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Research article

Potential effects of the invasive colonial ascidian (*Didemnum vexillum* Kott, 2002) on pebble-cobble bottom habitats in Long Island Sound, USA

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Abstract

The colonial ascidian, *Didemnum vexillum*, is a relatively recent invader to the east and west coasts of North America and since its appearance it has often become a dominant member of a variety of coastal communities in these regions. The species has the unique ability to colonize cobble-pebble substrates and form extensive mats in this habitat type. The mats essentially 'glue' the small pebbles and cobbles together and alter habitat complexity of the seafloor from a more three-dimensional system to a more two-dimensional one. We examined the potential impacts of the mat-forming activities on benthic macro-invertebrate population and community structure by comparing sets of samples collected inside and outside of the mats. Sampling was conducted at a site located in eastern Long Island Sound, USA, over a period of approximately one year using a corer and a suction sampler. Contrary to our prediction that the presence of the ascidian mats would reduce benthic species richness and abundance we found that these parameters either were not different or were significantly higher in samples taken inside *Didemnum* mats compared to samples collected immediately outside the mats. The presence of the mats did result in subtle shifts in benthic community structure and functional group dominance with greater numbers of infauna and deposit-feeders residing inside the mats compared to samples collected adjacent to the mats.

Key words: *Didemnum*, invasive ascidians, cobble bottom, benthic invertebrates

Introduction

The colonial ascidian, *Didemnum vexillum* Kott, 2002, is a relatively recent invader to the east and west coasts of North America (Bullard et al. 2007) and we first observed the species in southern New England in 2001 (Osman and Whitlatch 2007). Following its appearance in southern New England, *Didemnum vexillum* (hereafter referred to as *Didemnum*) populations have invaded a variety of habitats, including harbors and marinas (Auker and Oviatt 2008; Bullard and Whitlatch 2009), and Osman and Whitlatch (2007) have described the interactions of the species with other common members of shallow water fouling assemblages in Long Island Sound, USA. In addition to the establishment of populations in more protected shallow-water habitats, in 2002 we discovered that portions of deeper water (~30 m) pebble-cobble habitats in eastern Long Island Sound were heavily colonized by *Didemnum*. In these areas, the ascidian formed extensive mats on the seafloor similar to those described by Valentine et al. (2007) on Georges Bank, Gulf of Maine, USA.

The ability of *Didemnum* to colonize and form mats on the pebble-cobble seafloor habitats is unlike any of the other recent ascidian invaders (*Styela clava* Herdman, 1881, *Diplosoma listerianum* (Milne Edwards, 1841), *Ascidiella aspersa* (Müller, 1776), *Botrylloides violaceus* (Oka, 1927)) or native and long-term resident colonial ascidians (e.g, *Aplidium stellatum* (Verrill, 1871), *Aplidium constellatum* (Verrill 1871), *Botryllus schlosseri* (Pallas, 1776), *Didemnum candidum* (Savigny, 1816) found in Long Island Sound. In addition, there are no other resident benthic invertebrate species (e.g., sponges, bryozoans, coelenterates) capable of forming mat-like structures in this substrate type (pers. obs.). Individual *Didemnum* mats can be

up to several meters in area and the mats can occur over relatively large portions of the seafloor (i.e., tens to thousands of m^2; pers. obs., Valentine et al. 2007). The ascidian mats essentially "glue" small pebbles and cobbles together, filling in many of the interstitial spaces between the sediment particles and alter the habitat complexity of the seafloor from a complex three-dimensional system to a more two-dimensional one. The mats may also alter the flux of materials from the water-column to the sediment-column by creating a barrier to water flow at the sediment-water interface. Lastly, while relatively little is known about the effects of predators on the ascidian mats, *Didemnum* has a highly acidic tunic (Bullard et al. 2007) and congeneric species possess cytotoxic organic compounds (Vervoort et al. 1998) which may alter the foraging activities of epibenthic invertebrate (e.g., crabs, seastars) and vertebrate (e.g., fish) predators.

Species which are capable of significantly modifying a habitat are frequently called 'ecosystem engineers' because of their ability to cause physical changes in abiotic and biotic materials and exert direct or indirect controls on resource availability to other co-occurring species (Jones et al. 1994). The impacts of non-native marine ecosystem engineers on biodiversity and ecosystem services is reasonably well documented (see recent review of Wallentinus and Nyberg 2007), and we hypothesize that *Didemnum* is acting as an ecosystem engineer through its mat-forming activities. We also hypothesize the mats will significantly alter benthic community structure when compared to areas without the mats. We tested these hypotheses by examining whether the presence of the ascidian mats caused changes in macrobenthic community structure and diversity leading to altered functional group composition.

