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Original Article

Evaluating the interaction of the invasive tunicate *Didemnum vexillum* with the Atlantic sea scallop *Placopecten magellanicus* on open and closed fishing grounds of Georges Bank

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An invasive colonial tunicate (*Didemnum vexillum)* was initially observed on Georges Bank in 1998, and it has since spread in benthic environments on fishing grounds and areas closed to bottom-fishing. It can form dense mats on gravel substrates that are also a preferred habitat for the Atlantic sea scallop (*Placopecten magellanicus*), which supports one of the most valuable commercial fisheries in the United States. We used HabCam, a vessel-towed underwater imaging system, to investigate the spatial distributions of *P. magellanicus* and *D. vexillum* in a region that includes fishing grounds and an area protected from bottom-fishing. We found a negative relationship between *P. magellanicus* and *D. vexillum*, even after controlling for substrate and management status, suggesting that *D. vexillum* competes for habitat with *P. magellanicus*. We also applied the geostatistical method of universal kriging to interpolate the distribution of *D. vexllium* based on the covariables gravel, depth and area. Our results indicate that *D. vexillum* is more common in areas open to fishing than in the areas closed to fishing, even taking bottom substrate effects into account. *Didemnum vexillum* appears to have spread over portions of the northern edge of Georges Bank. This research evaluates potential fish and invertebrate habitat degradation caused by an invasive species.

Keywords: ascidians, biological invasions, essential fish habitat, fisheries, geostatistics, marine protected areas, non-indigenous species, sea squirt, universal kriging, vessel-towed underwater camera system.

Introduction

Marine invasive species can have large impacts on native biodiversity by modifying native habitat (Bax *et al.*, 2003; Coutts and Forrest, 2007; Molnar *et al.*, 2008; Smith *et al.*, 2014). Habitat modification by invasive species can interact synergistically with other drivers of environmental change such as global climate change, thereby exacerbating effects on native species (Didham *et al.*, 2007; Hellmann *et al.*, 2008; Rahel and Olden, 2008). Furthermore, invasive species can act as ecosystem engineers by changing the physical condition of substrates, habitat architecture, and can affect sedimentation and deposition of nutrients (Wallentinus and Nyberg, 2007). Additionally, invasive species can change the chemical composition of settling epibionts, when native species are replaced by introduced species (Wallentinus and Nyberg, 2007). Generally, the impacts of marine invasive species can result in decreased economic productivity from resources

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such as fisheries, aquaculture, and tourism (Lovell *et al*., 2006; Molnar *et al*., 2008; Williams and Grosholz, 2008; Vilà *et al*., 2010)

Georges Bank is a submerged plateau off the coast of New England, which has been characterized by high levels of primary productivity and has supported highly valuable commercial fisheries for several centuries (Fogarty and Murawski, 1998). The invasive sea squirt *Didemnum vexillum*, originating from Japan (Stefaniak *et al*., 2012), was first observed on Georges Bank in 1998 (Bullard *et al*., 2007). *Didemnum vexillum* has colonized at least 230 km^2 of pebble/gravel habitat in Georges Bank leading to concerns about the impact this species may have on valuable fishery resources (Valentine *et al*., 2007a). This global invader has several characteristics that contribute to its invasion success, such as early maturation, rapid colony growth as a result of asexual budding, ease of attachment to firm substrates, toleration of a wide temperature range and the ability to spread by colony fragmentation as well the lack of natural predators in the region (Valentine *et al*., 2007b; Carman *et al*., 2009, 2014; Lambert, 2009; Stefaniak *et al*., 2012; Stefaniak and Whitlatch, 2014). *Didemnum vexillum* can prevent other benthic organisms from settling and growing on colony surfaces by sequestering acidic and organic allelopathic compounds in its tunic (Valentine *et al*., 2007b; Carman *et al*., 2009). In particular, scallop spat cannot settle on *D. vexillum* colonies (Morris *et al*., 2009) and *D. vexillum* also can interfere with scallop swimming (Dijkstra and Nolan, 2011). Additionally, *D. vexillum* can thrive on gravel substrate that the Atlantic sea scallop (*Placopecten magellanicus*) prefers; thus *D. vexillum* may be able to reduce the habitat available to sea scallops. Furthermore, *D. vexillum* can also colonize the upper valve of adult scallops and other bivalves, which may affect their ability to feed (Valentine *et al*., 2007b; Carman *et al*., 2009). Therefore, *D. vexillum* exhibits a number of characteristics that allow it to successfully outcompete other benthic epifaunal and macrofaunal species for limited space. All of these traits combine to make it a threat to benthic marine habitats and fisheries in the area.

Colonies of *D. vexillum* on Georges Bank appear as thin encrusting layers or produce tendrils that protrude from thick encrusting mats. It can reproduce both sexually and asexually by budding, as well as fragmentation (Carman *et al*., 2014). Larvae from sexual reproduction swim for a few hours before attaching to a hard substrate and metamorphosing. However, asexual reproduction and fragmentation are probably responsible for the majority of it spread in the Georges Bank area (Lengyel, *et al*., 2009). *Didemnum vexillum* has become a concern as a nuisance species because it reproduces rapidly, has a long breeding season, fouls ship's hulls and maritime structures, and can invade productive marine habitats such as shellfish aquaculture sites and fishing grounds (Valentine *et al*., 2007b; Daley and Scavia, 2008; Carman *et al*., 2009).

