

Effects of small-scale disturbance on invasion success in marine communities

Safra Altman ^{*,1}, Robert B. Whitlatch

Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Rd, Avery Point, CT 06340, USA

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Abstract

Introductions of non-indigenous species have resulted in many ecological problems including the reduction of biodiversity, decline of commercially important species and alteration of ecosystems. The link between disturbance and invasion potential has rarely been studied in the marine environment where dominance hierarchies, dynamics of larval supply, and resource acquisition may differ greatly from terrestrial systems. In this study, hard substrate marine communities in Long Island Sound, USA were used to assess the effect of disturbance on resident species and recent invaders, ascidian growth form (i.e. colonial and solitary growth form), and the dominant species-specific responses within the community. Community age was an additional factor considered through manipulation of 5-wk old assemblages and 1-yr old assemblages. Disturbance treatments, exposing primary substrate, were characterized by frequency (single, biweekly, monthly) and magnitude (20%, 48%, 80%) of disturbance. In communities of different ages, disturbance frequency had a significant positive effect on space occupation of recent invaders and a significant negative effect on resident species. In the 5-wk community, magnitude of disturbance also had a significant effect. Disturbance also had a significant effect on ascidian growth form; colonial species occupied more primary space than controls in response to increased disturbance frequency and magnitude. In contrast, solitary species occupied significantly less space than controls. Species-specific responses were similar regardless of community age. The non-native colonial ascidian *Diplosoma listerianum* responded positively to increased disturbance frequency and magnitude, and occupied more primary space in treatments than in controls. The resident solitary ascidian *Molgula manhattensis* responded negatively to increased disturbance frequency and magnitude, and occupied less primary space in treatments than in controls. Small-scale biological disturbances, by creating space, may facilitate the success of invasive species and colonial organisms in the development of subtidal hard substrate communities. © 2006 Elsevier B.V. All rights reserved.

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1. Introduction

Although species range expansions and contractions are intrinsic ecological processes, there has been an increased rate of range expansion by nonindigenous species primarily due to human activities (Mooney and Drake, 1986; Carlton, 1989; Ruiz et al., 1997). Second to habitat loss, introduced species are thought to be among the most important causes for the decline of

* Corresponding author. Smithsonian Environmental Research Center, 647 Contees Wharf Rd, P.O. Box 28, Edgewater, MD 21037, USA. Tel.: +1 443 482 4251; fax: +1 443 482 2380.

E-mail address: altmans@si.edu (S. Altman).

¹ Current address: Program in Behavior Ecology Evolution and Systematics, University of Maryland, College Park, MD 20742 USA.

native species (Everett, 2000; Pimentel et al., 2000). The increased invasion rate has affected terrestrial, aquatic and marine systems promoting the potential for a global homogenization of species diversity (McKinney and Lockwood, 1999).

Coastal waters experience a heightened susceptibility to invasion and represent one of the most invaded systems on the planet as many bays, estuaries and near-shore waters are affected by stressors as a result of urbanization, exploitation of fisheries and shipping (Carlton and Geller, 1993; Carlton, 1989; Cohen and Carlton, 1998; Grosholz, 2002). Within a given region, estuarine invaders result in an increased variety of taxa and an increase in ecosystem impacts. The rate of range expansion for introduced coastal species appears to be more variable than that of terrestrial species and tends to show patterns of large range expansions over short time periods (Grosholz, 1996). This implies that introductions in coastal systems may have greater impacts on native communities than introductions in terrestrial systems.

Range expansions of invasive species may be affected by many factors including disturbance regimes within the invaded habitat. A number of classic studies have established the importance of natural disturbance and its effect on space allocation, recruitment, and subsequent interspecific competition and species composition in marine benthic communities (e.g., Dayton, 1971; Sousa, 1985; Connell and Keough, 1985; Sousa, 2001). Disturbance events typically lead to increased resources for potential colonizers. In hard substrate communities this is primarily in the form of increased available space for settlement and subsequent growth. While there is considerable variation in the frequency and magnitude of natural disturbance, small-scale events (e.g., 1–100 cm²) often occur more frequently than large-scale disturbances (e.g., 100 m² to km²; Connell and Keough, 1985; Sousa, 1985, 2001). Given sufficient variation in recruit densities, disturbances that are large in size are more likely to lead to changes in community assemblage and succession than small-scale disturbances (Petraitis and Latham, 1999). Although it is clear that disturbance severity, with cascading effects on spatial resources and competition, affects settlement and patterns and rates of succession (Underwood, 1998; Airolidi, 1998; Sousa, 2001), most studies have been restricted to examining the effects of complete removal of residents and have not looked at multiple levels of disturbance frequency or magnitude.

The question of how disturbance affects invasibility has been examined through theoretical and correlative terrestrial studies. While theory repeatedly predicts that increased disturbance should lead to increased invader success, results from empirical studies do not always

support this theory (Hobbs, 1989; DeFerrari and Naiman, 1994; Stachowicz et al., 1999; Seabloom et al., 2003; Gilbert and Lechowicz, 2005; Klein et al., 2005; Gross et al., 2005). The link between disturbance and invasion potential has rarely been studied in marine systems where dominance hierarchies, dynamics of larval supply, and resource acquisition may differ greatly from terrestrial systems (Sousa, 2001). While there is an abundance of evidence that disturbances can facilitate the invasion of non-native species in terrestrial and aquatic ecosystems (Sousa, 2001), only a few studies have focused on the influence of disturbance in promoting successful invasion in marine communities. After major storm-induced freshwater flow into San Francisco Bay in which native populations were reduced, Meng et al. (1994) and Nichols et al. (1999) found increased invasion rates of fish and non-native bivalves, respectively. In another study, fragmented eelgrass meadows were found to facilitate the growth of a non-indigenous mussel (Reusch and Williams, 1999), implying that disturbances resulting in fragmentation of eelgrass beds would increase the success of the invasive mussel. The majority of these studies focused on the effects of large-scale environmental disturbances and did not investigate the effect of small-scale disturbances on the susceptibility of communities to invasion.

Hard substrate assemblages provide an ideal system to study questions related to invasion dynamics because these communities can be manipulated over a range of different frequencies and magnitudes of disturbance. Highly localized, small-scale disturbances are typically driven by biological (e.g., predation by fish and crabs) processes, while low frequency, high magnitude disturbances are typically driven by physical (e.g., storms) processes (Hall et al., 1994, Sousa, 2001).

