

Maintenance of diversity altered by a shift in dominant species: implications for species coexistence

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ABSTRACT: Diversity can be maintained by the biological characteristics of species within communities, particularly dominant species. Invasions often result in shifts of dominant species. Despite the number of studies on invasion ecology, few have determined their long-term effect on diversity. In the present study, we coupled short- and long-term studies to examine the relationship between invasive species (colonial ascidians or sea squirts) and diversity and to discuss their implications for species coexistence. Diversity patterns between 2 panel studies (1979 to 1982; 2003 to 2006), one conducted before the establishment of invasive colonial ascidians, revealed an increase in species diversity. Short-term recruitment studies designed to elucidate mechanisms behind the patterns observed in our long-term studies suggest contrasting methods of maintaining diversity. Between 1979 and 1982, *Mytilus edulis* was a consistent spatial occupant whose hard shell provided secondary space for colonization by other species. In contrast, the 2003 to 2006 community was dominated by the seasonally abundant invasive colonial ascidians *Botrylloides violaceus* and to a lesser extent *Didemnum vexillum*, which do not provide secondary substrate. These species either senesce after reproduction or undergo seasonal regression and free space for colonization by other species. These studies suggest that the coexistence of species has shifted from a community in which diversity was maintained by secondary substrates to a community in which diversity is maintained by primary substrates. Additionally, they suggest that the community is undersaturated and could support more species, particularly those that seasonally utilize a limited resource (free space).

KEY WORDS: Species coexistence · Invasive species · Diversity · Species richness · Recruitment · Ascidians · Bivalves · *Mytilus edulis* · *Botrylloides violaceus* · *Didemnum vexillum*

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INTRODUCTION

In recent years, considerable effort has been directed towards studying invasive species and their ecological impacts on communities and ecosystems. Introduced species have been found to substantially alter species composition and ecological interactions within the invaded community. For example, observations of subtidal communities in Long Island Sound, USA, have shown a substantial displacement of native species by invasive ascidians (Osman & Whitlatch 1995a). Similar shifts have been found in the Gulf of Maine over a 25 yr period. Harris & Tyrrell (2001) witnessed a change in the development of rocky subtidal

communities, from a community that was historically comprised of kelp beds to a community dominated by invasive species, including a green alga (*Codium fragile* ssp. *fragile*), a bryozoan (*Membranipora membranacea*), and colonial ascidians (*Diplosoma listerianum* and *Botrylloides violaceus*). Recent studies in invasion biology have focused on identifying ecological components that render communities vulnerable to invasion (Levine & D'Antonio 1999, Lonsdale 1999, Stachowicz et al. 1999, 2002a, Lundholm & Larson 2004), examining characteristics that make species successful invaders (Levine 2000, Stachowicz & Byrnes 2006), and understanding the interactive effects of invasions on communities and ecosystems (e.g. Stachowicz & Tilman

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2005, Sala & Knowlton 2006, Stachowicz et al. 2007). Despite this continuing research, the mechanisms underlying the impacts of invasions on biological diversity and species coexistence are still not well understood (Stachowicz et al. 2007).

The maintenance of species diversity is commonly thought of as coexistence of species that use similar resources (Simberloff & Dayan 1991, Chesson 2000). As an example, assemblages of sessile invertebrates of fouling and cryptic communities feed on suspended material in the water column and require space for attachment. Diversity in highly competitive ecosystems can often be increased by the life-history characteristics or elimination of marine organisms (Dayton 1971, Sutherland & Karlson 1977, Connell 1978, Sousa 1984). Many marine species are seasonally dominant or have finite life-cycles that allow other species to become established in communities during their absences (Yund et al. 1997, Stachowicz & Byrnes 2006, Dijkstra et al. 2007a). During periods when competitively dominant species are absent, more resources (e.g. primary space) are available to other species (e.g. Sebens 1982). An alternative mechanism for increasing diversity in marine benthic communities is by providing a 3-dimensional surface that offers substrate for settlement of species (e.g. Jackson 1977, Osman & Whitlatch 1995b, Barnes 2001, Reiss et al. 2003). However, not all established adults increase diversity; in fact, some may reduce diversity by preventing other organisms from settling on their surfaces (Buss 1979, Bryan et al. 2003, Joullie et al. 2003). Thus, displacement of one dominant species by another species can affect diversity and the mechanism(s) of its maintenance, depending on their use versus the creation of available space.

The purpose of the present study was to examine the influence of invasive ascidians on the mechanisms that maintain diversity and their implications for species coexistence in a marine epifaunal community in the southwestern Gulf of Maine, New Hampshire, USA. We compared 2 long-term studies conducted at the same location—the first conducted before the ascidians arrived and the second conducted post-invasion. Short-term recruitment experiments were then designed to examine the influence of the dominant organisms in each community (pre-invasion and post-invasion) on species diversity. Results of these short-term experiments were compared with our long-term studies. Our pre-invasion dataset is an essential and unique component of our study, as most studies are only able to evaluate the impact of exotics after they have become established. Coupling short-term studies with pre- and post-invasion long-term datasets is critical to understand the mechanisms that underlay the relationship between invasions and community structure.

