Research Article

A decade of invasion: changes in the distribution of *Didemnum vexillum* Kott, 2002 in Narragansett Bay, Rhode Island, USA, between 2005 and 2015

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Citation: Auker LA (2019) A decade of invasion: changes in the distribution of *Didemnum vexillum* Kott, 2002 in Narragansett Bay, Rhode Island, USA, between 2005 and 2015. *BioInvasions Records* 8(2): 230–241, https://doi.org/10.3391/bir.2019.8.2.04

Received: 26 July 2018

Accepted: 1 December 2018

Published: 28 February 2019

Handling editor: Mary Carman

Thematic editor: April Blakeslee

Abstract

Didemnum vexillum, an invasive colonial ascidian, has colonized natural and artificial substrates in Narragansett Bay, Rhode Island (USA) since 2000, when it was first discovered in Newport Harbor. A survey of the bay in 2005 found *D. vexillum* at several coastal sites in the southern portion of the bay, dominating substrata by the end of its reproductive period. The current study examines the near-surface geographic distribution of the ascidian in the bay in 2015 at less than 1 m depth, a decade after the initial survey. According to this study, the ascidian has a more limited distribution in 2015 than in the earlier 2005 survey. Artificial substratum presence, estimated mean salinity, and distance from Providence ports are all positively associated with the 2015 presence of the ascidian in the bay based on results from a linear discriminant function analysis. There are few investigations of long-term changes in invasive species distribution. Based on the findings of this study, further investigation of the causes of long-term change in the geographic distribution and abundance of invasive species, as well as the long-term impacts of such changes on native communities, are recommended.

Key words: colonial ascidian, survey, discriminant function analysis, fouling species

Introduction

Invasive ascidians are a global concern in marine habitats (Lambert 2002). Ascidians are often dominant members of fouling communities, and they impact ecosystems by colonizing hard substrata, overgrowing important hard-shelled species, and altering available habitat (Bak et al. 1996; Lambert and Lambert 2003; Bullard et al. 2007a; Valentine et al. 2007b; Auker et al. 2014). Colonial ascidians are especially successful invasive species because they reproduce both sexually and asexually, and readily spread beyond their initial settlement by producing fragments that attach to new substrata (Bullard et al. 2007b). To thrive, ascidians only require a hard substratum for colonization and organic particulate matter (0.5–2 µm) for food (Bone et al. 2003; Bullard and Carman 2009; Colarusso et al. 2016). Thus, colonial ascidians often grow to dominate the substrata by the end of their sexual reproductive season (Auker and Oviatt 2008).

Didemnum vexillum Kott, 2002 is a colonial ascidian that has invaded many temperate marine habitats, including benthic areas in the northeastern

United States (Bullard et al. 2007a). The species likely arrived in the northeastern United States as a hitchhiker on introduced oysters (*Crassostrea gigas* (Thunberg, 1793)) in the 1970s (Dijkstra et al. 2007). It had come to the attention of invasion ecologists, fishery managers, and aquaculture industry stakeholders when it began to spread aggressively over farmed mussels and benthic substrata in New Zealand (Coutts 2002; Coutts and Forrest 2007). In 2000, a rapid assessment survey first sighted *D. vexillum* in Narragansett Bay, Rhode Island in Newport Harbor (Pederson et al. 2001). In 2002, another early sighting identified the ascidian growing above the low tide line on the dock of the University of Rhode Island's Graduate School of Oceanography (GSO) (USGS 2016). Additional reports of the ascidian throughout the bay soon followed these initial sightings (USGS 2016). By 2005, *D. vexillum* had become a dominant member of late summer communities at many sites throughout the bay (e.g., the GSO pier, Fort Wetherill Rhode Island DEM docks, and South Prudence T-Wharf) (Auker and Oviatt 2008). A 2005 survey found the ascidian at nine of 24 sites surveyed. Anthropogenic activity appeared to be a primary factor affecting the spread of the ascidian as the sites colonized were generally characterized by the presence of boats, moorings, and docks (Auker and Oviatt 2008). Artificial substrate is associated with increased abundance of nonnative ascidians, including *D. vexillum,* in many locations around the globe (Coutts and Forrest 2007; Glasby et al. 2007; Locke et al. 2007). However, Auker and Oviatt (2008) also found sites where *D. vexillum* grew on rocks in sheltered areas away from high human activity (e.g., at Beavertail Point State Park and Taylor Point on Conanicut Island), as did Valentine et al. (2007a) at Sandwich, Massachusetts.