The present study focuses on the effect of disturbance on invasion success in shallow water fouling communities in eastern Long Island Sound, USA, an urbanized estuary invaded by a number of species over the past 150 years. In this study, we examined the effects of small-scale disturbance magnitude and frequency on the successful space occupation by members of the fouling assemblage. To determine whether invaders that are relatively new to the system respond to disturbance in a similar manner to resident species, we addressed the effect of disturbance on the resident species and recent invaders. Once settled, fouling organisms fall into two growth forms — colonial and solitary. The two forms often differ in life history characteristics and growth strategy and their capacity to respond to disturbance and occupy open space may also differ. To address these potential differences, we examined the effect of

Table 1
Summary of the dominant fouling species found in experimental assemblages at the Avery Point study site

Taxonomic group	Species	Status	Growth form	Date of first collection or identification	Reference
Asciacea	<i>Ciona intestinalis</i>	Resident	Solitary	1838	(Couthouy, 1838; Van Name, 1945)
Asciacea	<i>Molgula manhattensis</i>	Resident	Solitary	1843	(DeKay, 1843; Van Name, 1945)
Asciacea	<i>Botryllus schlosseri</i>	Resident	Colonial	1870, 1830	(Binney, 1870; Van Name, 1945)
Asciacea	<i>Styela clava</i>	Recent Invader	Solitary	1970's	(Steneck and Carlton, 2001)
Asciacea	<i>Asciidiella aspersa</i>	Recent Invader	Solitary	Mid-1980's	(Steneck and Carlton, 2001)
Asciacea	<i>Botrylloides violaceus</i>	Recent Invader	Colonial	Mid-1970's	(Steneck and Carlton, 2001; Saito et al., 1981)
Asciacea	<i>Diplosoma listerianum</i>	Recent Invader	Colonial	Late 1980's	(Steneck and Carlton, 2001)
Asciacea	<i>Didemnid sp.</i>	Recent Invader	Colonial	Early 2000's	S. Altman, personal observations
Ectoprocta (Bryozoan)	<i>Membranipora membranacea</i>	Recent Invader	Colonial	Early 1970's	(Steneck and Carlton, 2001)
Ectoprocta (Bryozoan)	<i>Bugula neritina</i>	Recent Invader	Colonial	1990's	(R.B. Whitlatch, unpublished data)
Ectoprocta (Bryozoan)	<i>Cryptosula pallasiana</i>	Resident	Colonial	At Least 1900	(Sumner et al., 1911a,b)
Hydrozoa	<i>Obelia sp.</i>	Resident	Colonial	1873	(Verrill and Smith, 1873; Sumner et al., 1911a,b)

disturbance on species growth forms by focusing on colonial and solitary ascidians, both predominant invaders in the system. We also examined the dominant species specific responses within the community to determine whether resulting trends were due to single species or species complexes. As different stages of community development may not respond to disturbance in the same manner, community age was an additional factor considered through manipulation of 5-wk old and 1-yr old assemblages of fouling species.

2. Materials and methods

2.1. Study location and organisms

This study was conducted in eastern Long Island Sound, USA. Experiments were deployed on a floating raft at Avery Point, CT and observations were made in the vicinity of this location. The shallow subtidal fouling community of Long Island Sound consists of a number of dominant sessile taxa including ascidians, bryozoans, mussels, hydroids, sea anemones, sponges, and barnacles (see Osman and Whitlatch, 1995a; Stachowicz et al., 2002a).

Most sessile inhabitants of the New England fouling community have unclear geographical origins and many of the dominant species are soft bodied and have a poor fossil record. Many of the ascidians, for example, have

been observed in the region for over one hundred years and are thus considered established members of the resident community. For the purpose of this study, these will be referred to as resident species (Table 1). Several non-native species have invaded coastal New England fouling communities within the last three decades. These organisms will be referred to as recent invaders (Table 1).

2.2. Disturbance and recruitment estimates

To estimate the amount of small-scale disturbance in several subtidal fouling assemblages, photographic surveys were performed at three southeastern Connecticut, USA sites: Avery Point (41°19'15" N, 72°02'40" W), Bushy Point Rock (41°18'93" N, 72°03'18" W), and Ford's Marina (41°19'45" N, 71°59'11" W). Both Avery Point and Ford's Marina are protected sites and small boulders, docks and pilings are the most common hard substrates. Bushy Point Rock is a large boulder and the site is more exposed than the others. Ten haphazardly placed photo-quadrats (100 cm² each) were taken of the hard substrate assemblages to estimate spatial variability of unoccupied space in each site. Photographs were taken of the undersides of docks, dock pilings and rocks and boulders at depths ranging from 1–3 m below low tide. Images were analyzed with NIH Image J 1.29 software to estimate percent unoccupied

Table 2

Average open space and open patch size in natural subtidal fouling communities at three study sites

Site	Mean open space (cm ²)	SE	Mean patch size (cm ²)	SE
Avery Point	7.12	1.64	0.57	0.07
Ford's Marina	9.57	2.87	2.84	0.85
Bushy Rock	26.79	8.67	5.26	2.02
All sites	14.73	3.46	2.28	0.59

space within a 100 cm² area and the size of open patches. Predator presence (e.g., fish, crabs, predaceous gastropods) was observed and noted during 30 min intervals at the three sites. Water visibility at the sites typically varied between 2–4 m.

Temporal patterns of recruit abundance may relate to the eventual success of adults in the community. To consider the role that recruitment may have in determining the outcome of the community disturbance experiments, recruitment estimates of fouling organisms were obtained by deploying four replicate 10×10 cm PVC panels on a weekly basis. Panels, deployed from a

floating raft, were positioned at a depth of 0.5–1 m below the water surface and approximately 2 m above the bottom. All panels were oriented horizontally facing downward to minimize natural biological (e.g., predation, competition with macroalgae) and physical (e.g., sedimentation) disturbance. Panels were retrieved and replaced with new panels on a weekly basis and thus underwent consecutive, week-long deployments. Panels were examined under a dissecting microscope to enumerate and identify all organisms attached to the substrates to species.

2.3. Community experiments

This set of experiments consisted of manipulating disturbance in fouling communities that were grown on 10×10 cm PVC panels. Panels were deployed from a floating raft, in a manner similar to the recruitment panels, at the Avery Point site and were arranged haphazardly so that adjacent panels were composed of different disturbance treatments. All panels were initially deployed on 15 June 2001 and fouling communities were allowed to develop for 5 weeks prior to

