Latitudinal Gradients in Recruitment and Community Dynamics in Marine Epifaunal Communities: Implications for Invasion Success

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ABSTRACT. Although the latitudinal diversity gradient, where species diversity peaks at low latitudes, is well documented, much less is known about how species life history strategies differ among regions and the implications of these differences for community development trajectories and particularly for invasion dynamics. As a first step in trying to understand these factors, we contrast spatial and temporal variation in recruitment rates and resultant community development of epifaunal assemblages in regions along a latitudinal gradient from the temperate zone to the tropics. We exposed settlement panels in four regions: Long Island Sound (Connecticut), Chesapeake Bay and Virginia's Eastern Shore (Maryland and Virginia), Indian River Lagoon (Florida), and a portion of the Mesoamerican reef in Belize. Panels were deployed for either one to two weeks, to evaluate recruitment patterns, or one year, to monitor community development. We found that both recruitment and community development rates were inversely correlated with diversity, with the highest rates seen in temperate latitudes and the lowest in tropical Belize. Seasonal variability in recruitment also varied latitudinally, with strong summer pulses of recruitment in northern latitudes shifting to low and year-round recruitment at low latitudes. However, species turnover through time in communities becoming established was highest in Belize. We conclude with predictions regarding the implications these patterns may have on invasion dynamics at different latitudes.

INTRODUCTION

Latitudinal patterns in diversity have remained an important theme in ecology for more than a century, yet we still continue to debate the relative contributions of processes that may cause these patterns (Currie et al., 2004; Mittelbach et al., 2007). There are many environmental variables that change with latitude, and it is easy to correlate species distribution patterns with these factors. Unfortunately, it is as easy to find exceptions to these correlations. In addition, with increased transport of nonnative species (Ruiz et al., 2000), species distributions continue to be altered. Although latitudinal gradients in native species diversity are well documented, studies on terrestrial and freshwater systems suggest latitudinal gradients in invasion success occur as well (Sax, 2001). However, little work to date has examined this question in marine systems. Therefore, we have been documenting latitudinal differences in both the recruitment and the community development of

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marine epifaunal invertebrates as a first step in understanding latitudinal differences in species invasions.

The mode by which species successfully invade new habitats is a pressing ecological research issue (Rejmanek and Richardson, 1996; Williamson and Fitter, 1996; Moyle and Light, 1996). Current theory predicting the attributes of successful invaders has largely been developed in terrestrial environments and usually stresses the importance of life history traits associated with rapid reproduction and wide dispersal ability (Rejmanek and Richardson, 1996). In the far more open marine environment, ocean currents can disperse larvae and adults of many species for great distances over relatively short time periods (Jokiel, 1984; Scheltema, 1986). Additionally, man inadvertently transports countless individuals and species between discrete biogeographic provinces (Ruiz et al., 1997; Carlton, 1999). Given the generally good dispersal abilities of marine species, those attributes of new species that allow them to coexist with, or even displace, native species will be as important as dispersal ability to a species invasion potential.

The sessile invertebrate or epifaunal community is an excellent system in which to examine rigorously both the life history attributes that characterize successful invaders as well as those attributes of native communities that govern their susceptibility to invasion. Epifaunal communities occur in all coastal habitats and can be found in all biogeographic regions. These communities contain species with a variety of life histories, yet their principal species are usually permanently attached as adults and are easy to manipulate. Although the species within these communities differ among regions, they function in similar ways. Most have planktonic larvae as the main means of dispersal, feed from the water column, compete for limited available space, and are preyed on by a variety of mobile vertebrate and invertebrate predators. Because epifaunal species are sessile and relatively small in size, natural communities can develop on small discrete substrates, with larval dispersal and recruitment linking communities within a site or habitat as well as within a region. These attributes make them ideal systems that can be experimentally manipulated in the field to test directly hypothetical relationships while maintaining natural levels of abundance, species composition, and diversity.

Among epifaunal communities, a major difference is the number of available species that have some reasonable probability of recruiting to a particular site within a region. Osman and Dean (1987) found that these regional pools of species varied by almost an order of magnitude and that both the mean number of species found on individual substrates and the correlated richness at each site varied greatly among the study sites within each region, with overlap among sites in different regions. These patterns potentially result from (1) the low probability of recruits of many species in the regional species pool actually reaching a particular site during the course of investigation and (2) the high probability of local, within-site dispersal of species already present at a particular site. Alternatively, high predation and local extinction rates at some sites may prevent certain species in the regional species pool from colonizing these sites (Osman and Whitlatch, 1996, 1998). As a first step in trying to understand factors contributing to the local and regional differences in diversity and how these are likely to influence species invasions, we have been contrasting temporal variation in recruitment rates and resultant community development in regions along a latitudinal gradient from tropical to temperate regions.

METHODS

We deployed experimental panels in four biogeographic regions along the eastern seaboard of the United States and in the Caribbean Sea. These regions were Long Island Sound in Connecticut (LIS; 41°N), Maryland and Virginia's Chesapeake Bay and Eastern Shore region (CB; 37°N), the Indian River Lagoon in Florida (IRL; 27°N), and the vicinity of Carrie Bow Cay in Belize (BEL; 16°N). Polyvinyl chloride (PVC) panels, 100 cm^2, were abraded to facilitate settlement of invertebrates and were suspended on racks underneath docks. The panels were held horizontal with the experimental surface facing the seafloor.

Recruitment

To estimate recruitment in all regions, panels were sampled either weekly (LIS) or biweekly (CB, IRL, BEL). At the beginning of each sampling period, four clean panels were exposed at each of the field sites. After the one- or two-week exposure period the panels were collected and new panels were deployed. In the laboratory, all panels were examined under a dissecting microscope, and all attached invertebrates were identified to the lowest possible taxonomic unit (usually species) and counted.