Strayer et al. (2006) observed that most studies on invasive species focus on species distribution shortly (i.e. within a few years) after the invasion event, and such short-term studies limit the understanding of the long-term ecological impacts of species invasions. Morrison (2002) suggests that the most severe impacts of invasion occur immediately following the species appearance when it dominates its new habitat. The purpose of this study is to examine the distribution of *D. vexillum* on substrata within the top meter of the water surface in Narragansett Bay and, using a discriminant function analysis, examine the characteristics of sites where *D. vexillum* populations have been maintained from 2005–2015. I resurveyed sites in Narragansett Bay to determine how the geographic distribution of *D. vexillum* may have changed in the past ten years since the 2005 survey (Auker and Oviatt 2008). To maximize the coverage of the survey, I also added an additional 14 sites to the sites surveyed by Auker and Oviatt (2008). This study is one of the first attempts to examine change in *D. vexillum* geographic distribution over a period of ten years.

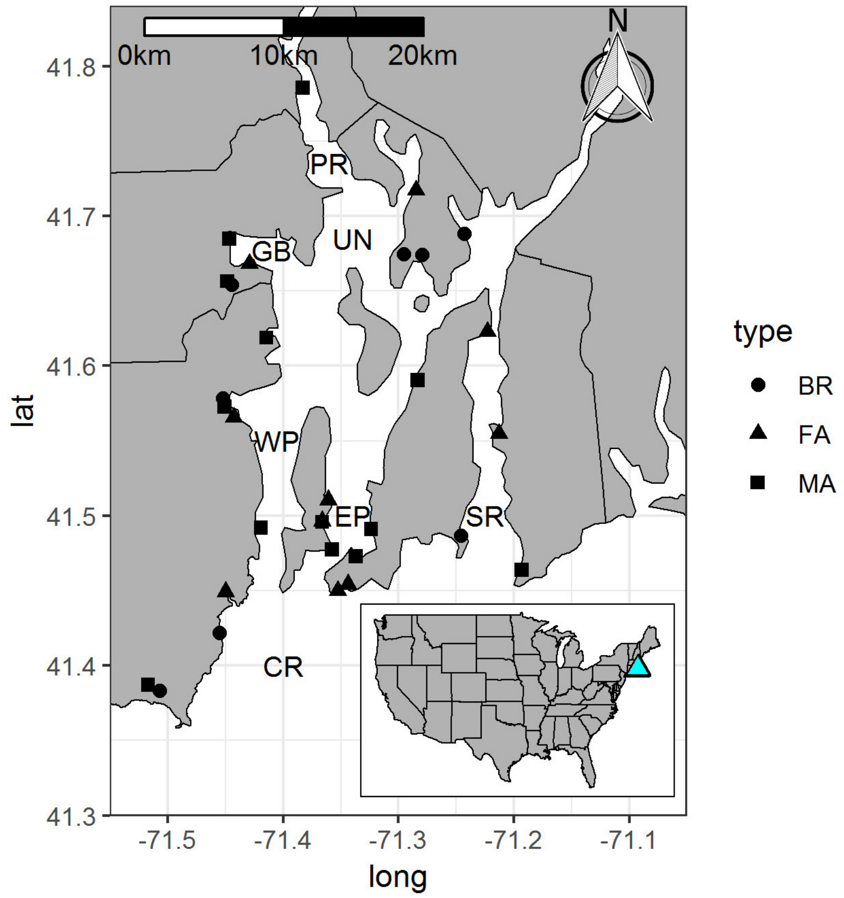

Figure 1. Map of sites in Narragansett Bay, Sakonnet River, and coastal Rhode Island that were visited during this study. CR = Coastal Rhode Island; WP = West Passage; EP = East Passage; SR= Sakonnet River; GB = Greenwich Bay; UN = Upper Narragansett; PR = Providence River. Circles denote boat ramp sites, triangles are fishing access sites (no boat ramps, docks, or piers), and squares show marinas and ports. For details see Supplementary material Table S2.