The Atlantic sea scallop (*P. magellanicus*) is a benthic bivalve mollusk that supports one of the highest valued fisheries in the United States, with total revenues reaching almost $500 million in 2013 (Lowther and Liddel, 2014). This fishery has recovered from a near collapsed state in the mid-1990s using a combination of conventional management measures such as effort control and gear regulations together with rotational and long-term closed areas (Hart and Rago, 2006). In particular, three areas on or near Georges Bank were closed to groundfish and scallop fishing in December 1994 (Murawski *et al*., 2000, Figure 1). Sea scallop biomass inside these closures increased over 20-fold between 1994 and 2004; however scallop biomass in these areas has subsequently declined somewhat after portions of these areas were reopened to fishing (Hart and Rago, 2006; Hart *et al*., 2013).

In this study, we evaluated the distribution of the invasive tunicate *D. vexillum* in Atlantic sea scallop habitat. We used the habitat camera mapping system (HabCam), a vessel-towed underwater camera system, to explore the spatial distribution of sea scallops and *D. vexillum* in areas protected and unprotected from bottom-fishing on Georges Bank to test if sea scallop density is lower in invaded areas. Additionally, we evaluated if *D. vexillum* spread is greater in areas open or closed to bottom-fishing. We also applied geostatistical techniques such as ordinary and universal kriging to determine the spatial distribution of *D. vexillum* cover across the entire study area. Georges Bank provides an important opportunity to determine how bottom fishing affects interactions in the benthic community because it is well monitored and substantial portions have been closed to bottom fishing since 1994. Activities such as scallop dredging and bottom trawling may have the potential to facilitate the spread of the invasive *D. vexillum* as a result of increased colony fragmentation (Morris and Carman, 2012), or the disturbance from bottom-fishing may open space for *D. vexillum* to colonize, although further studies are needed to evaluate specific mechanisms. We hypothesize that there will be a negative relationship between sea scallops and *D. vexillum.* This hypothesis is based on the literature that has demonstrated the tunicate's ability to prevent settlement of scallop spat and perhaps also increase mortality of adults (Morris *et al*., 2009). We also hypothesize that areas open to fishing will have greater cover of the invasive *D. vexillum* due to greater rates of disturbance and possibly also fragmentation of colonies from contact with fishing gear. This work can further our understanding of invasive species effects and how species interactions may affect habitat for fishery resources. Finally, possible management actions designed to mollify the negative impacts of the invasive *D. vexillum* on essential fish and invertebrate habitat are discussed.

Methods

Study area

Georges Bank is a shallow, highly productive, submerged plateau off the coast of New England that supports a number of 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). Interspersed within the gravel regions are large glacial erratics and boulders that can provide refuge sites for a diverse assemblage of organisms. Our study site is located in the northeastern portion of Georges Bank, in the area bounded between the Hague line dividing the United States and Canadian economic exclusive zone (E.E.Z.) on the east, and a boundary parallel to the Hague line on the west (Figure 1). The west portion of our sampling area was open to fishing while the portion to the east has been closed to all groundfish and scallop gear since December 1994, and is a part of Closed Area II. This area contains both sand and gravel substrates as well as high densities of sea scallops and *D. vexillum* in some locations.

Data collection

We collected data using a high-resolution imaging system, HabCam v2, to provide visual surveys of benthic marine organisms without disturbing the habitat itself (Howland *et al*., 2006;

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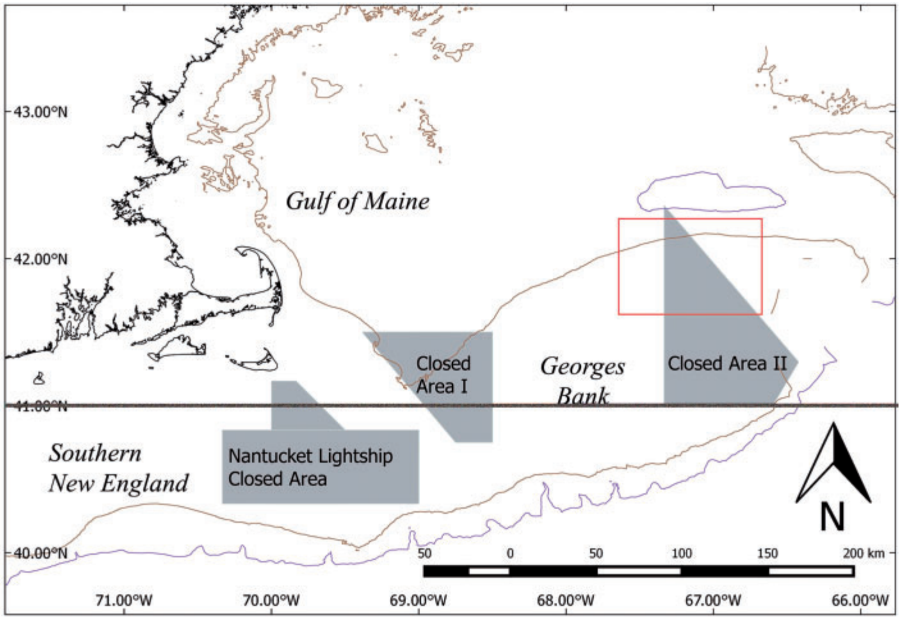

Figure 1. Georges Bank, with closed areas. Study area is shown in box.