Sample schedules varied by region as necessitated by recruitment patterns and destructive storm activity. Weekly sampling at the LIS Avery Point (AP) site began in 1991 and has continued unabated to the present. In the years 1991–1996 sampling was suspended during the winter months when almost no settlement occurs. From 1997 to the present, sampling was conducted continuously with biweekly sampling during the winter. The remaining LIS sites (Groton Long Point [GLP] and Mystic River [MR]) were added in 2001 and have been sampled on the same schedule as the AP site. Sampling in CB and IRL was begun in 2004 with two sites in each region. The CB sites were at the Smithsonian Environmental Research Center (SERC) in the upper Bay and at the Virginia Institute of Marine Science (VIMS) in the lower Bay. The IRL sites were the Smithsonian Marine Station (SMS) and the Ft. Pierce Inlet (Inlet). Sampling at the VIMS site was discontinued in 2007 after hurricane damage to the dock, and sampling at both IRL sites was suspended from September 2004 until March 2005 because of the loss of docks as the result of two hurricanes. Sampling in BEL began in December 2004 and continued through February 2006.

Data Analysis

Recruitment differences among sites within and across regions were compared by matching means for each sampling time and using paired t tests to analyze for significant differences. Wilcoxon signed-rank tests were also conducted for each pairing to eliminate the possible effects of large seasonal differences biasing the results. Because of the species differences among regions, analyses were done for total recruitment of all species, pooled invasive species, and pooled native species. Species identified as cryptogenic were included with the native species. The number of sampling periods varied greatly among the regions, and we conducted the analysis of each pair of stations using the maximum number of sampling periods in common based on the year and week of sampling. Data were corrected for exposure time to account for the one- and two-week sampling periods used in different regions.

Community Development

To measure difference in community development, experimental panels (same as above) were deployed for at least one year and nondestructively sampled for invertebrate richness. Four panels were deployed at each site (three per region) between July and August 2006 to a depth of 0.6 m below LLT and at least 0.5 m above the bottom. Panels in LIS, CB, and IRL were sampled iteratively 1, 3, and 12 months after deployment. Panels in BEL were sampled 3, 6, and 12 months after deployment. Panels were sampled with a dissecting microscope, and attached invertebrates were identified to the lowest possible taxonomic unit. Taxonomic richness on each panel was recorded.

RESULTS

Recruitment

Three types of recruitment patterns are evident. Within sites there are temporal patterns, among sites within regions there are fairly consistent relationships, and together these produce broader patterns among the regions.

Within-Site Temporal Patterns

Within each site there are temporal patterns in recruitment that result from seasonal cycles in reproduction and year-to-year variation in recruitment that can result from a variety of causes. Seasonal variability in recruitment is most evident in the two northern regions, LIS and CB, which experience large variations in temperature. In both regions recruitment is largely absent during the coldest winter months. The three sites in LIS are consistent in exhibiting peak recruitment in the late summer (Figure 1). Recruitment at the GLP site begins earlier and remains consistently higher than at the other sites throughout the whole season. This site is in shallower water and consequently experiences lower winter temperatures and higher summer temperatures (Osman and Whitlatch, 2007) and warms more quickly in the spring. At the CB sites, the majority of recruitment occurs in the spring and early summer, with a second, much smaller peak period in the autumn (Figure 1). Most dominant species in this region such as barnacles, bivalves, and polychaetes are planktotrophic with feeding larvae dependent on the spring and autumn plankton blooms. Recruitment in the remaining two regions, although temporally variable, exhibits no consistent seasonal cycle. Recruitment occurs year round at both IRL sites, with the inlet having somewhat higher recruitment in the summer (Figure 1). Recruitment at the SMS dock is dominated by several species of barnacles and has much more sporadic peaks. Finally, BEL recruitment was extremely low and demonstrated no obvious patterns.

Spatial Variability among Sites within Regions

Within the three regions with multiple sites we have observed fairly consistent differences among the sites. Based on the paired t tests of weekly differences in total recruitment over the period 2001 through 2007, the three sites in LIS were significantly different, with GLP > AP > MR

