Do artificial substrates favor nonindigenous fouling species over native species?

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Abstract

Exotic species are prominent constituents of fouling communities. If exotic fouling organisms colonize or compete better on a wider range of substrate types than native species, this may partially account for their high abundance in estuaries and bays. We used four artificial and four naturally occurring substrate types to compare initial settlement and percent cover of native and exotic fouling species through six months of community development. Both the identity of common taxa and the total number of species colonizing artificial versus natural substrate types were similar. Despite the similarities in species richness, relative abundance patterns between natural and artificial substrate types varied, particularly as the communities developed. Native species were initially in equal abundance on natural and artificial substrate types. Initially, the two most common exotic species, the colonial tunicates, *Botrylloides violaceus* Ritter and Forsyth and *Botryllus schlosseri* (Pallas), were also in similar, but low, abundance on artificial and natural substrates. As the communities developed, there was little change in abundance of exotic or native species on natural substrates. However, on artificial substrates the exotic tunicates increased dramatically and native species declined in abundance. Artificial surfaces may provide a novel context for competitive interactions giving exotic species a more "level playing field" in an environment for which they otherwise might not be as well adapted compared to long-resident native species. Additions of artificial substrates to nearshore environments may disproportionately favor exotic species by increasing local sources of exotic propagules to colonize all types of substrates.
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1. Introduction

Competition is a highly context dependent interaction. Theoretically, one might assume that given thousands of years of adaptation to their local environment, resident species should have inherent advantages when competing with nonindigenous species because the residents should be best adapted to local conditions (Byers, 2002). For an exotic species to become established in a novel, crowded community (i.e. with little "empty niche" space), let alone outcompete a native species, it would seemingly need to either enter an environment with conditions very similar to its home range or be so competitively dominant that environmental differences are inconsequential. The fact that most invasions fail (Williamson, 1996) suggests that these conditions are infrequently met. However, a third mechanism is

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also possible that may be partially responsible for the apparent increase in the rate of exotic species invasions (Cohen and Carlton, 1998). An invader may enter an environment that has been intensely altered by anthropogenic disturbance. These disturbances, if outside the magnitude, duration, or frequency of natural disturbances that affect communities, can create a mismatch between traits of the native species and the environmental conditions to which they have long adapted—a phenomenon termed selection regime modification (SRM) (Byers, 2002). Not only is this third mechanism powerful, but it is likely to increase as anthropogenic impacts continue at unprecedented rates in nearly all ecosystems on earth (e.g., Vitousek et al., 1997; Janzen, 1998). This mechanism may also help to explain, at least in part, the observed strong correlation of invasions in disturbed environments (e.g., Hobbs and Huenneke, 1992).

The SRM mechanism predicts that highly disturbed environments will have a greater abundance of exotic species and that the impact of invading species on native species will be greater in these environments. Marine fouling communities are excellent systems to test this hypothesis. Any hard surface in the marine environment is potential habitat for fouling species. For fouling organisms, artificial substrates represent an anthropogenically altered environment that is equally foreign to the evolutionary history of all species, both native and nonindigenous alike. Thus, artificial substrates have by our definition been in the marine environment for a brief period of time relative to the evolutionary history of the organisms involved. Substrate recognition and preference is a characteristic described for many taxa with planktonic life stages (e.g. McKinney and McKinney, 2002; Harrington et al., 2004; Vermeij, 2005). Proper recognition followed by adhesion and growth, are traits that should be heavily selected for in fouling species and these processes are likely strongly influenced by substrate type. Because fouling species are usually space limited, they compete vigorously and it is easy to manipulate the availability of their limiting resource by providing habitat, both natural and artificial. Furthermore, fouling communities represent a highly tractable, well studied system (e.g. Connell and Glasby, 1999; Connell, 2001; Stachowicz et al., 2002a) with a moderate number of exotic species to provide suitable resolution to test the predictions of the SRM hypothesis.