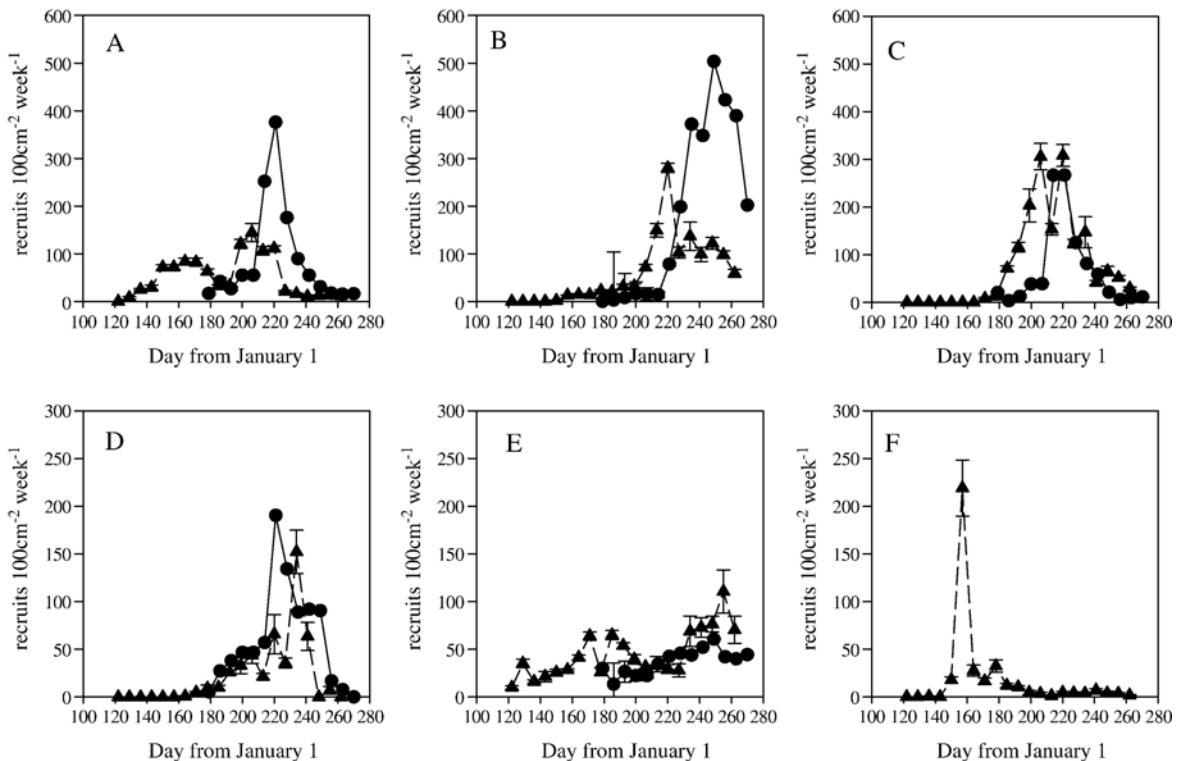


Fig. 1. Seasonal variation in the distribution of recruitment patterns for the dominant fouling species at the study site in 2001 (●) and 2002 (▲). A = *Botryllus schlosseri*, B = *Diplosoma listerianum*, C = *Bugula turrita*, D = *Molgula manhattensis*, E = *Cryptosula pallasiana* and F = *Sponge* sp. Error bars = ±1 SE of the mean. Note the difference in scale of the y-axis between rows. Experiments were conducted between days 201–266 in 2001 and between days 190–239 in 2002.

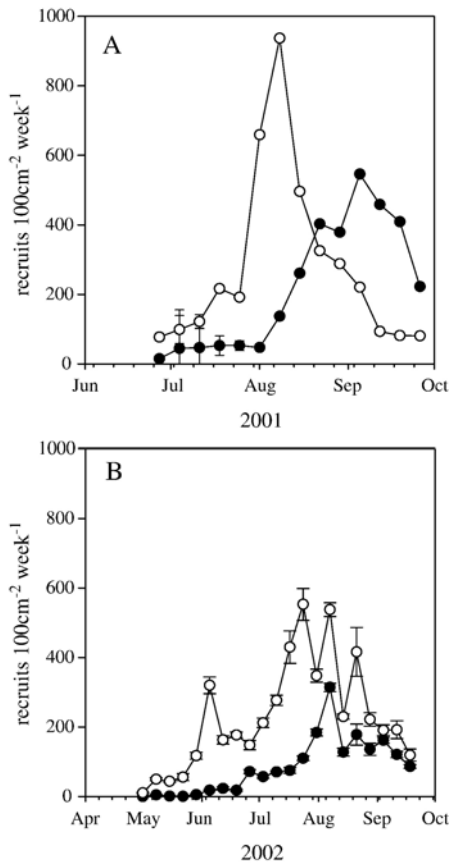


Fig. 2. Resident (open circle) and recent invader (closed circle) fouling species recruitment at the Avery Point study site, for 2001(A) and 2002 (B). Mean values \pm 1 SE.

manipulation. At this time $99\% \pm 0.8$ (average \pm 1 SE) of the available panel surface was covered. These panels will be referred to as 5-wk community panels. When the experiment began, the panels were dominated (>90% cover) by colonial and solitary ascidians. Specifically, *Botryllus schlosseri* (Binney, 1870), *Botrylloides violaceus* (Oka, 1927) and *Molgula manhattensis* (DeKay, 1843) occupied the majority of the primary substrate inhabiting $37\% \pm 4.05$, $27\% \pm 8.42$ and $27\% \pm 5.03$ (average \pm 1 SE) of the panel surface, respectively. All treatments began on 20 July 2001. We investigated three disturbance frequencies: a single disturbance (termed S), and biweekly and monthly disturbance (termed B, M, respectively). Panels in the S treatment were manipulated once, at the beginning of the experiment (20 July 2001). In addition to disturbance frequency, we manipulated the magnitude of disturbance by removing organisms from 20%, 48% or 80% of the panel surface. Thus, the experiment consisted of nine different disturbance treatments and one,

undisturbed control treatment. There were four replicate panels within each disturbance treatment.

Disturbances were created by randomly removing all organisms from sub-sections of the panels at different amounts and frequencies. Each panel was divided into a grid of 25 squares of equal area (2 cm \times 2 cm). Panels undergoing the 20% disturbance treatment had 4 randomly selected squares cleared, panels undergoing 48% disturbance had 12 squares cleared, and panels undergoing 80% disturbance had 20 squares cleared.

All panels were censused biweekly during the peak of the recruitment season (20 July 2001–24 September 2001). For each panel, we used a fifty point grid and identified all organisms occupying primary substrate (panel surface) at each point. In addition, we scanned all panels for species not identified during the point count. The total number of species found on the panel was used to estimate species richness. All panels were returned to the floating dock between sampling periods.