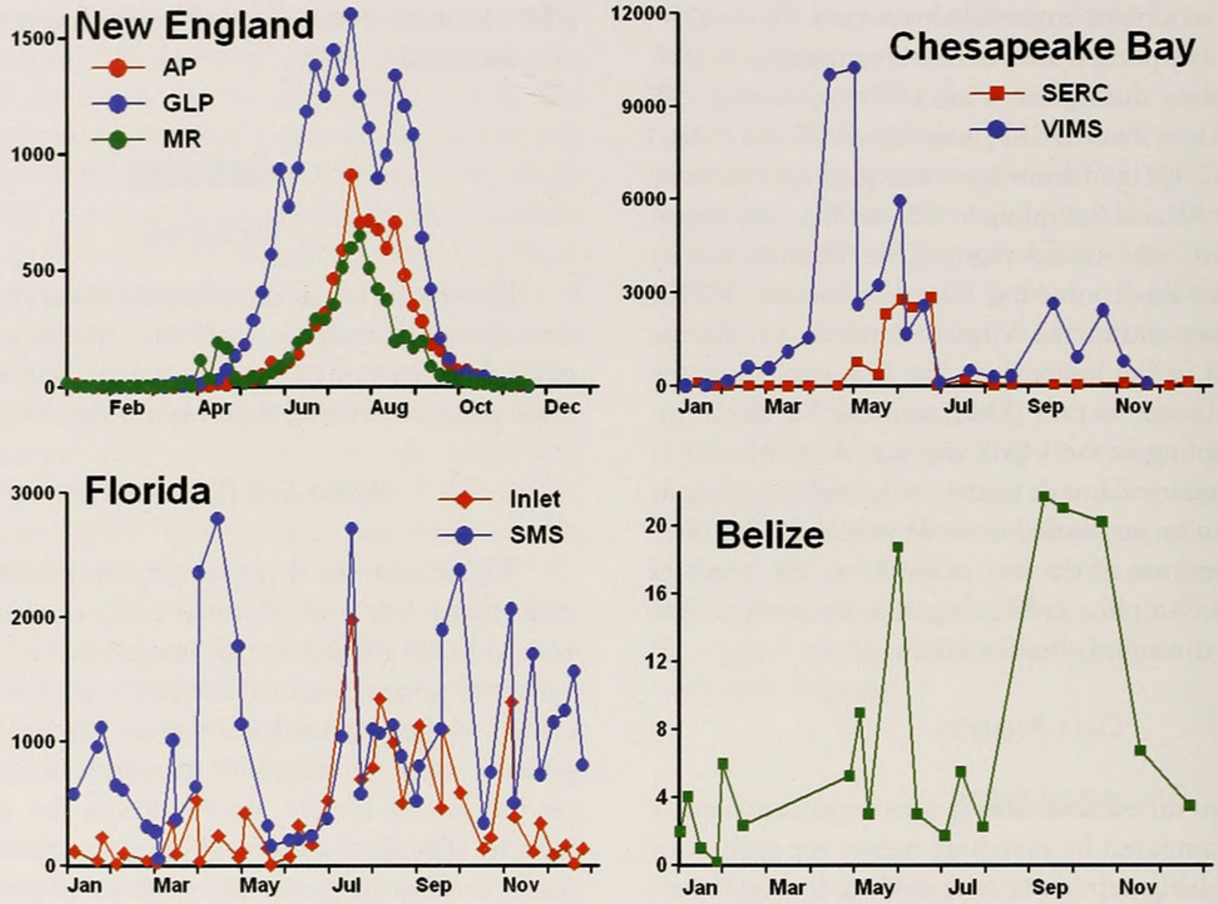

FIGURE 1. Comparison of temporal variation in mean recruitment in the four regions. Individual sites within regions are shown. Means were based on 1–6 years of data depending on region and the periods over which recruitment was measured (see Methods). Sampling sites are as follows: New England: AP = Avery Point, GLP = Groton Long Point, MR = Mystic River; Chesapeake Bay: SERC = Smithsonian Environmental Research Center, VIMS = Virginia Institute of Marine Science; Florida: Inlet = Ft. Pierce Inlet, SMS = Smithsonian Marine Station; Belize: Carrie Bow Cay.

(Table 1). Native species recruitment at the three sites showed the same pattern while the recruitment of invasive species was not significantly different among the sites (Table 2).

A similar analysis of the two CB sites for 2004 through 2006 found that total recruitment at the VIMS site was significantly greater than at the SERC site (Table 1). Recruitment at both sites was dominated by native barnacles, and invasive species recruitment was very low. Nevertheless both native and invasive species exhibited the same pattern as total recruitment (Table 2). Although experiencing similar variability in temperature, these two sites differ greatly in their salinity regimes. The SERC site is in the upper, low-salinity region of CB whereas the VIMS site is in the lower CB with higher salinities. In general fewer species recruit at the SERC site, and barnacle recruitment is much less.

Similarly, the two IRL sites differed significantly (2004–2006) in total recruitment, with SMS greater than Inlet (Table 1). Native and invasive species exhibited the same pattern (Table 2). Although there was little difference between the sites in temperature and salinity, they did differ in dominant species, which resulted in strong differences in total recruitment. Barnacle recruitment (six different species) was consistently much higher at the SMS site and this contributed greatly to the overall site differences. Most species of bryozoans as well as spirorbid worms had higher recruitment at the Inlet site. Figure 2 illustrates these differences.

The nonparametric paired analyses of the data from all three regions were almost identical to those above. The only difference was that in LIS invasive species recruitment was significantly greater at GLP than at either AP or MR.

Regional Patterns

The regional differences in temporal and spatial patterns in recruitment can be seen in Figure 1. In LIS the strong

TABLE 1. Results of paired analysis of mean recruitment between each pair of sites. Recruitment data were paired by sampling time. Mean values are for 2-week sampling periods and vary based on the number of sampling dates in common between any two pairs of sites (*df* = degrees of freedom;). Significant probabilities (Prob) are in **bold**.

			Total Annual Recruitment				
Site 1 [a]	Site 2 [a]	*df*	Mean 1	Mean 2	*t*-ratio	Prob > |*t*|	One-sided
Avery Point	Mystic River	229	474.5	299.2	6.39	**< 0.0001**	**< 0.0001**
	Groton LP	252	446.6	1000.4	8.60	**< 0.0001**	**< 0.0001**
	SERC	21	208.4	550.8	1.44	0.16	0.08
	VIMS	21	251.3	2206.2	2.99	**0.007**	**0.004**
	SMS	38	638.2	1010.0	2.22	**0.03**	**0.02**
	Inlet	36	607.5	607.5	1.37	0.17	0.09
Mystic River	Groton LP	234	296.7	996.8	9.63	**< 0.0001**	**< 0.0001**
	SERC	23	152.3	506.2	1.65	0.11	0.06
	VIMS	23	184.1	2097.8	3.22	**0.004**	**0.002**
	SMS	39	425.4	1068.1	4.15	**0.0002**	**0.0001**
	Inlet	38	451.2	459.9	0.09	0.93	0.46
Groton LP	SERC	21	698.5	550.8	0.52	0.61	0.31
	VIMS	21	761.3	2275.1	2.11	**0.05**	**0.02**
	SMS	39	1288.4	1050.5	0.91	0.36	0.18
	Inlet	37	1192.5	471.3	3.60	**0.0009**	**0.0005**
SERC	VIMS	17	381.6	1519.7	2.11	**0.05**	**0.03**
	SMS	10	341.6	685.3	1.18	0.26	0.13
	Inlet	10	341.6	242.1	0.42	0.68	0.34
VIMS	SMS	15	2694.9	903.9	2.38	**0.03**	**0.02**
	Inlet	15	2694.9	169.6	3.01	**0.009**	**0.004**
SMS	Inlet	71	1045.5	399.6	7.20	**< 0.0001**	**< 0.0001**

[a] Groton LP = Groton Long Point (GLP); SERC = Smithsonian Environmental Research Center; VIMS = Virginia Institute of Marine Science; SMS = Smithsonian Marine Station.

seasonality produces a relatively normal distribution in recruitment centered on the summer months of peak temperatures. Peak periods are relatively broad, with 1,000 to 2,000 recruits per panel per week. This overall pattern reflects the concentration of recruitment by most species in the summer period. Recruitment in CB is also seasonal but generally dominated by a few species, with sharp peaks in recruitment of 3,000 to 10,000 individuals per panel. The pattern in IRL is more diffuse with recruitment occurring throughout the year and several sharp peaks of 2,000 to 3,000 recruits per panel (barnacles) over a background of continuous recruitment. Individual species do have peaks in recruitment but they do not occur at the same time as in the northern regions. Thus, some species recruit in the winter and others in the summer, and this difference is reflected in the continuous total recruitment throughout the year. Finally, recruitment at the BEL site was extremely low, despite the much greater species diversity in the region.

