Effects of a non-native cyanobacterium on bay scallops (*Argopecten irradians*) in a New England seagrass ecosystem

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ABSTRACT

Bay scallops (*Argopecten irradians*) are an economically valuable species whose populations have declined in recent decades due in part to harmful algal and cyanobacterial blooms. Nantucket, Massachusetts hosts one of the last remaining bay scallop fisheries in the U.S., but recently documented the occurrence of a non-native cyanobacterium (*Hydrocoleum* sp.). *Hydrocoleum* can form dense mats in seagrass beds, the primary habitat of scallops, but is also diazotrophic, potentially augmenting bioavailable nitrogen to primary producers and fueling secondary production. We conducted surveys to explore the relationships between *Hydrocoleum* and scallop condition, reproductive potential, and density in eelgrass beds in Nantucket Harbor as well as effects of other habitat characteristics (e.g., eelgrass cover) on these same scallop traits. We found low *Hydrocoleum* cover during our sampling, but found fewer large scallops in plots with *Hydrocoleum*, suggesting that this size class may be especially vulnerable to negative effects of *Hydrocoleum*. Contrary to expectation, we found a positive correlation between *Hydrocoleum* cover and scallop condition. These patterns suggest that *Hydrocoleum* may enhance scallop condition, but also affect habitat use, highlighting the need for manipulative experiments to clarify mechanisms driving these relationships. Understanding how non-native species such as *Hydrocoleum* impact fishery species will help advance conservation and resource management efforts.

1. Introduction

Nonindigenous species (NIS) are affecting the biodiversity of marine systems (Molnar et al., 2008), including the health and productivity of economically important fisheries (Katsanevakis et al., 2014). Impacts of NIS on commercially important native species can occur through changes in habitat quality produced by NIS (Longepierre et al., 2005) or through direct effects of NIS on the survival and productivity of native species. For example, high abundance of an invasive tunicate (*Didemnum vexillum*) on Georges Bank in the North Atlantic is associated with lower abundance of sea scallops (*Placopecten magellanicus*), an economically important native fishery species in New England (Kaplan et al., 2018). NIS can also facilitate commercially important native species; for example, in the North Sea, shells of an invasive oyster (*Crassostrea gigas*) are the preferred settlement substrate of *Ostrea edulis*, a native oyster whose populations have locally collapsed due to overfishing (Christianen et al., 2018). As anthropogenic activities continue to accelerate the movement of marine species beyond their historic ranges (Miller and Ruiz 2014), these economic and ecological effects are likely to become more prevalent globally.

Bay scallops (*Argopecten irradians*) are an ecologically important and commercially valuable species along the Atlantic and Gulf coasts of the U.S that serve as key prey for mesopredators (Irlandi et al., 1999; Myers et al., 2007) and facilitate benthic-pelagic coupling and carbon sequestration (Wall et al., 2011). Historical assessments of scallop population sizes along the East Coast of the U.S. are largely based on estimates from the fishery, which has occurred since the mid-1800s, with landings averaging >300,000 bushels annually from 1950 to 1984 (MacKenzie 2008). However, after phytoplankton blooms ("brown tides") caused widespread die-offs in the mid-1980s, scallop landings declined 93% by 2010, and many populations have failed to recover since (Summerson and Peterson 1990; MacKenzie 2008; MacKenzie and Tarnowski 2018). Multiple factors could be contributing to this recovery failure, including recruitment limitation at low densities (Peterson and Summerson 1992), loss and fragmentation of seagrass beds (Irlandi et al., 1999; Hughes et al., 2009; Carroll et al., 2012), and continued proliferation of harmful algal or cyanobacterial blooms (Summerson and Peterson 1990; Meseck et al., 2007). While scallop populations remain

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low throughout their range, scallops still make important contributions to coastal economies, with landings of wild-caught, commercially harvested bay scallops exceeding $3.8 million annually in the U.S. between 2010 and 2018 (NOAA Fisheries, 2020).

Climate change and other anthropogenic factors (e.g., eutrophication) are increasing the prevalence and growth of cyanobacteria in coastal marine systems (O'Neil et al., 2012; Paerl and Paul 2012). The proliferation of cyanobacteria may have direct and indirect effects on bay scallop survival and condition (Fig. 1). Macroscopic, filamentous cyanobacteria can form thick mats along the benthos such that its biomass can exceed that of macrophytes such as seagrasses (Beer et al., 1986). Scallops rely on seagrasses for habitat throughout their ontogeny, with juveniles settling on seagrass blades and adults taking refuge at the plant/sediment interface (Belding 1910; Thayer and Stuart 1974). Blooms of filamentous cyanobacteria can reduce light penetration to seagrasses (Tiling and Proffitt 2017), limiting seagrass production, shoot density, and growth (Watkinson et al., 2005; Tiling and Proffitt 2017), which may negatively affect scallop densities (Bologna and Heck 1999). The addition of large amounts of dense biomass to seagrass beds may also limit scallop mobility (Raffaelli et al., 1998) and reduce habitat availability, potentially forcing scallops to occupy sub-optimal habitats that increase their likelihood of being consumed or harvested (Eby and Crowder 2002). Indeed, blooms of a filamentous mat-forming cyanobacterium (*Lyngbya majuscula*) substantially reduce the density of epibenthic organisms in mangroves and seagrass beds and decrease overall fish catch compared to non-bloom years (Pittman and Pittman 2005). Organisms may also avoid cyanobacterial mats because of localized changes in water chemistry. The decomposition of cyanobacteria can deplete dissolved oxygen and cause localized hypoxia (Paerl and Otten 2013), and reductions in flow under macroalgal canopies can reduce dissolved oxygen concentrations and negatively affect bivalve condition, growth, and survival (Gribben et al., 2009).

