

Invasive tunicate restructures invertebrate community on fishing grounds and a large protected area on Georges Bank

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Abstract Marine invasive species can profoundly alter ecosystem processes by displacing native species and changing community structures. The invasive tunicate *Didemnum vexillum* was first found on the northern edge of Georges Bank in 1998. It can form encrusting colonies on gravel substrates that are also a preferred habitat for a number of other invertebrates. In this study we used data collected via HabCam, a vessel-towed underwater imaging system, to investigate the distribution of *D. vexillum* and its relationship to other epibenthic macroinvertebrates in a portion of Georges Bank that includes fishing grounds and an

area protected from bottom-fishing. This novel technology provides imaging of epibenthic species distributions in areas of the benthic environment that were previously unobservable. We found that *D. vexillum* density is negatively correlated with the Atlantic sea scallop (*Placopecten magellanicus*), barnacles (genus *Balanus*), the tube anemone (genus *Cerianthus*), the green sea urchin (*Strongylocentrotus droebachiensis*), the globular sponge of the genus *Polymastia*, and Bryozoa. However *D. vexillum* is positively correlated with *Cancer* spp. Crabs, the tube forming polychaete, *Filograna implexa*, and *Asterias* spp. sea stars. The hypothesis that *D. vexillum* restructures the invertebrate community is supported by principal components analysis, revealing it as a primary driver of variation in the community when present. Additionally, there is an effect of the closed area as compared to fishing grounds on the structure of the invertebrate community and the abundance of certain species as consistent with previous studies, bottom-fishing affects invertebrate community structure. Principal components analysis revealed that bottom-fishing also appears to weaken clustering among species in the invertebrate community as compared to the community structure in the closed area. Biodiversity in high gravel sites of the epibenthic environment, as measured by the Shannon diversity index, also declined with increasing *D. vexillum* percent cover, while the open and closed areas were not significantly different in their level of biodiversity. *D. vexillum* appears to be the key driver of biodiversity decline in the epibenthos

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when present, rather than other processes such as direct disturbance and extraction from dredging. This research evaluates ecological responses to the presence of an invasive tunicate and suggests that this invasive species is a major force in shaping the ecological interactions in invaded areas.

Keywords Essential fish habitat · Vessel-towed underwater camera system · Sea squirt · Non-indigenous species · Ascidiaceans · Marine protected areas · Hurdle models · Hierarchical models

Introduction

Invasive species in marine environments have been shown to displace native species, change community structure and food webs, and alter fundamental ecosystem processes (Molnar et al. 2008). It has been difficult for researchers to disentangle the effects of habitat modification and invasive species on native species diversity leading to debate about the direct and indirect processes driving invasive species dominance (MacDougall and Turkington 2005; Didham et al. 2005; Chabrierie et al. 2008). Habitats with invasive species are generally modified by other processes, therefore it is frequently unclear if the invasive species drive native species loss and declines in biodiversity, if they are opportunists taking advantage of habitat modified by other processes in which low diversity enables their dominance, or if disturbance causes both ecological change and invasion independently (MacDougall and Turkington 2005; Didham et al. 2005; Chabrierie et al. 2008). While the driver hypothesis states that invasive species drive ecosystem changes, the passenger hypothesis posits that other processes drive ecological change and invasive species then are able to dominate environments as an indirect consequence (MacDougall and Turkington 2005). Although some studies have supported the passenger hypothesis (MacDougall and Turkington 2005; Chabrierie et al. 2008; Grarock et al. 2014; South and Thomsen 2016), other studies have found that invasive species are the drivers of ecological change (Hermoso et al. 2011; White et al. 2013). Another alternative hypothesis is the ‘back-seat driver’ hypothesis which states that the invasive species requires and benefits from disturbance to ecosystem processes leading to the decline of

native species, but then the invasive contributes to further declines of native species (Bauer 2012), which other studies have also supported (Berman et al. 2013; Fenesi et al. 2015). Although disentangling these forces is difficult, large scale in situ observations of invasive species in habitats characterized by different disturbance regimes can help elucidate the forces driving community change.

In 1998, an invasive sea squirt *Didemnum vexillum* was detected on Georges Bank, and has since colonized at least 230 km² of pebble-gravel habitat on Georges Bank (Valentine et al. 2007a, b; Bullard et al. 2007; Cohen et al. 2011; Moore et al. 2014). This tunicate originated from coastal Japan (Stefaniak et al. 2012) and is a global invader that has spread to Europe, New Zealand and both coasts of North America (Kott 2002; Bullard et al. 2007; Gittenberger 2007; Epelbaum et al. 2009; Cohen et al. 2011; Stefaniak et al. 2012; Moore et al. 2014). It is considered a nuisance species because it can foul ship hulls and maritime structures in addition to invading shellfish aquaculture sites and fishing grounds (Daley and Scavia 2008; Carman et al. 2009). *D. vexillum* can reproduce both sexually and asexually. However asexual reproduction and fragmentation are most likely the primary method by which the species spreads (Lengyel et al. 2009; Morris and Carman 2012), since larvae only remain in the water column for generally <1 day (Osman and Whitlatch 2007) and growth from fragments can also occur in cold water temperatures, which occur on the seafloor of Georges Banks (Carman et al. 2014). Even though there is limited information on the ability of this species to spread naturally via floating debris or other means, anthropogenic transport is considered the primary vector for the long-distance spread of this species (Osman and Whitlatch 2007; Herborg et al. 2009). The most probable transport vector for *D. vexillum* is direct transport of colonies fouled on aquaculture equipment, boat hulls, fishing gear or other mobile structures, or the indirect transport of colony fragments where small parts of the colonies break off during transport or disturbance by dredging or trawling (Herborg et al. 2009).

The characteristics of *D. vexillum* such as early maturation, rapid colony growth due to asexual budding, spread via colony fragmentation, ease of attachment to firm substrates, toleration of a wide range of temperatures, and the lack of natural

predators have resulted in rapid population growth (Bullard et al. 2007; Carman et al. 2009; Valentine et al. 2009). The combination of these characteristics leads *D. vexillum* to outcompete other benthic epifauna and macrobiota. For example, it has been shown to inhibit other benthic species from settling and growing on colony surfaces due to acidic and organic allelopathic compounds in their tunics (Valentine et al. 2007a; Carman et al. 2009; Morris and Carman 2012). A particular concern is that this tunicate has invaded the gravel habitat of the Atlantic sea scallop, which supports a highly valued commercial shellfish fishery on Georges Bank (Kaplan et al. 2017). Scallop spat are not able to settle on *D. vexillum*, so the invasion of this tunicate can make productive habitat inaccessible to scallops (Morris et al. 2009; Dijkstra and Nolan 2011; Kaplan et al. 2017). Additionally, in experimental studies scallops covered by *D. vexillum* became exhausted more quickly and were not able to swim as far as the control sea scallops without *D. vexillum* encrustation, which has implications for *D. vexillum*'s ability to increase sea scallop vulnerability to predation and limit their access to food rich habitats (Dijkstra and Nolan 2011).

