

Introduced species provide a novel temporal resource that facilitates native predator population growth

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Abstract Non-native species are recognized as important components of change to food web structure. Non-native prey may increase native predator populations by providing an additional food source and simultaneously decrease native prey populations by outcompeting them for a limited resource. This pattern of apparent competition may be important for plants and sessile marine invertebrate suspension feeders as they often compete for space and their immobile state make them readily accessible to predators. Reported studies on apparent competition have rarely been examined in biological invasions and no study has linked seasonal patterns of native and non-native prey abundance to increasing native predator populations. Here, we evaluate the effects of non-native colonial ascidians (*Diplosoma listerianum* and *Didemnum vexillum*) on population growth of a native predator (bloodstar, *Henricia sanguinolenta*) and native sponges

through long-term surveys of abundance, prey choice and growth experiments. We show non-native species facilitate native predator population growth by providing a novel temporal resource that prevents loss of predator biomass when its native prey species are rare. We expect that by incorporating native and non-native prey seasonal abundance patterns, ecologists will gain a more comprehensive understanding of the mechanisms underlying the effects of non-native prey species on native predator and prey population dynamics.

Keywords Apparent competition · Food webs · Colonial ascidians · Non-native · Invasive · Native predator

Introduction

A positive correlation between non-native prey and native predator populations suggests that non-native prey provide an additional food source that may lead to elevated native consumer and to reduced native prey populations (Roemer et al. 2002; Inger et al. 2010). This pattern is referred to as apparent competition, where abundance or distribution of consumers is changed by a prey species hence altering the population dynamics of the other prey species (Holt and Kotler 1987). Direct competition between invasive and native species has received much attention (e.g., Hamilton et al. 1999; Grosholz 2002). Apparent competition between non-native prey and native

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consumer and prey populations has received less attention. Given that non-native species are a potent force of local, regional and global ecological change (Ruiz et al. 1997; Baiser et al. 2010), it is critical to evaluate their effect on population dynamics of native consumers and their prey.

We assessed the effect of non-native prey species on growth of a native predator in a benthic marine system using pre- and post- invasion field surveys and laboratory experiments. Food web studies in benthic marine systems are rare (see Rilov 2009 for review), but they are critical because they generate the strongest trophic cascades in nature (Shurin et al. 2002). This is particularly true for the Gulf of Maine, a region of relatively low species diversity and a high degree of seasonality in species composition (e.g., Dijkstra and Harris 2009). Because species richness is low, any additional prey to the Gulf of Maine may have a larger impact on predator abundance compared to systems with high species richness that have a larger number of prey species from which to choose.

We examined pre- and post- invasion population structure in native predator (bloodstar, *Henricia sanguinolenta*) by surveying two sites in the Gulf of Maine where there is a long-term record of species composition and timing of introduced species (e.g., Harris and Tyrrell 2001). In the Gulf of Maine, non-native colonial ascidians (tunicates, sea-squirts) are recent and common members of hard natural and artificial substrates (Dijkstra et al. 2007). In particular, *Diplosoma listerianum* and *Didemnum vexillum* are recognized as prey by the native bloodstar (Dijkstra et al. 2007), a predator of native sponges (Witman and Sebens 1990; Shield and Witman 1993). We assessed predator growth when fed a traditional native sponge diet (*Haliclona oculata*) and a diet of the two most common non-native species at the two sites (*D. listerianum* and *D. vexillum*). Finally, we examined annual abundance patterns of non-native colonial ascidians and native/established sponges using a panel study spanning about 2 years. The addition of abundant competitively superior prey may result in direct competition between native and non-native prey (e.g., Wethey and Walters 1986; Bak et al. 1996), yet may also result in apparent competition between the species. The growing interest in addition of non-native prey species to community food webs indicates a need to evaluate potential mechanisms of population growth of their native consumers.