Materials and methods

Study area

Narragansett Bay is an estuarine system with a north-south salinity gradient. The northern part of the bay has low salinity; here, there is freshwater input, primarily through the Providence River and Taunton River via Mt. Hope Bay. High salinity is in the south at the bay's connection to Rhode Island Sound (Hicks 1959). Salinity throughout the bay stays above 20 psu, except within the Providence River (Hicks 1959). The estuary is approximately 40 km long and 19 km at its widest point, and covers a total area of 342 km^2 (Chinman and Nixon 1985). Of the three entrances to the bay, the East Passage is the only channel deep enough for commercial ships to pass through (Ely 2002).

Bay survey

In this study, I assessed 32 sites throughout Narragansett Bay, including sites in the West Passage, East Passage, Upper Narragansett, Providence River, Greenwich Bay, and Sakonnet River (Figure 1). These include 18 sites

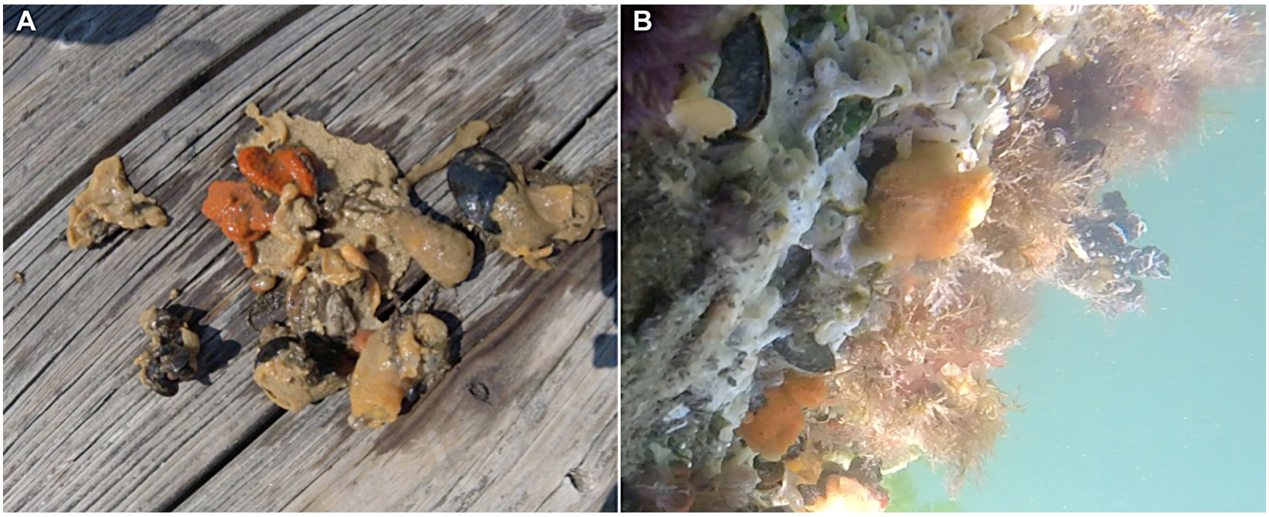

Figure 2. Photographs of *Didemnum vexillum* observed during the 2015 survey. A: Sample of fouling organisms, including a significant amount of *Didemnum vexillum* collected from the bottom of a floating dock in Jamestown, RI. B: Screenshot of video taken of floating dock just below water surface at Point Judith, RI. *D. vexillum* is easily seen, along with several other fouling organisms. Photographs by L. Auker.