Methods

Samples were collected at a site (41°18.197'N, 71°54.600'W) in eastern Long Island Sound at a water depth of ~30m. The site is characterized by a pebble-cobble bottom interspersed with large boulders and it experiences strong semidiurnal tidal currents reaching 50 to 100 cm sec^{-1}. Based on diver surveys of the site in 2001-2003, approximately 1 to 1.5 km^2 of the bottom was patchily carpeted with *Didemnum* mats. Individual mats were ~1.0 to 1.5 m^2 in area and

the mats were typically interspersed ~1.0 to 2.0 m from each other.

To assess the potential effects of *Didemnum* mats on benthic invertebrate species diversity and community composition, samples were taken inside and outside of individual mats by divers. Two different sampling methods were used. First, paired core samples (10.16 cm inside diameter, 14 cm depth) were taken; one positioned in the center of a mat and one ~1 m outside the edge of that mat. Four paired core samples were taken on 4 different sampling dates between July and September 2005 for a total of 32 samples. Samples were sieved through a 300 μm mesh screen, preserved in buffered 10% formalin and later transferred to 70% ethanol with rose bengal. Samples were sorted under a dissecting microscope (60x) and organisms were counted and identified to lowest practical taxonomic level. Second, a venturi air-lift sampler was used to quantify benthic invertebrate species and abundance over a larger area. The sampler collected all organisms within a 0.5m x 0.5m quadrat to a depth of ~1-3 cm. Sediment and organisms were collected in a 1.5 mm mesh bag attached to the end of the air lift sampler. Again, paired samples were taken inside and ~1 m outside of individual *Didemnum* mats. Four sets of paired samples were taken twice in September 2005 and once in July 2006 for a total of 24 samples. Samples were sieved through a 1.0 mesh sieve and processed in the same manner as the core samples.

For both sets of samples, taxa collected were categorized as infaunal or epifaunal and by trophic group (i.e. suspension feeder, deposit feeder or predator/scavenger) using classification schemes provided by Fauchald and Jumars (1979), Biernbaum (1979) and personal observations.

A Simpson's Diversity Index (SDI) was calculated for each sample, and data from each sampling date were analyzed separately. Samples taken inside and outside individual mats were compared using paired t-tests. A two-way Analysis of Variance (ANOVA) was used to determine the effects of *Didemnum* mats (sample location inside or outside of mat) and sampling date on total abundance. To graphically show relationships among invertebrate assemblages found inside and outside the ascidian mats, two-dimensional ordinations of multivariate data using non-metric multidimensional scaling (nMDS) were created using PRIMER 6 (Clarke and Gorley 2006). A two-way analysis of simila-

rities (ANOSIM) between inside and outside sample locations and date was used to determine differences in community composition.

Results

Although some differences were seen between the patterns derived from core and suction sampling, the general trends were quite similar. We discuss the two types of sampling separately but we have plotted many of the results together to make similarities and differences easier to visualize.

Core Samples

A total of 82 different taxa and 2489 individuals were identified in the 32 core samples. Samples were typically dominated by polychaete worms, bivalves and amphipods. Based on paired t-tests for individual sampling periods, the presence of *Didemnum* mats did not have a significant effect on total species richness for any sampling date although there was a trend of slightly higher species richness values for samples taken inside the mats compared to samples collected outside the mats (Figure 1A). SDI values showed no clear trend over the sampling dates and were not
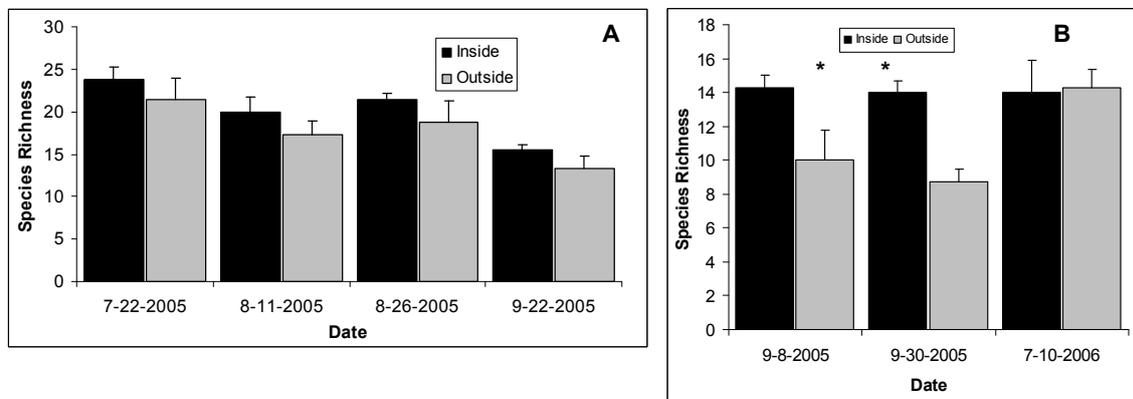