MATERIALS AND METHODS

Long-term experiments. Long-term comparisons of species diversity were quantified using 2 panel studies, conducted beneath a cement pier in Newcastle, New Hampshire, USA, at the University of New Hampshire's Coastal Marine Laboratory. The first study was initiated in 1979 with the goal of comparing succession between horizontal and vertical substrates (Harris & Irons 1982). Here, 8 horizontal and 8 vertical, predator-inaccessible 0.1 m² Plexiglas panels were deployed in July 1979 ~5 m below mean low water under the pier at the Coast Guard Station, Newcastle. This pier extends ~0.5 km into the channel of Portsmouth Harbor. The benthic substrate at this site was composed of fine sand/mud mixed with boulders. From 1979 to 1982, the fouling community on the pier was dominated by sponges, mussels, anemones, and large barnacles (Harris & Irons 1982). Soft corals, ascidians, bryozoans, and hydroids were less common and were interspersed throughout this assemblage. Panel arrays were suspended away from pilings to minimize predator access, though fish were not excluded. Any crabs or sea stars that were observed on the arrays were removed during monthly monitoring and photography. Identification and enumeration of individuals were conducted using the original photographic slides.

The second panel study was initiated in 2003 with the intention of determining any shifts in species composition and diversity and of assessing whether the maintenance of diversity had changed since the 1979 to 1982 study. The 2003 to 2006 study replicated the experimental design of the first study exactly, and panels were photographed monthly. Since the completion of the 1979 to 1982 study, 6 new species have become established in Portsmouth Harbor. These include the encrusting bryozoan *Membranipora membranacea*, the solitary ascidians *Asciidiella aspersa* and *Styela clava*, and the colonial ascidians *Didemnum vexillum*, *Botrylloides violaceus*, and *Diplosoma listerianum*. By 2004, all 3 colonial ascidians and *M. membranacea* occupied panels at our study site in Newcastle and were also found within the fouling communities occupying the beams supporting the pier. The 2 solitary ascidians had not yet been observed at this site, but do occur within the Portsmouth Harbor Region.

Slides and photographs of horizontal panels (facing the substrate only; n = 8) and vertical panels (1 side only; n = 8) taken approximately monthly from 1979 to 1982 and 2003 to 2006 (~1200 images) were digitized and downloaded into Adobe Photoshop 7.0. A few months from the 1979 to 1982 dataset are missing. Therefore, we excluded similar months from the 2003 to 2006 dataset for statistical analysis. For instance, if November 1980 were missing, then the equivalent

month (November 2004) of the 2003 to 2006 dataset would be excluded from the analysis. Data presented here are from July (1979 and 2003, respectively) to April (1982 and 2006, respectively). All individuals were counted and identified to species. The only exceptions to this occurred due to the difficulties of enumerating stolonating organisms and in differentiating epibionts from their basal individuals. Thus, abundances of hydroids were analyzed as percent cover, and *Molgula* sp./*Obelia* sp. were recorded as a species complex because *Obelia* sp. was a common secondary space occupant of the solitary tunicate *Molgula* sp. In addition to counting individuals, we recorded percent cover of the dominant structural members of each community (1979 to 1982, *Mytilus edulis*; 2003 to 2006, *Botrylloides violaceus*). Average monthly abundance data of individuals from horizontal and vertical panels were pooled for statistical analysis and ordination plots. Abundances from vertical and horizontal panels were pooled, as we wanted to compare total differences in community structure and composition. These data were used for statistical analysis and non-metric multidimensional scaling plot (nMDS) ordination. Comparison of community structure and composition between horizontal and vertical panels in 1979 to 1982 and 2003 to 2006 will be discussed elsewhere. A Kruskal-Wallis test on combined average monthly abundances of vertical and horizontal panels was used to detect differences in abundance (number of individuals; exception was hydroids) within a species between the 2 communities (1979 to 1982 and 2003 to 2006). A 1-way ANOVA was used to determine differences in average number of species and abundances of individuals found on panels per month. To determine whether the changes in species richness and abundance between the 1979 to 1982 and 2003 to 2006 communities were the result of the inclusion of the invasive species themselves (rather than their effects on the community), we performed calculations with and without invasive species.

To examine divergence in faunal composition between the 2 studies, a Bray-Curtis similarity matrix was constructed using abundances that were square-root transformed (Clarke & Warwick 2001). A nMDS plot and a 1-way analysis of similarities (ANOSIM) were calculated to examine differences in faunal composition between the 2 studies. The nMDS is a method that preserves species-specific formation and is sensitive in detecting changes in assemblage patterns (Clarke & Ainsworth 1993). ANOSIM is a non-parametric permutation test that applies the same (rank) similarity matrix used for nMDS ordination (after Clarke & Warwick 2001).