We predict that exotic species on average should be more abundant on artificial substrates than on natural substrates. There are two potential mechanisms that would lead to this pattern. First, if substrate recognition and selection is important, then relative to natural surfaces, native species will settle less on artificial surfaces. Native species could actively avoid artificial substrates either because they don't recognize them, or because they are suboptimal resources. For example, Anderson and Underwood (1994) reported higher recruitment by oysters and barnacles on concrete and plywood than on two artificial substrate types. Similarly, Bulleri (2005) described different recruitment patterns of epibiotic organisms on sandstone seawalls versus rocky shores. Second, native species should compete best on natural surfaces, to which they are accustomed, compared to artificial substrates. That is, the loss of a "home court" competitive advantage for native species on artificial substrates may lead to a higher abundance of exotic species on artificial substrate types. If native and exotic species are equally non-discriminating in their choices for settlement substrate, or if the environment is saturated with larvae, there may be few initial differences in settlement pattern by native and exotic species on different substrate types as the first mechanism specified. Differences may accrue only later as settled individuals (and colonies) grow larger, intensifying competition for space. In such a case, post-settlement processes, such as relative adhesion strength, relative growth rates, and additional competitive abilities, will have strong influence over final community structure on various substrate types.

Our hypotheses are more focused on native species settling or performing poorly on artificial surfaces rather than exotic species doing exceptionally well on these types of substrates. After all, artificial substrates are foreign for exotic species too. However, because competition is a context-dependent interaction that operates in relative, not absolute terms, we expect artificial substrates may erase much of native species' prior resident advantage. In contrast, native species are expected to compete more successfully on natural substrates on which they evolved. Granted exotic species may have evolved on these natural substrates as well, as these substrates are often ubiquitous, but on natural substrates the full environmental milieu to which the native is adapted should give it an advantage in context dependent competition. It is only on foreign substrate types that native species lose their relative competitive advantage.

Differences in the species composition of fouling communities on artificial substrates have long been recognized (Karlson, 1978; Anderson and Underwood, 1994; Underwood and Anderson, 1994; Bulleri, 2005). However, a systematic bias in the trends of native and exotic species as a function of substrate type has yet to be fully documented. A recently reported pattern of

exotic species predominance on artificial substrates in Elkhorn Slough, California USA strongly suggests such a systematic bias may exist (Wasson et al., 2005). As in many sedimentary estuarine environments, the only hard surfaces within Elkhorn Slough are provided by human-made structures. Wasson et al. (2005) found an approximately equal number of species in soft and hard habitats; however, exotic and cryptogenic species comprised 38% of species in soft sediment and 68% on hard substrates. Furthermore, exotic taxa covered the vast majority of space (84%) on the human introduced hard surfaces. The possibility of a high prevalence of exotic species in highly modified estuarine embayments has influenced surveys of incipient exotic species to target these types of environments (e.g., Pederson et al., 2005).

In this study we experimentally examine potential systematic trends in exotic and native species richness and abundance in fouling communities as a function of settlement substrate. By standardizing for substrate area and length of community development, we isolate the effect of substrate *per se*. By examining replicates of several types of artificial and natural substrates we intend to expose the generality of response of native and exotic species to the two substrate categories. Finally, comparison of the experimental results to our predictions will help to assess the potential of the SRM mechanism as an explanation for enhanced exotic species abundance and impact in disturbed environments.

2. Methods

To examine variation in exotic species success as a function of substrate type, four natural and four artificial materials were chosen. Natural substrate types were: shell, marble, slate, and wood. Artificial substrates consisted of aluminum sheet metal, styrofoam, PVC (polyvinylchloride), and rubber. The emphasis on our choice of artificial substrates was on materials that are well outside of the historical exposure of the fouling organisms, and thus not a part of their evolutionary history. While rubber and metal are not human-made materials, they are not substrates that would normally be encountered in a pristine estuarine environment. The natural substrates had relatively smooth surfaces due to being cut, but otherwise they were not modified in any way (e.g., wood was not pressure treated, rocks were unpolished). All substrates except the shell were flat 10 cm×10 cm panels that were glued to Plexiglass backing, secured with cable ties, and the Plexiglass was attached to metal brackets. The shell substrates were scallops that were very slightly convex and ~12.1 cm

wide and 11.7 cm long. In all cases, the center 68 cm^2 of the substrate was analyzed to standardize area searched and to minimize edge effects.