Figure 1. Average total benthic macrofauna species richness (± 1 s.e., n = 4) found in (A) core samples and (B) suction samples taken inside and outside *Didemnum* mats at different sampling times. Data were analyzed using paired t-tests and an * indicates a significance difference between the sample pairs (P < 0.05). Note differences in y-axis scales.
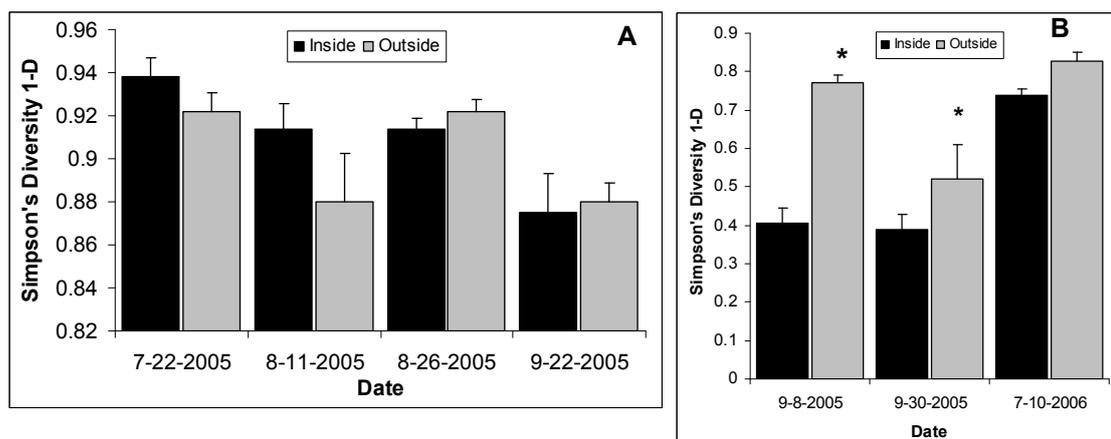

Figure 2. Simpson's Diversity Index values (mean ± 1 s.e, n = 4) of (A) core samples and (B) suction samples taken inside and outside *Didemnum* mats. Data were analyzed using paired t-tests and an* indicates a significant difference (P < 0.05).

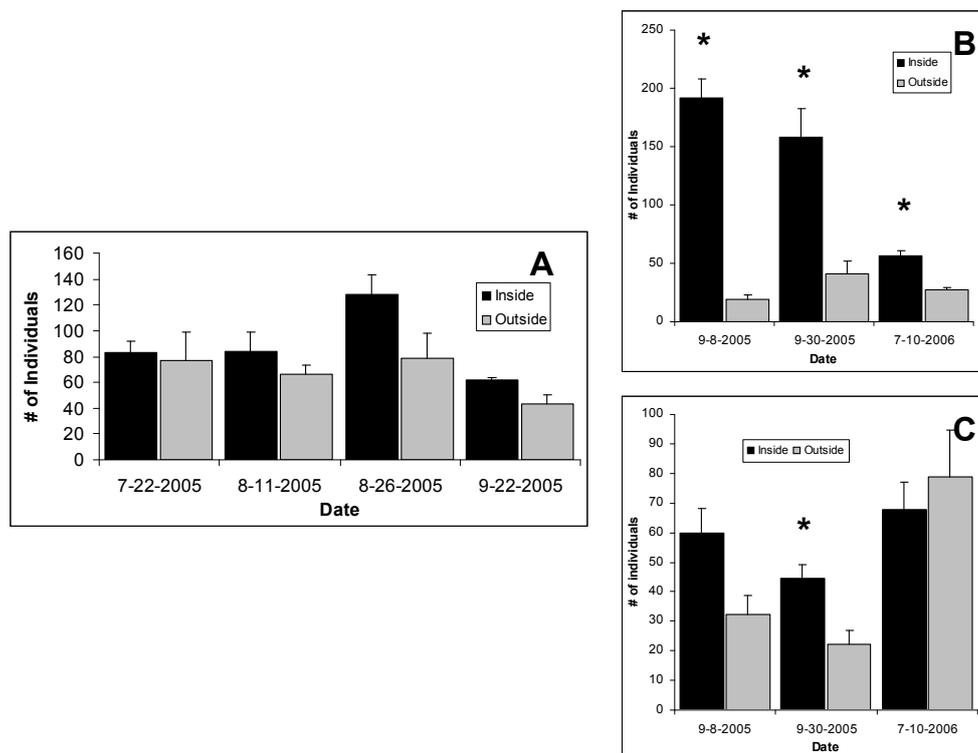**Figure 3.** A = average total abundance of macrofauna (± 1 s.e.) in core samples taken inside and outside *Didemnum* mats. B = average abundance of *Anachis* spp in suction samples taken inside and outside *Didemnum* mats. C = average abundance of macrofauna (except *Anachis* spp.) in suction samples taken inside and outside *Didemnum* mats. Data were analyzed using paired t-tests and an * indicates a significant difference (P < 0.05). Note differences in y-axis scales.