Given these patterns, we examined whether total annual recruitment was influenced by the regional differences in variability and peak abundances. Figure 3 shows the total mean annual recruitment for each of the sites; no general pattern is discernible from these data. Except for BEL, within-region differences in total annual recruitment are as great as, if not greater than, differences among regions. Figure 3 also shows the dominance of barnacle recruitment in both the low-diversity CB and high-diversity IRL regions, whereas bryozoans and ascidians dominate recruitment in LIS. Interregional differences in total recruitment, regardless of strong differences in temporal patterns, exhibited no pattern that could be associated with diversity or latitude.

Results from the paired analyses did show some regional differences (Tables 1, 2; see Figure 3). For total recruitment the VIMS site in CB had significantly greater recruitment than all other sites. The GLP in LIS and SMS in IRL were significantly greater than the Inlet IRL, SERC CB, and AP LIS

TABLE 2. Results of paired analysis of mean invasive and native recruitment between each pair of sites. Recruitment data were paired by sampling time. Mean values are for 2-week sampling periods and vary based on the number of sampling dates in common between any two pairs of sites. Significant probabilities (Prob) are in **bold**.

			Invasive					Native				
Site 1 [a]	Site 2 [a]	*df*	Mean 1	Mean 2	*t*-ratio	Prob > |*t*|	One-sided	Mean 1	Mean 2	*t*-ratio	Prob > |*t*|	One-sided
Avery Point	Mystic River	229	144.9	144.9	0.00	0.99	0.50	329.6	154.3	6.69	< 0.0001	< 0.0001
	Groton LP	252	133.7	145.9	0.67	0.50	0.25	312.9	854.5	8.91	< 0.0001	< 0.0001
	SERC	21	66.6	1.3	2.18	**0.04**	**0.02**	141.8	549.5	1.81	0.08	**0.04**
	VIMS	21	95.8	18.8	1.94	0.07	**0.03**	155.6	2187.4	3.14	**0.005**	**0.003**
	SMS	38	218.9	345.5	1.23	0.22	0.11	409.0	666.6	1.84	0.07	**0.04**
	Inlet	36	203.2	191.0	0.39	0.70	0.35	381.3	270.6	1.46	0.15	0.08
Mystic River	Groton LP	234	143.3	149.3	0.31	0.75	0.38	153.4	847.5	9.87	< 0.0001	< 0.0001
	SERC	23	35.8	1.2	2.27	**0.03**	**0.02**	116.4	505.0	1.86	0.08	**0.04**
	VIMS	23	28.9	24.0	0.60	0.55	0.28	155.1	2073.8	3.24	**0.003**	**0.002**
	SMS	39	199.9	355.9	1.85	0.07	**0.04**	225.4	712.3	4.37	**0.0001**	**<0.0001**
	Inlet	38	200.4	186.1	0.21	0.83	0.42	250.8	273.8	0.37	0.71	0.36
Groton LP	SERC	21	163.7	1.3	2.31	**0.03**	**0.02**	534.8	549.5	0.05	0.96	0.48
	VIMS	21	220.7	18.8	2.47	**0.02**	**0.01**	540.7	2256.3	2.47	**0.02**	**0.01**
	SMS	39	218.9	126.6	2.01	**0.05**	**0.03**	1069.5	705.0	1.50	0.14	0.07
	Inlet	37	203.2	−12.2	0.30	0.77	0.38	989.3	280.3	3.55	**0.001**	**0.0005**
SERC	VIMS	17	1.2	25.6	2.11	**0.05**	**0.02**	380.3	1494.2	2.05	0.06	0.03
	SMS	10	0.4	173.1	3.11	**0.01**	**0.006**	341.2	512.2	0.63	0.54	0.27
	Inlet	10	0.4	48.7	1.95	0.08	**0.04**	341.2	193.4	0.61	0.56	0.28
VIMS	SMS	15	11.0	239.4	3.23	**0.006**	**0.003**	2683.9	664.5	2.78	**0.01**	**0.007**
	Inlet	15	11.0	26.6	2.38	**0.03**	**0.02**	2683.9	143.0	3.02	**0.009**	**0.004**
SMS	Inlet	71	374.8	138.7	5.11	< 0.0001	< 0.0001	670.7	260.9	5.96	< 0.0001	< 0.0001

[a] R. = River; Inlet = Ft. Pierce Inlet.