Contrary to potential negative impacts, increased filamentous cyanobacterial cover may positively affect the density of epibenthic organisms such as scallops by increasing habitat complexity, as has been found with filamentous algae (e.g., Wright et al., 2014). Increased structure may itself provide more habitat for juvenile settlement (Gribben et al., 2009) or provide greater refuge from mobile predators whose movement can be impeded by thick algal mats (Bell and Westoby 1987), thereby reducing the physiological stress associated with predator exposure (Slos and Stoks 2008). In addition, filamentous nitrogen-fixing cyanobacteria can be an important source of bioavailable nitrogen that is readily utilized by phyto- and zooplankton (Karlson et al., 2015), primary food sources for suspension feeders such as scallops. Because nitrogen is often limiting in coastal marine systems (Howarth and Marino 2006), increased availability of nitrogen-rich phytoplankton in or near cyanobacterial mats may enhance scallop growth and body condition and reduce both intra- and interspecific competition for food, as has been shown in clams in the Baltic (Karlson et al., 2014). Increased nitrogen fixation by cyanobacteria may also increase nitrogen availability to seagrasses (García and Johnstone 2006) and enhance their above-ground growth (Lee and Dunton 2000), further increasing habitat complexity, which could positively affect scallop survival. Despite the variety of potential impacts of cyanobacteria on seagrass systems, we have little understanding of how they alter bay scallop survival, performance, and habitat use in the field.

Nantucket, Massachusetts hosts one of the last remaining wild bay scallop fisheries in the U.S., and supplied over half of Massachusetts' landings from 2010 to 2019 (National Marine Fisheries Service Fisheries Statistics Division, 2020). Nantucket maintains some of the largest expanses of eelgrass (*Zostera marina*) meadows in the region (>1335 ha, Massachusetts Department of Enviromental Protection, 2013), which may contribute to its relatively robust scallop populations (Bologna and Heck 1999; Carroll and Peterson 2013). The Town of Nantucket also began augmenting scallops populations through late-stage larval release in 2010. In 2008, annual subtidal surveys of Nantucket's eelgrass beds first documented the presence of a previously unobserved macroscopic, filamentous, benthic cyanobacterium (P. Boyce, unpublished data). The species was initially classified microscopically as belonging to the *Lyngbya* genus (P. Boyce, personal communication), but has since been classified via genomic techniques as a species of *Hydrocoleum* (Moisander et al., 2017). *Hydrocoleum* is a genus of diazotrophic (nitrogen fixing) cyanobacteria native to tropical oceans throughout the world (Palińska et al., 2015) and to our knowledge, previously reported only once in another temperate habitat (Magdalen Islands, Gulf of St. Lawrence, Péquin et al., 2017). The filamentous growth structure of *Hydrocoleum* facilitates the formation of thick mats that grow epiphytically on corals and seagrasses (Palińska et al., 2015). In its native range, cyanobacterial mats dominated by *Hydrocoleum* fix as much 1.7× more nitrogen per unit biomass than bare substrate and, along with another species (*Nodularia* sp.), contribute up to 19% of the nitrogen requirement for benthic primary production (Charpy et al., 2007). Certain species of *Hydrocoleum* produce toxins that can be harmful to shellfish (Méjean et al., 2010), but Moisander et al. (2017) found no evidence of

	Potential effect on scallops	Potential drivers
Negative ↓	*Condition index* *Gonadosomatic index* *Density* *Survival* *Habitat availability* **Narrower size range**	**Direct** • Complex structure reduces mobility, food availability, feeding efficiency • Decomposition reduces local dissolved oxygen **Indirect** • Reduction in light/flow to eelgrass reduces habitat quality
Positive ↑	***Condition index*** *Gonadosomatic index* *Density* *Survival* *Habitat availability* Wider/same size range	**Direct** • Production of bioavailable nitrogen increases food quality/quantity • Increased structure offers greater refuge from predators and habitat for settlement **Indirect** • Production of bioavailable nitrogen to eelgrass increases habitat quality/quantity

Fig. 1. Conceptual model of the potential positive and negative effects of *Hydrocoleum* sp., an invasive filamentous cyanobacterium, on bay scallops (*Argopecten irradians*) along with the potential mechanisms that drive these effects. Bolded text indicates relationships found in present study.

toxin-producing genes in *Hydrocoleum* samples from Nantucket. Sampling on Nantucket in 2014 suggested a negative correlation between *Hydrocoleum* cover and eelgrass cover and biomass (A.R. Hughes et al., unpublished data). Aside from these characteristics, little is known about the effects of this non-native, increasingly prevalent cyanobacterium on the abundance and performance of bay scallops; indeed, to our knowledge, this is the first report on the relationship between *Hydrocoleum* and bay scallops in the published literature.

