

Variability in site characteristics linked to bay scallop abundance but not tethered survival: Implications for restoration

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ABSTRACT

While predation impacts the abundance and distribution of prey species, the overall impact of predation varies with predator identity, predator density, and habitat complexity, among other factors. Numerous commercially and recreationally important prey species, such as bivalves, face intense predation that may affect management and restoration efforts. Therefore, predicting sites with elevated predation risk can be critical for successful restoration, although making predictions based on lab feeding assays may provide challenges. This study used bay scallops *Argopecten irradians* as a model organism to examine scallop abundance and survival in relation to predator density, habitat complexity, and predicted consumption, across multiple sites within the same estuary. Published predator-specific relationships between scallop consumption and habitat complexity were combined with field survey data to predict consumption potential at six sites in Shinnecock Bay, NY, USA. Using a series of Pearson correlations, the relationships between scallop abundance and tethered survival and site characteristics (habitat complexity, predator density, estimated consumption, scallop recruitment) were explored. Seagrass cover and recruitment of new individuals both strongly influenced scallop abundance, although tethered survival was not strongly correlated to any site metric (predator density, seagrass complexity, or estimated consumption). This study demonstrates potential issues when trying to link mesocosm studies to the field environment, such as sites with no seagrass but potentially confounding habitat complexity (i.e., *Crepidula fornicata*) and overestimates of consumption due to lack of realism in mesocosm studies. Overall, our study highlights the necessity of conducting field experiments to test mesocosm results, but also provides several valuable conclusions for shellfish restoration.

1. Introduction

Predation is often considered the most important factor affecting populations and communities (Connell, 1975; Menge, 1983). Post-settlement mortality from predation can determine recruitment and subsequent establishment and maintenance of benthic invertebrate populations (Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Carroll et al., 2012). Predators may impact prey through consumptive (Connell, 1975; Estes et al., 1998) and nonconsumptive pathways (Peckarsky et al. 2008), although multiple factors influence the impact of predators on benthic prey populations, including predator identity (Hill and Weissburg, 2013), predator density (Barbeau et al., 1994), prey

density (Eggleston et al., 1992), habitat complexity (Heck and Orth, 2006) and landscape composition and configuration (Hovel and Lipcius, 2001; Carroll et al., 2015a). Numerous bivalve prey populations, such as clams, oysters, and scallops, are commercially and ecologically important species, yet face continued threat of human overexploitation, necessitating management and restoration activities (Mackenzie 2008, Kraeuter et al. 2009). Thus, predicting patterns in predation and how they influence benthic populations is increasingly important for management, conservation, and restoration efforts.

While many predator species contribute to post-settlement mortality of benthic bivalves, decapod crustaceans are among the most important (Nelson, 1981; Menge, 1983; Seed, 1993; Rindone and Eggleston, 2011).

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Predatory decapods consume a wide variety of small invertebrate prey (Juanes, 1992), although their ability to consume bivalve prey is determined by claw and prey size (Juanes and Hartwick, 1990; Seed and Hughes, 1995; Ray-Culp et al., 1999; Aronhime and Brown, 2009). As such, predator identity and size can play a major role in the impact on prey populations. Larger bodied crabs, such as the blue crab *Callinectes sapidus* or the green crab *Carcinus maenas*, are often considered major benthic consumers capable of controlling shellfish populations (Eggleston, 1990; Eggleston et al., 1992; Seitz et al., 2001; Floyd and Williams, 2004; Miron et al., 2005; Wong, 2013). However, studies have demonstrated that smaller bodied crabs, such as xanthids, can also exert control over shellfish populations due to their abundance and density (Ray-Culp et al., 1999; O'Connor et al., 2008; Rindone and Eggleston, 2011; Johnson et al., 2014; Carroll et al., 2015b).

Structured habitats, such as seagrass beds or oyster reefs, often provide post-settlement shellfish refuge from predation (Heck and Orth, 1980; Ray-Culp et al., 1999; Grabowski, 2004; Warfe and Barmuta, 2004; Grabowski et al., 2008; Stoner, 2009). The prey refuge value of seagrass typically varies inversely with structural complexity (Leber, 1985; Heck and Orth, 2006; Carroll et al., 2015b). Prey survival is usually higher in the presence of seagrass, compared to unvegetated habitats (Heck et al. 2003), although the relationship between survival and seagrass density is considered nonlinear, with some threshold level of above- (Gotceitas and Colgan, 1989; Bartholomew, 2002; Lannin and Hovel, 2011) and below-ground complexity (Wong, 2013) at which prey survival stabilizes. This threshold response may be further complicated by predator identity, where the shape of the prey survival response across a range of seagrass densities may change across different predator species (Carroll et al., 2015b). Additionally, predator densities also tend to be positively correlated with habitat complexity (Eggleston et al., 1998; Lenihan et al., 2001; Hovel, 2003; Grabowski and Powers, 2004; Canion and Heck, 2009; Tait and Hovel, 2012), which could confound predictions of survival in the field based solely on habitat complexity. Therefore, the type of relationship between seagrass density and prey survival may vary considerably, based in part on landscape- and basin-scale patterns in predator identity and density.