Some of the panels used in the 5-wk community experiment were used to determine the influence of disturbance magnitude and frequency on community age. These panels were deployed at the study site after completion of the initial experiment for approximately one year. In June 2002, a subset of 16 randomly selected panels was censused, as described above, to confirm that the over-wintered species assemblages were similar in species composition and percent cover. The year-old assemblages were dominated by the solitary ascidians *Ciona intestinalis* (Couthouy, 1838), *Styela clava* (Herdman, 1881), *Asciidiella aspersa* (Müller, 1776) and *M. manhattensis*. These four species accounted for $22.5\% \pm 11.2$, $18.5\% \pm 3.1$, $12\% \pm 4.2$, and $12\% \pm 1.6$ (average \pm 1 SE) of the primary substrate, respectively. We randomly reassigned panels to treatments consisting of the same disturbance frequency as the 5-wk community experiment (single, biweekly, monthly). Magnitude of disturbance was reduced to two treatments of 20% and 80% because the 48% treatment showed intermediate results in the 5-wk community experiment. We analyzed 1-yr community panels in the same manner described for the first experiment and ran the experiment from 9 July 2002–27 August 2002.

2.4. Data analysis

To determine whether there were significant differences in open space in natural communities among the three sites, a one-way analysis of variance was run using total open space as a fixed effect. The same procedure was used to examine differences in the size of open patches, with patch size as a fixed effect.

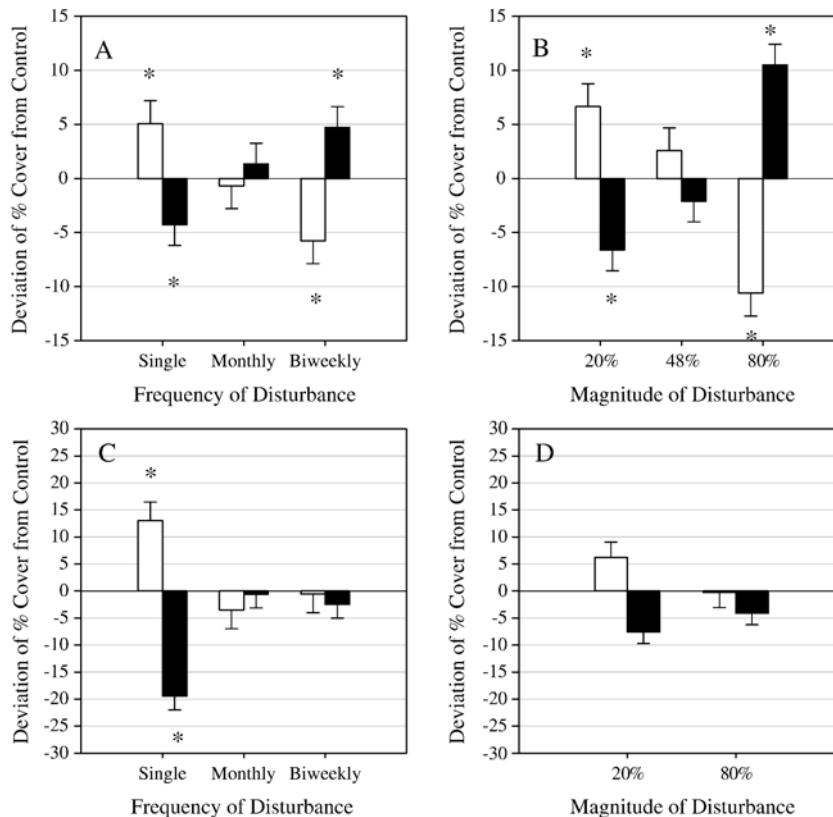


Fig. 3. Primary space occupation of invaders (black) and residents (white) plotted as deviation of % cover from control communities. (A–B) 5-wk community, (C–D) 1-yr community. Error bars = ± 1 SE of mean, * = significant difference from control ($p < 0.05$).

In experimental communities, percent cover of 1) invaders and natives, 2) colonial and solitary ascidians, and 3) individual space holders, was determined from biweekly census data for primary space. In order to detect deviations from the undisturbed community, an average control value was determined for each variable of interest (% cover of residents, % cover of invaders, etc.) for each sampling date. These control values were subtracted from treatment values to create a standardized data set for each variable. The degree of open space found in the control panels ranged from $1.3\% \pm 0.95$ (average ± 1 SE) to $16.0\% \pm 1.4$ in the 5-wk community and $6.0\% \pm 4.1$ to $14.5\% \pm 2.9$ in the 1-yr community. Three-way, repeated measures analysis of variance was run on the standardized data sets using the SAS 8e statistical software package (SAS Institute, Cary, North Carolina, USA). Disturbance frequency (S, M, B) and magnitude (20%, 48%, 80%) were treated as fixed effects while sampling date (time) was considered a repeated effect. In cases in which standardized data sets did not fit the assumptions of the model (e.g., Zar, 1997), they were arcsine or arcsine square root transformed. Once transformed, the model assumptions were met and

repeated measures analysis of variance was used. Post hoc tests consisted of Tukey pairwise comparisons. This approach allowed us to examine both the magnitude and direction of deviation from undisturbed control communities for the different variables of interest.

3. Results

3.1. Small-scale disturbance estimates

The range of open, unoccupied space observed in communities growing on natural substrates at the three sampling sites varied from 0–91% per 100 cm². The total open space per quadrat varied between sites: $7.12\% \pm 1.64$ (average ± 1 SE) at the Avery Point site, $9.57\% \pm 2.87$ at Ford's Marina and $26.79\% \pm 8.67$ at Bushy Rock (Table 2). There was significant variation between the amount of open space present at the Bushy Rock site and the two other sites (ANOVA, $F=3.31$, $p=0.05$; Bushy Rock, $t=4.56$, $p<0.001$). Across all sites, the average available space observed was $14.73\% \pm 3.36$. Although the amount of available open space ranged from very low to very high levels, the average available open space was