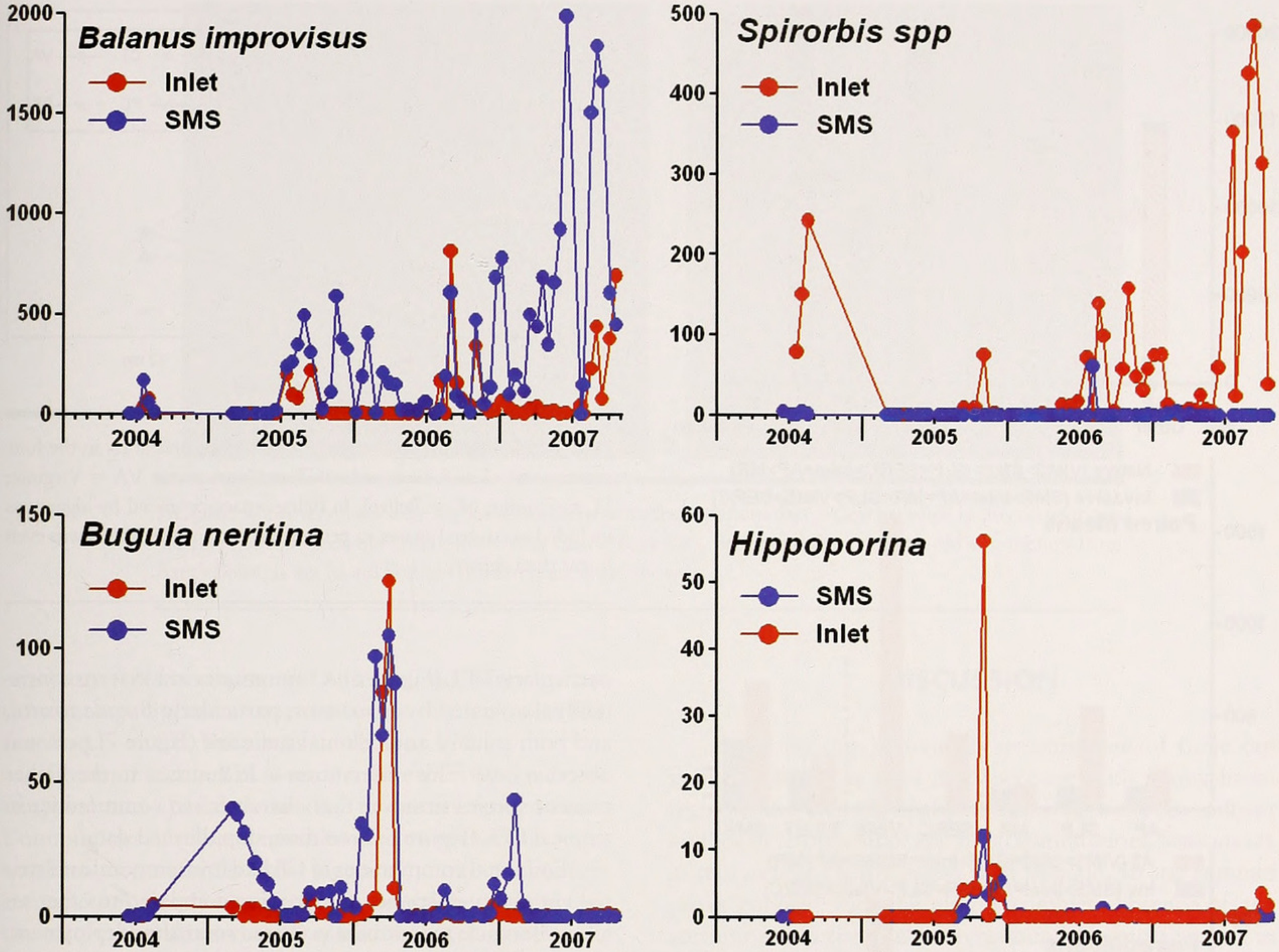

FIGURE 2. Comparison of recruitment at the two sites in Indian River Lagoon, Florida, for the barnacle *Balanus improvisus*, spirorbid polychaetes (*Spirorbis* spp.), arborescent bryozoan *Bugula neritina*, and encrusting bryozoan *Hipporina* sp.

sites, and all were greater than the MR LIS site. Recruitment of native species exhibited similar interregional patterns. However, for invasive species, recruitment was significantly higher in IRL than CB, with the LIS sites intermediate.

Community Development

Spatial and Temporal Variability

The speed of community development varied dramatically with latitude. The primary limiting resource, space, was quickly occupied in the temperate and subtropical regions by three months, compared to the tropical communities, which took close to a year to attain comparable spatial coverage (Figure 4). In the northernmost region, LIS, growth rates were particularly high, and at one site (AP) panels were completely covered after only one month, which is a striking comparison to comparably aged communities in BEL (Figure 5). These productive communities in AP were primarily composed of *Diplosoma listerianum*, an invasive colonial tunicate, and *Mogula manhattensis*, a solitary tunicate. These animals quickly became too heavy to remain attached to the panel and sloughed off, providing another flush of open space to recruiting species. This punctuated seasonal pulse of productivity of *Diplosoma* and *Mogula* did not occur at the other two sites in LIS, but growth rates remained high throughout the region.

Overall, communities in LIS experienced less temporal turnover in species composition than more southerly sites,

