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The influence of invasive ascidian diets on the growth of the sea star *Henricia sanguinolenta*

Kaitlin S. Van Volkom[1], Larry G. Harris[1] and Jennifer A. Dijkstra[2]

[1]Department of Biological Sciences, University of New Hampshire, Durham NH, 03824, USA and [2]School of Marine Science and Ocean Engineering, University of New Hampshire, Durham NH, 03824, USA

Original Article

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Author for correspondence:
Kaitlin S. Van Volkom, E-mail: kv1011@wildcats.unh.edu

Abstract

Invasive species can disrupt food webs by altering the abundance of prey species or integrating into the food web themselves. In the Gulf of Maine, there have been a suite of invasions that have altered the composition of the benthic ecosystem. These novel prey species can potentially benefit native predators depending on their nutritional value and relative abundance. We measured feeding instances of the native blood star, *Henricia sanguinolenta*, and changes in the seasonal abundances of invasive ascidian prey species. Results indicate that *H. sanguinolenta* forages optimally, as the blood star will prey on invasive ascidians when in high abundance, but feed on other species during periods of scarcity. Further, our study shows that blood stars prey on a wider variety of species than was previously known, such as small bivalves and barnacles. Additionally, we compared growth and reproduction of sea stars fed different combinations of invasive ascidians (*Diplosoma listerianum* or *Botrylloides violaceus*) or a native sponge (*Haliclona oculata*). Sea stars grew more on the native diet when compared with the invasive ascidian species, and *D. listerianum* appeared to be a superior quality food source when compared with *B. violaceus*. By comparing our data with historical data, we determined that there was a dramatic increase in sea star populations between 1980 and 2011, but then populations decreased by almost half from 2011 to 2016–2017. These data suggest that while invasive ascidians may have helped sea star populations at one point, sea stars are declining without their native food source.

Introduction

The introduction of an invasive species often reduces the population of native species through competitive exclusion and predation (Vitousek *et al*., 1996). Introduced species can greatly alter food webs in ways that directly affect native species (Carlsson *et al*., 2009). While much of invasion biology has focused on the negative predation impacts of invaders, these introduced species can also provide a novel resource, thereby benefitting native predators (Rodriguez, 2006). For example, increases in fish populations have been linked to consumption of planktonic stages of invasive copepods and polychaetes (Winkler & Debus, 1997; Sørensen *et al*., 2007), and the consumption of invasive gobies has been linked to greater growth and reproduction rates in water snakes (King *et al*., 2006).

A native predator may benefit from the addition of a novel prey in their diet; however, their fitness may decline if the invasive species completely replaces the native prey (Carlsson *et al*., 2009; Tablado *et al*., 2010; Pintor & Byers, 2015). High population densities of invasive zebra mussels have provided a beneficial food source for many turtles, birds and decapods (Molloy *et al*., 1994; Petrie & Knapton, 1999; Bulté & Blouin-Demers, 2008). Yet, a species of whitefish in the Great Lakes (*Potamopyrgus antipodarum* (Gray, 1843)) has declined in body condition as a result of predominately feeding on these mussels (Pothoven *et al*., 2001). Successive invasions can alter the environment by excluding native preferred prey, forcing native predators to consume potentially nutritionally deficient prey. Continually monitoring these invaded systems is important because not all species will react in the same manner to a change in diet. Feeding on invasive prey may even result in population declines that are not seen within the system until after a lengthy period of time.

Over the past 30 years, the repeated invasion of different colonial ascidians has greatly restructured the benthic communities in the Gulf of Maine (e.g. Dijkstra & Harris, 2009). *Botryllus schlosseri* (Pallas, 1766) was the dominant ascidian in the fouling communities from 1979 to 1980 (Harris & Irons, 1982), and it was subsequently replaced by *Botrylloides violaceus* (Oka, 1927) (Berman *et al*., 1991; Dijkstra & Harris, 2009; Dijkstra *et al*., 2011), *Diplosoma listerianum* (Milne Edwards, 1841) (Harris & Tyrrell, 2001; Carman & Roscoe, 2003; Dijkstra *et al*., 2007) and later *Didemnum vexillum* (Kott, 2002). The shift towards invasive species has led to the decline of some native benthic species in the southern Gulf of Maine and has led to prey switching by predators (Pratt & Grason, 2007; Lambert *et al*., 2016).