Dredging disturbances during commercial fishing for sea scallops reduce the diversity and abundance of benthic communities in the region (Auster et al. 1996; Collie et al. 1998). Further studies indicate that bottom-fishing gear damages epifaunal taxa, thereby reducing habitat complexity (Jennings and Kaiser 1998; Fogarty and Murawski 1998). Additionally studies have found that the spread of *D. vexillum* is greater in areas open to bottom-fishing and *D. vexillum* is negatively correlated with the commercially valuable Atlantic sea scallop *P. magellanicus* (Kaplan et al. 2017). However, no studies in this region have examined the interaction of disturbance from dredging with the spread of an invasive species and the relative influence of these processes on the macroinvertebrate community of Georges Bank. The presence of closed areas on Georges Bank provides a unique opportunity as a location for collecting control data to compare to a habitat disturbed by dredging on benthic community structure.

In this study we used photo-transects to explore the spatial distribution of benthic marine invertebrates and *D. vexillum* in areas protected and unprotected from bottom-fishing on Georges Bank. We hypothesize that the presence of *D. vexillum* alters the observable

primary cover in the epibenthic macroinvertebrate community and is the primary driver of macroinvertebrate biodiversity decline supporting the driver hypothesis of invasive species impacts. We assess how the invertebrate community changes in the presence of *D. vexillum* using principal components analysis and we evaluated correlations between invertebrate species density and *D. vexillum* density. We also investigate whether bottom-fishing influences associations among species using a principal components analysis, and assess if the abundances of these invertebrates is greater in areas open or closed to bottom-fishing. Using the closed area as a control to compare to the fished area, we evaluate if *D. vexillum* or disturbance and extraction from bottom-fishing is the main driver of biodiversity loss. This work can further our understanding of invasive species as a direct or indirect influence on biodiversity and ecological communities. The closed area, where bottom-fishing is prohibited, and the open area disturbed by bottom-fishing provide a natural experiment for assessing the impact of an invasive species relative to dredging extraction and disturbance on biodiversity of invertebrate communities.

Materials and methods

Study area

Georges Bank is a shallow, highly productive, submerged plateau with depths ranging up to 100 m deep off the coast of New England that supports several valuable commercial fisheries (Butman and Beardsley 1987). Surficial sediments of Georges Bank are dominated by large expanses of sand substrate interspersed with gravel and gravel/sand regions that mainly occur on its northern and western portions (Twichell et al. 1987). On the northeastern part of the bank, currents transport sand into deep water leaving gravel habitat along the northern edge. The study site is located in the northeastern portion of Georges Bank, inside and adjacent to a zone protected from bottom-fishing known as Closed Area II (Fig. 1). The portion to the west of 67°20' is open to fishing, while the portion to the east, in Closed Area II, has been closed to all groundfish and scallop gear since December 1994 and contains both sand and gravel substrates as well as high densities of *D. vexillum* in some locations

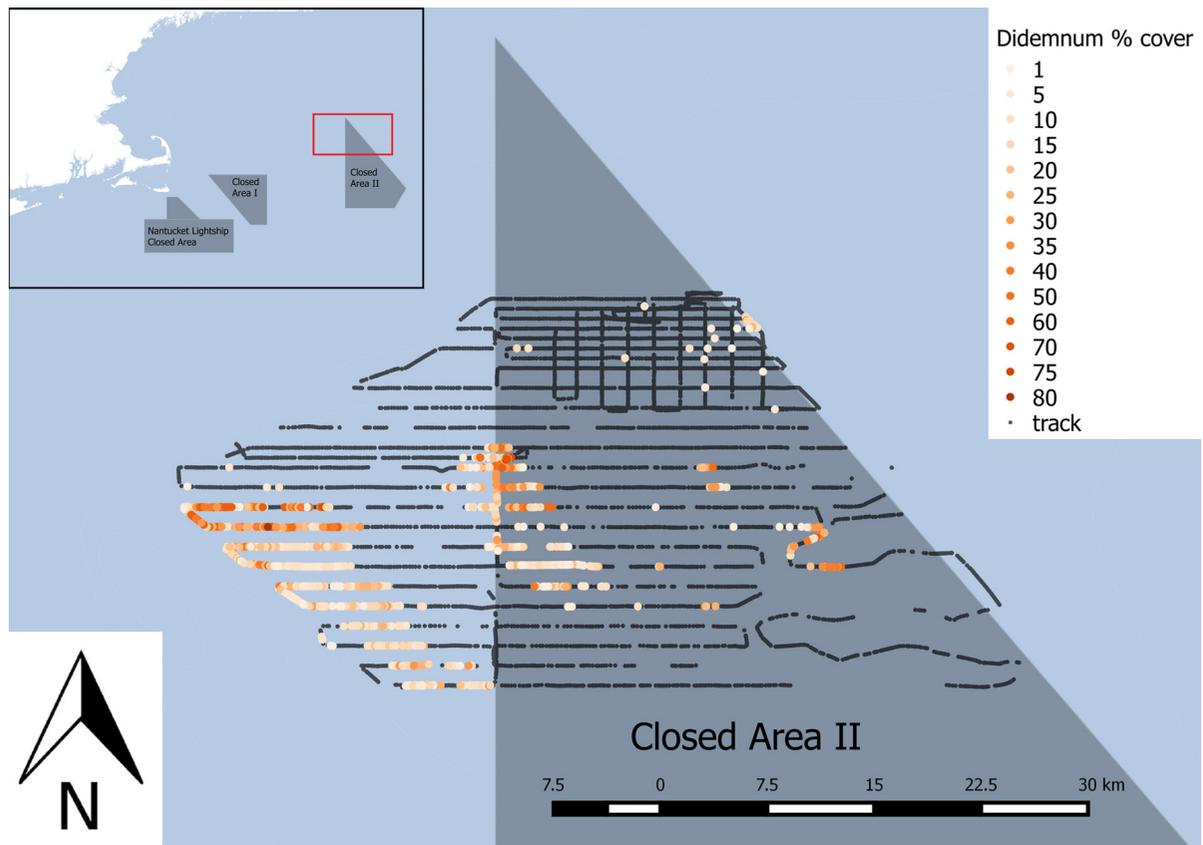


Fig. 1 Map of Closed Area II with HabCam track showing percent *D. vexillum* cover from 2012 survey

(Fig. 1). The area to the west of Closed Area II is open to fishing and therefore experiences benthic disturbance through bottom-fishing (Collie et al. 1998; Asch and Collie 2008). These two areas, one closed and one open to fishing, were utilized to compare the effects of *D. vexillum* on other benthic invertebrate species in areas of differing disturbance levels.

Data collection

The habitat camera mapping system (HabCam) is a vessel-towed underwater camera system which carries digital still cameras, strobes, and a variety of oceanographic sensors.

Data for this project were collected from HabCam version 2 (v2), an imaging system that provides visual surveys of benthic marine organisms without disturbing the habitat itself (Howland et al. 2006; Taylor et al. 2008; York et al. 2008). These data can be used to

evaluate physical features of the environment that drive spatial and temporal variability of benthic invertebrates. The HabCam vehicle is towed at speeds of 5–6 knots during which it collects data at a rate of about six images per second providing a continuous band of data input along the survey track, which ranged from 40 to 72 m depth. The equipment on HabCam v2 includes a digital still camera (UNIQ Vision, Inc. UP-1800-CL), and four machine vision strobes (Perkin Elmer MVS-5000) mounted in underwater housings placed radially around the camera 50 cm apart. Other sensors on HabCam v2 include a CTD (SBE 37-IS MicroCat, Seabird electronics Inc.) for conductivity and temperature measurements, a YSI 6600 Sonde multiparameter sensor, and a Benthos altimeter (PSA-916), which measures distance from the vehicle to the bottom. The data for this project were collected on the F/V *Kathy Marie* using HabCam v2 in July of 2012 (Fig. 1).