Five replicate brackets containing each of the eight substrate types were hung from floating docks so that the substrates faced down and were suspended ~3 m below the water surface. The substrates were deployed on May 16, 2004 at the town landing in Wells, Maine USA. The site is a busy commercial and recreational marina in an embayment with a naturally occurring mixture of soft and hard substrates. A water quality monitoring device is located at the pier. During the study period, salinities ranged from 29–35 ppt and water temperature ranged from 8.7 to 21.2 °C. In July, September, and October 2004, the substrates were removed from the brackets and brought to the laboratory for analysis. The major recruitment period for fouling species in New England is May to October (Stachowicz et al., 2002b), and previous investigations indicated that many fouling species begin to senesce in November (Tyrrell and Byers, unpub. data).

At the end of August, one of the brackets was lost when the piece of the dock that it was tied to was damaged; thus results are presented for four replicates of each substrate type. One metal substrate was lost before the July analysis and one slate and wood substrate were lost before the September analysis. Upon collection, each substrate was submerged in seawater and the center 68 cm^2 area was examined. To analyze the relative attractiveness of different substrate types as settlement space, a census was performed to quantify species richness. To compare how the amount of space occupied differed between substrate types, relative abundance was assessed by recording the identity of each species under 50 random points on a Plexiglass plate. We focused on quantifying the occupation of primary space, i.e. those species directly in contact with the supplied substrate. By September, the arborescent hydroid *Tubularia crocea* (L. Agassiz) had become extremely abundant, but we assessed primary space occupation under the canopy of *Tubularia*. The substrates were returned to the field after analysis to non-destructively follow the development of the communities through time.

For statistical analysis, species richness data were square root transformed and percent cover data were arc sine square root transformed. A repeated measures ANOVA was performed on species richness in July, September, and October as a function of substrate type (artificial versus natural). Cryptogenic species were grouped with exotic species for comparisons of richness of natives versus exotics (when cryptogenic species were excluded we got the same qualitative results across

substrate types). For percent cover analyses, a repeated measures ANOVA was used to compare the abundance of all native species on natural and artificial substrates in September and October. A second repeated measures ANOVA was used to compare the abundance of the nonindigenous tunicates, *Botrylloides violaceus* and *Botryllus schlosseri*, on natural and artificial substrates in the same two months. We focused on analyzing the abundance of these two nonindigenous tunicate species because these two species were conspicuous components of the community and the other nonindigenous and cryptogenic species occurred in only trace abundance in comparison. The substantial bare space on the panels in July (>50%) indicated that after only two months of community development, competition for space and species interactions in general were likely minimal, so we did not use the July data for abundance comparisons.

3. Results

A total of thirty-five species were encountered on the substrates, of these, three are nonindigenous (*B. violaceus*, *B. schlosseri* and *Membranipora membranacea* [Linnaeus]) and four are cryptogenic (*Bowerbankia gracilis* Leidy, *Cryptosula pallasiana* Levinson, *Electra pilosa* [Linnaeus], and *Campanularia* sp.) (Carlton, 2003). The four most abundant species in order were: *T. crocea* (native), *B. violaceus* (exotic), *B. schlosseri* (exotic), and the sponge *Halichondria panicea* [Pallas] (native). These four species occurred on every substrate type, indicating that these common species were able to colonize all substrate types. For the less common species, there were small variations in settlement between substrate types. For example, *Campanularia* sp. only appeared on shell while *M. membranacea* never colonized shell or marble
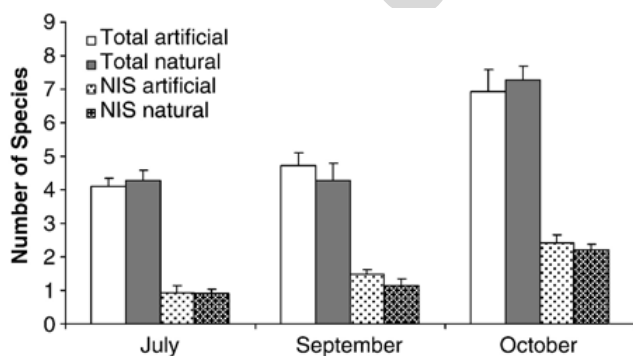

