine differences in the survival of recruits between *Watersipora* panels and control panels during the first three months of deployment in the field (October 2008-December 2008)

Total Survival

Source	df	SS	MS	F-ratio	P-value
Treatment	1	0.148	0.148	23.31	<0.0001
Days	1	0.002	0.002	0.38	0.548
Treatment|Days	1	0.016	0.016	2.57	0.126
Panel (Treatment)	18	0.114	0.006	1	0.497
Error	18	0.113	0.006		
Total	39				

Watersipora Survival

Source	df	SS	MS	F-ratio	P-value
Treatment	1	0.112	0.112	5.69	0.029
Days	1	0.128	0.128	9.1	0.008
Treatment|Days	1	0.024	0.024	1.72	0.207
Panel (Treatment)	17	0.336	0.02	1.41	0.245
Error	17	0.239	0.014		
Total	37				

Ascidean Survival

Source	df	SS	MS	F-ratio	P-value
Treatment	1	0.308	0.308	38.86	<0.0001
Days	1	0.005	0.005	0.66	0.428
Treatment|Days	1	0.032	0.032	3.97	0.062
Panel (Treatment)	18	0.143	0.008	0.99	0.505
Error	18	0.144	0.008		
Total	39				

Bryozoa Survival

Source	df	SS	MS	F-ratio	P-value
Treatment	1	0.038	0.038	0.95	0.342
Days	1	0.134	0.134	2.64	0.122
Treatment|Days	1	0.017	0.017	0.33	0.576
Panel (Treatment)	18	0.721	0.04	0.79	0.688
Error	17	0.862	0.05		
Total	38				

Porifera Survival

Source	df	SS	MS	F-ratio	P-value
Treatment	1	0.02	0.02	4.32	0.088
Days	1	0.02	0.02	3.57	0.117
Treatment|Days	1	0.02	0.02	3.57	0.117
Panel (Treatment)	6	0.028	0.005	0.83	0.591
Error	5	0.028	0.006		
Total	14				

Table 6: Results for each repeated measures ANOVA to determine differences in the percent cover of sessile invertebrates between panels treated with *Watersipora* and controls (within the last five months of deployment in the field: December 2008-May 2009).

Bugula neritena

Source	df	SS	MS	F-ratio	P-value
Treatment	1	0.319	0.319	0.07	0.79
Months	4	8.49	2.122	6.39	<0.0001
Treatment|Months	4	0.95	0.237	0.71	0.585
Panel (Treatment)	18	78.324	4.351	13.1	<0.0001
Error	72	23.92	0.332		
Total	99	112.001			

Bugula californica

Source	df	SS	MS	F-ratio	P-value
Treatment	1	4.789	4.789	3.51	0.077
Months	4	1.705	0.426	1	0.411
Treatment|Months	4	3.204	0.801	1.89	0.122
Panel (Treatment)	18	24.543	1.364	3.21	<0.0001
Error	72	30.571	0.425		
Total	99	64.811			

Watersipora spp.

Source	df	SS	MS	F-ratio	P-value
Treatment	1	661.661	661.661	171.26	<0.0001
Months	4	0.36	0.09	0.24	0.914
Treatment|Months	4	8.602	2.15	5.78	<0.0001
Panel (Treatment)	18	69.543	3.863	10.39	<0.0001
Error	72	26.785	0.372		
Total	99	766.95			

Botrylloides violaceus

Source	df	SS	MS	F-ratio	P-value
Treatment	1	2.615	2.615	1.12	0.304
Months	4	8.967	2.242	5.03	0.001
Treatment|Months	4	12.785	3.196	7.18	<0.0001
Panel (Treatment)	18	41.995	2.333	5.24	<0.0001
Error	72	32.07	0.445		
Total	99	98.432			

Botryllus sp.

Source	df	SS	MS	F-ratio	P-value
Treatment	1	48.726	48.726	28.88	<0.0001
Months	4	17.503	4.376	7.4	<0.0001
Treatment|Months	4	28.583	7.146	12.09	<0.0001
Panel (Treatment)	18	30.374	1.687	2.86	0.001
Error	72	42.552	0.591		
Total	99	167.737			

Distaplia occidentalis

Source	df	SS	MS	F-ratio	P-value
Treatment	1	0.359	0.359	0.72	0.407
Months	4	15.808	3.952	12.59	<0.0001
Treatment|Months	4	0.569	0.142	0.45	0.77
Panel (Treatment)	18	8.944	0.497	1.58	0.088
Error	72	22.598	0.314		
Total	99	48.277			

Didemnum sp.

Source	df	SS	MS	F-ratio	P-value
Treatment	1	125.135	125.135	12.18	0.003
Months	4	44.794	11.199	7.31	<0.0001
Treatment|Months	4	29.909	7.477	4.88	0.002
Panel (Treatment)	18	184.92	10.273	6.71	<0.0001
Error	72	110.252	1.531		
Total	99	495.011			

Corella inflata

Source	df	SS	MS	F-ratio	P-value
Treatment	1	104.151	104.151	8.58	0.009
Months	4	19.752	4.938	7.11	<0.0001
Treatment|Months	4	17.42	4.355	6.27	<0.0001
Panel (Treatment)	18	218.404	12.134	17.48	<0.0001
Error	72	49.974	0.694		
Total	99	409.701			

Ciona intestinalis

Source	df	SS	MS	F-ratio	P-value
Treatment	1	0.202	0.202	0.08	0.783
Months	4	0.193	0.048	0.13	0.97
Treatment|Months	4	2.959	0.74	2.04	0.097
Panel (Treatment)	18	46.387	2.577	7.12	<0.0001
Error	72	26.052	0.362		
Total	99	75.793			

Molgula manhattensis

Source	df	SS	MS	F-ratio	P-value
Treatment	1	1.346	1.346	0.38	0.545
Months	4	19.636	4.909	7.14	<0.0001
Treatment|Months	4	9.882	2.471	3.59	0.01
Panel (Treatment)	18	63.732	3.541	5.15	<0.0001
Error	72	49.528	0.688		
Total	99	144.124			

Bare substrate

Source	df	SS	MS	F-ratio	P-value
Treatment	1	93.957	93.957	48.84	<0.0001
Months	4	44.11	11.028	19.23	<0.0001
Treatment|Months	4	3.695	0.924	1.61	0.181
Panel (Treatment)	18	34.627	1.924	3.35	<0.0001
Error	72	41.299	0.574		
Total	99	217.688			

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