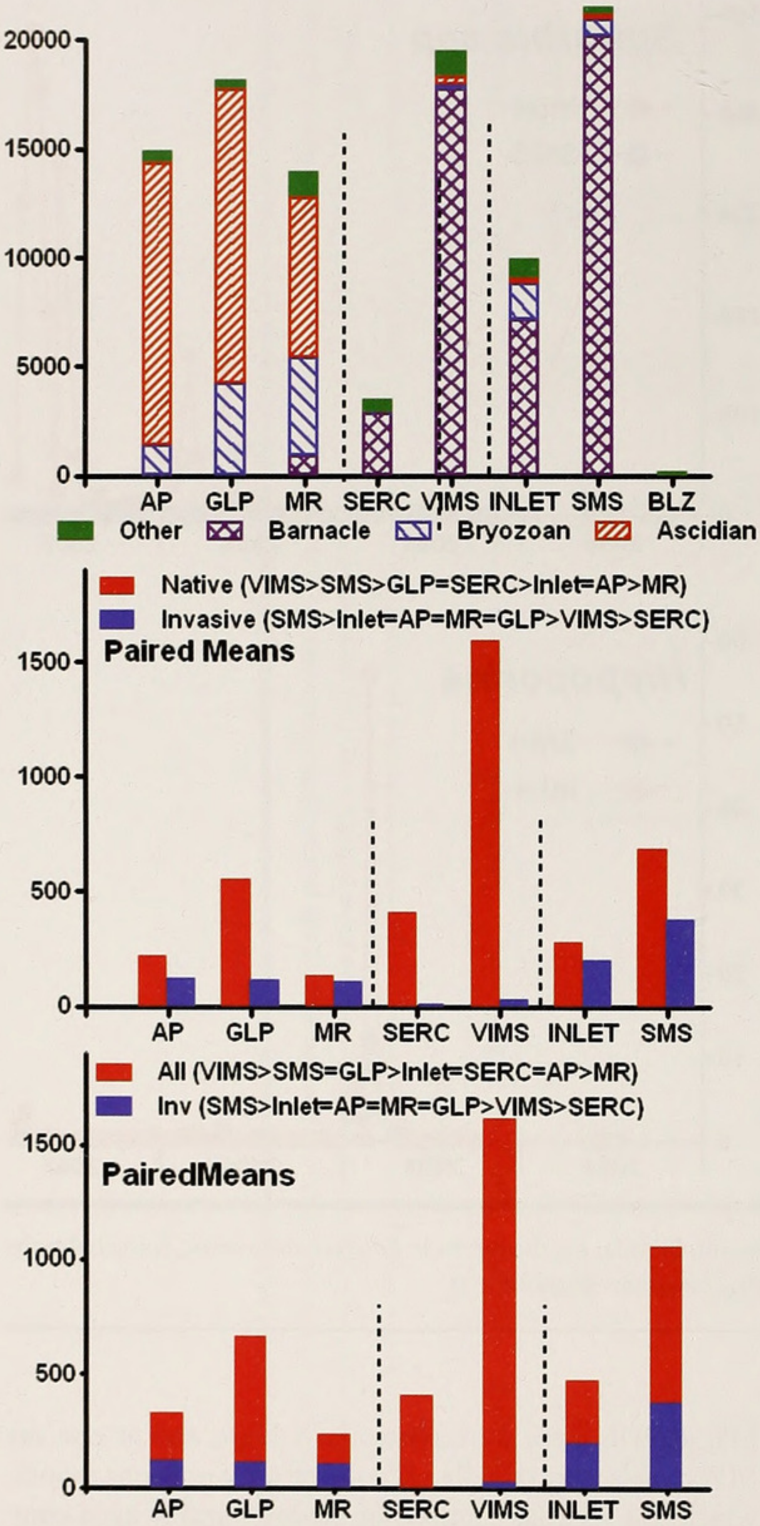

FIGURE 3. Comparison of recruitment among regions. Top: Total annual recruitment at each of the sites within regions. The contributions in each region of major taxonomic groups are represented by colored shading and/or scoring within the histogram bars. Middle: Mean recruitment of invasive (blue) and native (red) species by sites within region; significant differences are based on paired analyses (see Table 2). Bottom: Total mean recruitment by site showing the contribution of invasive (Inv) and native species. Dashed lines separate regions in all graphs.

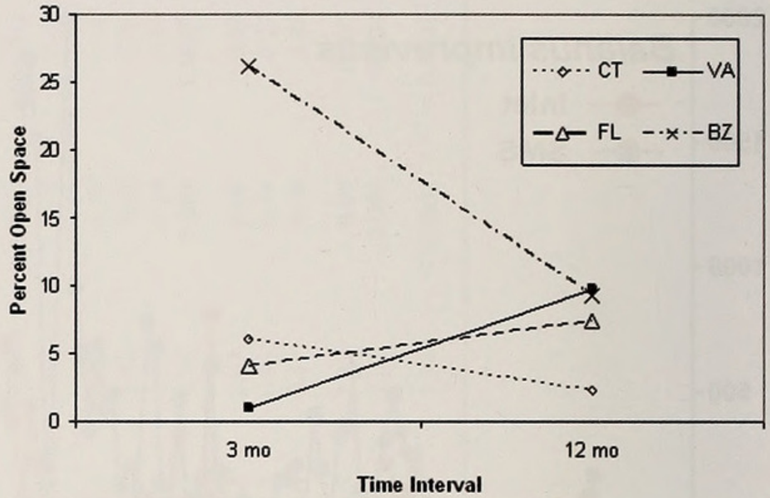

FIGURE 4. Total percent cover of open space on panels in the four regions after 3 and 12 months (CT = Connecticut; VA = Virginia; FL = Florida; BZ = Belize). In Belize, space occupied by algae was included as covered space, so percent cover of invertebrates was even lower than shown.

particularly BEL (Figure 6). Communities in LIS were consistently dominated by bryozoans, particularly *Bugula turrita*, and both solitary and colonial tunicates (Figure 7; personal observations). This observation is in contrast to the higher rates of species turnover that characterized communities in tropical BEL (Figure 6; Freestone, unpublished data).

Epifaunal communities in CB had low temporal and spatial variability in species composition compared to other regions. Barnacle recruitment occurred soon after deployment, in July 2006. After the first month, all panels had 99% to 100% cover (see Figure 4) and were almost completely covered with barnacles, with few other coexisting species. After three months, community structure still closely resembled the one-month communities; however, barnacles began to die and other species, such as *Mogula*, various hydroids, and sabellid polychaete worms recruited (see Figure 7). After one year, the primary layer of barnacles was less visible, having been covered with a thick layer of sediment tubes, mostly from amphipods and worms. Anemones were also common throughout. Panels deployed at the three sites were also very similar. Porifera were least common in CB when compared with other regions throughout the experiment.