Understanding the interactions between predators, prey, and habitat at locations within an estuary can be important for restoration and management of fisheries resources. For multiple shellfish species, restoration efforts focus on increasing abundances through transplants and seeding (Brumbaugh and Coen 2009, Arnold 2008). These efforts can come at considerable financial costs, and in some instances, these shellfish restoration efforts may fail due to predation (Peterson et al., 2001) and habitat-related issues (Powers et al. 2009). Bay scallops, *Argopecten irradians*, are a commercially important bivalve species that has experienced declines throughout their geographic range (Peterson and Summerson 1992, Tettelbach and Wenzel 1993, Arnold et al. 1998). Bay scallops have a long-recognized association with seagrass habitats which they use primarily as a predation refuge (Belding, 1910; Pohle et al., 1991; Irlandi et al., 1999), and they are subject to intense predation pressure from multiple benthic predators, predominantly crabs (Tettelbach, 1986; Bishop et al., 2005; Carroll et al., 2012). Studies have also identified alternative habitats which might also serve as predation refuges for bay scallops, including multiple algal species (Carroll et al., 2010; Hernandez Cordero and Seitz, 2014). Numerous restoration efforts of bay scallops have occurred throughout their range, with varied success (Fegley et al., 2009, Arnold 2011, Tettelbach et al., 2013). Thus, the bay scallop is a useful model organism for examining predation and habitat effects on population abundance and individual survival across multiple field sites.

Since interactions between bay scallops and their predators and habitats can influence restoration success (Fegley et al., 2009, Schmitt et al. 2016), our study aimed to examine factors that might influence scallop survival and density across multiple potential restoration sites. Specifically, we conducted field surveys to measure seagrass habitat complexity, predator densities, scallop spat settlement, and scallop

densities throughout Shinnecock Bay, NY, USA, which were used to estimate consumption. Additionally, we tethered scallops at the same sites to estimate survival and used data from mesocosm studies to estimate scallop consumption at the six field sites. We expected that tethered survival would correlate to scallop density, and that survival would be related to our estimate for consumption, which incorporated both predator density and habitat complexity.

2. Methods

2.1. Study site

Shinnecock Bay (SB) is a relatively shallow, bar-built estuary located along the south shore of Long Island, New York, USA, with a mean depth of ~2 m (MLLW) and semi-diurnal tides of 0.8 m (Carroll et al., 2008). It has major oceanic exchange from the south through the Shinnecock Inlet (40.8425 N, -72.4761 W) and receives periodic water pulses from the Peconic Estuary to the north when the tide gates in the Shinnecock Canal (40.8875 N, -72.5014 W) are opened. The major sources of freshwater input are via rainfall and groundwater. Six sites were selected in the eastern basin of the SB system (Fig. 1, Table 1) for this study. The sites were predominantly sandy bottom habitats, with seagrass coverage ranging from 0 to near 100%. Shoot density was counted in six replicate 25 × 25 cm quadrats (Table 1). At one site, Heady Creek, there was no seagrass but ~31% cover of the canopy forming, introduced alga *Codium fragile*, which has been demonstrated to offer a similar predation refuge for scallops as seagrass (Carroll et al., 2010). Additionally, Heady Creek was covered in a layer of living and dead *Crepidula fornicata* shells.