One of the native taxa that appears to be in decline is sponges (Dijkstra & Harris, 2009; Dijkstra *et al*., 2011) which are most abundant in the winter and spring (Harris & Irons, 1982; Dijkstra & Harris, 2009). Native sponges are known prey for the sea star *Henricia sanguinolenta* (Sheild, 1990; Sheild & Witman, 1993) and a previous study suggested that *H. sanguinolenta* is, in the absence of sponges, consuming invasive colonial ascidians (Dijkstra *et al*., 2013). Historically, during winter and spring, *H. sanguinolenta* fed on a wide variety of sponges, detritus, entoprocts and bryozoans (Sheild & Witman, 1993) and in summer and autumn, fed on other food sources, or relied on filter feeding (Rasmussen, 1965; Sheild & Witman, 1993). However, the proliferation of invasive ascidians in the autumn and winter now provide an alternate abundant food source for sea stars during a time of historic prey scarcity (Dijkstra *et al.*, 2013).

Much of the basic biology and ecology of *H. sanguinolenta* is still unknown, and with a continually shifting ecosystem, it is important to examine changes in native predators' diets. We use laboratory and natural field studies in combination with long-term population growth to understand the effect of invasive ascidians on growth and reproduction of *H. sanguinolenta*. In the field, we measured seasonal changes in the abundance of several invasive ascidian species and the corresponding feeding behaviour of *H. sanguinolenta.* As previous studies suggested that *H. sanguinolenta* is an optimal forager (Sheild, 1990; Sheild & Witman, 1993; Dijkstra *et al.*, 2013), we hypothesized that their feeding behaviour would fluctuate with annual changes in prey density. We then coupled field and lab studies to examine *H. sanguinolenta's* growth and reproduction when fed diets that mimic historical seasonal colonial ascidian and sponge abundance patterns. Further, we examined growth and reproduction of the sea star when fed *B. violaceus* and *D. listerianum* only. We hypothesized that they would exhibit higher growth on their native diet when compared with an invasive species diet.

Materials and methods

Monthly benthic surveys

To examine the relationship between seasonal changes in ascidian abundance and feeding by *H. sanguinolenta*, surveys were conducted monthly between July 2016 and November 2017 via scuba at Cape Neddick, Maine (43°10′8″N 70°37′2″W): a semi-protected rocky shallow site in southern Maine that is dominated by seaweeds and invertebrates. Three to five 1 m^2 quadrats were haphazardly placed at least 2 m apart on vertical rock surfaces, and if sea stars were feeding, the prey species was recorded. Density of sea stars (number per m^2) and ascidians (% cover) were recorded for each quadrat. Per cent cover of ascidian species was estimated by sub-sampling within the 1 m^2 quadrat with four, 0.25 m × 0.25 m gridded quadrats.

To examine long-term changes in the population structure of *H. sanguinolenta*, current data were compared with those collected in 1980 and in Dijkstra *et al.* (2013). Abundances of *H. sanguinolenta* in 1979–1980 were obtained by Dijkstra *et al.* (2013) from photographs taken by L. Harris. These data, and those in 2011 from Dijkstra *et al.* (2013) were collected using 0.25 m^2 quadrats. To compare these abundance values with the ones collected for this study, we multiplied them by four to standardize abundances to a 1 m^2 area. Only data from July and August were used, since these are the months that Dijkstra *et al.* (2013) surveyed. All three studies occurred at the same study site and in similar habitats.

Statistical analysis

The number of feeding individuals on each ascidian species was compared with the total per cent cover of ascidian species using a mixed model ANOVA in JMP Pro 15. Per cent cover was a fixed variable while month and ascidian species were considered random variables. A linear regression was performed to determine the relationship between per cent cover and the number of feeding individuals. To examine long-term changes in the population structure of *H. sanguinolenta*, abundances observed in 1979–1980, 2011, and 2016–2017 were compared using an ANOVA and a Tukey's HSD test using JMP Pro 15. These data were not distributed normally and could not be corrected with a transformation, and a Levine's test revealed that variances were unequal. Since the assumptions of equal variances and equal replicates was not met, a more stringent *P*-value of 0.01 had to be met for results to be significant.