Overall, communities in IRL retained almost complete phyla representation through time (Figure 7). All focal phyla were found on all panels in IRL after three months, and only Porifera had a very modest decline by one year. Species in these communities coexisted at very small spatial scales, with the result that IRL had the most diverse invertebrate assemblages at the panel scale after

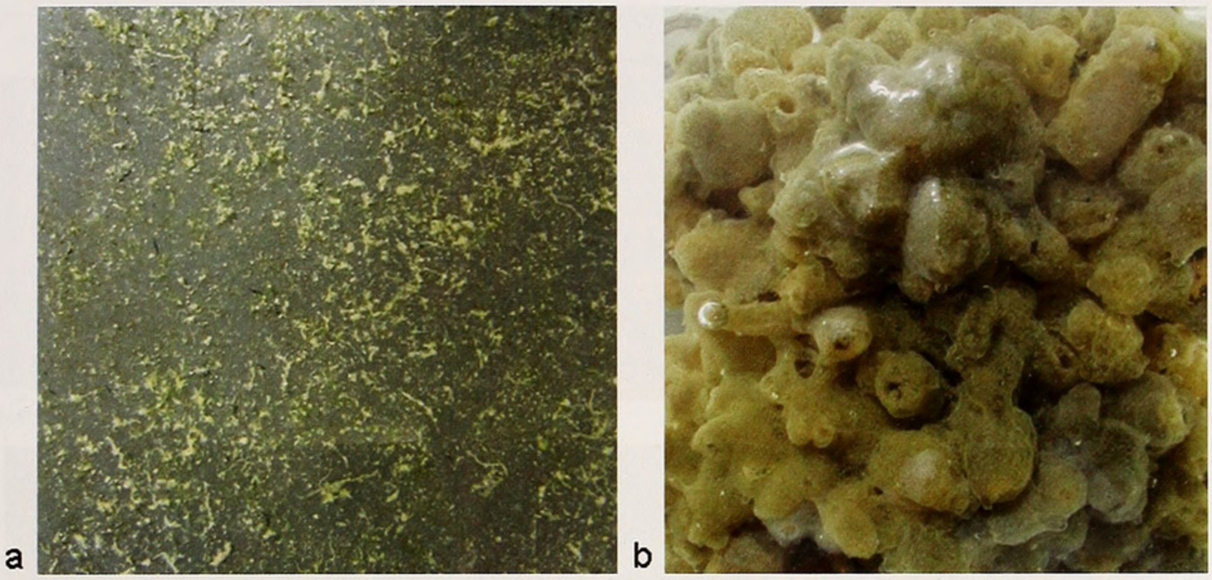

FIGURE 5. Growth rates were higher at northern latitudes, a pattern that is clearly visible in this comparison between (a) a 3-week-old community from Carrie Bow Cay, Belize and (b) a 4-week-old community from Avery Point, Long Island Sound (100-cm^2 panels are shown).

one year (Freestone, personal observation). More species turnover was apparent over the course of the year at IRL than in LIS or CB, but not as much as at BEL.

Communities in BEL were characterized by significant temporal and spatial variability in species composition. Communities developed much more slowly than did more northern communities (see Figure 4), and community composition clearly changed with time. These communities also varied at very small spatial scales, as panels that were deployed within a meter of each other harbored very distinct community assemblages with differing amounts of open space. In contrast to more northern communities, BEL communities were more consistently dominated by polychaetes, Cnidaria (sea anemones, hydroids, coral), and Porifera. After one year, Porifera clearly dominated the panels (Freestone, personal observation). Compared to the bushy and common bryozoan colonies that occur in LIS, bryozoans in BEL were generally very small, delicate, and rare.

Similar to the recruitment study, the largest difference in taxonomic composition of developing communities across all regions was the presence of barnacles. Barnacles were common in temperate and subtropical zones but were completely absent in BEL at 3 months. After 12 months, their dominance was still seen in CB and IRL, but barnacles were less common in LIS. However, only one barnacle on one panel was found in BEL. Although barnacles in temperate and subtropical zones are both intertidal and subtidal, barnacles are almost exclusively intertidal in BEL.

DISCUSSION

Based on our preliminary examination of these ongoing studies, it is clear that there are both strong intraregional and interregional patterns in both the recruitment and the development of epifaunal communities. Seasonality in recruitment clearly varies with latitude. Strong summer peaks coupled with the almost complete absence of any recruitment in the winter were found for most species in the temperate regions (LIS and CB). The strong dominance of barnacles in CB resulted in a bimodal pattern generally associated with the spring–fall plankton blooms upon which barnacle larvae feed. In IRL there was also a strong temporal variability in recruitment but neither a consistent seasonal pattern nor any similarity among species. Finally, in BEL recruitment was too low to discern any pattern. There were also fairly distinct patterns among sites within regions. In the temperate regions, sites showed consistent differences in numbers of recruits but little difference in the species recruiting at any one time or in the relative abundances of these species. In the subtropical IRL, there were greater differences between the two sites in the composition of the fauna recruiting at any one time. Based on the low recruitment and greater community variability among sites in BEL, it would appear that site differences in recruitment in the tropics are likely to be even greater.

The interregional variation in recruitment for native species was influenced by the variation in barnacle dominance, with the CB and IRL sites showing significantly


a
b

FIGURE 6. Time-series comparison of community development in (a) Long Island Sound after 1, 3, and 12 months and (b) Belize after 3, 6, 9, 12, and 20 months (100-cm^2 panels are shown). Greater species turnover occurred in Belize than in Long Island Sound.

higher recruitment than the LIS sites. However, the recruitment of invasive species varied in a similar manner to patterns described by Sax (2001). The tropical BEL site had little overall recruitment and no recruitment of invasive species, the subtropical IRL sites had the highest recruitment of invasive species, and the higher latitude temperate sites had lower recruitment of invasive species. The combined patterns of native and invasive species resulted in invasive species representing a much higher proportion of overall recruitment in IRL than in all other regions. In the low-diversity estuarine CB, invasive species contributed a very small proportion of total recruitment (see Figure 3).

Finally, even with the strong differences in recruitment reflected in the paired analyses, similarities in total annual recruitment were found between some sites in the three northern regions. This result suggests that the cumulative recruitment in more seasonal regions with strong peaks and in regions with little or no seasonality in recruitment can be similar.