Materials and methods

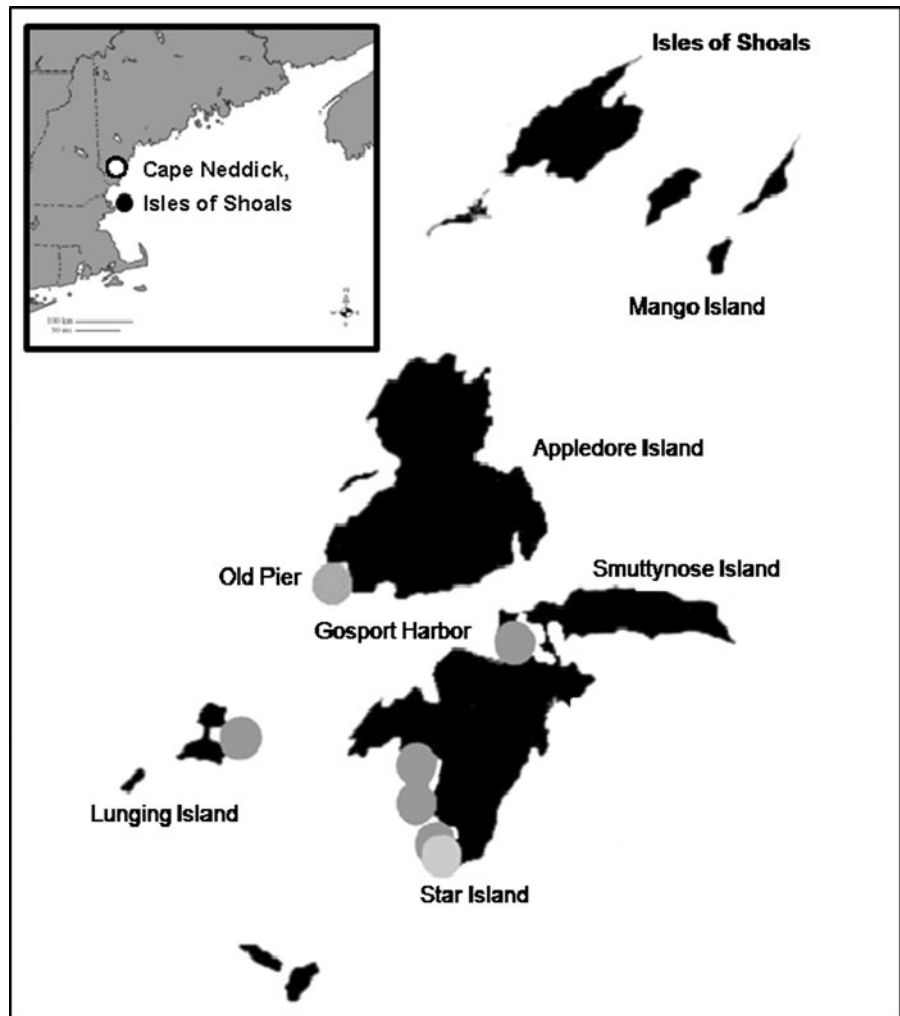
Study site and species

Pre- and post- invasion surveys documenting abundance and feeding behavior of *H. sanguinolenta* were conducted at the Isles of Shoals and Cape Neddick, ME. The Isles of Shoals is a cluster of islands located ~12 km off the coast of New Hampshire, USA and the Shoals Marine Laboratory is located on Appledore Island (42°59'19.35"N, 70°36'58.65"W; Fig. 1). Cape Neddick (43°09'57.31"N, 70°35'31.23"W) is a coastal site located in southern Maine (Fig. 1). Subtidal benthic and rocky intertidal communities at the Isles of Shoals and Cape Neddick are dominated by seaweeds and marine invertebrate filter feeders that compete for open substrate via overgrowth and chemical defense. While species compositions and densities of individual species are site specific, the composition of all hard bottom near shore benthic, fouling (communities on man-made structures) and intertidal communities studied to date in the Gulf of Maine are similar. Subtidal and intertidal rocky shores are dominated by seaweeds [e.g., *Ascophyllum nodosum* (rockweed) in the intertidal and *Saccharina latissima* (kelp) and the non-native *Codium fragile* spp. *fragile* (green fleece algae) in the subtidal]; fouling communities are dominated by sessile suspension feeding invertebrates. Within these habitats, non-native (e.g., *D. listerianum* and *D. vexillum*) and native (*Didemnum albidum*) encrusting colonial tunicates, and native sponges (*H. oculata*, *Chalinula loosanoffi* and *Halichondria panicea*) compete for open space.