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 fisheries such as the Atlantic sea scallop. The HabCam v2 vehicle is towed at speeds of five to six 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. The equipment on HabCam v2 includes a digital still camera (UNIQ Vision, Inc. UP-1800-CL), 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 by HabCam v2 in July of 2012. We also present the long-term sea scallop biomasses in the open and closed portions of the study area, based on the National Marine Fisheries Service Northeast Fisheries Science Center scallop dredge survey to help understand the effects of the closure on sea scallops prior to the invasion of *D. vexillum*. These data have been collected since 1982 using a modified 2.44 m New Bedford-style scallop dredge as the sampling gear; see (Hart and Rago, 2006) for more details on this survey.

Data processing

HabCam images were annotated to identify members of the invertebrate community, which were identified to the lowest taxonomic group possible for one in every 200 images. In total 5,309 images spanning locations within and adjacent to Closed area II were examined and annotated (Figure 2). All images used in the study were annotated by the same person (K.H.).

Scallops were separated into recruits ($\leq$75 mm shell height) and adults ($>$75 mm shell height) based on shell height obtained from image processing, which has been found to obtain comparable estimates with scallop lengths obtained from dredging (Taylor *et al.*, 2008). Data from image locations were overlaid onto geospatial vector data of Closed Area II and these data 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), which were subsequently separated for analyses. Density estimates for scallops were obtained by dividing scallop counts by the area of the field of view for each image. Sediment type and *D. vexillum* percent cover were determined for each image based on 5% increments.

Data analysis

Modelling the relationship between *D. vexillum* and scallop distributions

The effects of *D. vexillum* on adult and recruit scallop populations were analysed using generalized linear models, generalized additive models (GAMs), and non-linear least squares as a result of the non-linear nature of the relationship observed. Model fits from these three approaches were evaluated using the Akaike information criterion (AIC) and GAMs were selected to model the relationship based on the lowest AIC score (Burnham and Anderson, 2002). In order to reduce localized effects and issues with sample auto-correlation data for adult and recruit scallops, *D. vexillum* and proportional gravel cover were first averaged over 10 image blocks representing transect segments, covering ~1 km. Model residuals were examined visually and a variogram of residuals confirmed independence. Over-dispersion was detected in the scallop data; therefore a (quasi-) Poisson family was used in the GAM, in which the variance is given by $\Phi * \mu$, where μ is the mean density and Φ is the dispersion parameter, thus allowing variance to be greater than the mean. The proportion of gravel substrate and protected area category (i.e. open or closed to fishing) were used as a covariate and factor respectively in the GAMs to isolate the influence of *D. vexillum* on adult and recruit scallop distributions according to the formula:

$$\text{scallop density} \sim s(D.\ vexillum) + c^{*}\text{factor(Open/Closed)} + \text{proportional gravel cover} + \varepsilon$$

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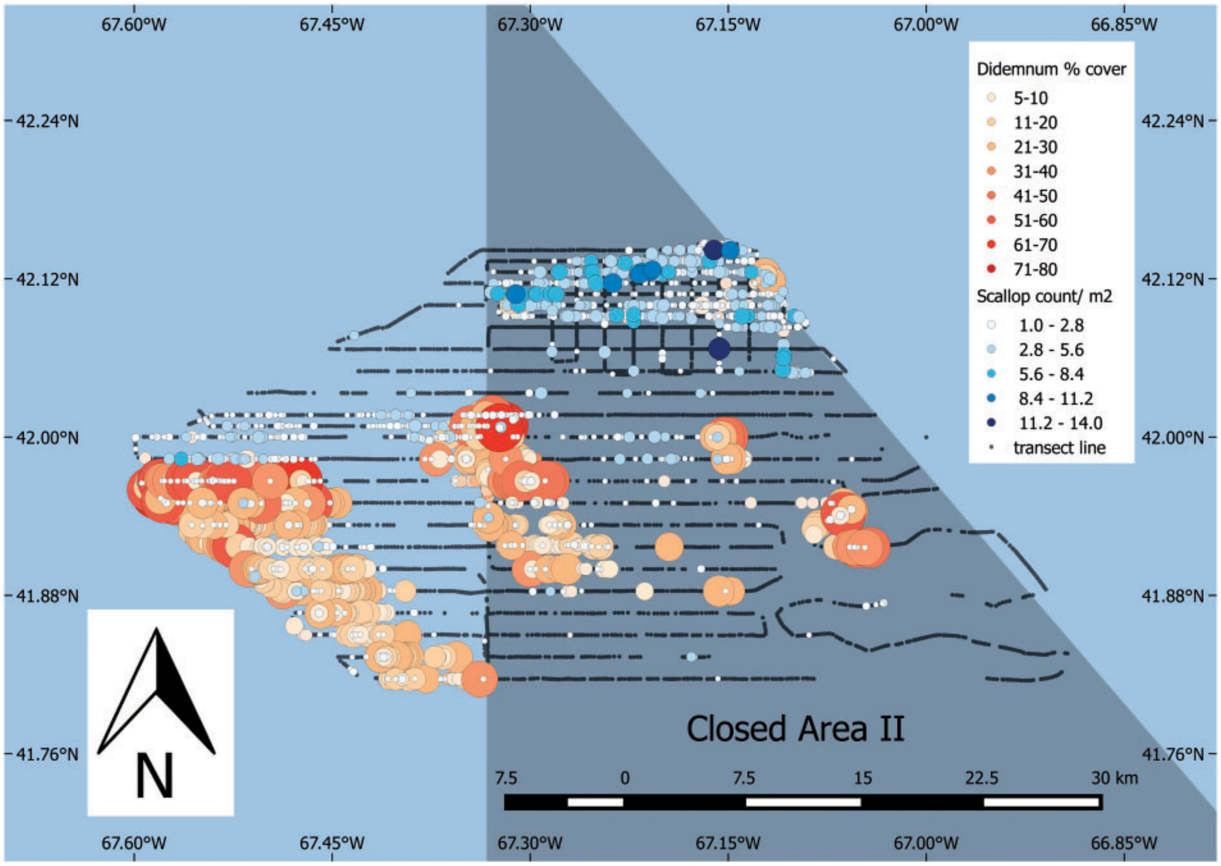