Discriminator species were calculated between 1979 to 1982 and 2003 to 2006 using the SIMPER statistic (SIMilarities PERcentages). A discriminator species has a relatively high and even distribution in most

areas of one assemblage, but is rare or absent in areas of another assemblage. Discriminator species were calculated by first computing the average dissimilarity in species composition between 1979 to 1982 and 2003 to 2006 (Clarke & Ainsworth 1993). The overall average dissimilarity was then broken down into separate contributions from each species and the consistency (i.e. monthly) with which each species contributed to the overall dissimilarity. Thus, a good discriminator species not only contributes importantly to the overall dissimilarity, but does so consistently (Clarke & Warwick 2001). Community analyses and graphs were generated using Primer 6.0 (Primer-E).

Short-term experiments. To determine the mechanisms driving diversity patterns in communities dominated by bivalves (1979 to 1982) and colonial ascidians (2003 to 2006), we conducted an experiment using 4 types of structural treatments: 2 types of biogenic structure (bivalves and colonial ascidians) and 2 controls (glue and no glue) and 3 sites. A total of 36, Plexiglas panels of 100 cm² (n = 3 for each treatment per site and n = 3 for each control per site) were deployed in July and August 2004 and July 2005.

Trials were carried out using 2 treatments with 50% cover of either bivalves (*Mytilus edulis* and *Anomia simplex*) or colonial ascidians (*Botrylloides violaceus*, *Didemnum vexillum*, and *Botryllus schlosseri*) and 2 controls (panels with glue and no glue). Each trial was performed at a separate site and was done to test the repeatability of the experiment. Species were collected from floating docks and glued to panels with Superhold Plastic Surgery glue. For glue controls, 50% of the surface was randomly covered in glue. Panels were suspended from floating docks and hung horizontally, ~0.5 m below the surface with experimental surfaces facing downward. Panels were left in the field for 2 wk, at which time they were collected and brought to the laboratory for analysis.

All individuals that settled upon adult individuals and free space on the panels were counted and identified to species (Pollock 1998, Bullard & Whitlatch 2004). A randomized complete-block 1-way ANOVA, with treatment levels as the independent factor, site as the block term, and recruitment (species and individuals) as the dependent variable, was used to test for differences in community structure on secondary space (bivalves and colonial ascidians) and primary space (free space on panels with adult individuals) (Table 1). Tukey-Kramer analysis set to 0.05 significance level was used to detect differences in settlement of species and individuals across structural treatment levels. All statistical analyses were generated using JMP software[®] (JMP 7, SAS Institute). To reduce heteroscedasticity, recruitment data were square-root transformed before analysis (Zar 1999).

RESULTS

Comparison between 1979 to 1982 (pre-invasion) and 2003 to 2006 (post-invasion) studies

Three invasive species not present in the 1979 to 1982 community became key members of the 2003 to 2006 community (Table 2). They include the colonial ascidians *Botrylloides violaceus* and *Didemnum vexillum* and the encrusting bryozoan *Membranipora membranacea*. *M. membranacea* is a pioneer species and exhibited its greatest abundance during the first 3 mo of community development (July to September; J. A. Dijkstra unpubl. data).

Differences in abundances of taxa were determined between 1979 to 1982 and 2003 to 2006 (Table 2). While differences in abundances of certain taxa were found between 1979 to 1982 and 2003 to 2006, we did not observe taxonomic losses or the addition of resident species that had not been present on the 1979 to 1982 panels. Faunal composition between 1979 to 1982 and 2003 to 2006 was significantly different, with apparent shifts in species composition and dominance of species (Fig. 1; ANOSIM: $R = 0.310$, $p < 0.001$; Table 2). According to a 1-way SIMPER analysis, the invasive colonial ascidians *Botrylloides violaceus* and *Didemnum vexillum*, the mussel *Mytilus edulis*, and the sponges *Haliclona loosanofi* and *Halichondria panicea* were the most important and consistent determinants of community dissimilarity between the 1979 to 1982 and 2003 to 2006 communities (Table 3). *B. violaceus* and, to a lesser extent, *D. vexillum* characterized the 2003 to 2006 community and have displaced the historically prevalent blue mussel *M. edulis* (Table 4). Abundances of *M. edulis* have significantly declined since the 1979 to 1982 study ($p < 0.001$; Fig. 2A). However, between 1979 and 1982 it was a dominant and persistent spatial occupant (Fig. 2A). Unlike *M. edulis*, overall abundances of colonial ascidians have significantly

Table 1. Randomized complete-block 1-way ANOVA, with structural treatment as the independent variable and site as the block term. Species richness and abundance were the response variables

	df	Sum of squares	F-ratio	Prob > F
Species richness				
Structural treatments	5	14.682986	38.2087	<0.0001
Block	2	0.159723	1.0391	0.3619
Error	46	3.535414		
Abundance				
Structural treatments	5	857.0559	34.8144	<0.0001
Block	2	10.1778	1.0336	0.3638
Error	46	226.4841		