from the 2005 survey by Auker and Oviatt (2008) and 14 additional sites not covered in the previous study. Because *Didemnum vexillum* inhabits substrata below the low tide line, I visited intertidal locations between one hour before and one hour after low tide during the weeks of July 29 through August 5, 2015. Sites on floating docks were visited outside of this time frame as ascidians were easily observed at all tide levels. The use of a GoPro® Hero+ digital video camera fitted with a waterproof housing and mounted on a floating hand grip (24.2 cm long) allowed me to record and confirm presence or absence of the ascidian underwater. Because *D. vexillum* reaches peak recruitment and dominates fouling communities by late September, I revisited sites where *D. vexillum* was absent in 2015 a year later in September 2016 to confirm its absence (Auker and Oviatt 2008). For sites where *D. vexillum* was present in 2016, but not observed in 2015, I counted the ascidian as "present" in the 2015 survey.

At each site, I surveyed 30–50 m of coastline for the presence of *D. vexillum*. *Didemnum vexillum* colonies are conspicuous on substrata below the water and are easily reached from floating docks for sampling (Figure 2). At sites where the ascidian was present, I collected colonies and preserved them in 70% isopropanol until return to St. Lawrence University, where they were preserved with 70% ethanol. Presence of external features (such as the characteristic "tendril" formation) and internal structures (e.g., spicules) confirmed that specimens collected were *D. vexillum*. At one site, Goat Island Causeway, *D. vexillum* was observed on pilings too far to safely reach from the surface. However, the characteristic tendrils formed by *D. vexillum* colonies were conspicuous on the dock pilings; this is a trait not shared by other ascidians, including the only other didemnid in this region, the encrusting *Didemnum albidum* Verill, 1871 (Gosner 1978).

I used the following variables to characterize each site:

- Site type: Sites were public fishing access points (i.e., no boat ramps or docks), public access boat ramps, or marinas.
- Substratum diversity: The types of substrata included artificial (floating dock, concrete, and nylon net) and natural (rock, wood, sand, shellfish, small gravel, vegetation, and mud) substrata.
- Vessels nearby: I counted boats, moorings, and commercial vessels within 1, 2, and 3 km radii of each site using high resolution aerial photography from Google Earth (2016).
- Salinity: The Narragansett Bay Fixed-Site Monitoring Network (NBFSMN) collects daily salinity data from several buoy sites throughout the bay. Since surface salinity is on a north-south gradient for the Narragansett Bay estuary, I produced a standard curve using buoy latitude and average daily salinity and average minimum salinity (mean salinity: $R^2 = 0.8045$; $P < 0.001$; minimum salinity: $R^2 = 0.848$; $P < 0.001$). Using this curve and site latitude, I estimated site salinities for each site. Figure 3 shows the standard curves produced for mean and minimum salinities, and Supplementary material Table S1 shows the salinity values for each site in the 2015 survey.
- Bay area: The sections of the bay included in the survey were Upper Narragansett, Coastal Rhode Island, Sakonnet River, East Passage, West Passage, Greenwich Bay or Providence Bay.
- Distance to ports: Using latitude and longitude data for each site, I measured the Haversine distance between each site and the three major commercial ports in Narragansett Bay (Quonset, Providence, and Newport) using the "geosphere" package in R (Hijmans 2015).

To compare sites visited in 2005 and 2015, I performed a linear discriminant function analysis on log-transformed variables in R using the "MASS" package (Venables and Ripley 2002; R Core Team 2014). Sites used in discriminant function analysis were only those that were visited in both years. Table 1 lists the two groups used for the linear discriminant function analysis. Group 1 (50% of the sites) includes sites where *D. vexillum* was absent in both 2005 and 2015, and Group 2 (50% of the sites) includes sites where *D. vexillum* was present in at least one of the years (2005 or 2015). The variables used in the analysis were slipped vessels within 1 km, distance to Newport, distance to Providence, estimated mean salinity, estimated minimum salinity, number of available artificial substratum types, and number of available natural substratum types. A Wilks' test within the "rrcov" R package determined if these variables were significantly different among sites (Todorov and Filzmoser 2009).