Figure 2. Chart of HabCam survey with scallop density (counts/m2) and *D. vexillum* percent cover. Size of data points scaled by density and percent cover.

where *s* represents a spline smoother, *c* is an estimated parameter, and ϵ is an error term. Temperature was also considered in all models, but not found as a significant predictor of scallop density thus it was eliminated as a predictor variable.

Determining the effect of the closed area on scallops and *D. vexillum*

The influence of the area closed to bottom-fishing on adult and recruit scallop density, and *D. vexillum* proportional cover from HabCam data were analysed using analysis of covariance (ANCOVA) with the proportional cover of gravel substrate as a covariate, since both *P. magellanicus* and *D. vexillum* are most abundant on gravel substrate. 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 effect of protected area on mean density of adult sea scallops, recruit scallops and *D. vexillum* proportional cover with greater than or equal to 50% gravel substrate is represented as "high gravel" and below 50% is represented as "low gravel" shown in Figure 4.

Interpolating *D. vexillum* distribution across the study area using geostatistics

The distribution of *D. vexillum* was modelled by universal kriging with gravel, depth and the categorical variable region, representing whether a point was inside or outside the closed area, as covariables using the R package gstat and sp (Pembesa, 2004; Bivand *et al.*, 2013). The universal kriging geostatistical approach results in the best linear unbiased estimates of the parameters and optimally weights each sample observation prediction (Cressie, 1993). A 100 × 100 grid was created for the study area to interpolate over using the spatial structure in conjunction with gravel, depth and area covariables. Gravel and depth were each spatially interpolated using ordinary kriging to provide input into the spatial linear model for predicting the proportional cover of *D. vexillum* (Supplementary Appendix S1). The exponential model was used to fit the variogram for both gravel and depth (Supplementary Appendix S1). The kriged estimates for depth and gravel were then used to create the prediction grid (Supplementary Appendix S2). Once this grid was created, gridded points were identified as being in Closed Area II or the region open to fishing and region was added as a grid co-variable (QGIS Development Team, 2015). A variogram was fit with a spherical model of the residuals from the linear regression with the covariates gravel and depth and the categorical predictor variable region (Supplementary Appendix S3). The universal kriging model applies the following equation where our interpolated value for *D. vexillum* (Z) is based on the covariables, gravel, depth and region and the variance-covariance matrix (η):

$$Z = \alpha(\text{gravel}) + \beta(\text{depth}) + \gamma(\text{region}) + \eta$$

where $\eta \sim \text{MVN}(0, \Sigma)$

This model is then used to demonstrate the interpolated density of *D. vexillum* infestation over the entire study area.

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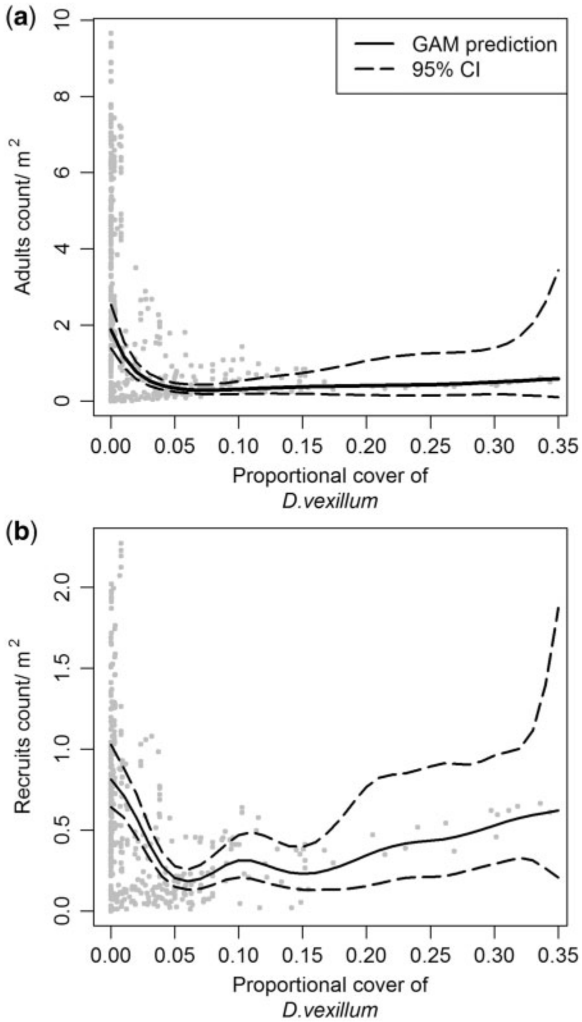

Figure 3. (a) Prediction of adult scallop density from the GAM response to *D. vexillum* proportional cover with gravel substrate held at its mean value in both open and closed areas shown with 95% CIs. (b) Prediction of recruit scallop density from the GAM response to *D. vexillum* proportional cover with gravel substrate held at its mean value in both open and closed areas with 95% CIs.