significantly affected by the presence of *Didemnum* mats (Figure 2A).

A two-way ANOVA showed that the total number of individuals did not vary significantly with the presence or absence of *Didemnum* mats (P = 0.85) or the sampling date (P = 0.29) or the interaction between them (P = 0.50) (Figure 3A). However, when the data from all dates were pooled, a paired t-test revealed there were significantly more individuals found within mats (P = 0.04). Significant differences in individual species abundances inside and outside the ascidian mats were observed for 10 of the 25 most abundant species (Figure 4). Paired t-tests indicated that nine species had significantly greater abundances inside the mats and one species had a significantly greater abundance outside the mats (Figure 4).

Thirty-eight taxa were exclusively found either inside or outside the mats at the study site. However, these species comprised <6.0% of the total number of organisms sampled and all but

two were represented by ≤4 individuals or were found in ≤2 samples (Mercer 2007). The epibenthic polychaete, *Lepidonotus squamatus* (Linnaeus, 1767), and the infaunal polychaete, *Eusyllis lamelligera* Marion and Bobretzk, were the only species that averaged ≥2 individual per sample and were present in >50% of samples. Both species were only found inside *Didemnum* mats.

Significantly higher abundances of infaunal organisms were found in samples taken within mats compared to those collected outside of mats (Figure 5A; paired t-test, P = 0.043). The abundance of epifaunal organisms was not significantly affected by presence of the ascidian mats. Paired t-tests also showed significantly higher abundances of deposit feeders (P = 0.035) and predators/scavengers (p = 0.046) in samples taken inside mats compared to those taken outside the mats (Figure 5A). The number of suspension feeders was not significantly affected by the presence of *Didemnum* mats.
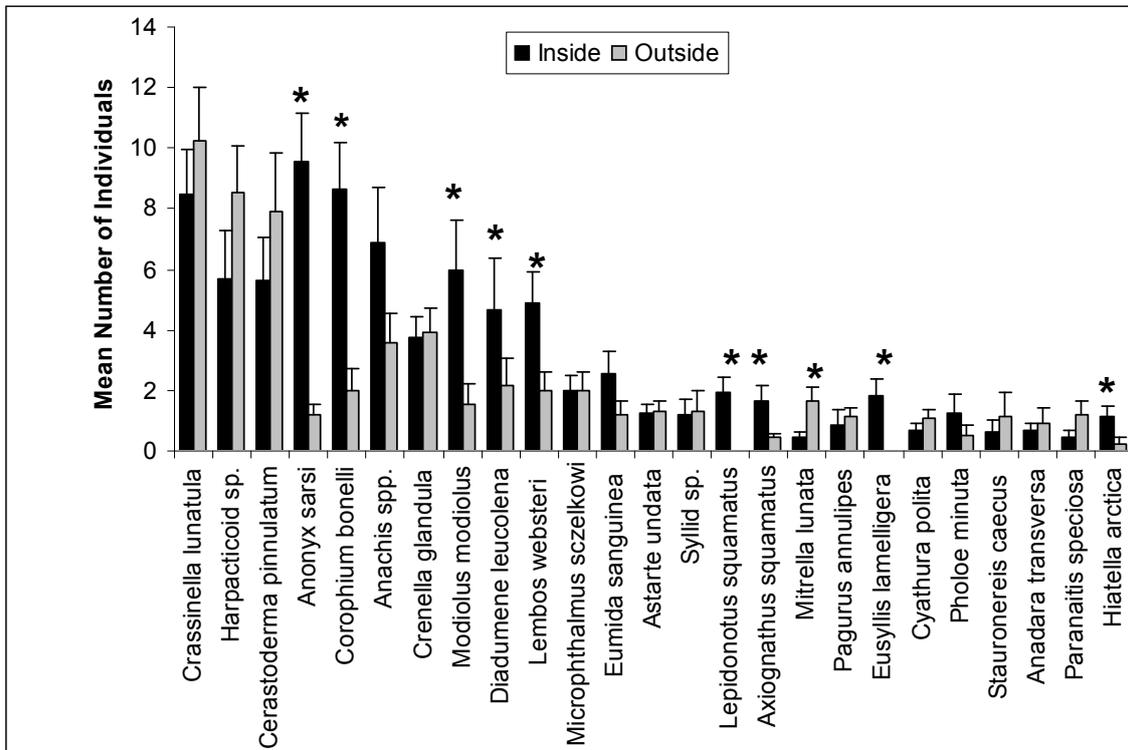
Figure 4. Average abundance (± 1 s.e, n = 16) of the 25 most abundant macrofaunal species found in core samples taken from inside and outside *Didemnum* mats. Data were analyzed using paired t-tests and an * indicates a significant difference (P < 0.05).
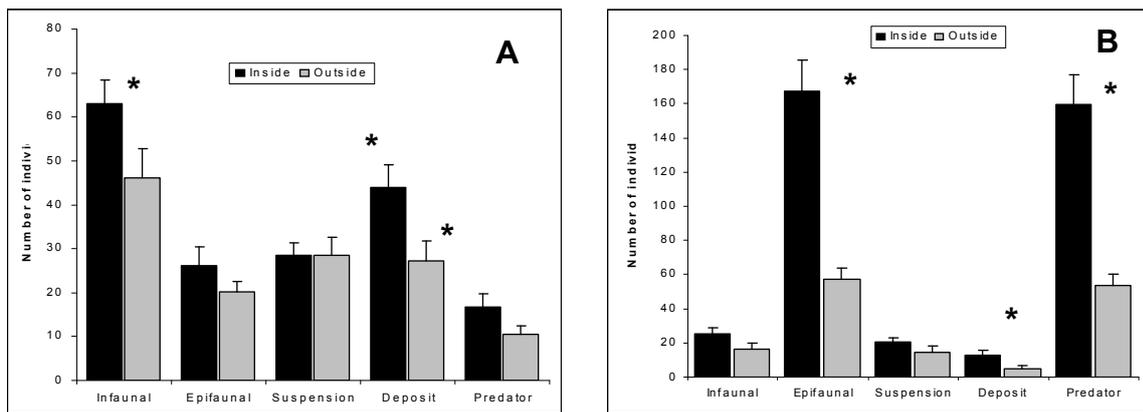