Field surveys were conducted to quantify the relationships among *Hydrocoleum* and overall bay scallop condition, gonadosomatic condition, and density in seagrass beds in Nantucket Harbor, Massachusetts. Relationships among other attributes of seagrass beds (e.g., eelgrass percent cover) and these same scallop indices were also examined. We hypothesized that *Hydrocoleum* presence and cover would negatively affect scallop density, condition index, and reproductive potential because scallops would avoid areas with high *Hydrocoleum* cover that might reduce these aspects of performance. Furthermore, we hypothesized that scallops would have higher condition index in areas with high seagrass and macroalgal cover. Overall, our work aimed to examine the potential impacts of non-native cyanobacterial blooms on an ecologically and economically important species.

2. Materials and methods

Nantucket is a 270-km^2 island 48 km off the coast of Massachusetts, USA (Fig. 2). Nantucket Harbor is a 19-km^2 shallow, semi-enclosed, euryhaline bay, with one entrance to the open ocean and little freshwater input (Howes et al., 2006). *Hydrocoleum* has been found in Nantucket Harbor in surveys conducted each September from 2008 to 2014 and 2019–2020, with a mean percent cover of 11% (±13% SD) across 28 sites surveyed (P. Boyce, unpublished data). Maximum coverage occurred in 2012, when the mean percent cover at all sites in Nantucket Harbor was 42%, and some sites had 100% coverage across plots surveyed (P. Boyce, unpublished data). In 2017, we established six sites with similar habitat characteristics in the mid-Harbor (Fig. 2 and Supplementary Information Table S1). Each site was comprised of a large (>1000 m^2) contiguous, subtidal (1.8–2.5 m MLLW) eelgrass bed with similar shoot densities (364.1 ± 186.1 shoots/m^2, mean ± SD, p = 0.6). Sites were >0.5 km apart and spanned a total distance of 3 km.

2.1. Surveys and scallop analyses

We explored the relationships between habitat characteristics and bay scallop (*Argopecten irradians*) density, condition index, and gonadosomatic index at six sites within Nantucket Harbor. Surveys were conducted at each site on one day each month from July–September 2017 (n = 3 sampling days; 18 July, 17 August, September 13, 2017). Surveys occurred on SCUBA during ebb tides, and sites were sampled in a random order each day. At each site, 0.25-m^2 quadrats (n = 6, N = 108) were placed randomly along a haphazard transect (30 m) that ran through a continuous eelgrass bed. Quadrats were always separated by at least 2 m along a transect line. In September, six additional, random 1-m^2 quadrats were surveyed at each site (N = 36). Quadrats were visually surveyed for *Hydrocoleum* percent cover, eelgrass percent cover, percent cover of macroalgae (mainly *Codium fragile*), and scallop density. Percent cover was determined by visual assessment.