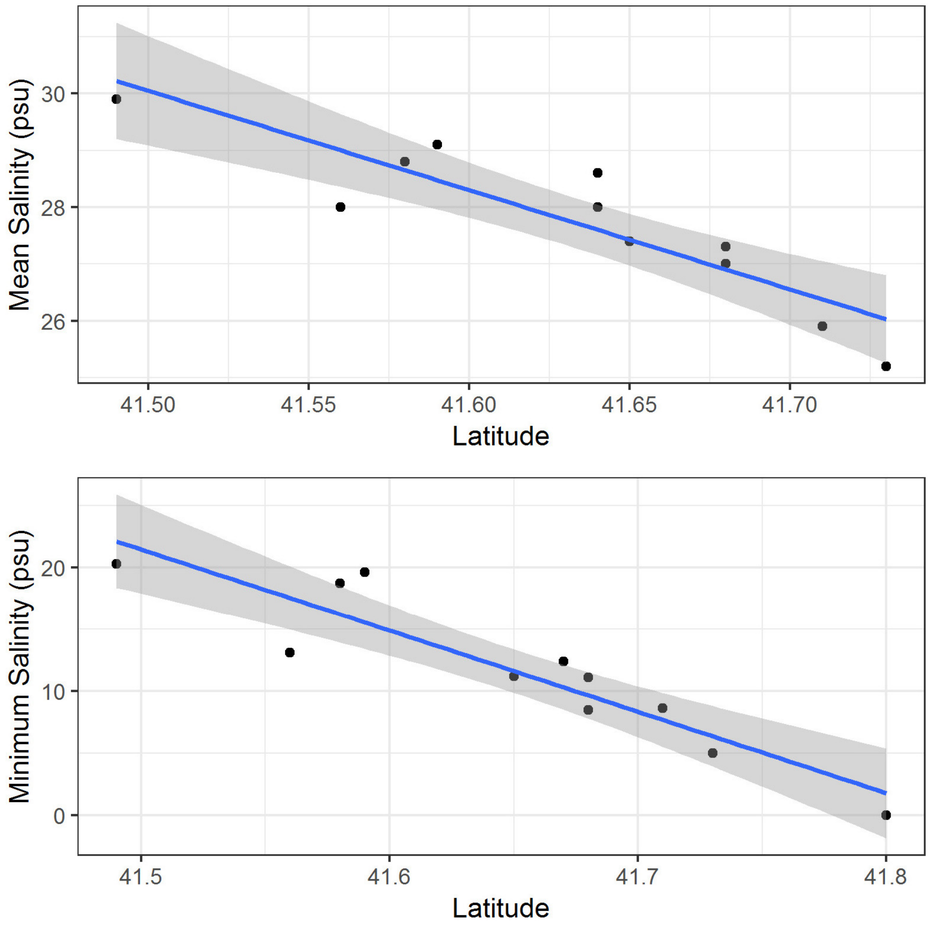

Figure 3. Standard curves for estimating salinity. The top graph represents the relationship between buoy mean salinity and latitude (Salinity = −17.481 (Latitude) + 755.516). The bottom graph represents the relationship between buoy minimum salinity and latitude (Salinity = −65.589 (Latitude) + 2743.395). The shaded area represents standard error.

Table 1. The sites belonging to each group for the linear discriminant function analysis were visited in both 2005 and 2015. Group 1 includes sites where *D. vexillum* was absent in both 2005 and 2015 (sites indicated here were visited in both years). Group 2 includes sites where *D. vexillum* was present in at least one of the years visited.

Group 1	Group 2
Brenton Point State Park	Beavertail Lot 4
Goddard Park Beach	Fort Adams Boat Ramp
Goddard Park Boat Ramp	GSO Pier
Jamestown Beach	Taylor Point
Kings Park Beach	Wickford Town Harbor
Narrow River Kayak Launch	Wilson Park
North Kingstown Town Beach	Conanicut Marina
Oakland Beach	Goat Island Causeway
State Pier 5	Great Island Bridge
East Greenwich Town Overlook	Fort Wetherill DEM