Table 2. Results of a Kruskal-Wallis test used to detect temporal change in species abundances between 1979 to 1982 and 2003 to 2006 ($n = 100$). ***significant difference at the 0.01 level in species abundances between the 1979 to 1982 and 2003 to 2006 communities; **significant differences at the 0.05 level; ns: not significant. *Mogula sp./Obelia sp.* recorded as complex

Species	Significance	Temporal (1979–1982; 2003–2006) changes in abundance
Porifera		
<i>Haliclona loosanofi</i>	***	Decrease
<i>Halichondria panicea</i>	***	Decrease
<i>Leucosolenia sp.</i>	ns	
<i>Halisarca sp.</i>	***	Decrease
Yellow encrusting sponge	**	Increase
Cnidaria		
<i>Ectopleura larynx</i>	ns	
<i>Obelia spp.</i>	**	Increase
<i>Metridium senelis</i>	***	Increase
<i>Ectopleura indivisa</i>	**	Decrease
<i>Hydractinia</i>	ns	
Mollusca		
<i>Anomia simplex</i>	ns	
<i>Mytilus edulis</i>	***	Decrease
<i>Hiatella arctica</i>	ns	
Gastropoda		
<i>Crepidula spp.</i>	ns	
Bryozoa		
<i>Membranipora membranacea</i>		Not present in the 1979–1982 community
<i>Bugula simplex</i>	***	Increase
<i>Bugula turrita</i>	**	Increase
<i>Schizoperella unicornis</i>	***	Increase
<i>Electra pilosa</i>	ns	
<i>Cryptosula pallasina</i>	ns	
<i>Bowerbankia</i>	ns	
<i>Hypothoa hyalina</i>	ns	
Encrusting bryozoans	ns	
Tunicata		
<i>Botrylloides violaceus</i>		Not present in the 1979–1982 community
<i>Diplosoma listerianum</i>		Not present in the 1979–1982 community
<i>Botryllus schlosseri</i>	***	Decrease
<i>Didemnum vexillum</i>		Not present in the 1979–1982 community
<i>Ciona intestinalis</i>	***	Decrease
<i>Mogula spp.</i>	**	Decrease
<i>Aplidium constellatum</i>	ns	
<i>Didemnum albidum</i>	ns	
<i>Mogula sp./Obelia sp.</i>	***	Increase
Crustacea		
<i>Balanus spp.</i>	***	Decrease
<i>Amphipod tubes</i>	**	Increase

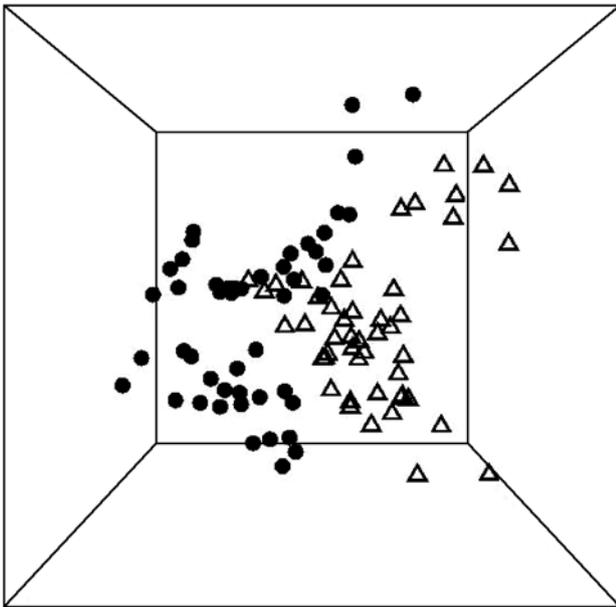


Fig. 1. Three-dimensional non-metric multidimensional scaling plot representing species assemblages between 1979 to 1982 (●) and 2003 to 2006 (△); stress 0.12. Each point represents monthly averages of abundance for both vertical and horizontal panels ($n = 100$). Significant differences in species composition were detected between 1979 to 1982 and 2003 to 2006 (ANOSIM: $R = 0.310$, $p < 0.001$)

increased (Table 2, Fig. 2B). Additionally, the invasive colonial ascidians *B. violaceus* and *D. vexillum* were seasonally dominant members of the 2003 to 2006 community (Fig. 2B). Highest spatial coverage of *B. violaceus* occurred in summer (June through August 2004 and July through September 2005) and of *D. vexillum* occurred in fall and winter (October through January 2004/2005 and November through February 2005/2006).