Long-term abundance of the sponge *H. panicea*

To determine if sponge abundance is declining in rocky intertidal habitats similar to the observed decline in subtidal habitats (Dijkstra and Harris 2009, Harris, L.G. unpub. data), long-term sponge abundance (*H. panicea*) in the rocky intertidal was documented by students in the Shoals Marine Laboratory Field Marine Biology and Ecology course between 1982 and 2006 (data presented here were vetted by H. Weeks at the Shoals Marine Laboratory). Twenty-eight permanent transects were established by markers in 1982 at 4.1 m above mean low water. Transects ran along fixed bearings and students

Fig. 1 Survey sites of *H. sanguinolenta* at the Isles of Shoals. 2005 to 2007 sites are marked with light gray circles. Dark circle is the survey site at Star Island between 1977 and 1978 (Hurlbert 1980)



sampled in areas that represented the typical slope and exposure of each transect. Students identified and recorded the abundance of organisms. Percent cover of *H. panicea* was assessed using a 20 cm² quadrat with a 16 square grid placed haphazardly along each transect. While abundance of *H. panicea* was documented at several of these rocky intertidal transects, only one had consistent long-term sponge data.

Survey of the bloodstar *H. sanguinolenta* and colonial ascidians

To document pre- and post-invasion densities of *H. sanguinolenta*, we compared its abundance at two sites [Star Island, NH (Isles of Shoals) and Cape Neddick, ME]. Surveys were conducted between June and August, 1977–1978 (reported in Hurlbert 1980) and

between June and August, 2005 and 2007 at a site 8 m below mean low tide off the western shore of Star Island (Fig. 1). At Cape Neddick, surveys were taken at ~6 m below mean low tide in April 1980 and 2011. *H. sanguinolenta* densities at Cape Neddick and Star Island were documented by either a 0.25 m² quadrat or by a 2.5 cm wand placed in the middle of each photograph. To establish that densities of bloodstars observed at Star Island reflected densities around the Isles of Shoals, we sampled 5 other sites between June and August, 2007 using a 0.25 m² quadrat (n = 10/site; Fig. 1).

To examine dominance of non-native colonial ascidians during times of their peak abundance, we recorded abundances of all non-native colonial ascidians (*D. listerianum*, *D. vexillum*, *Botrylloides violaceus* and *Botryllus schlosseri*) at 3 sites between

June and August, 2007 at the Isles of Shoals (Lunging Island, Gosport Harbor and Old pier) using a 0.25 m² quadrat (n = 10/site).

Feeding behavior and growth studies of the bloodstar *H. sanguinolenta*

We surveyed active feeding (stomach everted) events and recorded choice of prey of 190 *H. sanguinolenta* at two locations [Cape Neddick, ME (n = 114) and the Isles of Shoals (n = 76)] between July and August 2007 and 2010, using SCUBA. At the Isles of Shoals, 4 sites were sampled which included Lunging Island, Gosport Harbor, Old Pier and Star Island (Fig. 1).

To compare growth of the bloodstar on a diet of native and non-native prey, we carried out a feeding trial using *D. listerianum*, *D. vexillum* as our non-native diet treatments, *H. oculata* as our native diet treatment, and a no food treatment. Ascidian treatments were selected to represent the two most common non-native colonial ascidians found at the Isles of Shoals and at Cape Neddick. Using SCUBA, we collected small sized (0.15–1.40 g) *H. sanguinolenta* from Cape Neddick, ME in May 2010 and individually placed them in mesh-covered (7.2 cm × 6.5 cm) treatment mesocosms. Mesocosms were placed in a flow through system at the University of New Hampshire's Coastal Marine Laboratory. Initial star weights between treatments were not significantly different ($F_3 = 0.540$, $P = 0.66$). Treatments were checked weekly for food availability and food in containers was replaced as needed to ensure treatment individuals had an unlimited food supply. We measured the weight of the bloodstars underwater by placing the individuals in a pre-weighed container half-filled with seawater (Lambert et al. 2000). Bloodstars were weighed at 2 week intervals without blotting or other handling between May 20 and August 31. Any comparisons of growth include only those individuals that survived the entire observation period (*D. vexillum* n = 8; *D. listerianum* n = 9; *H. oculata* n = 7; No food, n = 8).

Temporal patterns of abundance of colonial ascidians and sponges

We assessed temporal patterns of percent cover of non-native and native prey using a panel study. Plexiglas panels (0.1 m²) were deployed in April 2008 and were photographed through December 2010.