In July, all scallop (n = 13) shell heights were measured in the field before scallops were released. In August and September, scallops (n = 57) were collected from a random subset of quadrats at each site. Scallops were immediately placed on ice and frozen in a −20 °C freezer upon returning to the lab for later analysis. After two months, scallops were thawed, measured for shell height (mm), opened, and dissected. Their gonadal tissue, somatic tissue, and shell were placed into separate, pre-weighed aluminum weigh boats, which were then dried to a constant weight in a drying oven (60 °C) for one week. Samples were then reweighed to quantify dry gonad, somatic, and shell mass. Individual scallop condition index (CI) was calculated by dividing total tissue mass by shell mass and scallop gonadosomatic index (GI) was calculated by dividing scallop gonadal tissue mass by total tissue mass. Condition index is often used as a proxy for instantaneous physiological state (Lucas and Beninger 1985) and gonadosomatic index as a proxy for future reproductive potential (Thompson and MacDonald 2006).
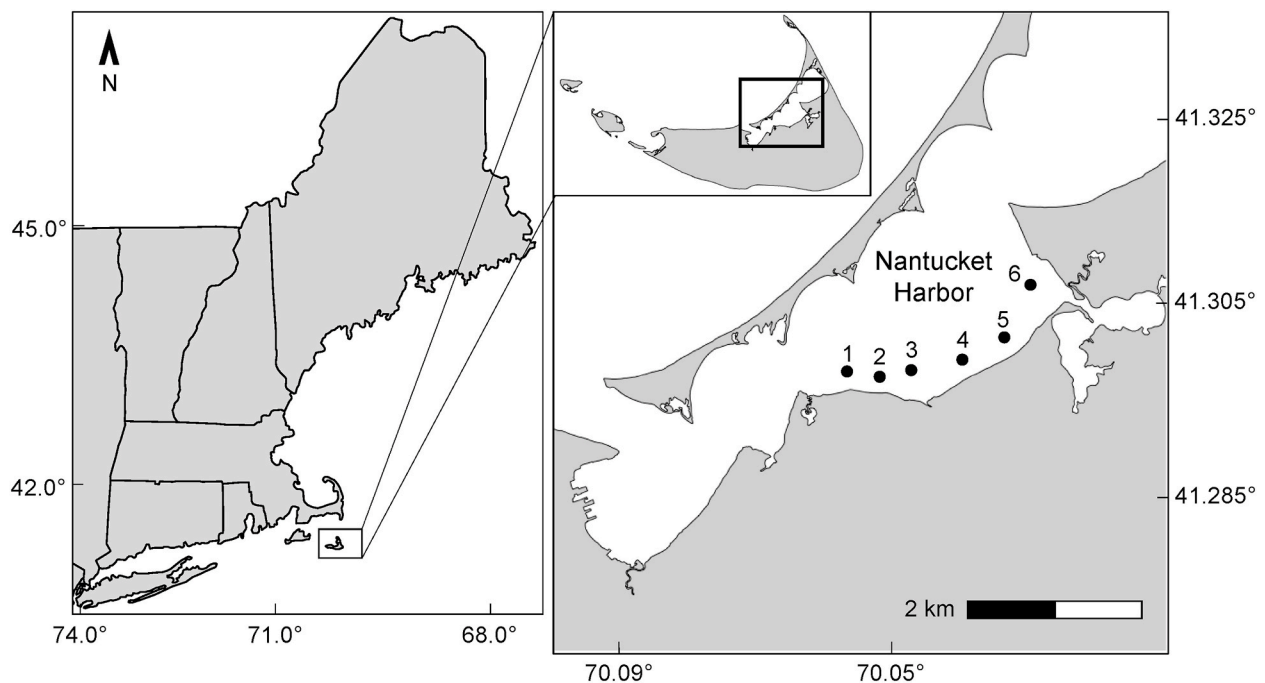

Fig. 2. Map of New England, USA (left panel) and Nantucket Island and Harbor (right panel) with locations of field sites indicated by filled circles. Site coordinates given in Supplemental Information, Table S1.

2.2. Statistical analyses

We explored whether multiple environmental and scallop variables explained variation in scallop CI, GI, and shell height using mixed multiple regression models conducted separately for each response variable. For CI and GI, predictor variables included *Hydrocoleum* percent cover, eelgrass percent cover, macroalgae percent cover, scallop density, and scallop shell height. For scallop shell height, predictor variables included *Hydrocoleum* percent cover, eelgrass percent cover, macroalgae percent cover, and scallop density. Month and site were included as a random effect in all models. GI and shell height data had a gaussian error distribution and were homoscedastic, so were analyzed with linear mixed effects models, but CI data were heteroscedastic, so were analyzed using a generalized linear mixed effects model with a gaussian error distribution and a log-link function. A separate multiple regression was used to quantify whether variation in scallop density was explained by *Hydrocoleum* percent cover, eelgrass percent cover, and macroalgae percent cover with a negative binomial error distribution to account for overdispersion in the count data (Zuur et al., 2009). Analyses were conducted on quadrat means (scallops from the same quadrat were averaged). All predictor variables were standardized and centered by their standard deviation to account for different measurement units. Because collinearity can bias parameter estimation, we calculated the variance inflation factor (vif) for each predictor. All predictors had low collinearity (Table 2), so we kept each variable in the model (Quinn and Keough 2002). Marginal R^2 values were calculated for the overall models using the MuMIn package (Bartoń 2020). Significant results of multiple regressions were plotted using added variable plots that show the relationship between the focal predictor variable and focal response variable while holding all other variables constant (*sensu* Moya-Laraño and Corcobado 2008).

Scallop size frequency distributions in quadrats with and without *Hydrocoleum* were explored using a Kolmogorov-Smirnov (K–S) test. Finally, a separate linear regression was conducted to explore the pairwise relationship between eelgrass percent cover and *Hydrocoleum* percent cover. Means and ranges of measured variables are shown in Table 1. Analyses were conducted in R (v.3.6.3) using the lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), car (Fox and Weisburg 2019), and MASS (Venables and Ripley 2002) packages.