Table 3. SIMPER (similarity percentage) results showing which species made the greatest contribution to the dissimilarity between 1979 to 1982 and 2003 to 2006 communities

Species	Average abundance (no. of ind. per panel)		Dissimilarity/ SD	Percent contribution
	1979–1982	2003–2006		
<i>Botrylloides violaceus</i>	0.00	2.04	4.47	8.62
<i>Mytilus edulis</i>	2.69	1.99	1.63	7.9
<i>Ciona intestinalis</i>	0.99	0.47	1.43	3.23
<i>Didemnum vexillum</i>	0.00	0.84	1.37	3.53
<i>Schizoperella unicornis</i>	0.27	0.7	1.36	2.64
<i>Haliclona loosanofi</i>	1.13	0.77	1.31	2.89
<i>Halichondria panicea</i>	0.86	0.73	1.31	2.78
<i>Metridium senelis</i>	0.38	0.59	1.24	2.4

Table 4. SIMPER (similarity percentage) results showing which species made the greatest contribution to the similarity within communities. *Mogula sp./Obelia sp.* recorded as complex

Species	Avg. abund.	Avg. sim.	Similarity/ SD	Percent contrib.
1982 to 1979				
<i>Mytilus edulis</i>	2.69	7.67	0.97	13.5
<i>Anomia simplex</i>	1.95	6.57	3.1	11.57
<i>Mogula sp.</i>	1.96	6.29	1.74	11.08
<i>Mogula sp./Obelia sp.</i>	1.88	4.84	0.92	8.52
<i>Botryllus schlosseri</i>	1.33	4.78	2.28	8.42
<i>Balanus spp.</i>	1.94	4.08	0.82	7.18
<i>Haliclona loosanofi</i>	1.13	3.53	1.27	6.22
<i>Leucosolenia sp.</i>	1.02	3.38	1.68	5.94
<i>Ciona intestinalis</i>	0.99	2.98	1.48	5.25
<i>Halichondria panicea</i>	0.86	2.08	0.95	3.66
2003 to 2006				
<i>Botrylloides violaceus</i>	2.04	7.76	4.37	13.75
<i>Mogula sp./Obelia sp.</i>	2.96	6.84	0.89	12.12
<i>Mytilus edulis</i>	1.99	6.1	1.73	10.8
<i>Anomia simplex</i>	1.69	4.25	1.29	7.54
<i>Mogula sp.</i>	1.56	3.58	0.98	6.34
<i>Botryllus schlosseri</i>	1.05	3.36	1.65	5.95
<i>Balanus spp.</i>	1.5	3.09	0.92	5.48
<i>Haliclona loosanofi</i>	0.77	2.29	1.19	4.05
<i>Didemnum vexillum</i>	0.84	2.12	0.94	3.76
<i>Schizoperella unicornis</i>	0.7	1.81	1.04	3.21
<i>Bugula simplex</i>	0.84	1.79	0.72	3.17
<i>Leucosolenia sp.</i>	0.72	1.76	0.97	3.12
<i>Halichondria panicea</i>	0.73	1.7	0.94	3.02

Species richness significantly increased between the first (1979 to 1982) and the second study (2003 to 2006; Fig. 3; $p < 0.01$), though the total number of individuals was similar (Fig. 3A,B included monthly averages for introduced species, while Fig. 3C,D excluded monthly averages for introduced species). Further examination of species richness and abundance as a function of succession within each of the 2 communities revealed species richness was consistently higher between 2003 and 2006 than between 1979 and 1982 (Fig. 4; Fig. 4A,B include monthly averages of species and abundances, while Fig. 4C,D exclude monthly averages of species and abundances). During the course of the experiments, species richness declined between 1979 and 1982, but no clear trend was observed between 2003 and 2006 (Fig. 4A).

Abundance in terms of species numbers showed a bell-shaped distribution between 1979 and 1982: low in Year 1, increasing in Years 2 and 3, and decreasing in Year 4 (Fig. 4B,D). In contrast, abundance increased steadily from 2003 to 2006.