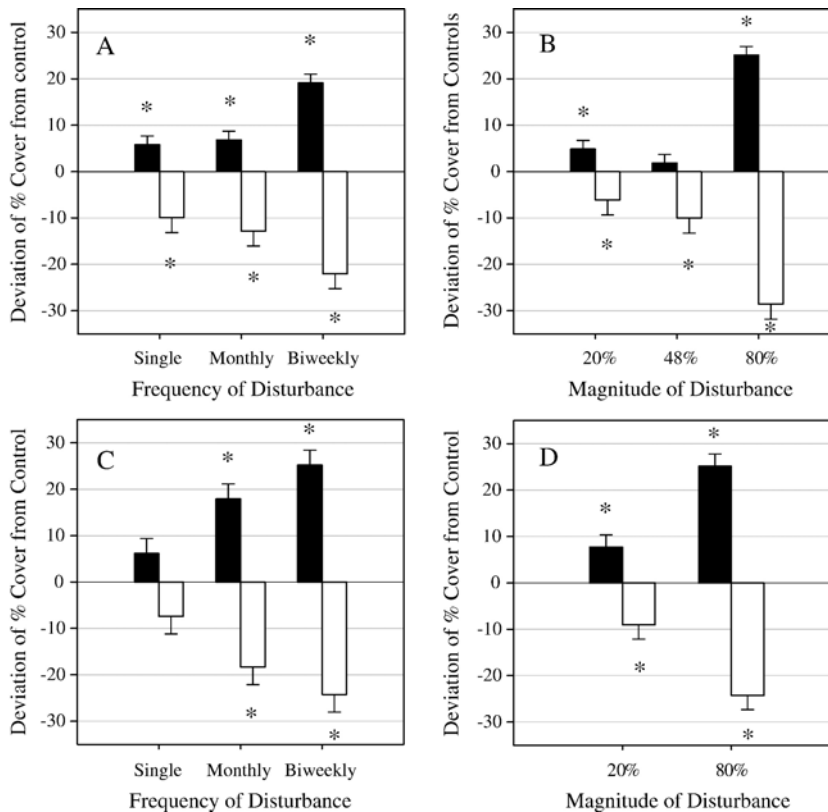


Fig. 4. Primary space occupation of colonial (black) and solitary (white) ascidians plotted as deviation of % cover from control communities. (A–B) 5-wk community, (C–D) 1-yr community. Error bars = ± 1 SE of mean. * = significant difference from control ($p < 0.05$).

moderate at all sites indicating that low magnitude disturbance events were most likely driven by biological processes (e.g., predation). The size of open patches also varied between sites (Table 2). The open patches at the Bushy Rock site were significantly larger than the open patches at Avery Point and Ford's (ANOVA, $F = 6.15$, $p = 0.003$; Bushy Rock, $t = 4.79$, $p < 0.001$, Table 2).

Potential predators observed at the three study sites included crabs (*Carcinus maenas* (L.), *Hemigrapsus sanguineus* (de Haan, 1835), *Libinia emarginata* (L.)), fish (e.g., *Tautoglabrus adspersus* (Walbaum, 1792), silversides and other small fish), carnivorous gastropods (*Mitrella lunata* (Say, 1826) and *Anachis lafresnayi* (Fisher and Bernardi, 1856)) and nudibranchs. At the Avery Point site, where community experiments were conducted, gastropod and nudibranch densities tended to be very low, but crabs and fish were more common than the other two sites.

3.2. Recruitment estimates

During summer 2001, the five most abundant species recruiting at the Avery Point site were the colonial ascidians

B. schlosseri and *Diplosoma listerianum* (Milne-Edwards, 1841), the solitary ascidian *M. manhattensis*, the tufted bryozoan *Bugula turrita* (Desor, 1848) and the encrusting bryozoan *Cryptosula pallasiana* (Moll, 1803). Combined, these species accounted for 62–94% of the total recruitment recorded from June through October 2001. All of these species had recruitment levels of at least 50 individuals $100 \text{ cm}^{-2} \text{ week}^{-1}$ at some point between June and October 2001, although the duration and intensity of recruitment varied among species (Fig. 1).

The same five species dominated recruitment during summer 2002. However, peak recruitment densities of both *B. schlosseri* and *D. listerianum* were approximately 200 individuals $100 \text{ cm}^{-2} \text{ week}^{-1}$ lower than peak recruitment densities of the same species in 2001 (Fig. 1). Other species showed patterns of similar recruitment magnitude and duration in both years. In addition, an unidentified sponge species also recruited at densities above 50 individuals $100 \text{ cm}^{-2} \text{ week}^{-1}$ during early June of 2002. During the 2002 recruitment season, these six species accounted for 75–98% of the total recruitment recorded at this site.

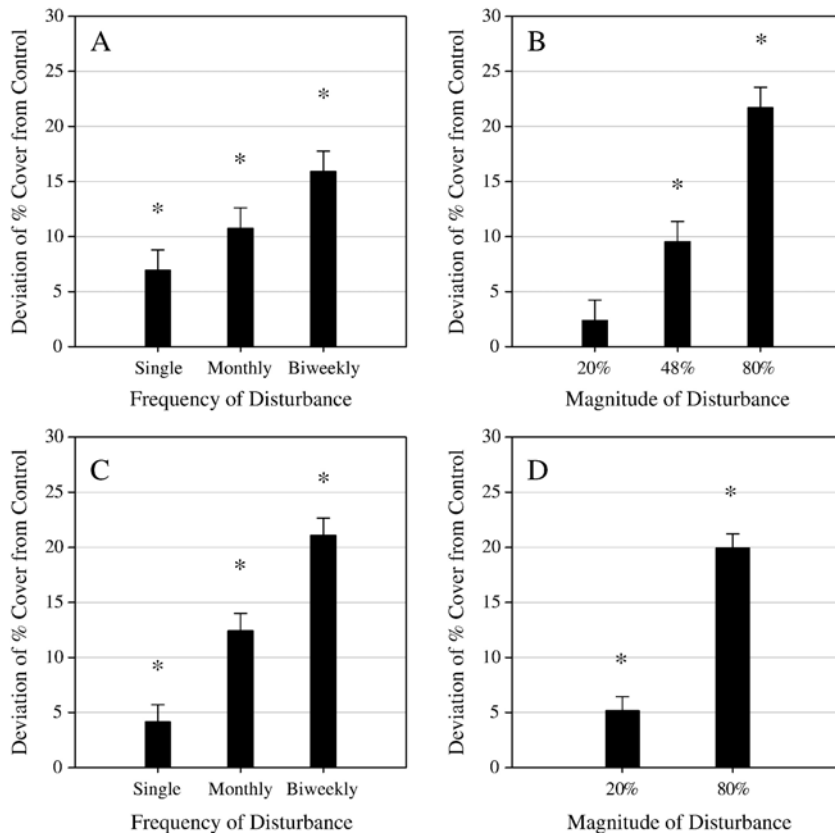


Fig. 5. Primary space occupation of *Diplosoma listerianum* plotted as deviation of % cover from control communities. (A–B) 5-wk community, (C–D) 1-yr community. Error bars = ± 1 SE of mean. * = significant difference from control ($p < 0.01$).

Recruitment of recent invaders and established residents showed different patterns depending on year. In 2001, resident species recruitment dominated and became extremely high in early August. The species contributing most to this pattern (63–89%) included *B. schlosseri*, *B. turrita*, and *M. manhattensis*. By late August, recruitment of recent invaders dominated (Fig. 2A). This was primarily due to high recruitment of *D. listerianum* combined with peaks in recruitment of *A. aspersa* and *B. violaceus*. In contrast, although the dominant species remained the same, resident recruitment was consistently higher than that of invaders during the entire recruitment period of 2002 (Fig. 2B).

3.3. Community experiments

Resident species in the 5-wk communities occupied significantly less primary space than residents in 5-wk control communities and this effect became stronger as disturbance frequency and magnitude increased (Fig. 3A–B). In contrast, recent invaders to the system showed a significant positive effect of disturbance

frequency and magnitude that resulted in increased primary space acquisition when compared to control panels (Fig. 3A–B). There was no consistent effect of time on primary space occupation in the 5-wk community experiment.