Figure 5. Comparisons of the abundance (mean ± 1 s.e.) of different benthic macrofaunal functional groups found inside and outside *Didemnum* mats. A = Core samples, B = Suction samples. Data were analyzed using paired t-tests and an * indicates a significant difference (P < 0.05). Note differences in y-axis scales.
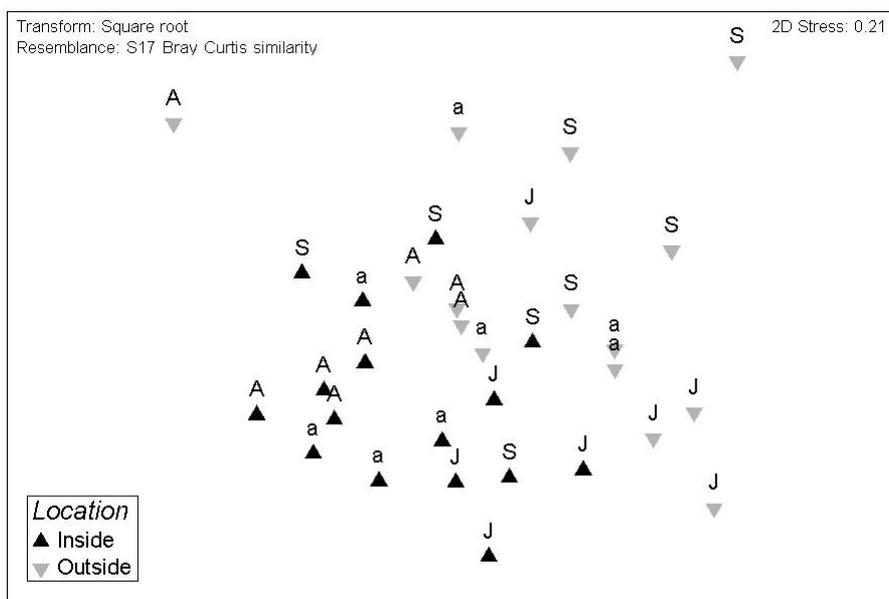
Figure 6. Non-metric multi-dimensional scaling plots of benthic macrofaunal community composition of core samples taken inside (triangles) and outside (inverted triangles) *Didemnum* mats. Plot based on a Bray-Curtis similarity matrix created from square root transformed abundance. Labels above the triangles indicate different sampling dates: J = 22 July 2005, a = 11 Aug 2005, A = 26 Aug 2005, S = 22 Sept 2005.

An nMDS analysis of benthic community composition indicated a separation of samples taken inside and outside the mats (Figure 6). A two-way crossed ANOSIM (presence of *Didemnum* mats and sampling date as factors) confirmed the ordination results. Community composition differed significantly between inside and outside sample locations (R = 0.216, P = 0.015). Also, community composition differed significantly between sampling dates (Global R = 0.267, P = 0.001) with pair-wise tests indicating significant differences between all dates except for the 11 Aug 2005 which was not significantly different from any of the other days.

Suction Samples

A total of 54 different taxa and 3195 individuals were collected in the 24 suction samples. Samples were typically dominated by gastropod and bivalve mollusks and crustaceans. Paired t-tests revealed a significantly higher species richness present in samples taken inside *Didemnum* mats than outside the mats for the first two sampling dates (P= 0.053, P= 0.032) but not for last sampling date (P= 0.9379) (Figure 1B). Despite having lower species richness and