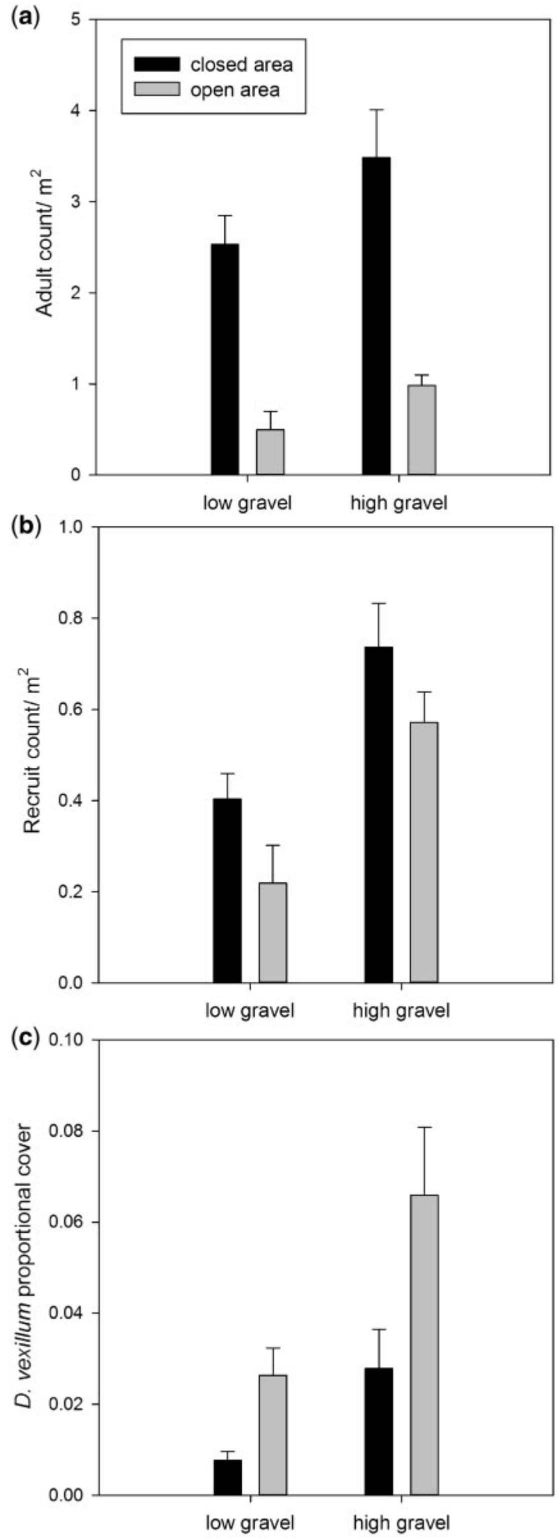

Figure 4. (a) Density of adult sea scallops in areas closed and open to bottom-fishing ($p < 0.001$) with gravel substrate ($p < 0.001$) (b) Density of recruit sea scallops in areas closed and open to bottom-fishing ($p > 0.05$) with gravel substrate ($p < 0.001$) (c) Proportional cover of *D. vexillum* in areas closed and open to bottomfishing ($p < 0.001$) with gravel substrate ($p < 0.001$). The "high gravel" category represents images with greater than or equal to 50% gravel cover, whereas the "low gravel" category is < 50% gravel. Error bars represent 95% CIs.

Results

Interaction between scallops and *D. vexillum*

Scallops and *D. vexillum* were located primarily in areas of high gravel substrate (Figure 2, Supplementary Appendix S2). The relationship for adult scallop density and *D. vexillum* essentially follows an exponential decline function with increasing *D. vexillum;* recruit scallop density showed a similar relationship (Table 1, Figure 3). Model predictions were made holding gravel substrate at the mean level from all sites to isolate the influence of *D. vexillum* on scallop density (Figure 3). At higher *D. vexillum* densities, the mean predicted recruit density also increased slightly (Figure 3b), but this is likely an artifact since there are few data points supporting this prediction as reflected by the increasingly large confidence intervals ($n = 20$ for recruits in areas with >0.15 proportional *D. vexillum* cover, as compared with a total $n = 530$). *Didemnum vexillum* has spread over portions of suitable scallop habitat primarily in the area open to fishing, though

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Table 1. Interaction between adult and recruit sea scallops with *D. vexillum* using GAMs with a Possion distribution.

Response variable	Explanatory variable	df or edf	Coefficient estimate (SE)	*p*-value	Deviance explained (%)
Adult density	*D. vexillum*	4.118		$p < 0.001$	53.6
	Area	1	−0.819 (0.128)	$p < 0.001$	
	Gravel	526	4.31 (0.525)	$p < 0.001$	
Recruit density	*D. vexillum*	5.307		$p < 0.001$	48.2
	Area	1	−0.214 (0.095)	$p = 0.02$	
	Gravel	526	1.20 (0.095)	$p < 0.001$	

Model fits are shown in Figure 3.