Results

Distribution observations

In 2015 and 2016, *Didemnum vexillum* was present at only 15.6% sites visited (n = 5) compared to 45% sites visited (n = 9) in 2005 (Auker and Oviatt 2008) (Figure 4). At four sites, *D. vexillum* was present in both 2005 and 2015 (Conanicut Marina, Fort Wetherill DEM, Goat Island Causeway,

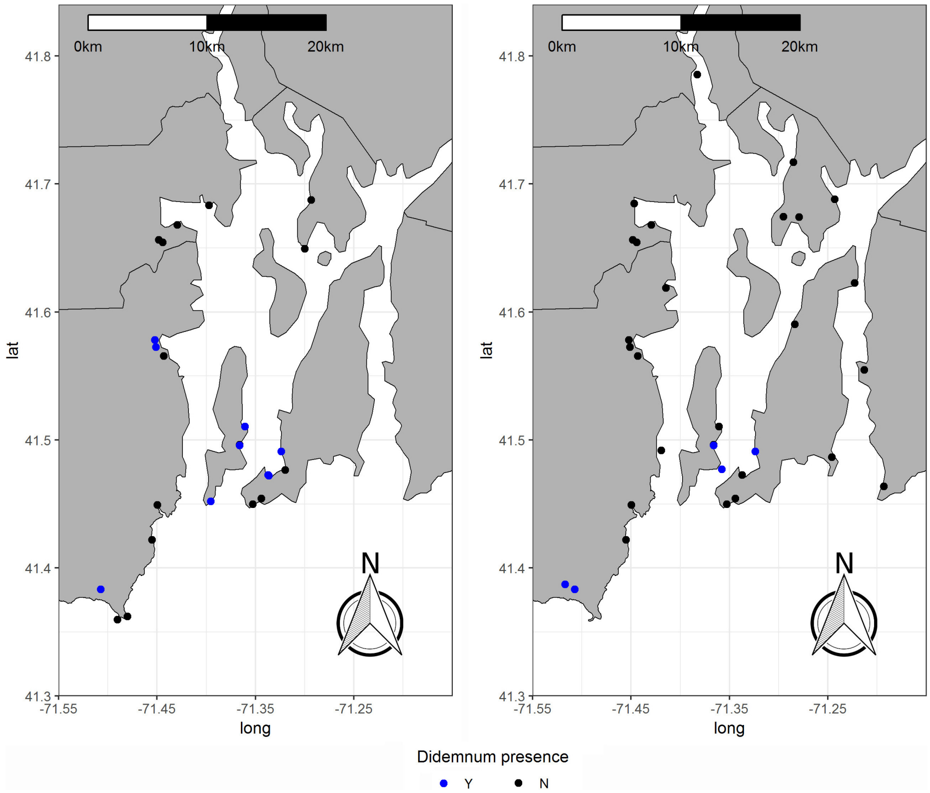

Figure 4. These maps show *Didemnum vexillum* presence (blue) and absence (black) in 2005 (left) and 2015 (right). For details see Supplementary material Table S2.

and Great Island Bridge). In 2005, *D. vexillum* was present in five sites where it was not present in 2015. In 2015, I visited an additional two sites where *D. vexillum* was present that were not visited in Auker and Oviatt (2008) (Table S2). The only site where *D. vexillum* was present in 2016, but not observed in 2015, was on the floating dock of the Great Island Bridge boat ramp. These colonies were small (3–5 cm in diameter) compared to colonies observed at other sites where *D. vexillum* was present.

Sites where *D. vexillum* was present were significantly further away from Providence than sites without the ascidian ($F_{1,30}$ = 7.138, p = 0.0121). However, there was no significant difference in distance from Quonset ($F_{1,30}$ = 3.413, p = 0.0746) or Newport ($F_{1,30}$ = 0.682, p = 0.415) between sites with and without the ascidian. There was also no significant difference in total number of vessels within 1 km ($F_{1,30}$ = 0.901, p = 0.35) between sites where the ascidian was and was not present in 2015 (Table 2).