2.2. Field surveys

We conducted field sampling of predator and scallop abundance during the summer of 2011. We quantified the abundance of the four most common scallop predators in this system: xanthids (predominantly *Dyspanopeus sayi*; Streib et al., 1995, Carroll et al., 2012), blue crabs *C. sapidus* (Bishop et al., 2005; Hernandez Cordero and Seitz, 2014), green crabs *C. maenas*, and spider crabs *Libinia* spp. (Tettelbach, 1986). This was accomplished via suction sampling, an effective in situ method for sampling decapods (Orth and van Montfrans, 1987; Johnson and Heck, 2006; Carroll et al., 2010). A 1 m² metal frame with a 1 m tall 1 mm mesh curtain was haphazardly thrown into the water from a boat and immediately suction dredged into a 750-µm mesh bag. Two 1 m² quadrats were suction sampled at each site on each visit. While we acknowledge that the mesh curtain did not extend to the surface at our sites, we made sure to capture any large mobile crabs immediately, since they were the most likely to escape the curtain, and then suction the entire area of the enclosure for smaller organisms which are more likely to hunker down into the habitat during a disturbance. Regardless, our abundance values are likely to be underestimates. The samples were then placed on ice, returned to the lab, and processed. Suction surveys were conducted at the six survey sites monthly, from June to September. Crabs were identified to species, sexed, and measured for carapace width. In addition to scallops, all other species were identified to the lowest possible taxon and counted.

2.3. Scallop larval settlement

Scallop larval settlement was monitored at the same 6 sites from early May to mid-October 2011 when bay scallop larvae may be present in the water column (Tettelbach and Weinstock, 2008). Spat collectors were modified after Ambrose Jr. and Lin (1991) and consisted of a 750-µm mesh spat bag measuring 38 × 78 cm (Atlantic Aquaculture), stuffed with a standardized piece (38 × 46 cm) of blue Netron® plastic mesh to keep the bag from collapsing, and a small Styrofoam float attached to each spat bag to extend it vertically. Sets of two spat bags were attached to a cinder block which was marked at the surface with a lobster buoy

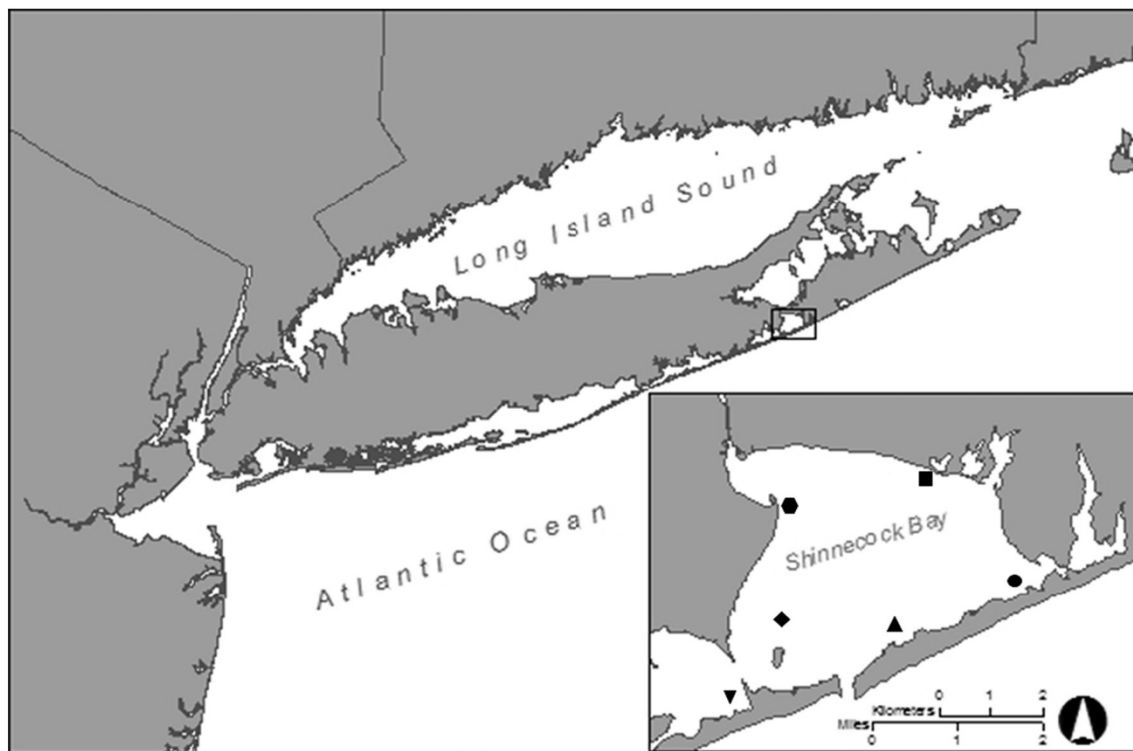


Fig. 1. Map of the study site, Shinnecock Bay, located on the east end of Long Island, New York. Shapes indicate sites where the hexagon is Cormorant Point, the upright triangle is East Shinnecock Bay, the diamond is Warner's Island, the square is Far Pond, the circle is Heady Creek and the down triangle is the Bridge.