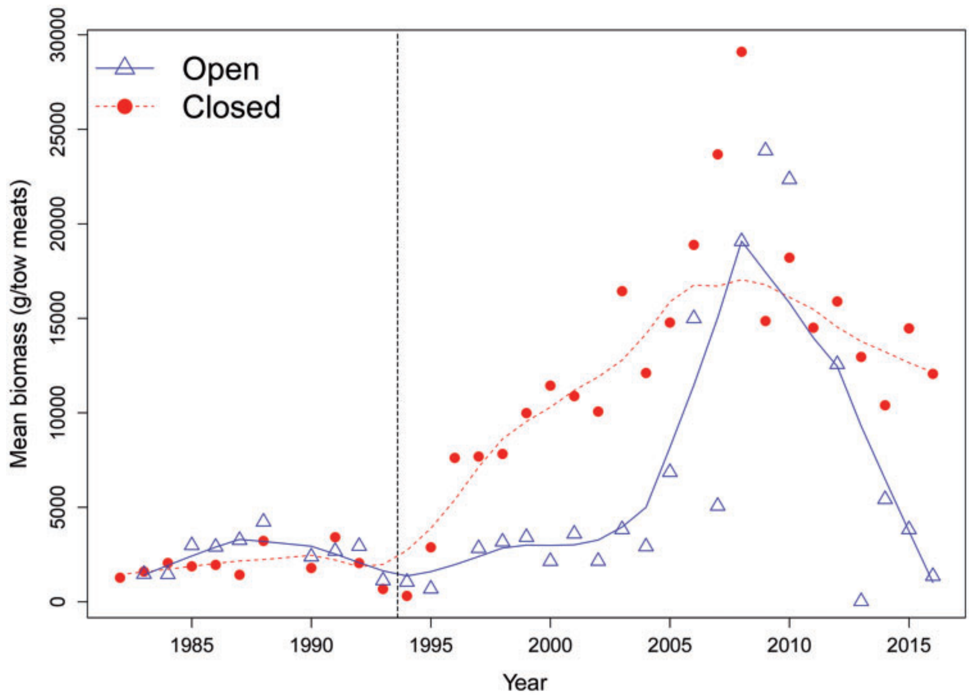

Figure 5. Mean scallop biomass in the open and closed portions of the study area, 1982–2016, from the NEFSC scallop dredge survey (Hart and Rago, 2006). The lines are lowess smoothers with stiffness of 0.25. The closed areas were put in place in December, 1994 (dotted vertical line).

it is also observed in the northern edge and on gravel habitat of Closed Area II (Figure 2).

The effect of the closed area on scallops and *D. vexillum*

Adult sea scallop density was significantly greater in the regions closed to bottom-fishing and positively correlated with gravel substrate, with a significant interaction between the two (ANCOVA, Region: $F_{1,526} = 99.87$, $p < 0.001$; covariate gravel estimate: 4.31, $F_{1,526} = 41.34$, p < 0.001; interaction: $F_{1,526} = 5.59$, $p = 0.02$, Figure 4a). However the interaction observed between gravel and region may be due to the large sample size rather than being biologically significant. Both the closed and open areas contained a large area of gravel habitat with proportions >35% in each (Supplementary Appendix S2). Recruits were not significantly greater in the region closed to bottom-fishing when using region as a blocking variable ($F_{1,526}$ 0.24, $p > 0.05$), however recruit density was positively associated to gravel substrates (gravel covariate estimate = 1.20, $F_{1,526} = 131.37$, $p < 0.001$; interaction not significant: $F_{1,526} = 0.24$, $p > 0.05$, Figure 4b). Proportional cover of *D. vexillum* was significantly greater in the regions open to bottom-fishing and positively associated to gravel substrate (ANCOVA; Region: $F_{1,526} = 89.49$, $p < 0.001$; covariate gravel estimate: 0.06; $F_{1,526} = 28.24$, $p < 0.001$; interaction not significant: $F_{1,526} = 0.13$, $p > 0.05$, Figure 4c). The highest densities of scallops are observed in the northern edge of Closed Area II, due to its protection status and ecological features such as a high portion of gravel habitat (Figure 2, Supplementary Appendix S2). Additionally, the time series of the dredge survey (1982–2015) for scallop biomass demonstrates the efficacy of the closed areas over time as evidenced by the increase in scallop biomass inside the protected area after it was closed in 1994 (Figure 5).

Interpolated estimates of *D. vexillum* distribution over the study area

The kriged estimates of gravel in the study area indicate that 39.8% of the study area is gravel habitat (Supplementary Appendix S1a). Universal kriging of *D. vexillum* using the gravel, depth and the categorical predictor region (inside or outside the closed area) as co-variables was conducted to demonstrate the proportion of the study area covered (Figure 6). Interpolated