We determined percent cover of colonial ascidians and sponges using a 100 point grid placed over each photo.

Statistical analysis

All data were analyzed using JMP 8.0©. To homogenize the variances, abundance data were square-root transformed and percent cover data were square-root arcsine transformed prior to analysis. One-way ANOVAs were then used to test for differences in pre- and post-invasion densities of bloodstars at the Isles of Shoals and Cape Neddick, ME. Two-way ANOVA (site × species) was used to investigate non-native ascidian distribution across sites at the Isles of Shoals. On finding significant differences, a Tukey–Kramer test set to 0.05 significance was used to assess pair-wise differences between treatments. A *t* test was used on results from our laboratory experiment that examined differences in initial and end weights of bloodstar on the same diet.

Results

Long-term abundance of the sponge *H. panicea*

Abundance of *H. panicea* was variable from 1982 to 1998 at the Isles of Shoals (Fig. 2). Since 1998, *H. panicea* has not been observed in the rocky intertidal on Appledore Island. These data correspond to observed long-term declines in sponges in the subtidal zone around the Isles of Shoals (Harris and Dijkstra, unpub. obs.), and Portsmouth Harbor (Dijkstra and Harris 2009).

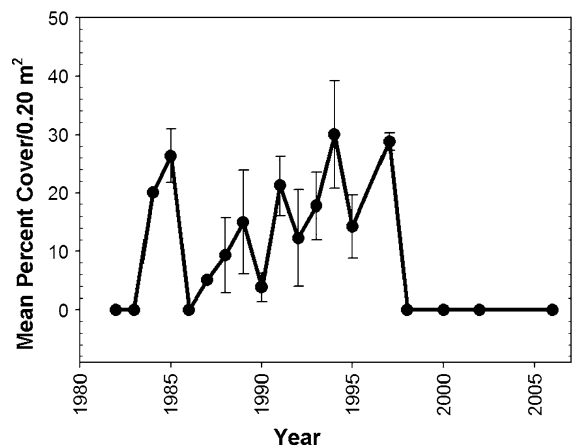


Fig. 2 Temporal pattern of sponge abundance in a low intertidal transect at Appledore Island, Isles of Shoals

Survey of the bloodstar *H. sanguinolenta* and colonial ascidians

Post-invasion densities of *H. sanguinolenta* were significantly greater than pre-invasion densities at the Isles of Shoal and at Cape Neddick ($F = 5.443$, $P < 0.025$, $F = 150.04$, $P < 0.01$, Fig. 3). Elevated *H. sanguinolenta* densities at Star Island reflected an overall increase at the Isles of Shoals ($P = 0.966$; Fig. 4).

In our 2007 surveys, *D. vexillum* and *D. listerianum* were the most common ascidians at the Isles of Shoals (Fig. 5). There was a significant main effect of species, site and an interaction between site and species (Table 1; $P < 0.05$, Tukey–Kramer). We observed

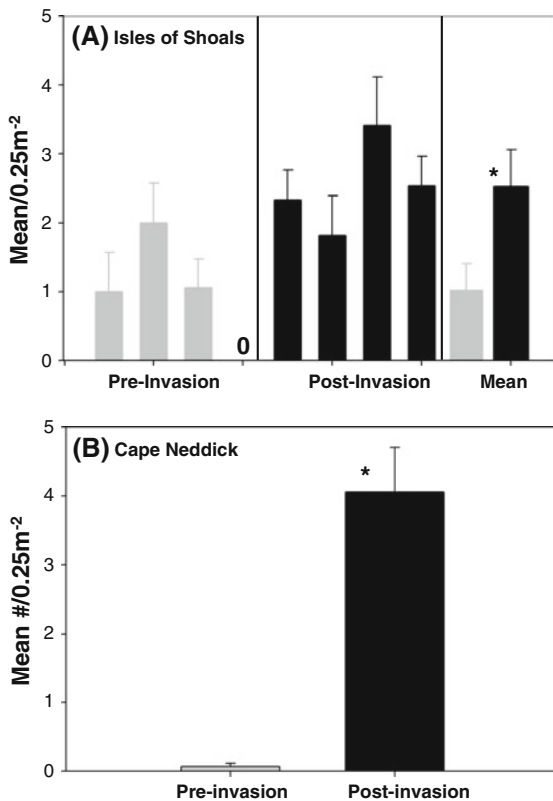


Fig. 3 a Mean abundance (+SE) of *H. sanguinolenta* between 1977–1978 pre-invasion (Hurlbert 1980) and 2005–2007 (post-invasion). Mean abundances are combined average abundances of *H. sanguinolenta* between 1977–1978 and 2005–2007. One-way ANOVA determined a significance difference ($*P < 0.025$) in abundance of *H. sanguinolenta* between the two time periods. b Occurrence of *H. sanguinolenta* between 1979–1980 and 2011 pre and post-invasion of invasive colonial ascidians at Cape Neddick, ME. ($*P < 0.01$)