3. Results

Hydrocoleum was found in 32% of all plots and at four of our six sites and mean overall percent cover was low (11.6% ± 23.0, mean ± SD). When present, *Hydrocoleum* covered an average of 36% of a plot (±29% SD). Scallop CI was positively associated with *Hydrocoleum* percent cover when all other variables were held constant (p = 0.04, R^2_{Adj} = 0.10, Table 2, Fig. 3). CI was also positively associated with scallop shell height (p = 0.009, R^2_{Adj} = 0.09, Table 2), but this relationship was driven by one outlier plot that contained only one small scallop (shell height = 22.5 mm, p = 0.39 without outlier, Supplementary Material,

Table 1
Sample size, mean, standard deviation, and range of scallop (*Argopecten irradians*) and environmental variables from our sampling on Nantucket, Massachusetts, USA in July, August, and September 2017.

Variable	n	Mean	SD	Range
Scallop				
Shell height (mm)	70	54.57	6.50	22.5–66.5
Condition index (CI)	57	0.158	0.029	0.069–0.197
Gonadosomatic index (GI)	57	0.093	0.055	0.007–0.202
Environmental				
Scallop density (m^{-2})	144	2.82	3.54	0–16
Hydrocoleum cover (%)	144	11.60	23.0	0–90
Zostera cover (%)	144	68.25	25.78	0–100
Macroalgae cover (%)	144	31.15	33.03	0–100

Table 2
Relationships between scallop condition index (CI), gonadosomatic index (GI), shell height, and density and relevant predictor variables (*Zostera* percent cover, *Hydrocoleum* percent cover, Macroalgae percent cover, Scallop density, and Scallop shell height) estimated from multiple regression mixed models. Parameter coefficients (estimates) are standardized and centered by their standard deviation to account for different units of measurement. Analyses were conducted on quadrat means. Bolded values indicate significant relationships (p < 0.05).

|	Parameter	Estimate	SE	t-/z-value	p-value	vif
CI R^2_{Marj} = 0.58	Intercept	−1.81	0.048	−37.74	**<2e-16**	
	Zostera	0.007	0.026	0.286	0.78	1.02
	Hydrocoleum	0.115	0.056	2.05	**0.040**	1.07
	Algae	−0.010	0.031	−0.33	0.74	1.11
	Scal. density	0.011	0.027	0.41	0.68	1.13
	Shell height	0.059	0.022	2.61	**0.009**	1.16
GI R^2_{Marj} = 0.12	Intercept	0.098	0.016	6.14	**1.7e-5**	
	Zostera	0.017	0.008	2.08	**0.046**	1.02
	Hydrocoleum	0.003	0.019	0.20	0.85	1.05
	Algae	−0.001	0.008	−0.17	0.86	1.02
	Scal. density	−0.001	0.008	−0.11	0.91	1.05
	Shell height	0.008	0.005	1.54	0.14	1.02
Shell height R^2_{Marj} = 0.01	Intercept	55.26	1.85	29.81	**<2e-16**	
	Zostera	−0.42	1.26	0.33	0.75	1.00
	Hydrocoleum	−0.08	2.22	−0.04	0.97	1.14
	Algae	0.29	1.17	0.25	0.81	1.08
	Scal. density	−0.79	1.25	−0.63	0.53	1.08
Density R^2_{Marj} = 0.04	Intercept	0.99	0.13	7.65	**1.97e-14**	
	Zostera	0.25	0.14	1.75	0.08	1.00
	Hydrocoleum	−0.18	0.15	−1.20	0.23	1.19
	Algae	−0.03	0.15	−0.17	0.86	1.19
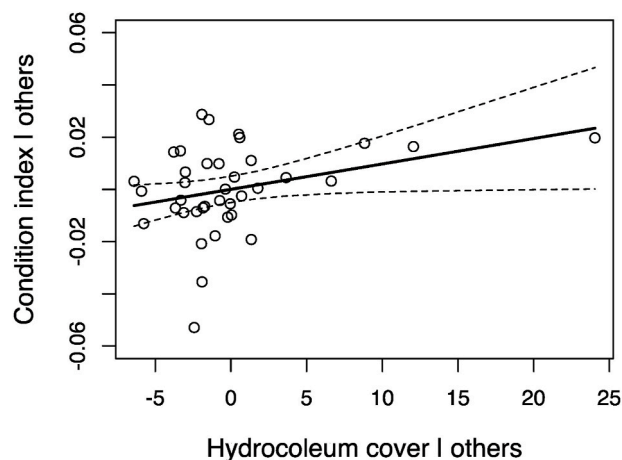
Fig. 3. Added variable plot showing the relationship between the residuals of *Hydrocoleum* percent cover (p = 0.04, R^2_{Adj} = 0.10) and scallop condition index when all other independent variables are held constant. Analyses were conducted on quadrat means. Dashed lines are 95% confidence intervals.