Data processing

HabCam images were annotated to distinguish members of the invertebrate community, which were identified to species, genus or family level depending on the species for one in every 200 images collected during the July 2012 survey by one of the co-authors (Karen Hopkins analyzed all images and participated in the 2012 survey). Thus, image analysis was standardized by having the same person analyze all photos. Species could be distinguished between the 5–10 mm range depending on the altitude of the camera. In total 5309 images were annotated for members of the invertebrate community both in and adjacent to Closed Area II (Fig. 1). This study focused on epibenthic diversity of organisms >5 mm in size and infaunal organisms or smaller bodied species were not assessed.

Locations of invertebrates were identified as being inside or outside of the closed area using the intersect and difference geoprocessing tools in Quantum GIS (QGIS development team 2015) and these were subsequently separated for analyses. Density estimates for each species were obtained by dividing species counts by the area of the field of view for each image. Sediment composition was evaluated visually based on the fraction of the image covered. Bryozoa and *D. vexillum* percent cover was also determined based on visual estimates of the fraction of the image that was covered.

Data analysis

Species interactions with D. vexillum

Correlations of benthic invertebrates with *D. vexillum* were assessed in the open and closed areas using hurdle models where the presence or absence of the species was modeled using a generalized linear model (GLM) under a binomial distribution, then the nonzero count data were modeled using a Poisson distribution to identify the relationship between the density of each species using *D. vexillum* as a predictor (Potts and Elith 2006). The coefficients from presence-absence and count model predictions were then multiplied to create the final hurdle model investigating the relationship between *D. vexillum* and other benthic species. Hurdle models were used since there were a large number of images containing zero species. Over-dispersion was

detected for many species; therefore for these species a Poisson quasi-likelihood was used to fit the GLMs, in which the variance is given by $\Phi * \mu$, where μ is the mean density and Φ is the overdispersion parameter, thus allowing the variance to be greater than the mean. Additionally, gravel substrate was used as a predictor in all models with gravel held at the mean value for model predictions to control for the effect of substrate, since substrate also was a main predictor of species distributions. The invertebrate taxa analyzed in this study tend to associate with particular substrates, with the majority of taxa having a strong association with gravel habitat. To avoid co-linearity only gravel substrate was used as a predictor. Data for all species and percent gravel cover were first averaged based on approximately 1 km blocks to reduce localized noise as well as spatial auto-correlation and then these data were used in hurdle models. Additionally, associations among species were assessed using principal components analysis (PCA) in the presence and absence of *D. vexillum* to assess if *D. vexillum* restructures associations among species. A scaled correlation matrix was used for all principal components analyses since species were assessed on different scales, as counts or percent coverage.

Disturbance effect on invertebrate community

The influence of disturbance caused by bottom-fishing in relation to the protected area on the invertebrate community was analyzed using analysis of covariance (ANCOVA) with the percentage gravel substrate as a covariate, since most of the species analyzed appear to correlate positively with gravel. Co-linearity was observed between the two most dominant substrate types, gravel and sand (adjusted $R^2 = 0.875$), and hence only gravel was used as a covariate in the analyses. The influence of *D. vexillum* and the disturbance effect were also assessed by measuring species diversity using the Shannon diversity index calculated per site. Areas containing high gravel (>50%) were separated from non-gravel areas for the site-level biodiversity analyses.

Results

A total of 16 taxa were resolved to the level of species or higher taxonomic group (genus, family and

phylum) in images processed. These included sponges (two genera: *Lophon* Günther, 1880; and *Polymastia* Bowerbank, 1862), sea stars (one genus: *Asterias* Linnaeus, 1758; and one species *Crossaster papposus* Linnaeus, 1767), anthozoan cnidarians (one genus: *Cerianthus* Delle Chiaje 1830), polychaete worms (one genus: *Mxyicola* Koch in Renier, 1847; and one species: *Filograna implexa* Berkeley, 1835), bivalves (one family: Mytilidae Rafinesque, 1815; and one species: *Placopecten magellanicus* Gmelin, 1791), barnacles (one genus: *Balanus* Costa 1778), crabs (two species: *Cancer borealis* Stimpson, 1895; and *Cancer irroratus* Say, 1817), Bryozoa (phylum), sea urchins (one species: *Strongylocentrotus droebachiensis* O.F. Müller, 1776) and ascidians (two species: *Boltenia ovifera* Linnaeus, 1767; and *D. vexillum* Kott 2002).

Species interactions with *D. vexillum*

Based on model fits using the hurdle models, species demonstrating a negative correlation to percent coverage of *D. vexillum* were the Atlantic sea scallop (*P. magellanicus*), barnacles (genus *Balanus*), the tube anemone (genus *Cerianthus*), the green sea urchin (*S. droebachiensis*), the globular sponge of the genus *Polymastia*, and Bryozoa (Fig. 2a–f). A positive correlation was observed with the *Cancer* crabs (*C. irroratus*, and *C. borealis*), sea stars of the genus *Asterias* (primarily *A. vulgaris*, but *A. forbesi* may have also been present), sponges of genus *Lophon*, and the lacy tubeworm (*F. implexa*) (Fig. 2g–k). Several species showed no significant correlation with *D. vexillum* in the hurdle models including the sunstar *C. papposus*, mussels of the family Mytilidae, marine worms of the genus *Myxicola* and the stalked tunicate (*B. ovifera*) (Fig. 2l–m).

HabCam images are shown of *D. vexillum* with some species which it positively associates with such as *Asterias* sea stars, the *Cancer* crab *C. borealis*, the encrusting sponge of the genus *Lophon* as well as species it negatively associates with, such as sea scallops (*P. magellanicus*) and barnacles (*Balanus* sp.) (Figure 3a–d). Sea stars appear to traverse areas with patchy *D. vexillum* infestation (Fig. 3c). However, no other species are apparent in areas that are almost entirely covered with *D. vexillum* (Fig. 3a).