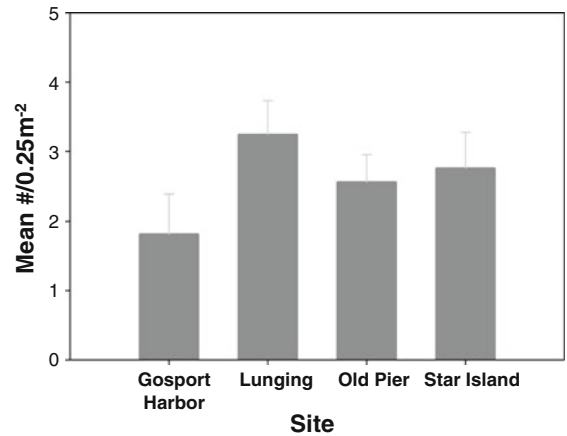


Fig. 4 Survey of *H. sanguinolenta* at four sites at the Isles of Shoals (Gosport Harbor, Lunging Island, Old pier and Star Island) between 2005 and 2007. Data presented are mean number of bloodstars (+SE)

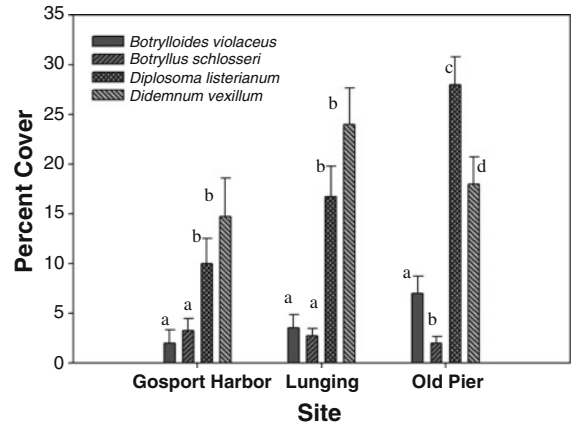


Fig. 5 Mean percent cover (+SE) of four colonial ascidians (*B. violaceus*, *B. schlosseri*, *D. listerianum* and *D. vexillum*) at three sites [Gosport Harbor, Lunging Island, and old pier] at the Isles of Shoals

very few native colonial ascidians and sponges at all sites, and none were observed in our quadrats.

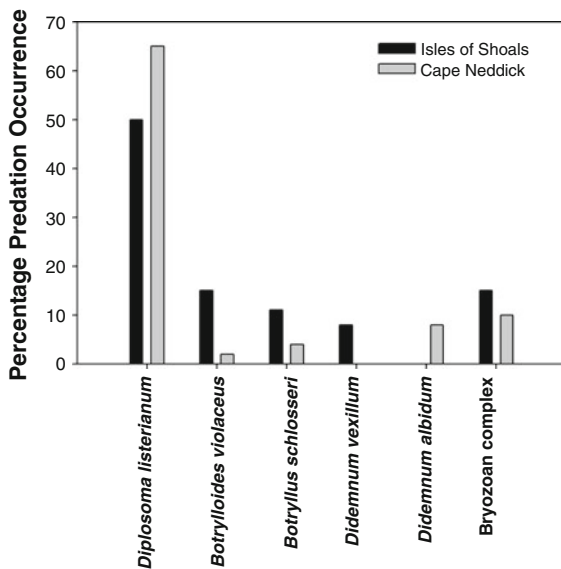
Feeding behavior and growth studies of the bloodstar *H. sanguinolenta*

Of the 76 *H. sanguinolenta* we observed actively feeding (demonstrated by an everted stomach) during dives at the Isles of Shoals, 50 % preyed on *D. listerianum*, 12 % on *B. violaceus*, 10 % on *B. schlosseri*, 9 % on *D. vexillum* and 15 % of bloodstars fed on debris composed of crushed barnacles and