abundance, areas outside the mats had significantly higher SDI values (paired t-test all dates combined, P = 0.004), due to the reduced dominance of the epibenthic predaceous gastropod *Anachis* spp. (Figure 2B). The average number of individuals of all taxa was significantly greater inside *Didemnum* mats for the two sampling dates in 2005 (paired t -test, P = 0.002, P = 0.019) but not for the July 2006 sampling date (paired t-test, P = 0.454). The difference in number of individuals inside and outside the mats was mainly due to the significantly greater numbers of *Anachis* spp. found inside the mats (Figure 3B). When *Anachis* spp. was removed from the analysis, the difference in number of individuals between inside and outside of mats was less and only the second sampling date showed a significant difference (paired t-test, P = 0.024) (Figure 3C). Significant differences in individual species abundances were observed for only 2 species other than *Anachis* spp. (Figure 7); the anemone *Diadumene leucolena* (Verrill, 1866) and the bivalve *Cerastoderma pinnulatum* (Conrad, 1831). While 30 taxa were found exclusively either inside or outside the mats, they represented only 1.5% of the total number of individuals sampled and occurred in very few of the samples (Mercer 2007).
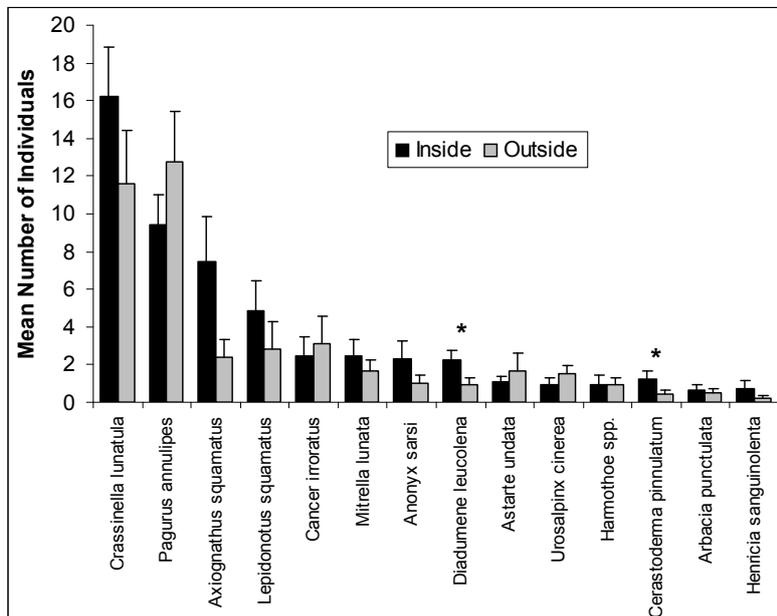
Figure 7. Average abundance (± 1 s.e, n = 12) of the 14 most abundant macrofaunal species found in 0.25 m² suction samples taken from inside and outside *Didemnum* mats. Data were analyzed using paired t-test and an * indicates a significant difference (P < 0.05) sample pairs.