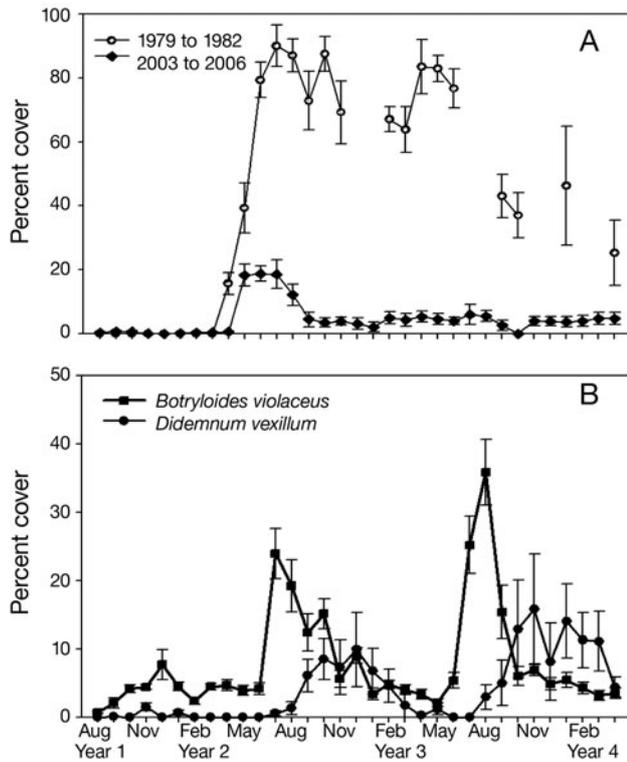


Fig. 2. (A) Percent cover (\pm SE) of the blue mussel *Mytilus edulis* between 1979 to 1982 and 2003 to 2006. Presence of *M. edulis* has significantly declined since 1982 ($p < 0.001$). Between 1979 and 1982, *M. edulis* dominated the panels for ~21 mo beginning in April 1980. (B) Annual percent cover (\pm SE) of the recent invaders *Botrylloides violaceus* and *Didemnum vexillum*

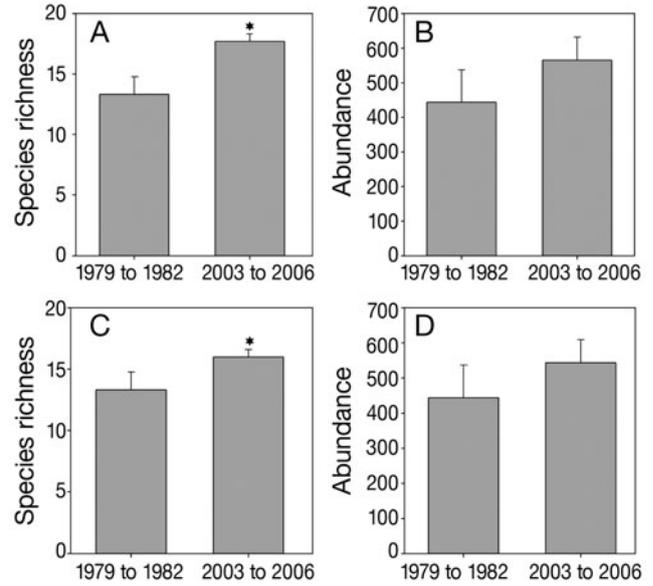


Fig. 3. Univariate measurements of species composition. Average monthly patterns of: (A,C) species richness and (B,D) abundance. (A,B) include invasive species; (C,D) do not. A 1-way ANOVA revealed a significant increase (*) in species richness in the post-invasion community (A: 1 df, $F = 13.656$, $p < 0.001$; C: 1 df, $F = 5.801$, $p < 0.018$). (A) includes invasive species in the calculations (mean = 17, SE = 0.62), while (C) (mean = 15, SE = 0.52) does not. Abundances of individuals were similar between the pre- and post-invasion studies when including invasive species (B: 1 df, $F = 0.024$, $p < 0.878$; mean = 566, SE = 66.98) in calculations and excluding invasive species (D: 1 df, $F = 0.006$, $p < 0.938$; mean = 551, SE = 100). Error bars were calculated using standard error

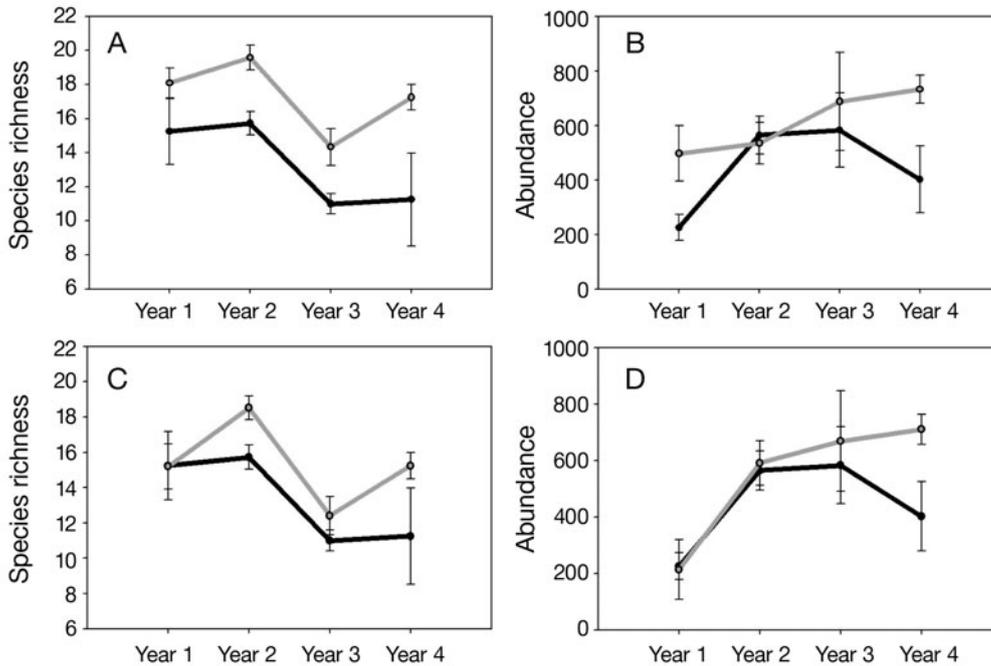


Fig. 4. Annual patterns of: (A, C) species richness and (B, D) abundance as a function of time since initial development between 1979 and 1982 (black line) and 2003 to 2006 (gray line). Annual average monthly abundances in (A) and (B) include abundances of invasive species, while (C) and (D) do not. Error bars were calculated using standard error