Table 1

Locations within Shinnecock Bay (SB), New York, USA. Eelgrass shoot density (SS m^{-2}), spat settlement, and scallop (Ai) density (individuals m^{-2}) for sites used to calculate the predicted predator intensity model. Densities are provided as mean \pm SE.

Site	Latitude	Longitude	SS Density	Total Spat	Ai Density
Far Pond	40.8784	-72.4582	454 \pm 25	332	0.50 \pm 0.27
Cormorant Pt	40.8738	-72.4904	611 \pm 47	1701	6.62 \pm 3.61
Warner's Island	40.8515	-72.4911	215 \pm 41	150	0.13 \pm 0.13
Bridge	40.8419	-72.5048	0	45	0
Eastern SB	40.8565	-72.4553	244 \pm 134	229	0
Heady Creek	40.8595	-72.4343	147 \pm 46 ^a	114	0.25 \pm 0.16

^a SS density equivalent of percent coverage of dominant macroalgae, *C. fragile*.

(Tettelbach et al., 2013). Three sets of collectors were deployed at each timepoint for a total of 6 collectors per site per sampling period. Initial deployments took place in the beginning of May; a second set of collectors was deployed 3 weeks later. On a 3-week basis, new sets of spat collectors replaced those which had been in the water for 6 weeks until the beginning of September, resulting in a mid-October final retrieval and a total of 6 sampling dates. During retrieval, spat bags were placed into individually labeled plastic garbage bags and returned to the lab where juvenile scallops were washed from the bags and retained on an 800- μ m mesh screen. Scallops were then sorted, enumerated, and measured to the nearest mm.

2.4. Field tethering experiment

To explore the predatory mortality on juvenile (i.e. vulnerable) scallops, we returned to the six sites in SB in late August 2014, when

predation rates were expected to be highest (Bishop et al., 2005; Carroll et al., 2010), to conduct a series of scallop tethering experiments. At each site, a screw anchor was established and three sets of 10 small (12–15 mm), tethered hatchery-reared scallops were deployed at 120-degree angles. Each scallop was tethered to a sod staple that was inserted into the sediment. The 10 scallops in each set were haphazardly distributed across a 1 m^2 area. The sod staples were labeled with bright pink labeling tape to allow effective recovery. Tethers were made from 3.6 kg strength Trilene® monofilament nylon line, 15 mm in length, and secured to the middle of the scallop valve with a \sim 2 mm loop using Zepa-Gap® cyanoacrylate adhesive and accelerant. The 15 mm tether length allowed scallops the ability to move and attach themselves to low seagrass blades, typical of scallops this size (Pohle et al., 1991). Tethers were collected after 24 h. A total of three consecutive deployments were done conducted within 1 to 2 days of one another.

Two sets of controls were used for each deployment to verify tether attachment and scallop health. In the first set of controls, four scallops were left behind in Stony Brook's Southampton Marine Science wet laboratory. The second set consisted of four tethered scallops deployed at each site inside of a 5-mm mesh predator exclusion cage (20 \times 10 \times 35 cm) – which was placed next to the site's screw anchor. None of the tethers detached in the laboratory and rarely did any detach in the field control (<5% of the time), therefore, all retrieved tethers with no scallops were interpreted as consumed.

Percent survivorship was calculated using the following equation:

$$S = \frac{N_t}{N_0}$$

where S is the calculated rate of survival, N_t is the number of scallops surviving after one day, and N_0 is the number of scallops deployed.

2.5. Estimating potential consumption

We estimated the consumption of the four dominant crab predators

collected during suction surveys: *D. sayi*, *C. sapidus*, *C. maenas*, and *Libinia* spp. (Table 2) at the 6 survey sites. We used simple calculations to estimate potential predation intensity on juvenile bay scallops each site using habitat specific consumption rates for each predator derived from mesocosm experiments (Carroll et al., 2015b), the density of predators, and time, using the following formula:

$$\text{Estimated consumption} = \sum_{i=1}^4 C_i \times \rho_i$$

where *Estimated consumption* for each site is the sum of the seagrass density-specific daily per capita consumption *C* by species *i* determined from prior mesocosm experiments and ρ_i is the density of species *i*. For each site *n*, C_i was predicted by inserting the mean seagrass density into predator-specific habitat-scallop survival relationships from Carroll et al. (2015b). These values were obtained from mesocosm experiments exploring scallop consumption across changing seagrass complexity where the same four crustacean predators were evaluated. Briefly, scallop survival displayed a linear relationship across different shoot density with *Carcinus* (scallops consumed = 16.6–0.010 * shoot density), and non-linear relationships with both *Callinectes* (scallops consumed = 9.9–0.69 * ln(shoot density)) and *Dyspanopeus* (scallops consumed = 7.6–0.56 * ln(shoot density)). There was no significant relationship for *Libinia* (Carroll et al., 2015b), however, consumption rates were lower in high seagrass complexity than no seagrass and low seagrass, so for the purposes of this study, scallop survival across seagrass shoot density in the presence of *Libinia* spp. was assumed to be linear (scallops consumed = 16.0–0.013 * shoot density). We acknowledge this assumption likely overestimates their consumption with increasing seagrass complexity. Additionally, since *C. fragile* offers a similar predation refuge to scallops as seagrass (Carroll et al., 2010), at Heady Creek, the only site with *C. fragile* present, we used the percent cover of *Codium* in our quadrats and estimated the shoot density required for the equivalent percent cover, using a shoot density-percent cover regression with data from Furman et al. (2017; Shoot Density = 6.12 * Percent Cover – 42.7; $p < 0.001$, $r^2 = 0.675$; Figure S1). This way, we calculated an estimated consumption for Heady Creek twice, once for zero seagrass, and once assuming that the *Codium* cover was an equivalent density of seagrass. Using these formulae, we calculated estimated consumption by the predator community based on the seagrass density at each site (Table S1). The ρ_i was calculated as the average density (individuals/m²) of species *i* across the four-month suction sample survey (values displayed in Table 2).

2.6. Data analysis

We were most interested in determining which variables (i.e., predator density, habitat complexity, estimated consumption, spat settlement) might best predict scallop density and survival across our sites to inform restoration efforts. Therefore, in order to explore these potential relationships, we conducted a series of three Pearson correlation matrices; 1) including all sites with measured seagrass density (Heady Creek = 0 seagrass); 2) including all sites with estimated seagrass

Table 2
Mean predator density of the four target decapod species at each site (\pm SE).

	Far Pond	Cormorant Pt	Warners Island	Bridge	ESB	Heady Creek
<i>Dyspanopeus sayi</i>	31.2 ± 4.4	44.0 \pm 12.1	58.4 \pm 16.3	89.3 ± 38.4	41.6 \pm 19.2	222.5 ± 61.3
<i>Callinectes sapidus</i>	13.1 ± 3.7	5.5 \pm 1.5	1.4 \pm 0.7	0.1 \pm 0.1	0.6 ± 0.3	2.6 \pm 2.2
<i>Carcinus maenas</i>	0	0	0.3 \pm 0.2	0.3 \pm 0.2	0.4 ± 0.3	0.4 \pm 0.3
<i>Libinia</i> spp.	0.3 ± 0.2	0.8 \pm 0.5	1.4 \pm 0.8	0.4 \pm 0.2	0.1 ± 0.1	0.5 \pm 0.3

density using measured *C. fragile* cover at Heady Creek (see above); and 3) Heady Creek excluded due to the high amount of habitat complexity formed by *Crepidula* beds which are not accounted for in our consumption estimates. By using these correlation matrices, we determined any potential relationships between and among variables. Given the small sample size (5 or 6 sites), we considered any $r > 0.75$ to be a strong correlation and relationships significant at an α of 0.1. All analysis was conducted using SigmaStat analytical software.

3. Results

3.1. Field surveys

While many species were identified and enumerated via suction sampling, mud crabs, *D. sayi*, were the dominant decapods encountered during the suction surveys. Over 3900 mud crabs were collected in 48 suction samples across all 6 sites and 4 time points, comprising 69% of the total decapod crustacean catch (Table 3). For the other target predator species, 187 blue crabs, 27 spider crabs, and 10 green crabs were counted across all sites and collections. We also identified at least 7 other decapod crustaceans, 4 different predatory gastropods, 1 echinoderm, and 2 potential fish predators that might consume post-set scallops at different life stages. There was spatial variability in densities of the four target decapod crustaceans (mud, blue, green and spider crabs; Table 2).