Experimental growth studies

Sea stars were collected from Cape Neddick, Maine in late summer, 2016. Ascidians were collected from Cape Neddick, ME, the University of New Hampshire pier in New Castle, NH and Hawthorne Cove Marina, Salem, MA. *Haliclona oculata* were collected from the University of New Hampshire's pier. After collection, animals were maintained in a flow-through system for one week at the University of New Hampshire's Coastal Marine Lab in New Castle, NH. Sea stars in the multi-food treatments were held at 16°C with a chiller. Sea stars in the single-food treatments were held at ambient temperature (~20°C) because of a shortage in chillers. Though sea stars were not fed, they are able to filter feed and were kept in a flow-through system, so it is possible that they were filter feeding. Prior to the beginning of the experiment, individuals were weighed and placed in polyethylene cups (1 individual per cup) that had a height of 7.62 cm and a diameter of 7.62 cm at its widest (total volume, 236 ml^3). The sides of the containers were cut and replaced with a plastic netting (3 mm × 4 mm mesh size). They were given a surplus of food each week and they were weighed twice a month thereafter.

Multi-food growth experiments

To mimic pre- and post-invasion seasonal cover of invasive ascidians and sponges, four diet treatments were performed (1) *Diplosoma listerianum*: *Haliclona oculata* (DH, N = 17); (2) *Botrylloides violaceus*: *Haliclona oculata* (BH, N = 17); (3) No food: *Haliclona oculata* (NH, N = 17); (4) No food (*N*, N = 17) (Table 1). Ascidian diets were given in the autumn, a time when they are dominant in the community, while sponges were given in the winter. Treatments 1 & 2 represented the proposed current diet, Treatment 3 represented the proposed historical, pre-invasion diet, and Treatment 4 was a negative control. Autumn was designated as the time from 1 September to 30 November, and winter was from 1 December to 10 March.

Initial body masses between the different treatments were not significantly different from one another (0.15–0.74 g, mean = 0.39 g; $F^3_{76} = 0.4091$, $P = 0.7469$). Animals were maintained at water temperatures between 14–16°C using a chiller from 1 September until 26 October 2016. After October, the chiller was removed and the animals were maintained at ambient water temperatures (4–15°C). Sea stars were switched to their native sponge diet on 1 December 2016 (Treatments 1–3). These experiments concluded on 10 March 2017, after which animals were relaxed in an 8% MgCl solution and cut into five sections through the oral disc. Diet is directly tied to both growth and reproduction in sea stars, so a high-quality diet should lead to large pyloric caecae and gonads. Each arm was dissected along the ambulacral grooves and the gonads and pyloric caecae were removed. Animals were sexed and the wet weight of the gonads and pyloric caecae were measured on an OHAUS Adventurer scale.

Single-food growth experiment

In addition to the seasonal multi-food growth experiments, we wanted to examine the effect of single food non-native ascidian diets on sea star growth and reproduction. Sea stars were fed a diet of *B. violaceus* (N = 10) or *D. listerianum* (N = 17) from 4 August 2016 to 10 March 2017. Each treatment had sea stars of

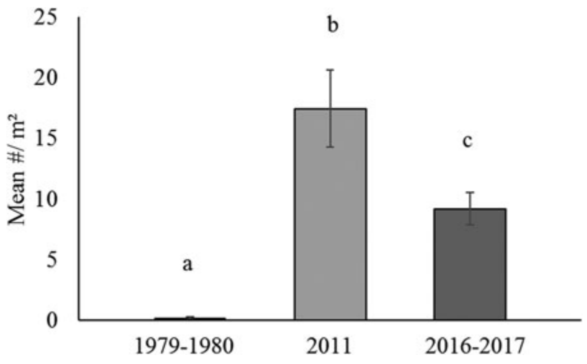

Fig. 1. Population densities of *H. sanguinolenta*. Mean abundances are combined average abundances of *H. sanguinolenta* between 1979–1980, 2011 (Dijkstra *et al*., 2013), and 2016–2017. These data represent sea star populations observed between July and August. Differing letters represent statistical differences and error bars are the standard error.

a similar weight distribution (0.25–1.2 g, mean = 0.53 g) and initial weights between treatments were not statistically different ($F^1_{25} = 0.2522$, $P = 0.6199$). These ascidians were chosen as they are known components of the sea star's diet, abundant in the Gulf of Maine, and projected ocean warming is predicted to increase their abundance in rocky subtidal communities (Stachowicz *et al*., 2002; Dijkstra *et al*., 2011, 2017). The experiments concluded on 10 March 2017, and dissections were completed as described above.