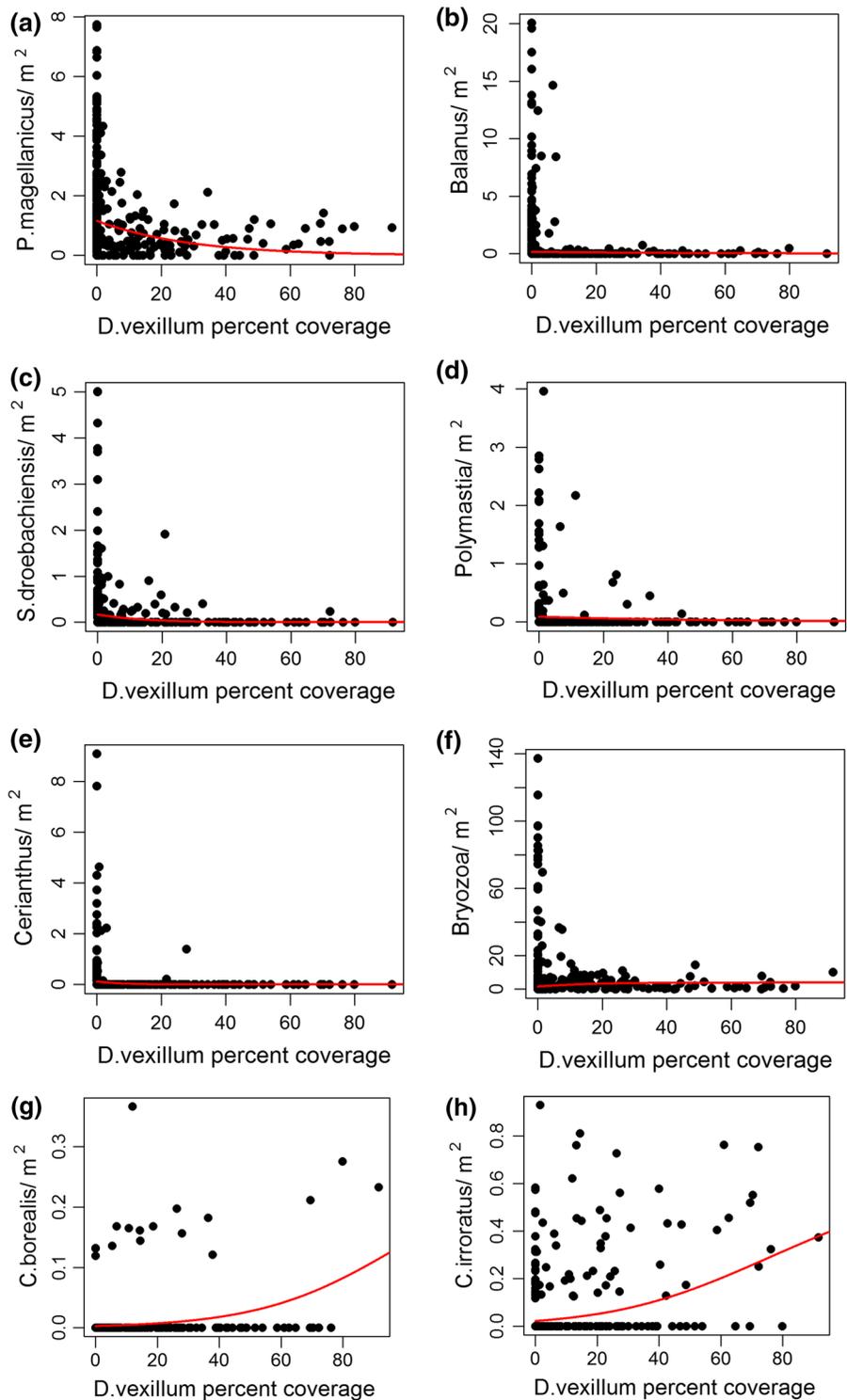
In high gravel habitat, principal components analysis (PCA) demonstrated that *D. vexillum* was a strong driver of variation among sites when present in the

community in closed and open areas (Fig. 4). The invertebrate community without *D. vexillum* appears to be characterized by three distinct associations, whereas groupings among these species are rearranged in the presence of *D. vexillum* (Fig. 4a–d). The community of species that exists in the area despite the presence of *D. vexillum* is comprised of species such as the sunstar *C. papposus*, Bryozoa, mussels of the family Mytilidae, and the stalked tunicate *B. ovifera*, which appear in the PCA as a distinct community orthogonal to the *D. vexillum* community (Fig. 4b, d). Also, the marine worm (*Myxicola*), the sunstar *C. papposus* and the Jonah crab (*C. borealis*) were not found in open area sites without *D. vexillum*, showing overall lower species richness. The sunstar *C. papposus* was also not present in closed area sites without *D. vexillum*. However, absence of *C. papposus* and *C. borealis* in particular areas may simply be due to these species being relatively rare on Georges Bank. The total number of *C. papposus* sunstars found was 19 individuals identified in 5309 images annotated in this study, while 18 Jonah crabs *C. borealis* were observed. By contrast, over 100 individuals of all other invertebrate species in this study were observed; relative abundances of the study species is shown in a rank abundance plot (Fig. 7 in Appendix).

Disturbance effect on invertebrates

The effect of disturbance from bottom-fishing in comparison to the protected area was assessed using ANCOVA with significant interactions shown (Table 1, Fig. 5a, b). Barnacles of the genus *Balanus*, sea scallops (*P. magellanicus*), the green sea urchin (*S. droebachiensis*), Bryozoa, mussels (family Mytilidae), the marine worm (genus *Myxicola*), globular sponges (genus *Polymastia*), and the stalked tunicate (*B. ovifera*) were more abundant in the closed area than the open area (Fig. 5). On the contrary, species found in greater abundance in the area open to bottom-fishing include: *Asterias* sea stars, the tube anemone (genus *Cerianthus*), the encrusting sponge (genus *Lophon*), the sunstar *C. papposus*, *D. vexillum*, the lacy tubeworm (*F. implexa*), and the *Cancer* crabs (Fig. 5). Associations among taxa change in the open area as compared to the closed area indicating bottom-fishing influences these relationships (Fig. 4a–d). A cluster of taxa associated with *D. vexillum* is present in both the open and closed area PCA, though this group

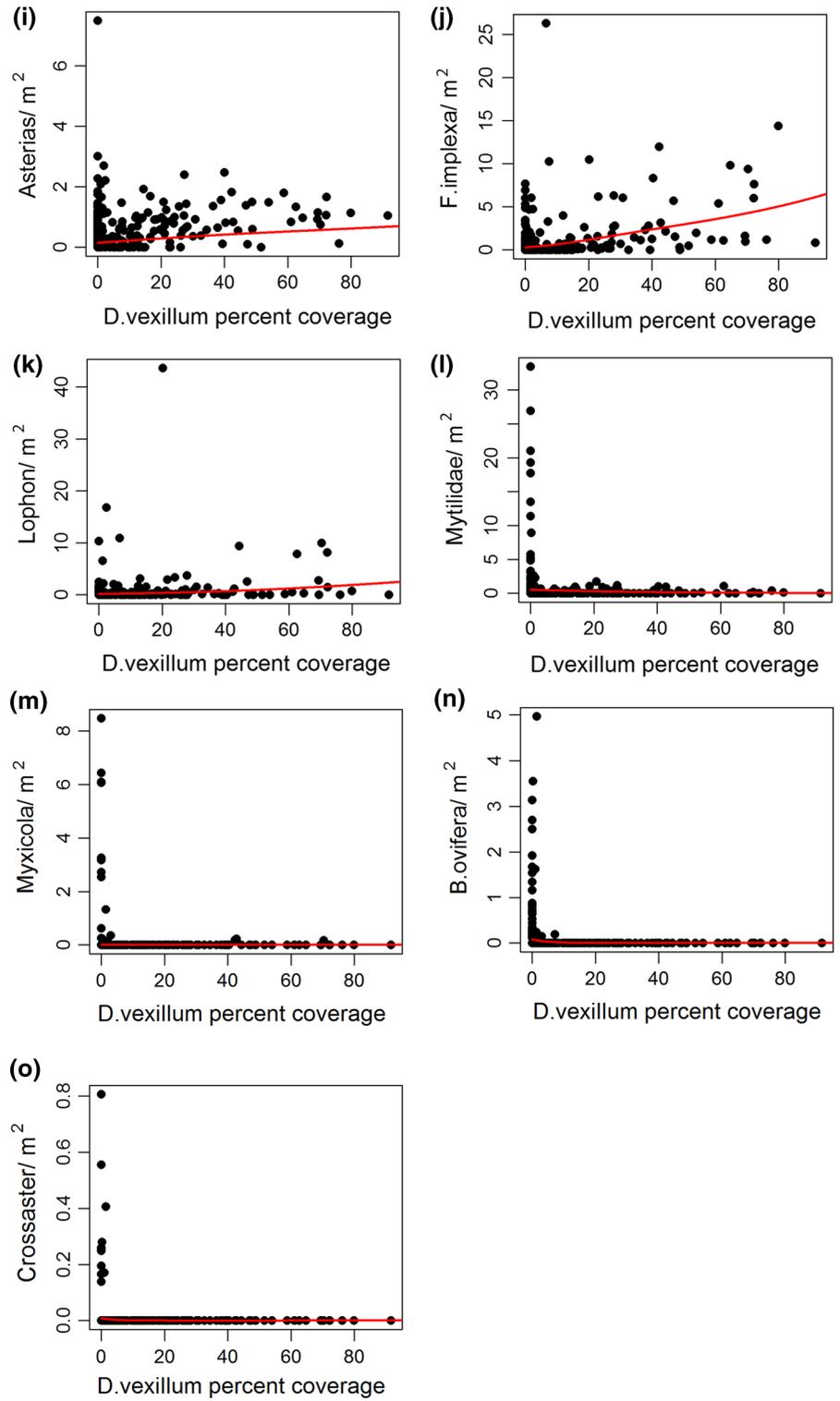
Fig. 2 Model fits for relationship of *D. vexillum* and other invertebrate species in benthic community using hurdle models