Fig. S1). There was no relationship between scallop CI and eelgrass percent cover, macroalgae percent cover, or scallop density (Table 2). Multiple linear regression revealed no relationship between scallop shell height (SH) and *Hydrocoleum* percent cover, eelgrass percent cover, macroalgae cover, and scallop density (Table 2). However, *Hydrocoleum* presence influenced scallop size distribution (K–S test, D = 0.43, p = 0.02, Fig. 4). Shell heights of 54 scallops from 35 *Hydrocoleum*-absent plots and 16 scallops from 11 *Hydrocoleum*-present plots were measured.
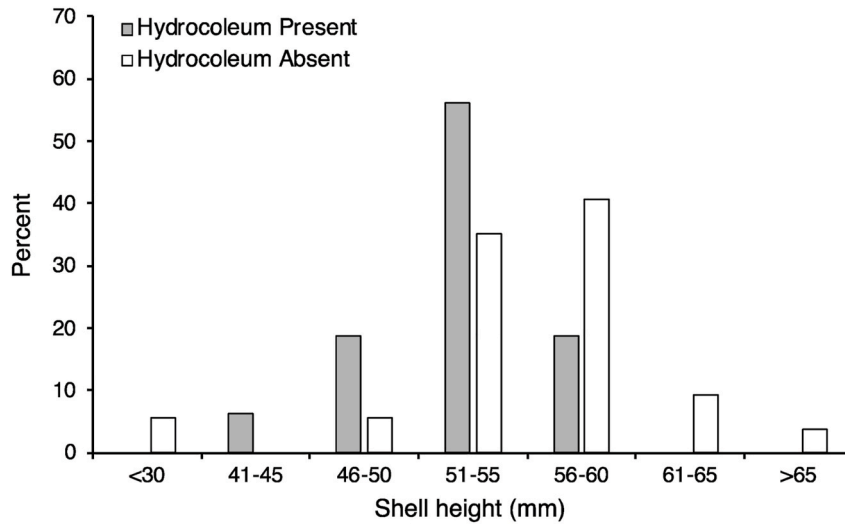
Fig. 4. Size distribution (shell height, mm) of scallops (*Argopecten irradians*) found in our surveys in plots with and without *Hydrocoleum*. 54 scallops from 35 *Hydrocoleum*-absent plots and 16 scallops from 11 *Hydrocoleum*-present plots were included in this analysis.

In plots without *Hydrocoleum*, 54% of scallops were in the largest three size classes observed (>56 mm shell height), while these large scallops made up only 19% of the scallops in plots with *Hydrocoleum*. Moreover, scallops in the largest (>61 mm) size class were absent from plots with *Hydrocoleum*, but made up 13% of scallops in plots without *Hydrocoleum*.

Scallop GI was positively associated with eelgrass percent cover when all other variables were held constant (p = 0.05, R^2_{Adj} = 0.09, Table 2, Fig. 5). There was no relationship between scallop GI and *Hydrocoleum* percent cover, macroalgae cover, scallop density, or scallop shell height (Table 2). There was no relationship between scallop density and *Hydrocoleum*, macroalgae, or eelgrass percent covers (Table 2) and no relationship between eelgrass and *Hydrocoleum* percent cover (linear regression, $F_{1,142}$ = 2.5, p = 0.1).

4. Discussion

Despite relatively low incidence and cover during our sampling, *Hydrocoleum* affected multiple aspects of scallop performance and habitat use. Counterintuitively, there was a weak but positive association between *Hydrocoleum* cover and scallop condition (Fig. 3). Scallop

Fig. 5. Added variable plot showing the relationship between the residuals of eelgrass (*Zostera marina*) percent cover (p = 0.05, R^2_{Adj} = 0.09) and scallop (*Argopecten irradians*) gonadosomatic index when all other independent variables are held constant. Analyses were conducted on quadrat means. Dashed lines are 95% confidence intervals.

size distributions also differed between plots with and without *Hydrocoleum*: scallops from the smallest (<30 mm shell height) and largest (>61 mm) size classes observed in our study were absent from plots with *Hydrocoleum* (Fig. 4).

While size-dependent effects of *Hydrocoleum* on scallops may be important, the mechanisms underlying the patterns we observed cannot be discerned from our study because so few juvenile scallops were found in our surveys (n = 3) and we did not test the underlying mechanisms driving changes in habitat use by larger scallops. Our conceptual model (Fig. 1) presents hypotheses as to why there might be fewer large scallops in plots with higher *Hydrocoleum* cover. Specifically, large scallops might behaviorally avoid *Hydrocoleum* because 1) its complex structure reduces scallop feeding efficiency or food availability, as can occur in complex eelgrass beds (González-Ortiz et al., 2014) or 2) it reduces eelgrass cover by negatively affecting light and flow (Tiling and Proffitt 2017) that are important for eelgrass growth. Alternatively, large scallops might have higher mortality rates in plots with *Hydrocoleum* if 1) *Hydrocoleum* reduces scallops' ability to escape from mobile predators, as can occur with branching algae (Raffaelli et al., 1998) or 2) *Hydrocoleum* decomposition leads to localized hypoxia, which occurs with other cyanobacteria even at low density (Pittman and Pittman 2005) and more strongly affects older, larger-bodied bivalves (Clark et al., 2013). Our survey data suggest that the effects of *Hydrocoleum* on scallops do not operate through its effects on eelgrass, and scallops in this largest size class (>61 mm) may have reached a size refuge from benthic predators (Tettelbach 1986); however, each potential mechanism should be tested in future work to elucidate size-specific responses of scallops to *Hydrocoleum*.