Significantly greater abundances of epifaunal organisms (paired t-test, P = 0.001) were found in samples taken inside mats compared to those outside the mats (Figure 3B). Paired t-tests showed significantly higher abundances of deposit feeders (P = 0.029) and predators/scavengers (P = 0.001) in samples taken inside mats (Figure 5B). Suspension feeders were not significantly affected by the presence the ascidian mats (P = 0.17). When *Anachis* was removed from analysis the differences in epifaunal and predator/scavengers were no longer significant.

Community composition differed significantly between inside and outside samples locations (R = 0.531, P = 0.002; two-way crossed ANOSIM). An nMDS analysis of community composition (Figure 8) indicated that benthic community composition inside and outside the *Didemnum* mats were different for the two sampling dates in 2005. However, community composition of samples collected in 2006 showed no effect of the ascidian mats. Pair-wise tests showed that the two sampling dates in September 2005 did not differ significantly (R = 0.188, P = 0.1); however the 2006 sampling date was significantly different than both of the 2005 dates (R = 0.802; P = 0.004; R = 0.792, P = 0.002).
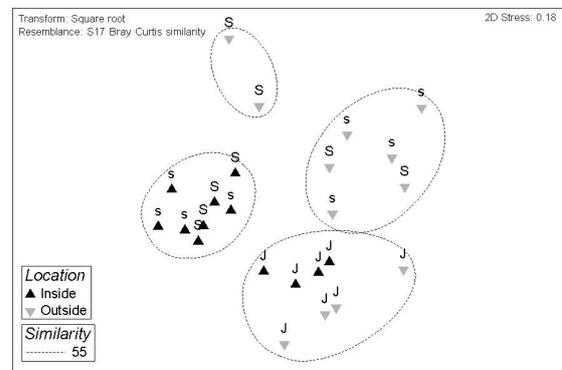

Figure 8. Non-metric multi-dimensional scaling plots of benthic macrofaunal community composition of 0.25 m² suction samples taken inside (triangles) and outside (inverted triangles) *Didemnum* mats. Plot based on a Bray-Curtis similarity matrix created from square root transformed abundance data. Labels above the triangles indicate different sampling dates: s = 8 Sept 2005, S = 30 Sept 2005, J = 10 July 2006. Solid lines indicate samples that are 55+% similar according to the CLUSTER analysis routine in Primer 6 (Clarke and Gorley 2006).

Discussion

We hypothesized that the unique ability of *Didemnum vexillum* to colonize deeper-water pebble-gravel substrates and form extensive mats on the seafloor would result in it having dramatic effects on the resident fauna by altering habitat complexity and structure. Contrary to our prediction that the presence of the ascidian mats would reduce benthic species richness and abundance, total abundance and richness of epifaunal and infaunal species were either not different or were significantly higher in samples taken inside *Didemnum* mats compared to samples collected immediately outside the mats. The presence of the mats did result in subtle shifts in community structure and functional group dominance.

Typically, introduced marine ecosystem engineers that increase habitat complexity tend to cause local species diversity to increase, while engineers that decrease habitat complexity cause species diversity to decrease (Crooks 2002). For example, Beekey et al. (2004a) found a positive relationship between zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) aggregations and the diversity of benthic species in soft sediment freshwater habitats. This was attributed to the increase in habitat complexity provided by the mussels and shells of dead individuals to the relatively flat and homogenous soft substrate surrounding the mussel aggregations. However, the relationship between habitat complexity and diversity does not always hold true. For example, Castel et al. (1989) found that macrofaunal densities decreased in beds of Pacific oysters (*Crassostrea gigas* (Thunberg, 1793)) in the Mediterranean compared to sediments without the oysters, even though these beds are structurally much more complex than the bare substrate. These decreased densities were attributed to the reduced sediment oxygen levels created by the oyster beds.