is more closely clustered in the area closed to bottom-fishing than the area open to bottom-fishing. However, *Asterias* sea stars and the crab *C. borealis* associate

more closely with the *D. vexillum* community in the area open to bottom-fishing, but are not part of that community in the closed area (Figs. 3, 4).

Fig. 2 continued



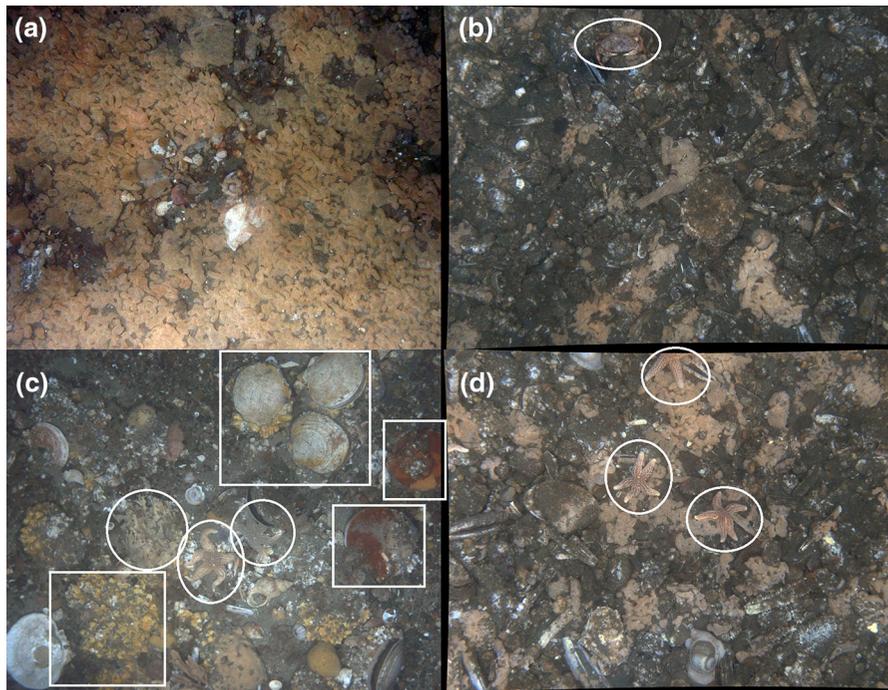


Fig. 3 Images from Habcam with invertebrate species positively associating with *D. vexillum* shown in *circles*, species with negative association with *D. vexillum* shown in *squares*. **a** *D. vexillum* covering benthic environment. **b** *Cancer* crab with

D. vexillum patches. **c** Sea scallops (*P. magellanicus*), barnacles (*Balanus*), sea stars (*Asterias*), and encrusting sponge of the genus *Lophon*. **d** Sea stars (*Asterias*) over *D. vexillum* patches

Didemnum vexillum and bottom-fishing impacts on biodiversity

Biodiversity as measured by the Shannon index per site for areas with high gravel cover demonstrated a decline with increasing *D. vexillum* percent coverage (Fig. 6). Additionally the Shannon index as measured per site was not significantly different between the areas open and closed to bottom-fishing (Table 2). The total abundance of all counted taxa in the closed area was 4459 individuals, whereas in the open areas the total abundance was 1150 individuals. *D. vexillum* and Bryozoa were assessed by percent coverage and not included in count totals or biodiversity index calculation.

Discussion

The presence of *D. vexillum* appears to shift associations among taxa since it is a major driver of variation among sites when present in the community. Increasing percent coverage of *D. vexillum* also induced a

decline in biodiversity of macroinvertebrates as measured by the Shannon index, although the effect of the different extractive pressure and disturbance regimes, as measured by sites in areas open or closed to bottom-fishing, had no significant effect on the decline in biodiversity (Fig. 6; Table 2). This finding indicates that *D. vexillum* is the major driver of biodiversity decline among macroinvertebrates in the epibenthic environment particularly when it comes to dominate the community, rather than other causes of habitat modification such as disturbance and extraction via bottom-fishing. Our results on the effects of *D. vexillum* on invertebrate biodiversity corroborate another study on the impact of *D. vexillum* on epifauna and macrofauna on Georges Bank, which used bottom photographs and a Naturalist dredge to determine that *D. vexillum* percent cover was inversely related to macrofauna and appears to outcompete epifaunal and macrofaunal taxa (Lengyel et al. 2009). In contrast, the results from a study conducted in Long Island sound at shallower depths (30 m), sampled below *D. vexillum* colonies using core samples and suction samples and did not find significant differences in invertebrate