Statistical analysis

Differences in the final body mass among treatments were compared for three time periods: autumn, winter and the total length of the experiment. These values were compared in R Studio (V 3.2.2) using an ANCOVA with the initial weight for each time period as the covariate, and further analysed with a Tukey's HSD test. The same statistics were run using week 1 as a starting date and significance patterns remained the same, so week 3 was chosen as our starting point. Single food and multi-food experiments were analysed separately since they ran for different time periods and started at different temperatures.

Growth rate was calculated using the following formula: ((Final Mass − Initial Mass)/(Initial Mass × Number of Weeks)) × 100. The growth rate for the autumn, for the winter, and total growth were calculated independently. Growth rates in the autumn were calculated using the third week as the initial mass, since animals in all treatments lost weight during the first two weeks of the experiment, likely due to stress from the lab environment and not treatment effect (Bose *et al*., 2019). The final pyloric caeca mass was standardized by using the organ to body mass ratio and an ANOVA and Tukey's HSD test was run using JMP Pro 13.

Results

Monthly benthic surveys

Sea star population density at Cape Neddick, Maine has decreased significantly ($F^2_{102} = 36.8385$, $P < 0.0001$) since 2011 (Dijkstra *et al*., 2013) (Figure 1). The data from 1979–1980 represent the population of sea stars before the invasion of colonial ascidians, where the population density of sea stars was 0.19 individuals m^{-2}. The data collected in 2011 was after the invasion of ascidians, and the density of sea stars was 17.4 individuals m^{-2}, and densities recorded during this study have almost halved at 9.2 individuals m^{-2}.

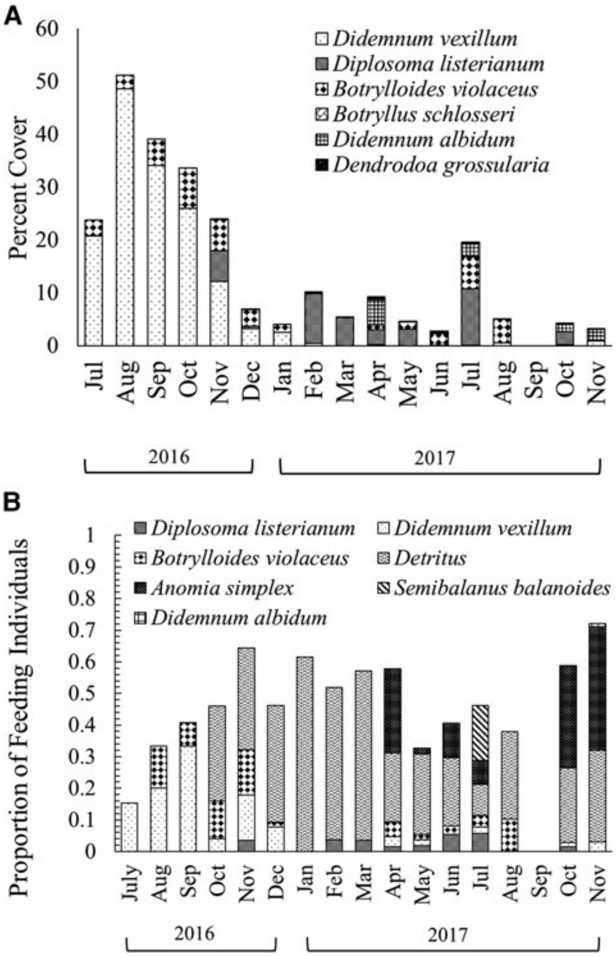

Fig. 2. Annual fluctuations in per cent cover of ascidian species (A) and feeding behaviour of *H. sanguinolenta* from 2016–2017 (B). Bars in Figure 2B show the proportion of animals that fed on a certain species, and the empty space above represents the proportion of animals that were not feeding. Different bar patterns represent diet. Data were not collected in September 2017 due to Hurricanes Harvey and Jose. As ascidian abundance declines, *H. sanguinolenta* begins consuming detritus and the jingle shell, *A. simplex*.