In general, disturbance-mediated patterns of space occupancy observed in the 5-wk community experiment were similar to those of the 1-yr community experiment. Recent invaders responded positively to increased frequency and magnitude of disturbance (Fig. 3C–D). However, this effect was only statistically significant in terms of disturbance frequency, and was driven by significant differences from controls in the S treatment (Fig. 3C). Resident species responded in an opposite manner, by displaying a decrease in space occupancy as disturbance frequency increased. This was also driven by a significant difference in the S treatment. There was no consistent effect of time on primary space occupation in the 1-yr community experiment. In cases where time did have an effect on space occupation, there were no significant interactions between time and disturbance frequency or magnitude.

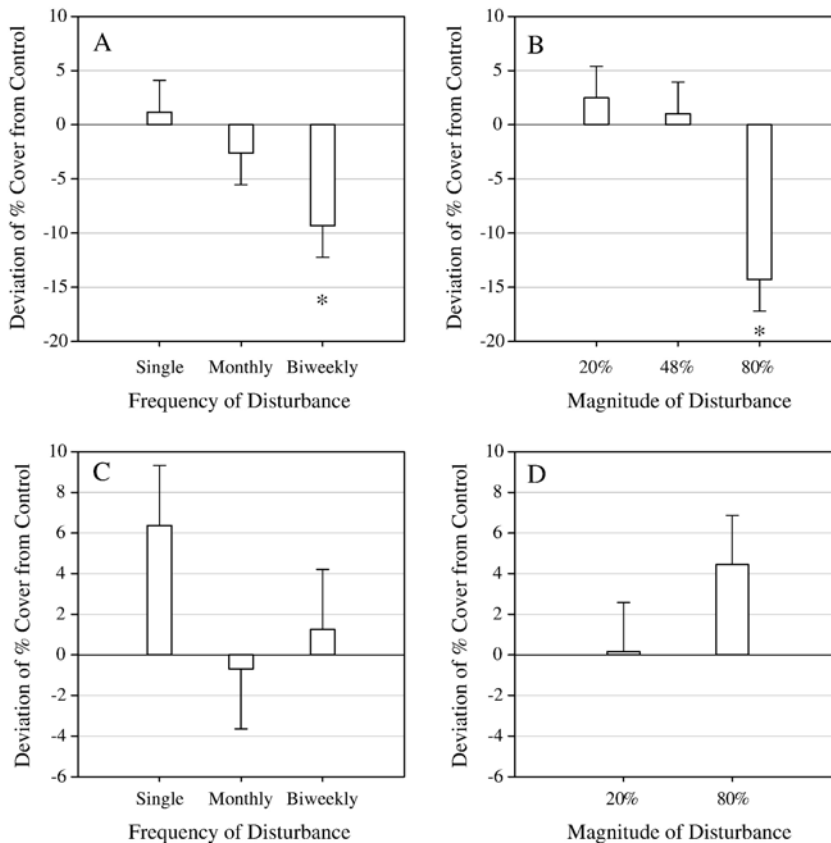


Fig. 6. Primary space occupation of *Molgula manhattensis* plotted as deviation of % cover from control communities. (A–B) 5-wk community, (C–D) 1-yr community. Error bars= ± 1 SE of mean. *=significant difference from control ($p < 0.05$).

Solitary ascidians in the 5-wk old community showed a significant decrease in primary space acquisition in response to all disturbance frequencies (S, M, B) and for the 48% and 80% magnitudes of disturbance (Fig. 4A–B). In contrast, colonial ascidians showed a significant increase in response to disturbance frequency (S, M, B) and magnitude (20%, 80%) when compared to controls (Fig. 4A–B).

Year-old communities also showed a significant negative effect of disturbance on solitary ascidians coupled with a significant positive effect on colonial ascidians (Fig. 4C–D). Specifically, solitary ascidians occupied significantly less primary space than controls at intermediate and high disturbance frequencies (M and B treatments), and at all disturbance magnitudes tested (Fig. 4C–D). Colonial ascidians in the 1-yr community treatments occupied more space than control communities. These effects were significant at the same frequencies and magnitudes as discussed for the solitary growth forms (M, B and 20%, 80% treatments).

Of the recent colonial invasive species, *D. listerianum* had a significant positive response to disturbance

magnitude and frequency in both the 5-wk and 1-yr old communities. In the 5-wk community, all frequencies tested (S, M, B) as well as the 48% and 80% disturbance magnitudes differed in the amount of primary space occupied by *D. listerianum* in controls at $p < 0.01$ (Fig. 5). In the 1-yr old community, the primary space occupied by *D. listerianum* at all frequencies tested (S, M, B) as well as the 20% and 80% disturbance magnitudes differed from the controls at p values of less than 0.01 (Fig. 5). *Botrylloides violaceus*, also displayed a positive response to disturbance, but these trends were not significantly different from control values. *Bugula neritina* settled at extremely low levels throughout the 5-wk community experiment and did not result in any significant responses or trends.

Neither *A. aspersa* nor *S. clava*, both solitary invasive ascidians relatively new to the study site, showed significant responses to disturbance in the 5-wk community. Although the trends were not statistically significant, both species had negative responses to increased disturbance magnitude. In the 1-yr community, only *S. clava* showed a significant negative response to increased