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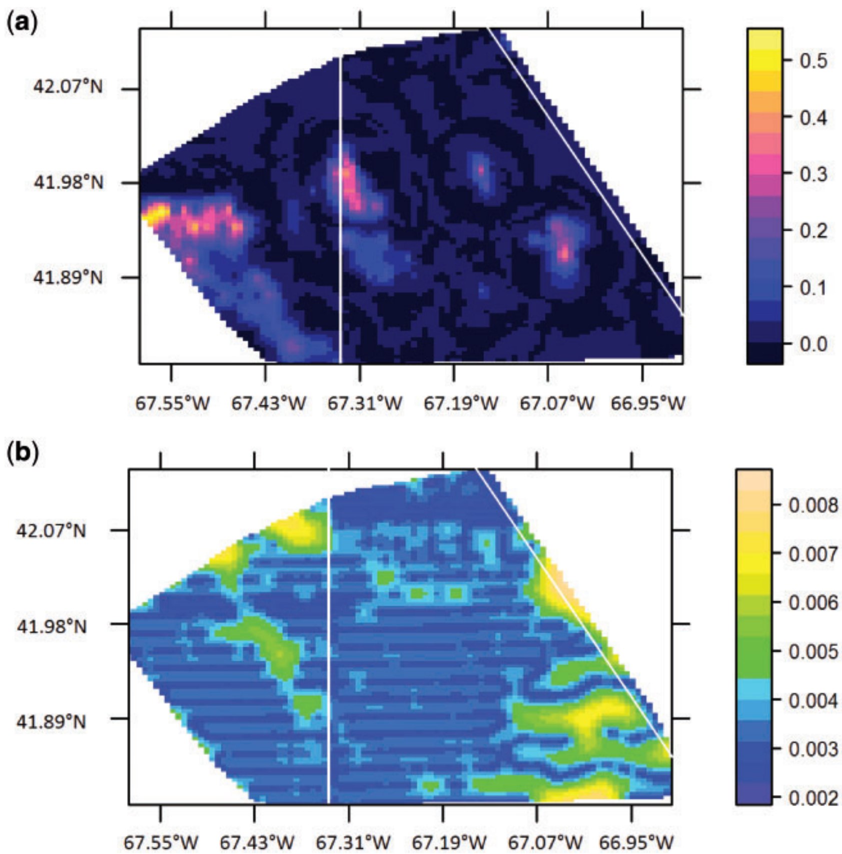

Figure 6. (a) *Didemnum vexillum* proportional cover from universal kriging estimates. (b) Variance from universal kriging estimates. Closed area II is located in between white boundary lines.

values are as high as 51.7% of area covered with *D. vexillum* in some cells of the prediction grid, with a mean value of the total study area covered being 2.9% (Figure 6). The variance of the interpolated proportional cover is also demonstrated showing areas with lower data coverage have higher variance (Figure 6). *Didemnum vexillum* is shown to cover significant portions of the study area, with the greatest density shown in the region open to fishing adjacent to Closed Area II.

Discussion

The effect of the invasive *D. vexillum* on Atlantic sea scallop habitat

The results from this study demonstrate the negative relationship of the invasive *D. vexillum* on sea scallop distributions. We found *D. vexillum* cover is negatively related to adult and juvenile sea scallop densities in both areas that were open and closed to bottom-fishing, and densities of *D. vexillum* were much greater in the region open to fishing, even after controlling for substrate. Additionally, scallops as well as *D. vexillum* appear in greater densities in areas of high gravel substrate, suggesting there is competition for habitat. Our interpolated estimates of gravel proportional cover indicate that 39.8% of the study area is gravel substrate, which is preferred habitat for both scallops and *D. vexillum*. Scallop spat cannot settle on *D. vexillum*, likely as a result of its acidic tunic (Morris *et al.*, 2009). In addition to overgrowing the gravel, ascidian colonies also can cement grains together making is more difficult for scallops to burrow into the substrate (Mercer *et al.*, 2009). Therefore, colonization of gravel substrate by *D. vexillum* turns preferred sea scallop substrate into unsuitable habitat. It is unlikely that *D. vexillum* is outcompeted by scallops in the closed area because *D. vexillum* has been observed to smother scallops and other bivalves by using their shells as substrate (Bullard *et al.*, 2007; Carman *et al.*, 2009). The interpolated estimates of *D. vexillum* demonstrate that it covers significant portions of the study area. In some areas over 50% of the habitat is covered by *D. vexillum* with the mean of the total study area being around 2.9%. In regions open to fishing the mean proportional cover of *D. vexillum* was over 6%, indicating the spread of this invasive species has the potential to cause a loss of fishing grounds and yield for New England fisheries, though more data is necessary to determine the effects of *D. vexillum* on fishery productivity.

Bottom-fishing methods can cause fragmentation, and therefore may spread *D. vexillum* colonies (Bullard *et al.*, 2007; Morris and Carman, 2012). Fragments of *D. vexillum* colonies can lodge in fishing gear and spread to other areas (Daley and Scavia, 2008). Additionally sea scallops are typically shucked at sea and discarded scallop shells colonized by *D. vexillum* could potentially generate new colonies (Daley and Scavia, 2008). There may also be a possibility that bottom disturbance caused by fishing gear facilitates the spread of *D. vexillum* by clearing the substrate of established native epifauna (Collie *et al.*, 1998; Hermsen *et al.*, 2003). Additionally, the disturbance created from bottom-fishing can also generate more organic matter in the benthos, which

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could be a significant food source for filter-feeding *D. vexillum* colonies. These mechanisms may explain the relatively lower proportion of *D. vexillum* observed in areas closed to bottom-fishing, as found in this study. Alternatively, other factors may also account for the observed differences in *D. vexillum* abundances such as oceanographic conditions, or the initial location where *D. vexillum* was introduced on Georges Bank, which was most likely in the open area via hull-fouling of vessels or commercial fishing gear. Even if bottom-fishing gear is a primary vector for the spread *D. vexillum*, it can spread by other natural mechanisms, and thus it may eventually occur in greater densities in the closed area.