Similarly, there was spatial variation in scallop densities on the bottom across the 6 sites. At two sites, no scallops were collected across the entire sampling season; one of these sites had no seagrass cover while the other had moderate seagrass cover. The highest scallop abundance occurred at Cormorant Point, with 6.6 ± 3.6 individuals per m² for all collections. This comprised 88% of all scallops collected via suction sampling. The other three sites had low scallop densities: ≤ 0.5 individuals per m² (Table 1, Fig. 2).

3.2. Scallop larval settlement

Peak settlement occurred on 8 August, yielding 58% of scallops collected. However, collectors retrieved on 19 July and 30 August, just before and after the peak settlement, comprised 22% and 14% of the total scallops collected. Little recruitment occurred in other periods. Overall, we collected 2505 scallop spat in collectors, with substantial variability among collection sites. Mean spat per collector varied from 0 to 200 ± 24 , and total spat per site from 45 to 1701, with the most spat occurring at Cormorant Point (Table 1, Fig. 2).

3.3. Tethering experiments

During the predation experiments, 24-h scallop survival varied from ~25% at the Bridge to ~64% at Heady Creek, although the four other sites with a range of seagrass density (215 ± 41 to 611 ± 47 , mean \pm SE, Table 1) exhibited between 41 and 50% scallop survival (Fig. 2). The equivalent seagrass density to the 31% cover of *C. fragile* at Heady Creek was estimated to be 147 shoots m⁻².

3.4. Estimated consumption

The estimated consumption of scallops by the predator field ranged from ~199 scallops per day at ESB to >1000 (*Codium* cover converted to equivalent seagrass density) or >2000 (*Codium* not converted to seagrass) scallops per day at Heady Creek. The large range of estimated consumption was driven by the most abundant predator in the system - mud crabs *D. sayi* (Fig. 3).

3.5. Correlations between variables

When considering all sites and the actual seagrass density (i.e.,

Table 3

Species densities across all suction samples and sites ($n = 48$), separated into broad taxonomic groups. Species that were considered potential predators for some life stage of scallop (post-set, juvenile and adult) are noted in bold.

Group	Scientific name	Common name	Total	% of group	% of total	
Decapods	<i>Dyspanopeus sayi</i>	Mud crab	3920	68.52	47.22	
	<i>Hippolyte zostericola</i>	Zostera shrimp	835	14.60	10.06	
	<i>Crangon semptemspinosa</i>	Sand shrimp	278	4.86	3.35	
	<i>Pagurus longicarpus</i>	Long-clam hermit	272	4.75	3.28	
	<i>Callinectes sapidus</i>	Blue crab	187	3.27	2.25	
	<i>Palaemonetes sp.</i>	Grass shrimp	133	2.32	1.60	
	<i>Cancer irroratus</i>	Rock crab	45	0.79	0.54	
	<i>Libinia emarginata</i>	Spider crab	27	0.47	0.33	
	<i>Carcinus maenas</i>	Green crab	10	0.17	0.12	
	<i>Ovalipes ocellatus</i>	Lady crab	9	0.16	0.11	
	<i>Portunus gibbesii</i>	Blue swimmer crab	3	0.05	0.04	
	<i>Portunus spinimanus</i>	Blue swimmer crab	2	0.03	0.02	
	Gastropods	<i>Iyanassa obsoleta</i>	Mud snails	1542	87.22	18.58
		<i>Urosalpinx cinerea</i>	Oyster drill	107	6.05	1.29
		<i>Eupleura caudata</i>	Thick-lip drill	53	3.00	0.64
		<i>Anachis sp.</i>	Dove snails	41	2.32	0.49
		<i>Ilyanassa trivittata</i>	3-lined mud	17	0.96	0.20
		<i>Littorina littorea</i>	Littorine	5	0.28	0.06
		<i>Busycotypus canaliculatus</i>	Knobbed whelk	1	0.06	0.01
		<i>Busycon carica</i>	Channeled whelk	1	0.06	0.01
<i>Euspira heros</i>		Whelk	1	0.06	0.01	
<i>Mercenaria mercenaria</i>		Moon snail	1	0.06	0.01	
Bivalves	<i>Argopecten irradians</i>	Bay Scallop	127	45.52	1.53	
	<i>Mercenaria mercenaria</i>	Hard clam	92	32.97	1.11	
Fish	<i>Mya arenaria</i>	Softshell clam	60	21.51	0.72	
	<i>Gobiosoma bosc</i>	Naked goby	318	85.25	3.83	
Echinoderms	<i>Syngnathus fuscus</i>	Northern Pipefish	22	5.90	0.27	
	<i>Pseudopleuronectes americanus</i>	Winter flounder	14	3.75	0.17	
	<i>Myoxocephalus aeneus</i>	Grubby	9	2.41	0.11	
	<i>Gasterosteus aculeatus</i>	stickleback	8	2.14	0.10	
	<i>Opsanus tau</i>	Toadfish	1	0.27	0.01	
	<i>Tautoglabrus adspersus</i>	cunner	1	0.27	0.01	
	<i>Asterias sp.</i>	Sea star	153	95.63	1.84	
	<i>Sclerodactyla briareus</i>	Sea cucumber	7	4.38	0.08	