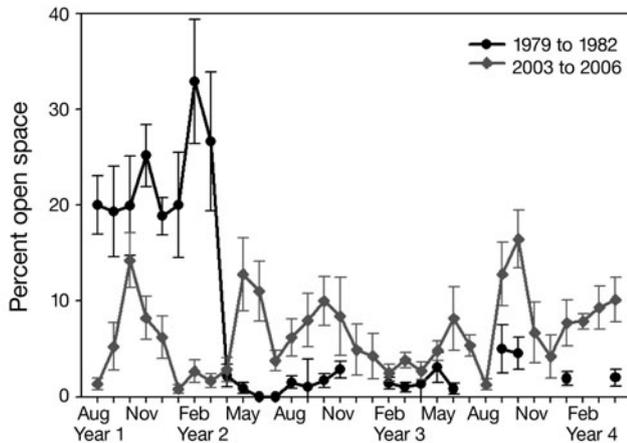


Fig. 5. Percent available bare space (\pm SE) between 1979 to 1982 and 2003 to 2006. Total bare space increased ($p < 0.05$) since the initial study. Between 1979 and 1982 free space was more prevalent before the recruitment of mussels in April 1980, while primary space was stochastically available between 2003 and 2006 ($p < 0.05$)

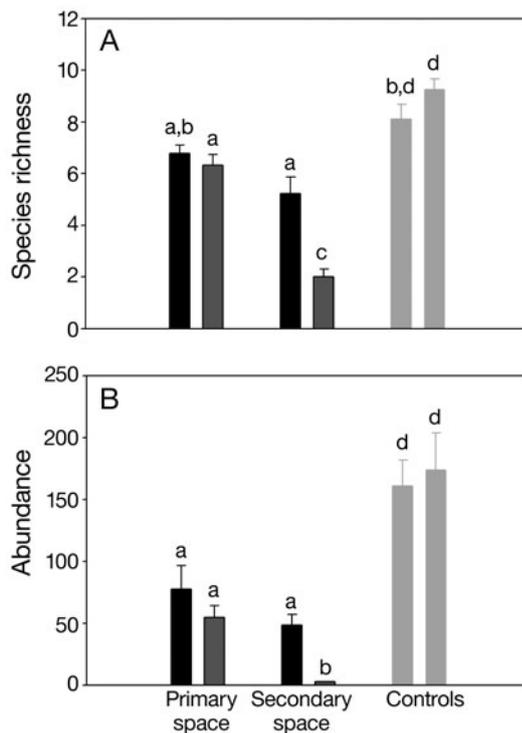


Fig. 6. The 2 wk experiments testing the response of settling larvae to secondary space provided by colonial ascidians and bivalves and to free space on panels with established adults. The Tukey-Kramer test revealed significant differences in (A) species richness and (B) abundance of recruits on bivalves versus colonial ascidians ($p < 0.05$). Additionally, secondary space provided by bivalves acted similarly to primary space on panels with established adults. No significant differences were detected on free space adjacent to adults on panels. Species richness and abundance were significantly higher on control panels than on either panel with established adults ($p < 0.05$). Different letters above bars represent significant differences

In addition to changes in community composition and species richness, there were also significant differences in the prevalence of open space between the 2 communities (Fig. 5). Between 1979 and 1982, the availability of space was linked to mussel recruitment, as a greater percent of primary space was available before the settlement of mussels in April 1980. In contrast, an increase in colonial ascidians corresponded to an increase in primary space that was stochastically available between 2003 and 2006.

Short-term experiments

A 1-way complete-block ANOVA revealed that more individuals and species settled on (1) secondary space provided by bivalves than on secondary space provided by colonial ascidians (Fig. 6) and on (2) control panels than on panels with bivalves or colonial ascidians (Fig. 6). No significant differences were detected in the numbers of species or individuals that settled on secondary space provided by bivalves than on primary space on panels with established adults (Fig. 6; Tukey-Kramer set to $p < 0.05$).

DISCUSSION

The present study reveals that invasive species can alter the primary mechanisms of coexistence if the structural role and life-history characteristics of the invading dominant species are significantly different than the structural role and life-history characteristics of the native dominant species. The pre-invasion community was dominated by the perennial bivalve *Mytilus edulis*; its hard shell maintained coexistence by providing secondary substrate for the settlement of competent larvae. In the post-invasion community, the invasive annual colonial ascidians *Botrylloides violaceus* and, to a lesser extent, *Didemnum vexillum* displaced *M. edulis* as the dominant species on the panels in spite of predators being excluded. Unlike bivalves, many colonial ascidians possess a chemical defense that deters secondary settlement (e.g. Bryan et al. 2003, Joullie et al. 2003) and inhibits predation (Lindquist et al. 1992, Pisut & Pawlik 2002). Species coexistence in the post-invasion community was maintained instead by an increase in primary space that was facilitated by senescence and/or regression of the seasonally dominant non-native colonial ascidian species.