Autogenic ecosystem engineers can transform habitats because their growth comprises an integral part of the altered environment and can provide new habitat for species (Castilla et al. 2004). In the case of *Didemnum*, the mats may serve as novel habitat for benthic species. Some invertebrates capable of living beneath the mats may be using the mats for shelter and protection from epibenthic predators. For example, Beekey et al. (2004b) found that colonization of soft sediments by zebra mussels significantly reduced

the foraging efficiencies of benthic predators. The ascidian mats may be providing protection from predators that could explain the higher abundances of some species of infaunal invertebrates found beneath the mats. There was a general lack of large epibenthic predators in the areas colonized by *Didemnum* while areas surrounding the mats were commonly inhabited by crabs and demersal fish (pers. obs.). If *Didemnum* mats do reduce the foraging abilities of benthic predators, the mats could have important impacts on fishery resources similar to those hypothesized by Valentine et al. (2007) for portions of the Gulf of Maine which have been invaded by *Didemnum*.

Animal-mediated modification of benthic habitats has long been recognized to influence not only the biotic but also the abiotic properties of these habitats (McCall and Tevesz 1982). It is likely that the mats of *Didemnum* alter benthic-pelagic coupling and influence the biogeochemical cycling of many nutrients and elements by creating a physical barrier between the underlying seafloor and the water column above. This physical barrier created by the ascidian mats may influence dissolved oxygen exchange between the sediments and overlying water leading to hypoxic conditions in the sediment, which might influence benthic diversity and alter community structure (Diaz and Rosenberg 1995). However, Beekey et al. (2004a) found that despite the severe oxygen depletion in the sediments below zebra mussel beds, most infaunal invertebrates responded positively to zebra mussel colonization Similar results were found in this study with infaunal abundances generally higher in areas covered by *Didemnum* mats compared to outside of the mats. The degree to which the ascidian mats alter benthic-pelagic coupling processes and the properties of the substrates beneath the mats should be explored.

Despite the increase in both macrobenthic species abundance and richness inside *Didemnum* mats, there was a significant decrease in SDI values inside the mats compared to outside the mats. This is largely explained by the higher dominance of the epifaunal predaceous gastropod *Anachis* found inside the mats. A likely explanation for the occurrence of higher abundances of the gastropods is that laboratory studies have shown that the gastropod can forage on both living and recently dead *Didemnum* colonies (Mercer 2007; but see Osman and Whitlatch 2007).

The winter dieback of *Didemnum* mats in eastern Long Island Sound (pers. obs.) might explain the differences in community composition observed between the September 2005 suction sampling dates and the July 2006 date. The last sampling date, which was nearly a year after the first two dates, showed fewer significant differences than the first two dates when inside and outside locations were compared with paired t-tests. The number of *Anachis* was also significantly lower in July than in September (Mercer 2007). As *Didemnum* increases in biomass and area covered following the winter die back, *Anachis* may exhibit a numeric response to increased food availability resulting in more *Anachis* later in the summer when *Didemnum* mats cover the greatest amount of seafloor.

The continued growth and spread of *Didemnum* in southern New England is likely inevitable. As a relatively new invader to southern New England waters, the full magnitude of the effect this species may have on ecosystem structure and function has yet to be determined. This study highlights some of the effects that *Didemnum* has on the abundance and biodiversity of benthic macrofauna inhabiting pebble-cobble substrates. Despite the unique ability to form extensive mats on pebble-cobble substrates throughout New England, we found that the mats minimally influenced benthic macro-invertebrate species abundance and richness in these habitats in eastern Long Island Sound. Clearly additional studies are needed to assess whether the ascidian mats are providing a predator refuge for some benthic species and how subtle shifts in macrofaunal functional group composition caused by the presence of the mats may influence higher trophic levels in coastal ecosystems. In addition, cobble substrates are an important recruitment habitat for the American lobster (*Homarus americanus* Milne Edwards, 1837) and their limited availability may represent a demographic bottleneck for lobster production (Wahle and Steneck 1991). The role *Didemnum* mats may play in affecting lobster recruitment and subsequent population dynamics warrants further study.

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