Table 1 Survey of colonial ascidians at 3 sites around the Isles of Shoals

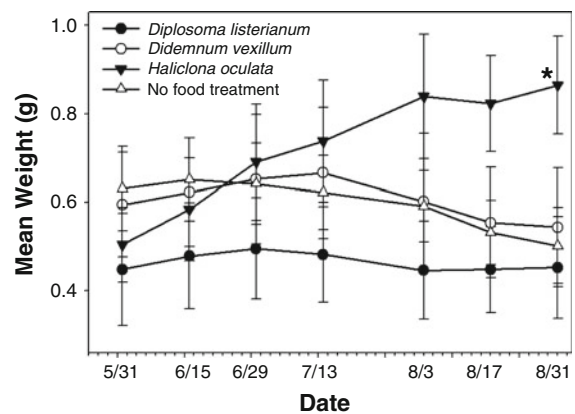
	<i>df</i>	Mean square	F ratio	Prob > F
Species	3	39.8627	17.1342	<0.0001
Site	2	32.1439	13.8164	<0.0001
Error	234	2.3265		
Gosport Harbor				
Species	3	9.56217	5.1435	0.0027
Error	75	1.85907		
Lunging				
Species	3	35.0655	23.0913	<0.0001
Error	75	1.5186		
Old Pier				
Species	3	19.9259	7.1862	0.0003
Error	75	2.7728		

One-way ANOVA with site as the block term found site was a significant factor. Significant differences in abundance in ascidians were found within sites. A Tukey–Kramer test set to 0.05 significance was used to determine significant differences in ascidian abundance within sites (see Fig. 5)

**Fig. 6** Feeding surveys of *H. sanguinolenta* at Isles of Shoals and Cape Neddick. Bryozoan complex refers to a mixture of broken barnacles shells and bryozoans

bryozoans (bryozoan complex; Fig. 6). Of the 114 *H. sanguinolenta* we observed during dives actively feeding at Cape Neddick, 64 % preyed on *D. listerianum*, 1 % on *B. violaceus*, 2 % on *B. schlosseri*, approximately 10 % on *D. albidum*, and 10 % on a bryozoan complex (Fig. 6). Sponges were not observed in our quadrats and were rarely observed at the Isles of Shoals and Cape Neddick. We did not witness *H. sanguinolenta* feeding on sponges.

Growth rates of *H. sanguinolenta* showed considerable variation among diets (Fig. 7). Bloodstars fed

**Fig. 7** Mean wet weight (\pm SE) of *H. sanguinolenta*. Asterisks denote significant differences between beginning and end weights

H. oculata increased weight over the first two months and then plateaued; overall, they grew significantly more than individuals in the other diet treatments ($t = 2.29$, $P < 0.041$). Bloodstars on either non-native diet did not significantly lose or gain weight [$(P < 0.98$ (*D. listerianum* $t = 0.02$, and *D. vexillum* $t = 0.02$)] compared to their initial weights, while bloodstars lacking food exhibited a steady, but not significant ($t = -0.61$, $P < 0.27$), decline in weight.

Temporal patterns of abundance of colonial ascidians and sponges

Non-native colonial ascidians and native sponges showed opposing seasonal dominance patterns with high percent cover of non-native prey observed in