Given that blooms of other cyanobacteria decrease the body mass of local benthic organisms (Pittman and Pittman 2005; Persson et al., 2011), it was surprising that scallop condition was positively associated with *Hydrocoleum* cover. Our results appeared to show a positive relationship between scallop shell height and condition index, but this trend was entirely driven by one small (22.5 mm shell height) scallop in its own plot (Fig. S1). Without that plot, there was no relationship between shell height and CI (p = 0.39), but the weak but positive relationship between *Hydrocoleum* cover and CI remained (p = 0.03). *Hydrocoleum* was not very prevalent in our study (observed in 32% of plots at 11.6 ± 23.0 percent cover, mean ± SD), and the potential for strong negative effects of filamentous cyanobacteria on body condition may not manifest at the low coverage we observed. Rather, we hypothesize that at low coverage, *Hydrocoleum* may improve scallop condition through three potential mechanisms (Fig. 1): greater production of bioavailable
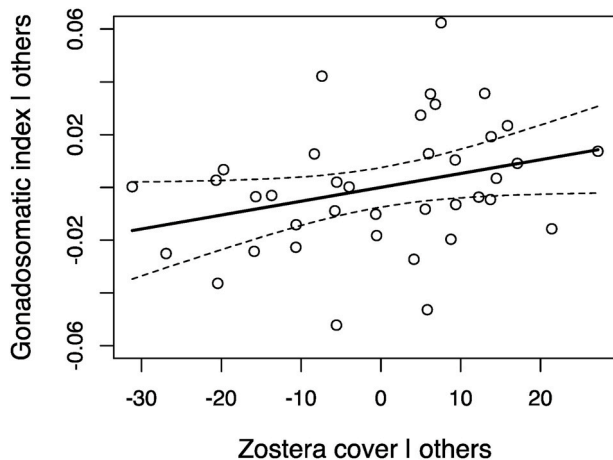
nitrogen that increases 1) scallop food quantity/quality or 2) eelgrass cover or 3) increased structure that provides greater refuge from predators, which could reduce scallop physiological stress. Importantly, we recognize that these hypotheses, if operating, directly contrast those that would support the potential size-specific patterns described above. So while different mechanisms are likely operating for the effect of *Hydrocoleum* on scallop CI and size range, we have chosen to present all testable hypotheses in order to guide future work on this topic. However, because we found no relationship between *Hydrocoleum* and eelgrass percent cover, we hypothesize that changes in scallop food quantity/quality or changes in predation rate are the most likely mechanisms driving the weak, positive association between *Hydrocoleum* cover and scallop condition.

Hydrocoleum collected on Nantucket possesses the nitrogenase gene (Moisander et al., 2017), and has been classified as a diazotroph that can fix nitrogen gas (N_2) to create bioavailable forms of inorganic nitrogen (e.g., ammonium and nitrate). This bioavailable nitrogen can be utilized by phytoplankton, increasing phytoplankton biomass and nitrogen and carbon content (Lesutienè et al., 2014), which would translate into higher quality food for suspension feeding bivalves like bay scallops (Shriver et al., 2002). Because inorganic nitrogen is limiting on Nantucket (2.5% of the total nitrogen pool, Howes and Samimy 2017), any small increase in bioavailable nitrogen produced by *Hydrocoleum* may have outsized effects, resulting in higher scallop condition. Indeed, cyanobacteria can fuel secondary production in the Baltic Sea, particularly by fast growing plankton and crustaceans but also by longer-lived bivalves, and can account for 50–80% of production by these species during a cyanobacterial bloom (Lesutienè et al., 2014). While a bloom was likely not occurring during our surveys and *Hydrocoleum* was associated with only modest increases in scallop condition index, a larger bloom may contribute to more substantial changes in scallop condition. Interestingly, scallops can also consume other microflora and organic matter in their immediate vicinity (Davis and Marshall 1961) and may inadvertently consume *Hydrocoleum* directly, which could also benefit growth (Perga et al., 2013).