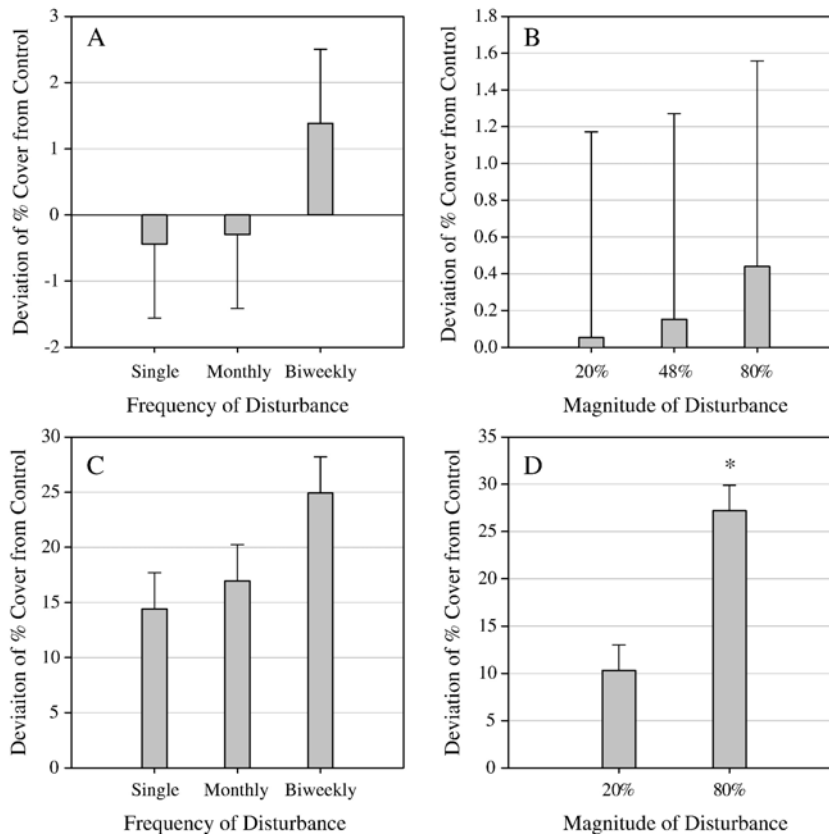


Fig. 7. Empty space plotted as deviation of % cover from control communities. (A–B) 5-wk community, (C–D) 1-yr community. Error bars = ± 1 SE of mean. * = significant difference from control ($p < 0.01$).

magnitude of disturbance (ANOVA $F = 11.37$, $p < 0.01$). The response was driven by a significant difference between the amount of space the species occupied under 80% disturbance regimes versus controls.

In the 5-wk community, the only resident colonial that showed a significant response to disturbance was the hydroid *Obelia* sp. In terms of both frequency and magnitude, the effect of disturbance on *Obelia* sp. space occupancy was positive (frequency ANOVA $F = 5.62$, $p < 0.01$; magnitude ANOVA $F = 5.85$, $p < 0.01$). In the 1-yr community, *Obelia* sp. displayed the same positive trends (frequency ANOVA $F = 4.31$, $p = 0.03$; magnitude ANOVA $F = 15.02$, $p = 0.001$). The encrusting bryozoan *C. pallasiana* also displayed a significant response to disturbance magnitude for both levels of magnitude manipulated (20%, 80%) in the 1-yr community (magnitude ANOVA $F = 16.89$, $p = 0.001$). This effect was, however, negative.

The only resident solitary species that occupied a substantial amount of primary space in the treatments was the ascidian *M. manhattensis*. This species was negatively impacted by increased disturbance frequency

and magnitude in the 5-wk community. This was driven by significant differences between the biweekly disturbance and control treatment as well as the 80% disturbance and control treatment (Fig. 6). There were no significant trends with regard to *M. manhattensis* in the 1-yr old community.

Empty space in control panels increased from $\sim 1\% \pm 0.9$ to $\sim 19\% \pm 3.4$ (mean, ± 1 SE) during the course of the first experiment. There were no significant differences between empty primary space in the 5-wk community controls or treatments (Fig. 7). This indicates that disturbance regimes created available space but did not limit space occupancy. Even though the disturbance treatments created available space, within two weeks, the space on these panels was filled to the same degree as the undisturbed control substrates. In the 1-yr old community, empty space in control panels ranged from 5%–15% (\pm SE of 2.2 and 2.8, respectively). Disturbance treatments differed significantly from controls as disturbance magnitude increased, but did not differ from controls under increased disturbance frequency (Fig. 7).

Overall species richness in the 5-wk community ranged from 4–19 species per panel and did not statistically differ between any of the disturbance treatments and the controls. The communities exposed to the highest frequency and magnitude of disturbance appeared to display slightly lower species richness (7–15 species) than control and other disturbance treatment values; however, this trend was not statistically significant. The 1-yr old community had a species richness range between 9 and 18 species per panel. There were no statistical differences between control and treatment values of species richness with increased disturbance frequency. However, increased disturbance magnitude lead to a significant decrease in species richness in the 1-yr communities (ANOVA $F=9.88$, $p=0.005$).

4. Discussion

In shallow subtidal benthic invertebrate communities, the allocation of primary space is largely affected by small-scale disturbances. For example, small-scale natural disturbances which result in the death of community members include the direct and indirect effects of predation (e.g., fish, crabs), removal of individuals by intra- and interspecific competition, and abiotic disturbances such as storm events (e.g., Osman, 1977; Sousa, 1979a,b; Russ, 1980; Mook, 1981; Davis and Wilce, 1987; Davis, 1988; Bertness et al., 1989; Hurlbut, 1991; Osman et al., 1992). In the subtidal hard substrate communities examined in the present study, bare patches of primary substrate were ubiquitously present and routinely comprised 0–91% with an average of 15% of the available surface area. These open patches of substratum were most likely created by small-scale predation events. Crabs and fish were the most prevalent predators observed at the field sites and are likely the agents of small-scale disturbances observed on the hard substrates (K. B. Heinonen, personal communication; S. Altman, personal observation).

Our results indicate that increased frequency of small-scale disturbance facilitated the growth of recent invaders in the fouling assemblages. The recent invaders responded positively to increased disturbance frequency regardless of the age of the community and dominated recruitment into experimentally disturbed areas. Increased magnitude of disturbance also facilitated recent invader success, although this effect was only significant in the 5-wk community. As the community aged, individual organisms were larger at the onset of disturbance treatments and occupied almost twice the amount of primary space compared to individuals in the 5-wk assemblages. Thus, fewer organisms occupied the

disturbed area in the 1-yr assemblages and fewer organisms were removed although the amount of space disturbed did not change between the 5-wk and 1-yr community experiments. This may explain the decreased impact of disturbance magnitude on invasion success in the 1-yr community. In addition, older, larger organisms may be more efficient at filling open space. This has been observed in blue mussel (*Mytilus edulis* (L.)) patches where lateral movement of adults and gregarious settlement of conspecifics following a disturbance promoted positive feedback mechanisms that maintained the mussel patch (Petraitis and Latham, 1999). In addition, a larger, colonial individual has a greater perimeter from which to expand than a smaller, individual and could fill an open patch in a shorter time frame. An alternate explanation is that the year-old communities were more stable, leading to an increased resistance to patch openings at low frequencies. For example, ribbed mussels, *Guekensia demissa* (Dillwyn, 1817), that form aggregations composed of different age classes are less susceptible to disturbance from ice scouring and crab predation than both younger mussels and mussels not forming aggregations (Bertness and Grosholz, 1985). Community stability has also been associated with decreased susceptibility to invasions. Stachowicz et al. (2002a) showed that the fouling assemblages found at Avery Point were more stable in terms of biomass and productivity when community diversity levels were high because space was filled more consistently. Concurrently, communities with higher species richness were also more resistant to invasion (Stachowicz et al., 2002a).