Heady Creek = 0), seagrass density had strong positive correlations with spat settlement ($r = 0.811, p = 0.05$) and on-bottom scallop density ($r = 0.744, p = 0.09$; Fig. 4). Tethered scallop survival was not correlated to any of the other surveyed or estimated variables. When we used *C. fragile* percent cover to estimate an equivalent seagrass density, the overall patterns remained the same, although the positive relationships between seagrass and both spat settlement ($r = 0.835, p = 0.039$) and on-bottom scallop density ($r = 0.776, p = 0.07$; Fig. S2) strengthened. When Heady Creek was excluded from the analysis, several new relationships emerged. Seagrass density negatively affected estimated consumption ($r = -0.769$) and had strong positive relationships with spat settlement ($r = 0.823$) and scallop density ($r = 0.768$; Fig. 5). In addition, scallop survival exhibited strong negative correlations with predator density ($r = -0.786$), estimated consumption ($r = -0.893$), but not with seagrass

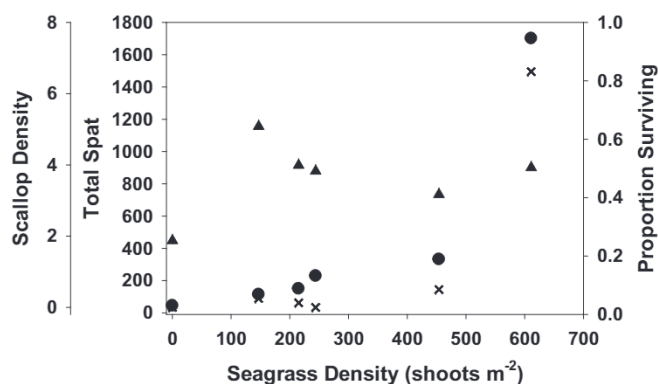


Fig. 2. Scallop density (Xs), total scallop spat (circles), and scallop survival (triangles) across the range of seagrass shoot density at sites across Shinnecock Bay, NY, USA. The cover of *Codium fragile* at the Heady Creek site was used to approximate seagrass shoot density for a similar percent cover (see methods), resulting in a value of ~ 147 shoots m^{-2} .

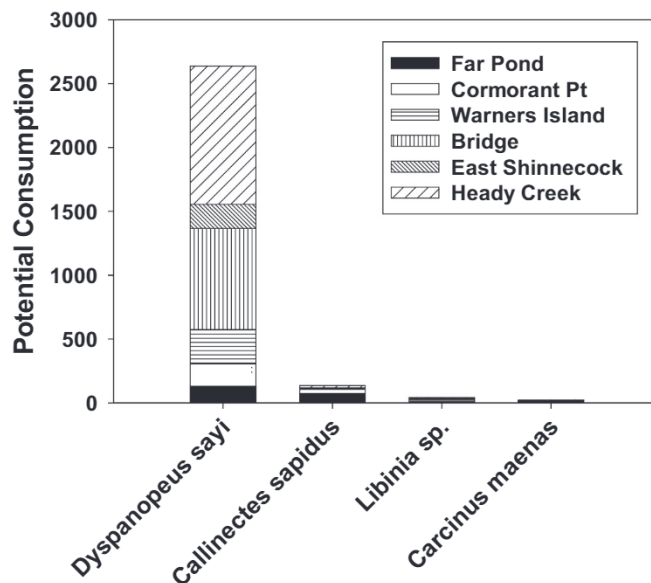


Fig. 3. Stacked bar plot illustrating the potential numbers of scallops consumed by each predator per day, with the stacked bars representing each study site. Scallop consumption was calculated using mesocosm consumption rates and field densities of predators (individuals m^{-2}).

density (Fig. 5). For all analyses, the strongest relationship was always between scallop recruitment and scallop density ($r > 0.99$ and $p < 0.0001$).