Fig. 1. Total number of species (±1 SE, solid bars) and number of nonindigenous and cryptogenic species (NIS) (±1 SE, stippled bars) on artificial (light colored bars) and natural substrate types (dark colored bars).
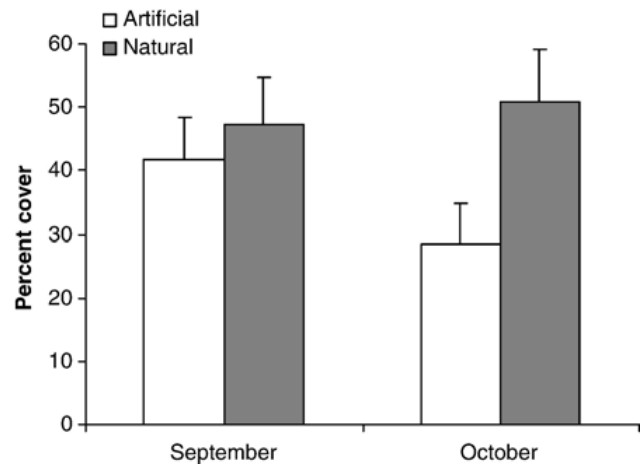

Fig. 2. Percent cover of all native taxa (per 68 cm^2 ±1 SE) on artificial and natural substrate types. Open bars indicate artificial substrate types and shaded bars indicate natural substrate types.

substrates. Generally, species lists were very similar between all of the substrate types.

Average species richness was similar on each of the substrate types (e.g. in October mean = 7.10, SE ± 0.38). The total number of species did not differ between substrate categories (Fig. 1, $F_{1,27} = 0.014$, $p = 0.91$), indicating that the relative attractiveness of natural versus artificial substrate types was very similar. The number of species on the substrates increased with time ($F_{2,26} = 26.75$, $p < 0.001$), but the time by substrate type interaction was not statistically significant ($F_{2,26} = 0.67$, $p = 0.52$).

Despite similarities between natural and artificial substrates in the species richness patterns, there were strong differences in the amount of space occupied by native and exotic taxa between these two substrate categories. The percent cover of native species on natural substrates increased only slightly from 47% in September to 51% in October (Fig. 2). However, on artificial substrates, natives declined from 42% in September to 28% in October. This differential decline in native percent cover on artificial substrates relative to natural substrates was significant (time by substrate type interaction: Fig. 2, $F_{1,27} = 4.96$, $p = 0.035$). The effect of time alone on the amount of space occupied by native species was not significant ($F_{1,27} = 2.34$, $p = 0.14$), and the effect of substrate type alone was also not significantly different ($F_{1,27} = 1.77$, $p = 0.19$). The statistical results were qualitatively similar when *T. crocea* (the most abundant native species) was examined individually.

The second and third most abundant species across substrate types were the nonindigenous tunicates, *B. violaceus* and *B. schlosseri*, whose abundance

comprised 90% of total nonindigenous abundance. The amount of space occupied by these two exotic species significantly increased through time (Fig. 3, $F_{1,27}=$ 41.56, $p<0.0001$) and their percent cover increased significantly more on artificial than natural substrates through time (time by substrate type interaction: $F_{1,27}=7.18$, $p=0.012$); substrate type alone was not significant ($F_{1,27}=1.60$, $p=0.22$). Specifically, the two exotic tunicates occupied similar amounts of space on artificial and natural substrates in September (8% and 9%), and by October had increased to 16.5% on natural substrates and to 36% on artificial ones (Fig. 3). *Botrylloides* occupied 45% of primary substrate on the PVC substrate in October (Fig. 4A), which was notably higher than its abundance on any of the natural substrate types (maximum was 17% on slate) and *Botryllus* was much more abundant on metal (21%, Fig. 4B) than on the other substrate types. Despite the strong increases in exotic tunicate abundance on artificial substrates, the total abundance of fouling organisms was similar between natural and artificial substrate types in October (Fig. 4C), because the increase in exotics on artificial substrates was compensated by a decrease in native abundance (Fig 2).

4. Discussion

Our study focused specifically on substrate type as a determinant of fouling community structure. We found that average species richness patterns did not differ as a function of substrate type. Thus, in this system it appears that natives and exotics alike appear physiologically capable of settling on a variety of substrates. However, a large difference was observed in the relative abundance
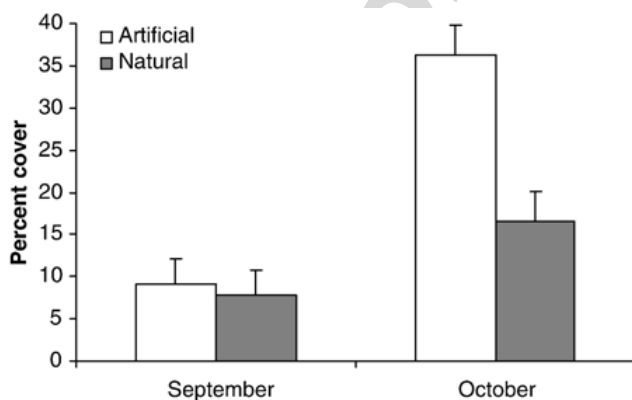