The general trend of disturbance promoting invader success has been documented in a number of terrestrial and aquatic habitats. Investigations of grassland taxa have found that disturbance was necessary for the establishment of non-indigenous grasses (Petryna et al., 2002; Burke and Grime, 1996; Hobbs and Huenneke, 1992). Experimental manipulation demonstrated that interactions between multiple types of disturbance such as grazing, soil disturbance and eutrophication, were found to have an increased effect on invader success (Burke and Grime, 1996; Hobbs and Huenneke, 1992). Literature reviews of pine and woody plant invasions indicated that the majority of plant invasions occurred in disturbed habitats (Rejmánek and Richardson, 1996). Studies of non-indigenous fish in California streams also found that increased disturbance facilitated invasion (Moyle and Light, 1996). Minchinton (2002) found that mats of stranded wrack (dead plant material) created patches of open space that enhanced the seaward spread of *Phragmites australis* in a coastal New England

marsh. The present study is unique in focusing on the marine community and on small-scale disturbances likely created by biotic agents.

Species richness was significantly different from the controls only in the year old community under the maximum disturbance magnitude treatment. In this case, decreased species richness was coupled with increased disturbance as well as increased invader success. These findings concur with other fouling community studies linking resident species diversity to invasion success (Stachowicz et al., 1999, 2002a). However, this pattern was not seen in the majority of the disturbance treatments where species richness did not differ from the controls. Terrestrial grassland studies linking disturbance to invasion success have reported a similar pattern (Petryna et al., 2002).

In terms of growth forms, colonial ascidians were more successful than solitary ascidians in occupying primary space following disturbance. This finding is consistent with Jackson's (1977) predictions that colonial species should be the dominant space holders under disturbance regimes. This is primarily a result of their ability to grow and reproduce asexually. Colonial animals extend laterally as they grow and therefore increase the amount of primary space they occupy. In contrast, solitary species often grow up and away from the substrate, greatly reducing spatial competition with colonial species and only slightly increasing primary space occupancy (Jackson, 1977). Jackson (1977) also argued that most solitary species, due to their decreased ability as space competitors, depend on disturbance events as a source for recruitment opportunities and use generalist strategies of rapid growth, small size and short generation time to settle and grow. Small-scale disturbance events can be more harmful to solitary species, as the entire animal can be removed by the event, whereas small-scale disturbances may only remove a portion of an individual colonial species and may not necessarily lead to death of the colony. In cases when indeterminate growth is sufficiently strong, colonial species will occupy space rapidly and may also inhibit recruitment and settlement of other organisms (Osman and Whitlatch, 1995a,b).

Colonial ascidians were more successful in acquiring space than solitary ascidians with response to increased disturbance magnitude, frequency and community age. When examined at the species level, the trends were primarily driven by the recent invader *D. listerianum*. Aside from general competitive advantages of colonial over solitary growth forms, *D. listerianum*'s ability to rapidly occupy primary space likely results from its increased growth rates at warmer water temperatures

when compared to resident colonial ascidians (Stachowicz et al., 2002b), its ability to fuse with conspecific colonies (Bishop and Sommerfeldt, 1999), its capacity to migrate after settling (Svane and Young, 1989), and its relatively high recruitment rates during the course of the experiments. *D. listerianum* is also one of the few species which regularly recruits on other species but few species recruit on it (Osman and Whitlatch, 1995b). Colonial didemnid ascidians, such as *D. listerianum*, have been shown to be competitively dominant in cryptic coral reef systems. For example, Buss and Jackson (1979) found that an unidentified didemnid ascidian was the competitive dominant in 94% of the interspecific interactions reported. In the subtidal hard substrate community of southern New England, *D. listerianum*, shows similar competitive dominance. In contrast, this species was not an important competitor in Florida subtidal hard substrate assemblages and did not respond positively to disturbance (Mook, 1983). *D. listerianum*'s competitive advantage may be related to the length of time it has been established in an area. For example, subsequent to invading the southern Gulf of Maine in the early 1980's, *B. violaceus* became the competitive dominant in the community. By 1985, *B. violaceus* was still dominant, but had decreased in abundance by half (Berman et al., 1992). As an invader that has recently entered the community, *D. listerianum* may have some competitive advantage that it does not have when it is an established resident.

Many of the negative effects of disturbance on space occupancy of the resident species were driven by the solitary ascidian *M. manhattensis*. This species can form dense aggregations, similar to colonial growth forms, as a result of the gregarious larval settlement on the tunics of conspecific adults (Svane and Young, 1989; Monnoit, 1965). As the recruits grow, the aggregation becomes heavy, adults often die, and the entire aggregation can detach from the primary substrate (Stachowicz et al., 2002a; S. Altman personal observations). Small-scale disturbances likely accelerate the detachment process and decrease *M. manhattensis*' ability to occupy open space. Although *M. manhattensis* recruits will settle on bare substrate, the tendency for limited dispersal of its recruits and its preference for settlement on adults makes it difficult for this species to fill open space rapidly.

Although the species comprising the resident pool have been members of New England hard substrate assemblages for at least one hundred years, many have cryptogenic, or unknown, geographic origins. Because this study demonstrates disturbance facilitates dominance of recent invaders over resident species, and resident species may in fact be established but non-indigenous

members of the community, disturbance could potentially facilitate reduction in the abundance of resident invaders by recent invaders. Documentation of an invader displacing another invader has been reported in intertidal New England habitats with the Asian shore crab *H. sanguineus* replacing the green crab *Carcinus maenas* (L.) (Lohrer and Whitlatch, 2002). In New England subtidal hard substrate communities, another unidentified colonial didemnid species has also invaded in the past four years and currently ranges from (at least) the southern Gulf of Maine to the Chesapeake Bay (Bullard et al., 2007-this issue; L. Harris, G. Ruiz, A. Hines, personal communication). In Long Island Sound, in areas in which this species recruits, its rapid abundance and coverage of the majority of available substrate is striking (S. Altman, personal observations; Osman and Whitlatch, in press). Further studies of the impact of small-scale disturbance in the hard substrate community could determine the role of disturbance in facilitating both competitive dominance and the replacement of one didemnid invader by another.

The results of this study highlight the impact of small-scale disturbance on the success of invaders, particularly invaders that are new to a system and exhibit colonial growth. The success of *D. listerianum* in occupying space indicates that frequency and magnitude of disturbance are important factors in invasion success not only in terrestrial and aquatic habitats, but in marine habitats as well. In addition to the biological disturbance mimicked in this study, coastal systems are experiencing frequent, human-mediated disturbances that make limited resources such as space and nutrients available. Coastal systems often simultaneously experience increased anthropogenic stress as well as increased risk of invasion (Grosholz, 2002; Cohen and Carlton, 1998; Carlton and Geller, 1993; Carlton, 1989). This combination of stressors means that coastal regions are more susceptible to invasion, and are, at the same time, more susceptible to high frequency, low magnitude disturbance which, the results of this study indicate, can further facilitate the invasion process.

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