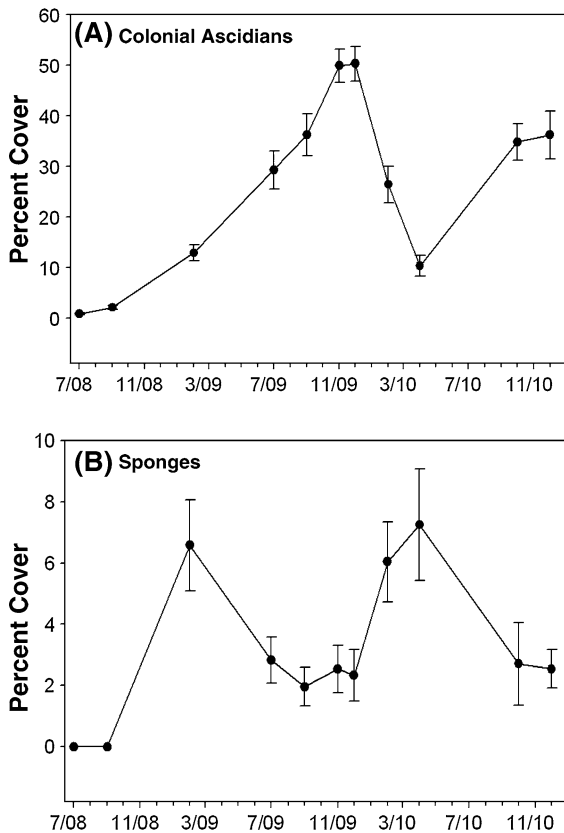


Fig. 8 Mean percent cover (\pm SE) of **a** colonial ascidians and **b** sponges and on Plexiglas panels (0.1 m^2) deployed in April 2008 and sampled seasonally through 2010. Dates refer to month/year

summer and fall months. Percent cover of native prey was highest during the winter and late spring (Fig. 8).

Discussion

Our results indicate that introduced prey can indirectly increase a native predator population by providing resources that are seasonally opposed to its native prey. Here, we show that consumption of non-natives will not directly result in greater predator biomass, but will sustain it, and limit the loss of biomass, during periods of absence of its native prey. Therefore, the addition of non-native prey may lead to increased native consumer pressure on native species (a process known as apparent competition), similar to the effects of non-native dune plants on rodents and native plants (Dangremond et al. 2010). However, direct competition between competitively superior non-native

colonial ascidians and sponges also likely contributed to the observed decline in native sponge prey, particularly in the intertidal zone (Wetthey and Walters 1986; Bak et al. 1996).

Other factors that may favor native predator population growth are temperature and rising plankton concentrations. Water temperature has increased over the last 30 years in the Gulf of Maine (Fogarty et al. 2008; Dijkstra et al. 2011). Though increasing sea surface temperature may positively influence population growth of many non-native species (Westerman et al. 2009), warmer waters may limit reproduction and growth of native species (Sorte et al. 2010; Moore et al. 2011). *H. sanguinolenta* is a cold water northern temperate species (Mah and Hansson 2011), and warming waters may likely restrict its growth and reproductive output. Another factor that may lead to elevated bloodstar densities is greater plankton concentrations. Although plankton concentrations have increased in the Gulf of Maine since the early 1980s (Pershing et al. 2005), and Anderson (1960) suggests that *H. sanguinolenta* filters particles from the water column, our results, along with others (Vasserot 1961), indicate positive growth can only occur when preying on larger food items. Though we did not witness sponge predation by the bloodstar during our field surveys, most likely because they were carried-out during a season when sponges are scarce, predation by bloodstars on sponges has been well documented (Hurlbert 1980; Witman and Sebens 1990; Shield and Witman 1993). Given that warmer temperatures and greater plankton concentrations are unlikely to enhance populations of *H. sanguinolenta*, the temporal mismatch in peak abundance of native and non-native prey likely resulted in the observed greater post-invasion bloodstar populations. Optimal foraging theory predicts that predators will switch their diet to include temporally abundant species (Hughes 1979).

Although our laboratory studies did not show significant weight gain of bloodstars on a non-native diet, they maintained weight on the non-native diet ((*D. listerianum* +1 % mean weight gain, *D. vexillum* -9.1 % mean weight loss), relative to the no food treatment (-21.4 % mean weight loss)). The offset seasonal distribution patterns of non-native and native prey, coupled with the results from the growth experiment suggests the native predator began its “growing” season at a higher biomass than it would in

the absence of non-native prey. More biomass at the beginning of the season when the native prey is available leads to larger individuals that can directly (e.g., produce more offspring) or indirectly (e.g., higher nutrient reserves that can be transferred to juveniles) support reproductive efforts that increase population size.

Many terrestrial, freshwater and marine species undergo seasonal cycles of appearance and disappearance (Tonn and Magnuson 1982; Lechowicz and Koike 1995; Stachowicz and Byrnes 2006), yet studies that include seasonal distribution of native and non-native prey species are few. We show that non-native prey enhanced growth of the native predator population by providing a source of food during periods of rarity or absence of its native prey. Therefore, temporal native and non-native prey distribution patterns should be considered in future studies and be incorporated in models of the effects of non-native species on native consumer and prey populations.

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