Linear discriminant function analysis

The variables used (slipped vessels within 1 km, distances to Newport and Providence, estimated mean and minimum salinities, and number of available artificial and natural substratum types) maximized the distinction between sites where *D. vexillum* was absent and where *D. vexillum* was present for at least one of the years (Wilks' λ_7 = 0.1261, p < 0.001). The variables that contributed the most to the linear discriminant function analysis, and

Table 2. Characteristics of sites where *Didemnum vexillum* was present and absent. Except for "Number of sites" all values are means ± standard deviation.

	Sites with *D. vexillum* present	Sites with *D. vexillum* absent
Number of sites	5	27
Mean salinity (psu)	30.98 ± 1.00	28.80 ± 1.72
Minimum salinity (psu)	24.92 ± 3.75	16.75 ± 6.44
Mean number of vessels within 1 km	441.60 ± 195.94	303.93 ± 310.66
Distance to Quonset (km)	17.09 ± 6.74	12.27 ± 5.12
Distance to Providence (km)	39.50 ± 6.88	26.10 ± 10.74
Distance to Newport (km)	10.18 ± 9.65	13.20 ± 7.14
Mean number of artificial substrata	0.80 ± 0.45	0.41 ± 0.57
Mean number of natural substrata	0.60 ± 0.55	1.00 ± 0.83
Mean number of substrata types	1.40 ± 0.55	1.40 ± 0.64

Table 3. Coefficients of the linear discriminant function analysis.

	Linear Discriminant
Slipped (1 km)	−0.249
Distance to Providence	8.025
Distance to Newport	−0.790
Artificial Substratum	2.961
Natural Substratum	−1.143
Estimated mean salinity	16.816
Estimated minimum salinity	−12.184

maximized the difference between the two groups, were distance from Providence, estimated mean and minimum salinities, and presence of artificial substrata (Table 3).

Discussion

The colonial ascidian *Didemnum vexillum* was present at fewer sites in Narragansett Bay in 2015 when compared to a similar study from 2005 described in Auker and Oviatt (2008). In the current study, there was an increased likelihood of ascidian presence on artificial substratum and at locations in the southern part of the bay. Though *D. vexillum* was a dominant member of the late summer and autumn benthic community in Narragansett Bay in 2005, it has appeared to decline in surface distribution since the data published in Auker and Oviatt (2008). There are several factors that could have caused a population decline of the ascidian in the bay, though it must be stressed that the current study focused only on characteristics of sites that increased the likelihood of *D. vexillum* presence and did not focus on determining the *causes* of ascidian near-surface population decrease.

Factors that can lead to population declines in invasive species include competitive exclusion by other species, predation on the invasive species, introduction of a new predator, or the introduction of a parasite or disease (Lockwood et al. 2013). However, it is unlikely that any of these factors have influenced *D. vexillum* in Narragansett Bay. Like other colonial ascidians, *D. vexillum* is a strong spatial competitor (Bullard et al. 2007a; Rajbanshi and Pederson 2007). Predation on *D. vexillum* is also limited.

There are no known predators of the ascidian during warmer months when the ascidian is actively producing secondary metabolites and sequestering sulfuric acid (Bullard et al. 2007a); in fact, in some cases, mats of the ascidian may actually protect infaunal invertebrates from predators (Mercer et al. 2009) and provide associational resistance to overgrown organisms like mussels (Auker et al. 2014). Finally, there are no reports of diseases or parasites of *D. vexillum*.

In Narragansett Bay, one potential reason for *D. vexillum* decline is fluctuating surface salinity. Like most ascidians, *D. vexillum* grows poorly at salinities less than 26 psu (Bullard and Whitlatch 2009). In 2015, all sites with *D. vexillum* present were in the southern portion of the bay, where salinity is more stable due to the greater distance from the mouth of the Providence River and other freshwater inputs at the northern end of the bay. Salinity at sites where the ascidian was observed in this study did not fall below 20 psu (Table S1). Surface waters in northern Narragansett Bay experienced sharp drops in salinity in 2010 and 2012 due to heavy spring rains and flooding (NBSFMN 2005-2010). The distribution of ascidians is limited by spatial variations in salinity (Millar 1971; Stoner 1992; Vázquez and Young 2000; Lambert 2005; Auker and Oviatt 2008). Vázquez and Young (2000) found that some species of ascidians from the order Aplousobranchia, a group that includes *D. vexillum*, only survived above 22 psu. Generally, colonial ascidians require higher salinities for positive growth (Epelbaum et al. 2009). Drops in salinity may have played a role in reducing populations in the bay, but this hypothesis requires further investigation.