Fig. 3. Percent cover (± 1 SE) of the nonindigenous tunicates *Botrylloides violaceus* and *Botryllus schlosseri* on artificial and natural substrate types. Open bars indicate artificial substrate types and shaded bars indicate natural substrate types.
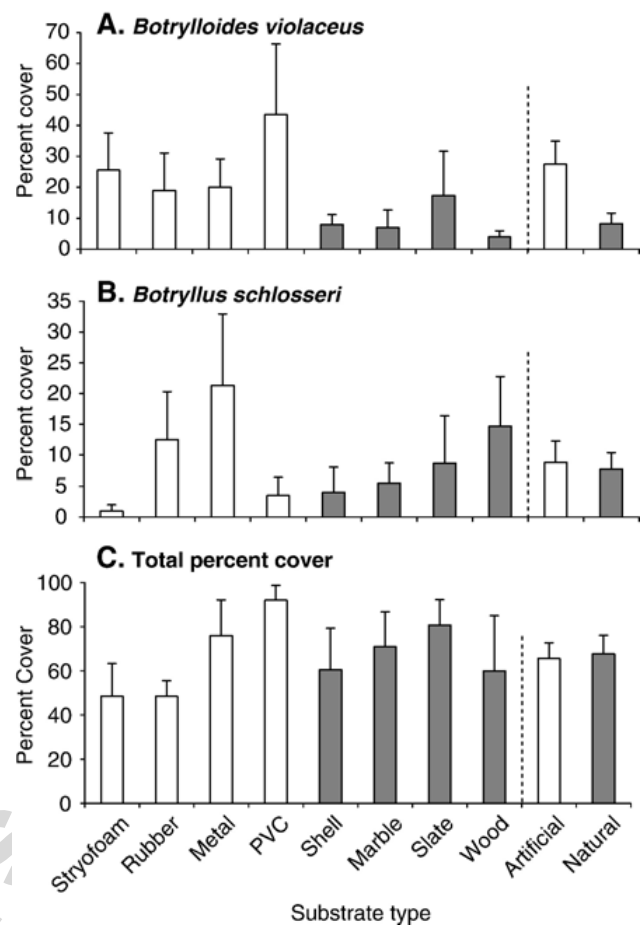

Fig. 4. Percent cover (± 1 SE) of fouling organisms on all substrate types in October 2004. Open bars indicate artificial substrate types and shaded bars indicate natural substrate types. A) *Botrylloides violaceus*, B) *Botryllus schlosseri* and C) all species combined.

of exotic and native species between the two substrate categories due to post-settlement processes (e.g. relative adhesion strength, growth rates, and competition). The exotic tunicates, *Botrylloides* and *Botryllus*, increased dramatically on artificial substrates through time at the expense of native species abundance, which declined. In contrast, *Botrylloides* and *Botryllus* increased only slightly on natural substrates; native species on these same substrates did not change, indicating that the slight increase in exotics was primarily due to their occupation of bare space. Exotic species were thus disproportionately enhanced on artificial surfaces, as predicted by the SRM hypothesis. Our results are consistent with post-settlement processes driving the observed pattern and suggest that a lack of shared evolutionary history of any species with artificial substrate types weakens potential competitive advantages of native species on such surfaces.

The abundance of native species was strongly dominated by *T. crocea*, which has an upright growth

form in comparison with the prostrate form of the two nonindigenous tunicates, *Botrylloides* and *Botryllus*. Obviously these growth form differences may affect relevant, substrate-influenced properties such as adhesion and growth. While it might have been insightful to compare natives and exotics with similar growth forms, we were primarily interested in species invasive status as a contributor to their relative abundance on various substrate types, and none of the native colonial (i.e. prostrate) tunicates of this region are common in fouling communities.