In BEL, the epifaunal communities were quite spatially variable in community composition even at the smallest scale of panels at each site. This pattern is consistent with the spatial heterogeneity hypothesis for the latitudinal diversity gradient, which states that abiotic variability in tropical systems allows more species to coexist (see Davidowitz and

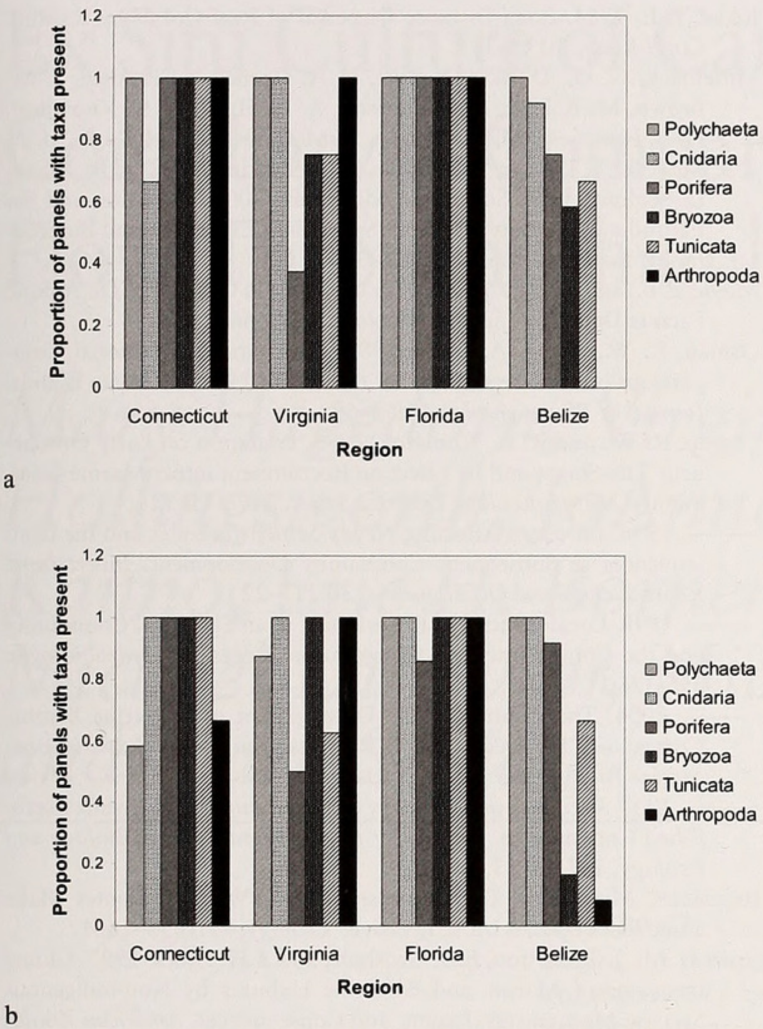

FIGURE 7. Proportion of panels that had listed taxa present at (a) 3 months and (b) 12 months by region.

Rosenzweig, 1998). Interestingly, in contrast to the abiotic variation that characterizes other systems, such as terrestrial plant–soil relationships, the settlement panels were identical in size and material, so substrate composition was not a source of variability. While it is possible that differences in subtle small-scale variation in currents or eddies could drive community variability, a more parsimonious explanation is that propagule supply is very low and sporadic. Community developmental trajectories may therefore be more a result of random recruitment from a limited larval pool rather than spatial variability in abiotic conditions.

Another possible explanation that has strong theoretical underpinnings is that biotic interactions, such as predation, are also strong and spatially variable in the tropics (Schemske, 2002). Although this hypothesis has not been empirically tested in a comprehensive experiment, the idea that biotic interactions are stronger in the tropics has received much theoretical attention (Mittelbach et al., 2007). Visual observations of the communities in BEL support this hypothesis. For example, we commonly observed grazing or saw indirect evidence of grazing (i.e., abrasions) on the panels from indiscriminate consumers, including gastropods, crabs, and fish. While predation undoubtedly occurs in temperate environments (Osman and Whitlatch, 1995, 1998, 2004), overall interaction strengths may be weaker and more spatially predictable in northern latitudes. Sporadic and low larval recruitment, spatially variable predation, and low growth rates in areas of low productivity are all potential contributors to the spatial and temporal variability of tropical epifaunal community development.

Our main goal has been to document and contrast recruitment and community development patterns among regions along a latitudinal gradient to ascertain potential differences in the ability of nonnative species to invade these systems. Except for our sites in BEL, all the regions we have been studying have nonnative species present, and such species are often dominant within these epifaunal communities. In LIS we have found that early recruitment of invasive ascidians in years with warm winters (Stachowicz et al., 2002a) and their dominance at harbor sites without native predators that prey on their recruits (Osman and Whitlatch, 1995, 1998, 2004) have contributed to their successful invasion. The strong and consistent timing of recruitment of native species certainly can create an opening for invaders that can recruit outside this window. In CB recruitment is even more constrained temporally with much higher numbers of recruits, again creating potential temporal windows for invasion. However, as our community development data have shown, the communities in both these temperate systems develop rapidly and thus quickly limit resources for new species. Studies in LIS (Stachowicz et al., 2002b) have shown that as community diversity within these systems increases, the communities become more resistant to invasions, mostly by increasing the likelihood of limiting open space.

In IRL, space was also rapidly occupied and the amount of open space remained low after three months. In addition, the diversity within this system is higher, and some species are recruiting at any time of the year. Based on the results of the LIS study (Stachowicz et al., 2002a) these factors should increase the resistance of this system to invaders. Although we have found several invasive species at our study sites, none of these species appears to be particularly abundant or dominant. Finally, in BEL we have observed much more diverse and spatially variable communities. Recruitment and the rates of community development are low, and this situation certainly allows spatial resource to be available for much longer periods of time, which should create a greater window for species invasion. However, the extremely high diversity of both epifaunal species and predators may inhibit invasion success. It is also likely that, given the spatial variability in communities, invaders will face completely different communities at each site as well as temporal variability in communities within sites. Although it is much too early in our studies to link latitudinal variation in recruitment or community development to invasion success, our preliminary results do suggest that there is a correlation between decreasing invasion success and increasing diversity, increasing community variability, and the reduction in recruitment windows in less seasonal environments, with species varying greatly in the timing of recruitment.

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