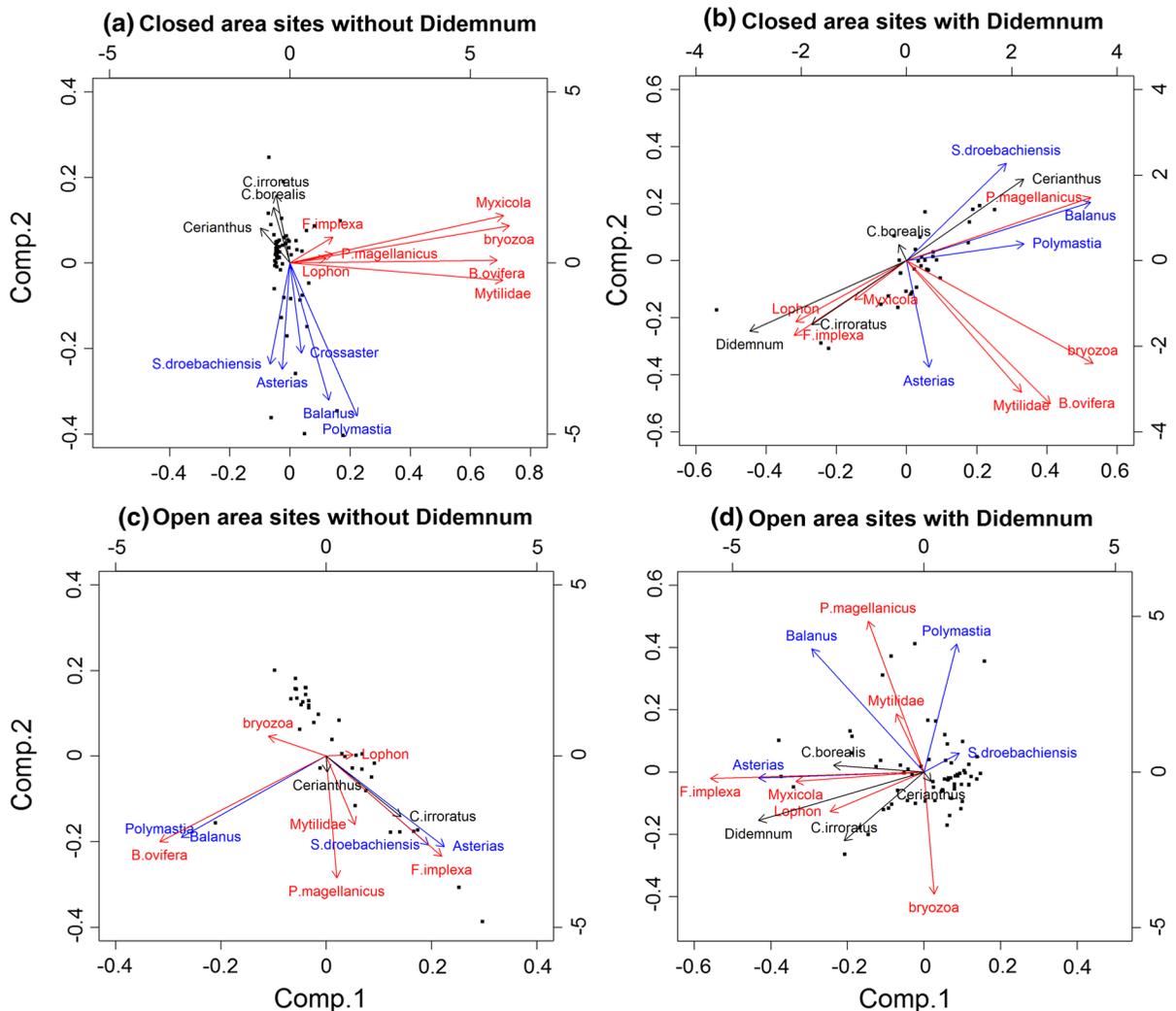


Fig. 4 Sites with > 50% gravel substrate **a** closed areas without *D. vexillum*, PC 1 = 0.23 proportion of variance, PC 2 = 0.11, **b** closed areas with *D. vexillum* present, PC 1 = 0.27,

PC 2 = 0.20, **c** open areas without *D. vexillum*, PC 1 = 0.24, PC 2 = 0.21 and, **d** open areas with *D. vexillum* present, PC 1 = 0.18, PC 2 = 0.14

richness between samples taken from *D. vexillum* mats and those taken outside, with infauna and deposit feeders actually having greater abundance in areas covered by *D. vexillum* (Mercer et al. 2009). Additionally, a study conducted in Alaska also at shallower depths (4–7 m) than our study did not find a significant relationship between *D. vexillum* cover and overall species richness or abundance though significant differences between infested and uninfested plots were found for sessile species, but not for mobile fauna (McCann et al. 2013).

The results from our study apply to the epibenthic environment of depths ranging from 40 to 70 m on

Georges Bank and not to infaunal biodiversity, which was not assessed in this study. Assessing invertebrate communities found within sedimentation and deeper than the epibenthic environment may yield different results on the impact of *D. vexillum* on benthic communities. Nonetheless, our results are consistent with other studies from our study area, but contrast to studies of *D. vexillum* from other areas and depth ranges (Lengyel et al. 2009; Mercer et al. 2009; McCann et al. 2013). It is also necessary to note that in this study several taxonomic groups were not discernable to species level, with some being evaluated at genus, family or phylum. Therefore, results and the

Table 1 Closed area effect on invertebrate taxa of Georges Bank

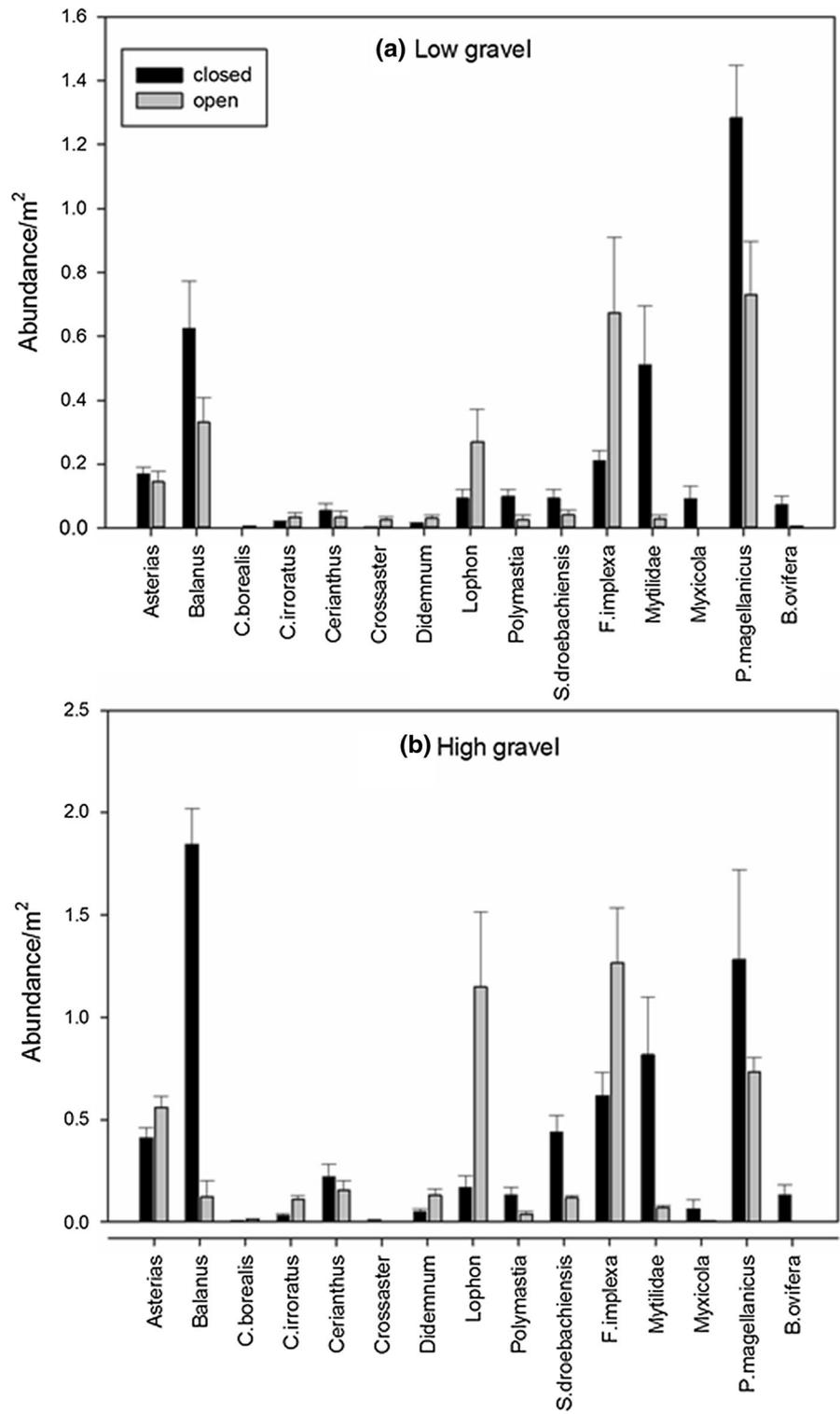
	Taxa	Closed area effect (\pm)	Gravel coefficient	Interaction
Analysis of covariance (ANCOVA)	<i>Balanus</i>	*** (+)	0.021**	**
	<i>P. magellanicus</i>	*** (+)	0.016***	
	<i>Asterias</i>	*** (-)	0.009***	
	<i>S. droebachiensis</i>	* (+)	0.006***	**
	Bryozoa	*** (+)		
	Mytilidae	** (+)		
	<i>Cerianthus</i>		0.004***	
	<i>Mxyicola</i>	* (+)		
	<i>Lophon</i>	*** (-)	0.001**	**
	<i>Polymastia</i>	* (+)		
	<i>Crossaster</i>			
	<i>Didemnum</i>	*** (-)	0.13***	**
	<i>F. implexa</i>	*** (-)	0.01***	
	<i>B. ovifera</i>	** (+)		
Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$	<i>C. irroratus</i>	*** (-)	0.0003***	*
	<i>C. borealis</i>	**(-)	1.06×10^{-4} *	