Historically, mussels became the dominant species on panels and ropes suspended between pier pilings that were deployed in July 1979 and February 1980 (Harris & Irons 1982, present study). While dominance by *Mytilus edulis* is one of potentially many states before

the introduction of *Botrylloides violaceus* and *Didemnum vexillum*, the decline of mussels on ropes and panels deployed in February 2003, July 2003, and April 2008 suggests a pattern of reduced mussel abundance (J. A. Dijkstra & L. G. Harris unpubl. data, present study), though the mechanism is unclear and requires further investigation. In addition, the shift in species dominance between 1979 and 2006 was not likely the result of a region-wide decline in mussels, as mussel populations actually increased following overfishing of the green urchin *Strongylocentrotus droebachiensis* in the Gulf of Maine after 1995 (Harris & Tyrrell 2001, Witman et al. 2003, Siddon & Witman 2004).

The present study shows a positive relationship between the number of introduced species in a community and the average monthly species richness, despite a shift in dominance from a species that provided secondary substrate, e.g. mussels, to one that does not provide secondary substrate, e.g. colonial ascidians. All resident species found in the pre-invasion study were also observed in the post-invasion study. However, when excluding invasive species in our analyses, the average number of species able to occupy panels was still higher in the post-invasion community, suggesting that the life history of invasive species, rather than the invasive species themselves, is driving the increase in species richness observed between 2003 and 2006. Therefore, maintenance of species diversity has changed as a result of a shift in the structural role and life history of dominant species. *Mytilus edulis* is a dominant primary space occupant in intertidal and subtidal communities (Harris & Irons 1982, Petraitis 1995). Like all bivalves, its shell provides a stable surface for the settlement of secondary space occupants (Jackson 1977, Sutherland & Karlson 1977, Sutherland 1978, Dean & Hurd 1980, Osman & Whitlatch 1995b, Barnes 2001), but inhibits the amount of primary space available for settlement (present study). In contrast, *Botrylloides violaceus* and *Didemnum vexillum* are seasonally dominant species. *B. violaceus* grows during the spring and summer months (asexual reproduction), sexually reproducing, senescencing, and finally sloughing off panels, leaving open space for colonization. In contrast to other groups, colonial ascidians have smooth surfaces that often inhibit the attachment of species. Additionally, they have evolved chemical defenses that are highly effective deterrents to larval settlement (e.g. Buss 1976, Bryan et al. 2003, Joullie et al. 2003, Marti et al. 2003, present study). Increased availability of primary space in the post-invasion community likely counteracted the inhibitory characteristics of colonial ascidians, as higher numbers of individuals and species settle on primary versus secondary substrates (e.g. Osman & Whitlatch 1995b, Stachowicz et al. 2002a, Clark & Johnston 2005, Dijkstra et al. 2007b, present study).

Many studies have shown a correlation between local species richness and regional species richness. For instance, an increase in local species richness accompanied by a rise in regional species richness was found for corals in the Indo-Pacific (Karlson et al. 2004), in wetlands along the northern Coastal Range of California (Freestone & Harrison 2006), and in various biogeographic regions from 62° S to 63° N (Witman et al. 2004). Mortality of dominant individuals not resulting from competition or predation, e.g. senescence, can lead to local temporal stochasticity of free space in subtidal communities (Connell 1978). Senescence of colonies or individuals from a single species eliminates them from an area and opens that area to recolonization, thereby, preventing competitive exclusion of species. The life-history cycle, e.g. senescence of invasive colonial ascidians, in this system created a community that is susceptible to colonization and can support regional increases in species richness.

The investigations described here also provide insight into the coexistence of species. A well-developed body of theory on species coexistence suggests that coexistence can be driven by temporal patterns of resource use (e.g. Abrams 1984, Chesson 1985, Warner & Chesson 1985, Chesson & Huntly 1997). Temporal changes in species presence and absence, resulting from environmental variation in a community, create patches of free space that can modify competition and enable species coexistence in local communities (Chesson 2000, Stachowicz et al. 2002b, Leibold & Chase 2003, Leibold et al. 2004, Stachowicz & Tilman 2005). Environmental variation in temperate zones tends to occur regularly (i.e. seasonal) and, in the absence of predation, to drive the appearance and disappearance of species in communities, as with the annual senescence of *Botrylloides violaceus* in the present study (e.g. Minchin 1992, Stachowicz et al. 2002b, Philippart et al. 2003, Kirby et al. 2007). A shift in dominance from a perennial species to an annual species creates annual temporal competitive relief, enabling species coexistence in this community.

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