Certainly microtopographic differences existed between our substrate treatments. In part, we embraced these differences because such properties are what make each substrate distinct. However we also standardized for these differences somewhat by using natural substrates in slightly processed forms. For example, the wood, slate, and marble substrates were cut and smoothed to expose a flat surface, thus their surfaces were less rugose than they would be in nature, and therefore more similar to (the typically smooth) artificial substrates. This reduction in microtopography of natural substrates resulted in substrate surface characteristics being more uniform between natural and artificial substrate treatments, which helped to isolate substrate composition, *per se* as a major factor driving our results.

Coastal infrastructure such as pilings, buoys and floats are often constructed of the artificial materials that we used in this experiment. We included PVC as an artificial substrate type because it is commonly utilized for fouling community studies. Our study, like others (e.g., Anderson and Underwood, 1994; Glasby, 2000), suggests careful consideration of substrates used for experimental purposes. For example, Connell and Glasby (1999) reported differences in community structure between artificial substrates and natural rocky reefs in Sydney, Australia. They suggested that these artificial substrates are not surrogates for natural rock substrates, but rather they present a novel habitat type for fouling taxa. Smith and Rule (2002) similarly showed that assemblages of motile fauna recruiting to artificial surfaces were not representative of adjacent natural communities. Particularly in the case of exotic species studies, it may be helpful to recognize that, relative to natural substrates, artificial substrates may result in unnaturally depressed abundance of native species and enhanced abundance of invasive tunicates and other exotic species. Not only does substrate type affect the performance of some types of species, ubiquitous exotic species such as tunicates may differentially thrive on certain types of artificial substrates that are commonly used for ecological studies. Thus, in general, our results suggest that communities do not just develop differently on artificial substrates, but that the artificial substrates may be systematically biased in their reflection of natural communities.

The ability of exotic tunicates to occupy and maintain substantial amounts of space on artificial substrates likely contributes to their success in highly modified estuarine embayments. Human structures may attract and even promote nonindigenous species by differentially benefiting them. For example, in a thorough system-wide assessment of Elkhorn Slough, CA, exotic species were heavily dominant on novel, hard substrates (Wasson et al., 2005). Similarly, the spread of the problematic, newly identified tunicate *Didemnum vexillum* in New Zealand may have been facilitated by artificial substrates in the marine environment. This tunicate attaches to a wide variety of substrate types and forms lobes than hang down from docks, wharves and boat bottoms. These lobes are easily dislodged by wave activity allowing the tunicate to spread to the seafloor and other surfaces (A. Coutts, pers. comm.).

The patterns we documented focused on the two highly abundant exotic tunicates, *Botrylloides* and *Botryllus*. Many of the exotic and cryptogenic species in this system were too sparse to provide necessary resolution to determine if they exhibited the same relative abundance patterns as these two nonindigenous ascidians. However the power of the SRM prediction is in the aggregate prediction it makes for exotic species as a whole. We believe that species identity will always be important in establishing dominance; however, on artificial substrates, or in disturbed environments in general, the SRM mechanism predicts that on average the identity of those species is increasingly likely to be nonindigenous.

The communities we studied are annual and a majority of the species senesce every winter. If allowed to persist year-round, we believe the dominance by exotic tunicates on artificial substrates would have been greater because of their high rate of increase right up through peak abundance and into senescence. Thus, highly modified embayments in milder climates that have perennial fouling communities may have even stronger skew to nonindigenous species. If true, the extension of this idea also has implications for global climate change. Specifically, warmer water temperatures that promote perennial community persistence may also enhance exotic species relative abundance (Stachowicz et al., 2002b). Rising ocean temperatures, in concert with steadily increasing coastal and offshore infrastructure, which often provides artificial and altered settling habitats, could lead to substantial increases in exotic fouling species.

Fouling communities are an attractive choice for manipulation and testing of ecological hypotheses. The dependence of these communities on substrate as habitat allows disturbances or habitat alterations to be easily imposed. We chose a particular habitat alteration, namely the substitution of artificial settling surfaces for natural ones, to ascertain how developing fouling communities are affected. We have demonstrated that systematic variation in community development patterns is based on the interaction of substrate type and native and exotic status. However, further investigation into the specific mechanisms behind the apparent loss of advantage for native species on artificial substrate types is warranted. Nevertheless, to avoid contributing to the spread and proliferation of exotic species, coastal managers should consider limiting the amount of submerged artificial substrates and avoiding destruction of naturally occurring hard substrates in coastal and estuarine habitats.

Acknowledgments

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