The time series from the scallop dredge survey (1982–2015) demonstrates a dramatic increase in scallop biomass after the closed areas were put in place in 1994 in both the closed and open areas as a result of management efforts that decreased fishing mortality (Hart and Rago, 2006). In particular, the closure of a portion of our study site as part of Closed Area II induced substantially greater densities of adult scallops as a result of its protection from bottom-fishing, but at best, only a weak, non-significant effect was observed for recruits. The strong closed area effect on adults that are targeted by the scallop fishery is to be expected, but recruits (<75 mm) are much smaller than the 102 mm ring size of commercial scallop gear, and thus most recruits would pass through the gear and not be captured. Although patterns observed in recruitment from a single year class should be treated with caution, the fact that recruitment was higher in the area closed to fishing, even controlling for substrate, might be due to the lower levels of *D. vexillum* in the protected area. Moreover the spread of *D. vexillum* in our study area coincides with a decline in scallop biomass beginning in 2010, based on the dredge survey data, due in part to reduced recruitment in this area. Thus, the productivity of the scallop fishery may be affected by the inhibiting effects of *D. vexillum* on scallop settlement and recruitment, though further data is necessary to determine the impact on the fishery. Fish populations may also be affected by the spread of *D. vexillum*. The gravel substrate where *D. vexillum* is found in greatest density also serves as important nursery grounds for juvenile cod and haddock (Collie *et al*., 2000), as well as spawning grounds for Atlantic herring, so *D. vexillum* may alter habitat and food availability for several commercially important species. Additionally, allelopathic chemicals from *D. vexillum* overgrowing on substrates may negatively impact the viability of eggs of fish that rely on gravel pavement for spawning sites such as Atlantic herring (Dijkstra *et al*., 2007).

Management considerations

In order to manage the spread of *D. vexillum*, further research is necessary to evaluate which of these mechanisms contribute most significantly to spreading this species. Habitat restoration efforts that include attempts to remove *D. vexillum* from some areas might be considered. Other marine pest species such as jellyfish, ctenophores, nemerteans, snails, sea urchins, polychaetes, burrowing shrimps, crabs, and fishes may be amenable to biological control efforts, though strategies adopted from terrestrial realms require special considerations for marine environments (Lafferty and Kuris, 1996; Secord, 2003). Sea urchins (*Strongylocentrotus droebachiensis* and *Strongylocentrotus franciscanus*) are predators of *D.vexillum*, though in experimental tests these urchins preferred other food sources when available (Epelbaum *et al*., 2009). The periwinkle (*Littorina littorea)*, which is also not indigenous, is a predator of *D. vexillum*, but it is of limited value since it only consumes senescing *D. vexillum* and is an intertidal to shallow subtidal snail (Valentine *et al*., 2007b; Carman *et al*., 2009). Predators were not successful at controlling fouling from *D.vexillum* on Pacific oysters in experimental treatments (Switzer *et al*., 2011). Thus options for biological control of *D.vexillum* are limited.

Manual eradication methods have been used by shellfish aquaculturists since *D. vexillum* is a shellfish pest capable of encapsulating and smothering bivalves (Carman *et al*., 2009). For example, chemical and mechanical treatments have been shown to reduce fouling from *D. vexillum* in oyster aquaculture, though survival of oysters was also reduced in lime-treated treatments (Switzer *et al*., 2011). Eradication methods such as smothering with dredge material, filter fabric, and plastic, as well as manual removal and treating boat hulls with dilute bleach have been used in Shakespeare Bay, New Zealand (Coutts and Forrest, 2007). Smothering by dredge material killed 100% of colonies occupying an $\sim$3200 m^2 area of relatively homogenous seabed substrate, although efforts were not successful in completely eradicating *D. vexillum* from the region. However these methods can also have negative effects on native species, thus eradication methods must be used with caution. Additionally, while these methods may be useful for control in small-scale near shore environments, they would be more difficult and expensive to attempt on Georges Bank and may not have lasting benefits (Coutts and Forrest, 2007).

As with many marine invasive species, limiting the spread of *D. vexillum* will require controlling transport vectors that facilitate its spread such as vessel fouling, aquaculture, and commercial fishing gear (Tamburri *et al*., 2002; Bax *et al*., 2003; Daley and Scavia, 2008). *Didemnum vexillum* most likely spreads through fouling of vessel hulls, aquaculture transfers and commercial fishing (Acosta and Forrest, 2009; Herborg *et al*., 2009). Maintaining databases on transport vectors such as ship movement will provide information that can be used to develop risk assessment programs to control the transport vectors for *D. vexillum* and other nonindigenous species (Daley and Scavia, 2008; Acosta and Forrest, 2009; Herborg *et al*., 2009). Additionally environmental niche models combined with vector models can provide spatially explicit predictions of the potential distributions of the invaders to inform risk assessments (Herborg *et al*., 2009). This information can be used for regulatory agencies to control transport vectors through voluntary or mandatory practices that minimize the risk of spreading *D. vexillum*. Given the value of the sea scallop fishery, controlling the spread of this invasive species has both economic and ecological importance.

Conclusions

In this study, we demonstrate a negative relationship between sea scallops and the invasive species *D. vexillum* on commercially important fishing grounds. We also demonstrated that there are higher concentrations of *D. vexillum* in areas open to bottom-fishing than areas closed to bottom-fishing. Future studies should evaluate the relationship between fishing effort and the spread of this invasive species, to determine the degree to which bottom-fishing is propagating the spread of this invasive and the potential for protected areas to mitigate habitat degradation caused by *D. vexillum*. Management of this invasive species may require coordinated efforts to restore degraded habitat and limit its spread

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through the various transport vectors discussed. Future studies should address more long-term monitoring efforts of this invasive species to determine its impact on commercially valued fish species.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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