Per cent cover of ascidian species ($F = 18.8418$, $P < 0.0001$) was found to have a significant effect on feeding behaviour, but given our more stringent *P*-value, month was not ($F = 18.8418$, $P = 0.0308$). Per cent cover explained 72% of the variation in the feeding behaviour of *H. sanguinolenta* ($R^2 = 0.7208$, $P < 0.0001$). The recorded number of feeding instances did not significantly change over the year, nor did the number of sea stars feeding on a particular ascidian species. Per cent cover of detritus, *Anomia simplex* (Mabille, 1895) and *Semibalanus balanoides* (Linnaeus, 1767) were not measured and thus not included in the above statistic. Ascidian abundance was highest in late summer of 2016 and then declined throughout the winter, and high ascidian abundance was not seen again (Figure 2A). In the late summer of 2016, sea stars mainly fed on *D. vexillum* (Figure 2B), which was also the most abundant ascidian at that time of year with cover ranging between 34–48% (Figure 2A). Individuals were also observed feeding on *B. violaceus* at the end of summer (2–5% cover). Ascidian abundance continued to decline into the winter season to ~4% in January, and sea stars continued to feed on detritus. In the late winter, sea stars preyed on *D. listerianum* after it appeared on the substrate (5–9% cover).

In spring, the native ascidians *Dendrodoa grossularia* (Van Beneden, 1846) (<1%) and *Didemnum albidum* (Verrill, 1871) (~5%) were seen, but no sea stars were observed feeding on these species (Figure 1). During this time, sea stars were observed

Table 1. Multi-food diets were switched in late December from an ascidian to a sponge diet

	Autumn 2016	Winter 2017
DH	*Diplosoma listerianum*	*Haliclona oculata*
BH	*Botrylloides violaceus*	*Haliclona oculata*
NH	No supplemental food	*Haliclona oculata*
N	No supplemental food	No supplemental food

consuming a small native bivalve, *A. simplex* (Figure 2B), which is the first recording of *H. sanguinolenta* feeding on *A. simplex*. In March and April, the abundance of both *D. vexillum* and *D. listerianum* increased, and sea stars began to feed on these species, despite their low abundances (0–9% cover). *Henricia sanguinolenta* continued to eat detritus during the spring.

In July, sea stars were observed feeding on small barnacles, *S. balanoides*, which is another previously undocumented food source (Figure 2B). In August 2017, sea stars fed solely on *B. violaceus* and detritus. Data were not collected in September, due to a series of hurricanes that came through the Gulf of Maine. In October and November 2017, there was an increase in the native ascidian *D. albidum*, but only one sea star was observed feeding on it. Sea stars fed mainly on detritus, and newly settled *A. simplex* individuals, as ascidian per cent cover was very low during this time (Figure 2A). No sponges were seen during the course of this study.

Experimental growth studies

Multi-food growth experiments

During this experiment, sea stars were observed feeding on all food items. Overall, sea stars that were fed had higher final body masses than those that were not fed ($F^{3}_{62} = 12.161$, $P < 0.0001$) (Table 2). When looking at the final total body masses, sea stars on the DH and BH diet were similar, and sea stars that were fed the BH diet were similar to both DH and NH. In the autumn months, sea stars on the DH diet had similar body masses to those on the BH diet ($F^{3}_{62} = 4.0494$, $P = 0.01079$). Sea stars on the BH diet had body masses that were statistically similar to all other treatments. (See Table 1 for treatment descriptions.) In the autumn, all sea stars, regardless of treatment, lost body weight, while in the winter, individuals fed sponge exhibited positive growth, and those that were not fed continued to lose weight. Overall, sea stars that were fed exhibited positive growth, while those that were not lost weight.

Animals on the DH diet had a higher pyloric caeca to body mass ratio than those that were not fed ($F^{5}_{61} = 3.5957$, $P = 0.0065$). Those on the NH and BH diets were statistically similar to both the DH and no food diet (Figure 3). All treatments had similar gonad mass to body mass ratios ($F^{5}_{61} = 1.3345$, $P = 0.2618$).