conclusions drawn may be different if taxonomic groups were discernable to species level. Additionally, organisms were identifiable in images when larger than 5 mm therefore, our study evaluates the relationship of *D. vexillum* with macroinvertebrates only and the effect of *D. vexillum* on smaller bodied invertebrates may differ than the results shown. Future studies may evaluate the relationship of *D. vexillum* on invertebrates smaller than 5 mm by collecting grab samples, which would also enable higher taxonomic resolution.

Macroinvertebrate taxa associated together in the absence of *D. vexillum* appear to aggregate based on a positive or negative association with *D. vexillum*, creating a realignment in the invertebrate community when it is present (Fig. 4). *D. vexillum* positively associates with some invertebrates, which may have more tolerance to the acidic tissues the tunicate produces, while it appears to have negative associations with other key species of the benthic environment that may be more sensitive to its presence. For example the Cancer crabs *C. borealis* and *C. irroratus*, the lacy tubeworm *F. implexa* and *Asterias* sea stars are positively correlated with *D. vexillum* when modeling each species' response to *D. vexillum* independently (Fig. 2). In assessing the multivariate PCA of high gravel habitat, more motile species, such as the Cancer crab *C. irroratus*, as well as less motile species such as the lacy tubeworm *F. implexa*, the

marine worm *Myxicola* and the encrusting sponge of the genus *Lophon* seem to form a distinct community with *D. vexillum*. Conversely species such as barnacles of the genus *Balanus*, the Atlantic sea scallop (*P. magellanicus*), the tube anemone of the genus *Cerianthus*, the green sea urchin (*S. droebachiensis*), and mussels of the family Mytilidae negatively correlate to *D. vexillum*. It is important to note that the majority of taxa which negatively associate with *D. vexillum* are also less abundant in the area open to bottom-fishing since these species are more sensitive to disturbances due to bottom-fishing (Asch and Collie 2008), or in the case of *P. magellanicus*, directly harvested. Other studies have shown that disturbed habitat is more susceptible to invasive species (Lozon and MacIsaac 1997; Marvier et al. 2004), which was also found in this study since the open area disturbed by bottom-fishing is more heavily invaded. Furthermore, *D. vexillum* may be more abundant in the open area since fishing vessels are likely a vector for its spread (Herborg et al. 2009); dredging may fragment colonies that can attach to bottom-fishing gear and further its spread in the benthos. Therefore, the disturbance caused by dredging and commercial fishing vessels acting as a vector for its spread may interact to introduce and then allow *D. vexillum* to proliferate in the more disturbed habitats. Alternatively, the space opened by dredging could allow for the highly fecund *D. vexillum* to take advantage of disturbed habitat

Fig. 5 The effect of the closed area on abundances of benthic invertebrate taxa in **a** low gravel and **b** high gravel habitats. ANCOVA results are reported in Table 1



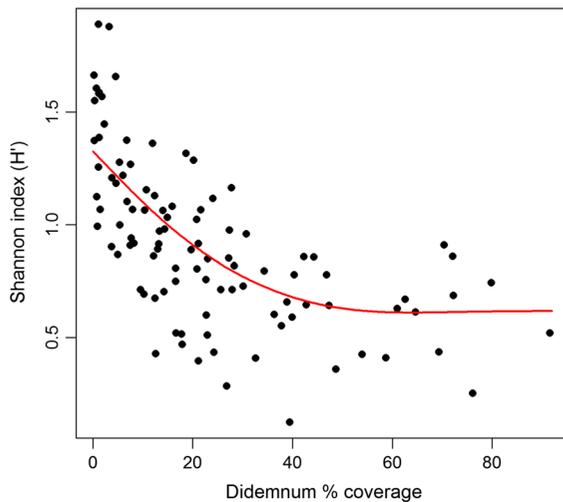


Fig. 6 *Didemnum vexillum* impacts on biodiversity as measured by Shannon index of biodiversity per site in high gravel habitat only. A generalized additive model was used to predict Shannon index response to *D. vexillum*, gravel percent cover and Area (closed or open) (Table 2)

more quickly than other species. However, once the area has been invaded by *D. vexillum*, its presence, rather than the process of bottom-fishing is likely the strongest driver of biodiversity decline.

Since several taxa analyzed in this study have a negative correlation with the presence of *D. vexillum*, there may be a decline in the abundance of members of the invertebrate community in areas infested with *D. vexillum*. Alterations to the benthic habitat on Georges Bank due to *D. vexillum* may also affect productivity of fisheries in the region since the gravel habitat it prefers is also habitat for juvenile fishes and scallop spat, though more research is necessary to determine this invasive species' impact on fishery productivity. Predators of *D. vexillum* include sea urchins (*S. droebachiensis* and *S. franciscanus*, though *S. franciscanus* is a Pacific coast species), although in experimental tests these predators prefer other food sources when available (Epelbaum et al. 2009).

Unexpectedly, the green sea urchin (*S. droebachiensis*) was found to be negatively correlated to *D. vexillum* and is not part of its community cluster in either open or closed area PCAs when *D. vexillum* is present. Another study in New Zealand indicated that sea star and sea urchin predators may limit the spread of *D. vexillum* (Forrest et al. 2013), although the species of predators examined in these studies are not found on Georges Bank. Therefore the spread of *D. vexillum* on Georges Bank may at least be partially due to the lack of natural predators and competitors.

The lacy tubeworm *F. implexa*, was found to positively associate with *D. vexillum* and is part of the same community in the multivariate analysis. Consistent with other studies, encrusting taxa such as the lacy tubeworm have been found in disturbed shallow habitat in high densities and are known as early colonizers (Asch and Collie 2008; Collie et al. 2009). The lacy tubeworm may also have a relationship with the *Cancer* crabs, since crab species are also known to utilize the calcareous tubes the lacy tube worms produce as habitat to reduce risk of predation (Heck and Hambrook 1991). Furthermore, laboratory experiments have indicated that *Cancer* crabs can prey on other species of solitary ascidians such as *Ascidella aspersa*, *Ciona intestinalis*, and *Styela clava*, which are not found on Georges Bank, but not on colonial ascidians such as *D. vexillum* (Dijkstra and Harris 2007).