In both 2005 and 2015, anthropogenic activity, represented as "boat ramp" or "marina" site type in Auker and Oviatt (2008) and by the presence of artificial substrata in this study, played a role in predicting *D. vexillum* presence. Ascidians are common colonizers of marine hard substrate (Jackson 1977). Artificial substrates, in particular, provide a stepping stone for *D. vexillum* invasion into a region because these structures provide additional substrate for nonnative ascidians when natural hard substrate is scarce (Coutts and Forrest 2007; Locke et al. 2007). These habitats increase the risk of invasion and have greater numbers of non-native species than native species when compared to natural substrate (e.g., reefs) (Glasby et al. 2007). For sites visited in both Auker and Oviatt (2008) and this study, there was no change in site usage from 2005 to 2015.

In this study, the geographic extent of *Didemnum vexillum* is further restricted, and therefore it appears less dominant, than it was in the early 2000s when it was first reported in Narragansett Bay. Understanding the long-term ecological impacts of species invasions is limited because most studies on invasive species focus on the period shortly after invasion (i.e. within a few years) (Strayer et al. 2006). Studies that return to invasive populations long after these initial invasion events are rare; those that have been conducted seem to suggest that the most severe impacts occur immediately following the initial phase of invasion (Morrison 2002). Invasion impacts may reduce in severity over time once invasive species have become established in a new habitat. Evolution of the invasive species, shifts in community structure, and changing abiotic variables may all impact the ecological interactions within the invaded community and reduce the impact of the invader (Strayer et al. 2006). However, there are several potential models for invasion impact that remain to be tested but seem to be supported by observed patterns in the field. For example, it appears that although invasive populations go through post-invasion boom-bust cycles, the long-term abundance of an invader is maintained by available space and food availability (Strayer and Malcolm 2006). According to my study, the primary factors that correlated with increased presence of *D. vexillum* abundance in Narragansett Bay were availability of artificial substrata and distance from Providence (which correlates with increasing salinity). These findings agree with Bullard et al. (2007a) who describe anthropogenic changes in the environment, limited food availability, and salinity fluctuations as factors that likely limit the long-term distribution of ascidians.

D. vexillum is more abundant in offshore, deeper waters due to the stable temperatures and higher salinities found in this environment (Bullard et al. 2007a; Valentine et al. 2007b). A survey of shallow water sites at low tide cannot delineate the entire distribution of the ascidian in an estuarine environment, and it should not be used as such. However, when this study is compared to the results from Auker and Oviatt (2008), it is clear that significant changes have occurred in Narragansett Bay *D. vexillum* populations over the past decade. Future research should endeavor to determine the extent and stability of *D. vexillum* populations on the Narragansett Bay seabed, similar to mapping efforts in Georges Bank by Kaplan et al. (2017) and York et al. (2008). Deep-water populations may act as a reservoir that can replenish surface populations that have been impacted by disturbance events at the surface in estuarine habitats (Lewin 1986).

Acknowledgements

This research was made possible from funding provided by the St. Lawrence University Biology Department. The author would also like to thank Frederick Auker, Jason Signore, Stephan Bullard, and Chris Deacutis for field assistance and advice. I would like to thank S. Bullard and members of the SLU faculty writing group, particularly Jeffrey Maynes, for comments and suggestions on the manuscript during all stages of writing. I would also like to thank all of the private marinas mentioned herein for permitting me access to their floating docks and facilities. Finally, detailed comments from the associate editor and anonymous reviewers greatly improved this manuscript.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Estimated mean and minimum salinity for each site based on a standard curve of Narragansett Bay Fixed-Site Monitoring Network buoy latitudes and salinity values.

Table S2. *Didemnum vexillum* presence at sites in this study

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