Macroscopic filamentous cyanobacteria such as *Hydrocoleum* adds dense, complex structure even at low coverage. In the northeastern U.S., scallops are most frequently consumed by mobile predators such as crabs, whelks, and fish (MacKenzie 2008), which are often less efficient consumers in dense vegetation (Goshima and Peterson 2012; Carroll et al., 2015). Higher quality refuge habitats afforded by greater *Hydrocoleum* cover may reduce predator densities or foraging efficiencies, thereby decreasing predator-driven physiological stress effects in scallop prey. Prey that are exposed to predators often have lower condition (i.e., less tissue mass standardized for size) and are less efficient at converting energy that they consume into body mass, but these effects are diminished when prey have access to higher quality refuges (Donelan et al., 2017). Any reduction in the threat of predation offered by refuge in *Hydrocoleum* could therefore mitigate these effects in scallops and improve their performance. Future work during years with more substantial *Hydrocoleum* coverage should build on our study, including testing the hypotheses presented in Fig. 1, to help further elucidate if and how *Hydrocoleum* contributes to increases in scallop condition.

Hydrocoleum had positive effects overall on overall scallop condition, yet there was no relationship between *Hydrocoleum* and scallop gonadosomatic index (GI). Hence, any additional nutrients that may be derived from *Hydrocoleum* are not preferentially allocated toward scallop gonadal or shell growth. However, there was a positive relationship between eelgrass percent cover and scallop GI (Fig. 5). This may have emerged because of the positive effect of eelgrass cover on refuge quality, which can reduce predator encounters and increase prey growth and growth efficiency as described above. Reductions in predator-associated stress may have allowed scallops to allocate more energy to gonad development, which is often more energetically costly than somatic growth (MacDonald and Thompson 1985). Because our sampling occurred in the mid-to late-summer prior to scallops' second annual

spawn on Nantucket (see below, Hall et al., 2015), gonadal growth at this time of year may be especially important (Sastry 1970). Our results confirm the findings of others (Irlandi et al., 1995; Carroll et al., 2015) that suggest that high quality eelgrass beds are an important factor in promoting healthy bay scallop populations.

Surprisingly, there was no relationship between *Hydrocoleum* and eelgrass percent cover. However, mean percent cover of *Hydrocoleum* was low, which suggests that a bloom was not occurring on Nantucket during our sampling. Effects of *Hydrocoleum* might be stronger in years when *Hydrocoleum* is more abundant, which often occurs on Nantucket (see above, P. Boyce, unpublished data). It is also possible that potential negative effects of *Hydrocoleum* on eelgrass do not manifest at lower levels of *Hydrocoleum* cover or manifested in eelgrass traits we did not measure (e.g., above- or below-ground biomass). Alternatively, nitrogen fixation by cyanobacteria can augment eelgrass growth and production, as shown in other systems (Hamisi et al., 2009), so *Hydrocoleum* may actually enhance eelgrass production. Further exploration of the direct and indirect interactions among scallops, eelgrass, and *Hydrocoleum* will facilitate more effective resource and habitat management efforts.

Despite thorough visual inspections of eelgrass blades within our plots, very few juvenile scallops were found, likely because of the time of year of our sampling. Scallops spawn twice each year on Nantucket, once in May through early July and once in the fall. Scallops from the first spawn can reach adult size (40–55 mm shell height) prior to overwintering (Hall et al., 2015), while scallops from the fall spawn overwinter at an average height of 10 mm (Tettelbach et al., 2011). Hence, although small scallops could have been observed throughout our sampling timeframe, scallops from the first spawn may have grown large enough by August and September to be indistinguishable from one-year-old adults. We did not quantify the presence of an annual growth ring, making it impossible to distinguish between early- and late-spawned scallops from the prior year. The lack of very small scallops (<20 mm) suggests that the second annual spawn had not yet occurred.

Our results suggest that *Hydrocoleum* impacts scallops in both predictable and counterintuitive ways and provide an important foundation upon which to build future work. *Hydrocoleum* has not yet been described in New England except on Nantucket (Moisander et al., 2017) and has been reported in only one other temperate system to our knowledge (Gulf of St. Lawrence, Péquin et al., 2017), and it appeared to affect scallop performance even at low coverage. Hence, our results report previously undescribed effects of a nonindigenous cyanobacterium on an economically-valuable and historically-important fishery. Our work suggests that at lower prevalence, *Hydrocoleum* may have modest, positive effects on scallop condition, though large scallops may behaviorally avoid or suffer higher mortality in areas with higher cover. Nantucket hosts one of the last remaining bay scallop fisheries in the United States, so it is crucial to develop a more mechanistic understanding of the potential for nonindigenous species such as *Hydrocoleum* to impact scallop populations to manage its fishery more effectively. More generally, climate change is likely to enhance the prevalence and severity of cyanobacterial blooms in many coastal systems (Paerl and Huisman 2009), which may have detrimental effects on critical estuarine and coastal habitats and associated economically valuable and ecologically important species.

CRediT authorship contribution statement

Sarah C. Donelan: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization. **A. Randall Hughes:** Conceptualization, Methodology, Writing – review & editing. **Geoffrey C. Trussell:** Conceptualization, Methodology, Writing – review & editing. **Jonathan H. Grabowski:** Conceptualization, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2021.105427.

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