Bottom-fishing also appears to restructure some associations among species as found in our multivariate analysis. Most species associated with *D. vexillum* are scavengers that are more abundant in the open area impacted by bottom-fishing. Specifically *Asterias* sea stars, and the crab *C. borealis* were more closely associated with species found in the *D. vexillum* community in the open areas whereas these species were not associated with the *D. vexillum* group in the closed areas (Fig. 4). *Asterias* sea stars were also found to be more abundant at disturbed sites in high

Table 2 Generalized additive model fit for Shannon index response to *D. vexillum*, gravel and area (open or closed) predictors

Response variable	<i>D. vexillum</i> (edf)	Area (SE)	Gravel (edf)
Shannon index	***	-0.065	*
Deviance explained = 65%	(3.91)	(0.05)	(6.60)
		Not significant	

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

gravel habitat (Fig. 5), which may be explained by the fact that they scavenge and have been reported to feed on organisms damaged by bottom-fishing (Ramsay et al. 1998; Jenkins et al. 2004). Sea stars may be tolerant of *D. vexillum* tissues as demonstrated by their close spatial association in HabCam images (Fig. 3). Moreover, sea star predation as well as intra and interspecific interactions among sea stars have been shown to affect the distributions of invertebrate prey species (Gaymer et al. 2004; Shank et al. 2012). The most motile species analyzed in this study are the *Cancer* crabs and their motility may enable them to inhabit and traverse areas infested with *D. vexillum* without having a significant negative impact on their distribution in these areas. Moreover, *Cancer* crabs are also scavengers that may colonize disturbed habitats and consume prey items damaged or discarded from bottom-fishing (Collie et al. 2009). Studies have shown that they utilize chemical cues to detect, locate and identify food items (Rebach 1996); thus the presence of discards and prey items damaged by bottom-gear may attract these crabs to the open area. Scavengers including *Cancer* crabs and *Asterias* sea stars in the Irish Sea have been shown to aggregate around damaged scallops in particular, having implications for an increase in incidental scallop mortality caused by dredge gear (Jenkins et al. 2004). *Cancer* crabs have also been shown to break open even lightly damaged scallop shells (Jenkins et al. 2004). Therefore, *Cancer* crabs higher abundance in the open area may be explained by greater access to food resources as a result of bottom-fishing.

Bottom-fishing may alter interactions among species that together drive variation among the sites as observed in the PCA. The clustering among three species groups identified by color in the closed area PCA without *D. vexillum* appears more diffuse and not as tightly clustered in the open area PCAs (Fig. 4). Species may associate with each other to form mutualistic relationships that serve an ecological purpose such as predator avoidance in the case of *Cancer* crabs using calcareous tubes formed by the lacy tubeworm *F. implexa* (Heck and Hambrook 1991), although this relationship may be altered in the presence of bottom-fishing if these tubes are crushed. Generally, scallop dredging on Georges Bank creates a high level of disturbance as compared to natural disturbances created by storm events (Jennings and

Kaiser 1998). Previous research has shown that areas impacted by bottom-fishing are found to have lower abundance of organisms, lower species richness and lower diversity as compared to areas that are undisturbed (Collie et al. 1998; Asch and Collie 2008). Additionally, bottom-fishing affects the physical structure of the benthos and benthic community functional groups (Tillin et al. 2006; Hinz et al. 2009). Heavily trawled areas have been found to have greater abundances of motile animals, as well as infaunal and scavenging invertebrates, while attached filter-feeding, and larger more sedentary animals are more abundant in areas with lighter trawling effort (Tillin et al. 2006). However our results indicate that area as a factor did not have a significant effect on the decline in biodiversity as measured by the Shannon index per site, which was driven primarily by *D. vexillum*.

Studies conducted in the Gulf of Alaska and Irish Sea show that most motile organisms are less severely affected by chronic and experimental trawling than Anthozoa, sponges, Bryozoa, tubicolous polychaetes and barnacles (Freese et al. 1999; Bradshaw et al. 2002). Species with softer tissues are more vulnerable to bottom-fishing impacts as compared to encrusting species with more durable or hard exteriors (Asch and Collie 2008). In this study encrusting sponges of the genus *Lophon* were more abundant in the open area than the closed area whereas globular sponges of the genus *Polymastia* demonstrated the opposite relationship since their softer tissues may make them more sensitive to bottom-fishing impacts (Asch and Collie 2008). The effects of bottom-fishing may be cumulative, therefore small-scale experimental studies cannot capture longer-term large-scale spatial and temporal trends that can be extrapolated to the ecosystem level (Hinz et al. 2009). In contrast to small-scale experimental studies, this observational study evaluates a large area in situ providing detailed observations of ecological interactions in the northern edge of Georges Bank, though more data is needed to evaluate trends over time.

Didemnum vexillum may also be more widespread in habitat disturbed by dredging since disturbed habitats are generally more susceptible to invasive species (Lozon and MacIsaac 1997; Didham et al. 2007). It is also present in the closed area, albeit at lower densities than the open area; however, even in

the closed area, its presence still has a strong impact in driving variation among sites. *D. vexillum* appears to be a key driver of ecological change in the study area regardless of disturbance regime, which is consistent with other studies supporting the driver hypothesis of invasive species impacts on native communities (Light and Marchetti 2007). The area effect, representing different levels of disturbance from bottom-fishing processes, was not significant in affecting the Shannon index as measured per site, which would be expected to show a significant effect if bottom-fishing was a driver of biodiversity loss as indicated in the passenger and back-seat driver hypotheses (MacDougall and Turkington 2005; Bauer 2012). Therefore, the results from this study are most consistent with the driver hypothesis in characterizing the effects of this invasive species on biodiversity.

In this study we examined interactions of an invasive tunicate *D. vexillum* with other taxa of the invertebrate community on Georges Bank and found it appears to restructure the invertebrate community when present. This study demonstrates the impact of this invasive tunicate is stronger in altering the ecological community and biodiversity than direct disturbance caused by bottom-fishing. Furthermore, we have demonstrated the extensive impacts an invasive species can have on benthic communities and biodiversity using advanced technology for observing a commercially important region over a large scale. Large scale in situ studies comparing fished and protected areas provide valuable insights into understanding ecological interactions in these communities, which can be used to implement ecosystem-based strategies into marine management.

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Appendix

See Fig. 7.

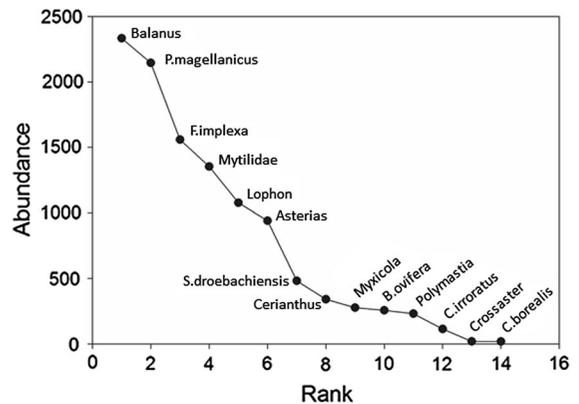


Fig. 7 Rank abundance plot of all count taxa found in the study area

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