Single-food growth experiment

There was no difference in the final autumn body masses between treatments, and sea stars on both treatments lost weight during this period ($F^{1}_{24} = 0.5328$, $P = 0.4725$) (Table 3). However, in the winter, those that ate *D. listerianum* had higher final body masses than those that consumed *B. violaceus* ($F^{1}_{24} = 2.996$, $P = 0.00627$) (Table 3). Overall, animals on both treatments lost weight during this experiment, but those that were fed *D. listerianum* lost less weight than those that were fed *B. violaceus* ($F^{1}_{24} = 8.1467$, $P = 0.00875$). Animals that consumed *D. listerianum* had a higher pyloric caeca mass to body ratio than those that were on the *B. violaceus* diet (Figure 4) ($F^{1}_{25} = 5.5718$, $P = 0.0264$), but there

Table 2. Average weekly growth rates and final average body masses of sea stars on different diets in autumn, winter, and over the entire experiment

		Autumn Growth Rate (%/week)		Autumn Final Mass (g)		Winter Growth Rate (%/week)		Winter Final Mass (g)		Total Growth Rate (%/week)	
Treatment	*N*	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE
B. violaceus: *H. oculata* (BH)	17	−0.551	0.256	0.362	0.023	0.767	0.398	0.417	0.028	0.179	0.217
D. listerianum: *H. oculata* (DH)	17	−0.923	0.300	0.395	0.019	1.243	0.274	0.470	0.023	0.259	0.131
No additional food (N)	17	−0.927	0.225	0.331	0.020	−0.612	0.092	0.301	0.023	−0.705	0.094
No additional food: *H. oculata* (NH)	17	−0.862	0.597	0.341	0.019	0.768	0.248	0.381	0.023	0.064	0.273

N, number; SE, standard error.

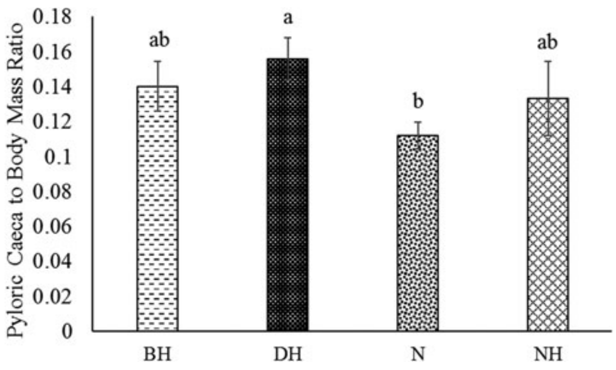

Fig. 3. Final pyloric caecae mass to body mass ratios. The treatment abbreviations are as follows; BH: *Botrylloides violaceus* and *Haliclona oculata*, DH: *Diplosoma listeranium* and *Haliclona oculata*, N: no food, NH: no food and *Haliclona oculata*. Different letters represent statistical differences and error bars are the standard error.

were no differences in gonad mass to body ratios among treatments ($F^1_{25} = 0.0793$, $P = 0.7806$).

Discussion

Our study reveals a decline in sea star populations since 2011 with concurrent declines in sponge populations. Further, our results, along with Dijkstra *et al.* (2013), showed that *H. sanguinolenta* lost weight when fed an ascidian diet, and gained weight on a sponge diet. This is the first study to examine annual changes in feeding behaviours of *H. sanguinolenta*, and highlights (along with others, e.g. Rasmussen, 1965; Sheild, 1990; Sheild & Witman, 1993; Dijkstra *et al.*, 2013) that it is a generalist predator that feeds opportunistically. Our work shows that sea star feeding behaviour increased with higher per cent cover of ascidian species, but that sea stars are not preferentially feeding on a particular species. In contrast to studies that suggest *H. sanguinolenta* feeds mainly on sponges and ascidians, this study demonstrates that individuals will consume the jingle shell, *A. simplex*, the barnacle, *S. balanoides*, as well as deceased or molted crab exoskeletons, *Cancer* spp. These species likely require a longer handling time than sponges or ascidians, and are probably eaten when there are not many other prey options available.

We hypothesized that sea stars that consumed ascidians prior to feeding on sponges would have higher final body masses than those that were starved prior to feeding on sponges. This proved to be true for sea stars that consumed *D. listerianum* prior to eating sponges, but was not true for those that consumed *B. violaceus* before sponges. Additionally, when exposed to single food diets, individuals that consumed *D. listerianum* had higher final body masses when compared with *B. violaceus*, and they also had higher pyloric caecae masses. These results suggest that *D. listerianum* is a better food source than *B. violaceus* and may contribute to growth in the field. Although growth on a diet of *H. oculata* was not directly compared with growth on an ascidian diet in this study, a previous study did directly compare the two, and found that sea stars had higher growth when consuming *H. oculata* than invasive ascidians (Dijkstra *et al.*, 2013). Combined, our results indicate that invasive ascidians do not contribute to growth, but help to alleviate starvation as individuals fed *D. listerianum* in the autumn gained more weight when they switched to a sponge diet. The combination diets were designed to represent a system in which sea stars were able to feed on invasive ascidians in the autumn and sponges in the winter. While this may be a possibility in some areas of the Gulf of Maine where sponges are still present, these diets were not reflective of the benthic ecosystem at Cape Neddick, ME.

Table 3. Autumn, winter, and total growth rates and final average body masses of sea stars on single food diets

		Autumn Growth Rate		Autumn Final Mass		Winter Growth Rate		Winter Final Mass		Total Growth Rate	
		(%/day)		(g)		(%/day)		(g)		(%/day)	
Treatment	*N*	Mean	±SE	Mean	±SE	Mean	± SE	Mean	±SE	Mean	±SE
B. violaceus	10	−1.68	0.441	0.415	0.047	−0.296	0.172	0.383	0.0009	−0.805	0.152
D. listerianum	17	−1.63	0.239	0.438	0.031	0.542	0.225	0.478	0.065	−0.368	0.110

N, number; SE, standard error.

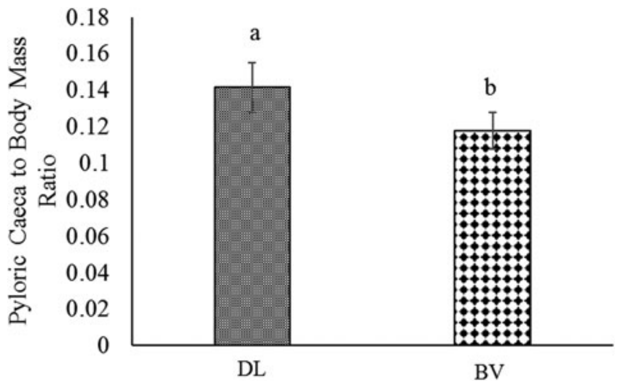

Fig. 4. Ratio of pyloric caeca to body mass of animals that consumed either *D. listerianum* or *B. violaceus*. Different letters represent statistical differences and error bars are the standard error.

Sea stars are feeding on ascidians in the field, but they did not exhibit positive growth while feeding on these species in the lab. Since growth is directly linked to maternal output (Georgiades *et al*., 2006), it follows that there should be declines in population sizes. Although there was an increase in sea star populations between 1980 and 2011 (Dijkstra *et al*., 2013), the populations at Cape Neddick, ME have almost halved in the five years since that study. It is possible that sea star populations increased between 1980 and 2011 because sea stars had access to both native and invasive food sources, and were not yet affected by rising temperatures in the Gulf of Maine. While this study did not record sea star populations in multiple locations across the Gulf of Maine, this is still a precipitous drop in population size at this site. No sponges were seen at this site during this 17-month study, and our study and Dijkstra *et al*. (2013) have demonstrated that sponges are superior prey to ascidian species. In other locations across the Gulf of Maine, there are sponge populations remaining (personal observations), and future studies should compare these areas with sites where sponges no longer remain.

The Gulf of Maine has warmed more rapidly than 99.9% of the world between 2004 and 2016 (Pershing *et al*., 2015). Winter temperatures have seen moderate increases, yet changes in summer water temperatures have been pronounced (Dijkstra *et al*., 2017). While sea stars can withstand brief periods of warming, long-term exposure to high temperatures can result in Sea Star Wasting Disease (Staehli *et al*., 2009; Van Volkom, 2018) or death (Van Volkom, personal observation). Given these repeated, heightened temperatures in combination with the presence of sub-optimal food sources, a decline in sea star population is not unexpected.

As the prevalence of invasive species in the Gulf of Maine continues to increase, and benthic food webs continue to shift (Dijkstra & Harris, 2009; Dijkstra *et al*., 2017), predators will have to adapt to a continually changing food web. As shown by our field data, predators may not be able to rely on consistent food sources from year to year, and generalist predators will be highly favoured. If invasive species and increasing water temperatures continue to diminish or remove native species from ecosystems, specialist predators will struggle to find the food sources that they need. Even generalist predators, such as *H. sanguinolenta*, that can change their diet to opportunistically feed on whichever prey species is available, are still struggling to grow and reproduce. While some native predators have the capacity to alter their diet and take advantage of novel food sources, this does not mean that they will be able to thrive in this altered ecosystem. With the compounded pressures of climate change and radically invaded ecosystems, we may soon see the decline of more native predators.

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