4. Discussion

The ability to predict predation can be critical for selecting sites in many marine restoration projects, where costs of maintaining organisms or protecting them in the field can place burdens on the limited resources available for these efforts. During this study, the 6 sites surveyed in Shinnecock Bay, NY, which represent a range of conditions that might be considered in bay scallop restoration efforts, habitat complexity, predator identity and density, estimated consumption, actual predation, and scallop settlement, all exhibited spatial variation. The Bridge, a site with no seagrass and little other habitat complexity, had the lowest tethered-scallop survival and no on-bottom scallops. Cormorant Point, the site with the highest seagrass cover and the highest scallop

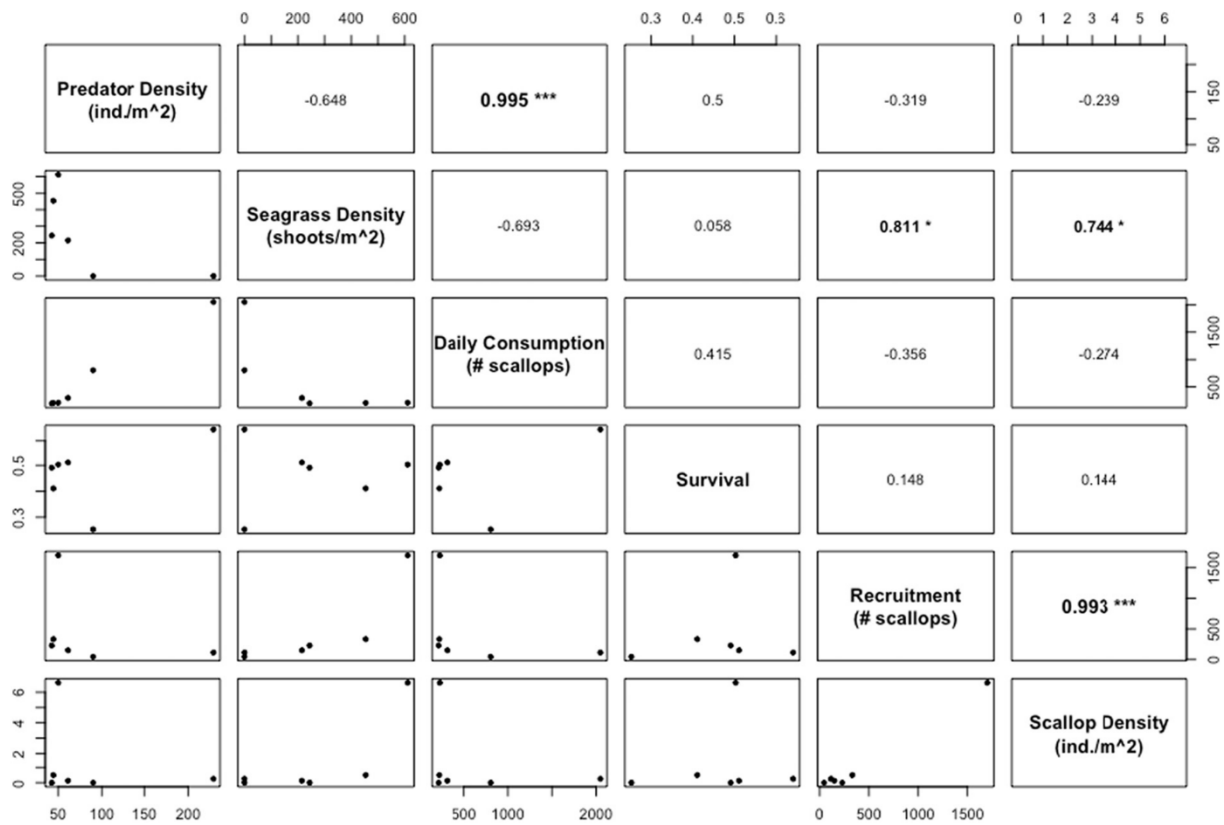


Fig. 4. Pearson correlation matrix plots showing relationships between predator density, seagrass density, estimated consumption, scallop survival, scallop recruitment, and scallop abundance for all sites, with Heady Creek represented as zero seagrass. Significant relationships are signified with bold font and an asterisk ($0.1 > \alpha > 0.05$), two asterisks ($0.05 > \alpha > 0.01$) or three asterisks ($\alpha < 0.01$).

recruitment exhibited the greatest on-bottom density of scallops despite moderately high predation rates. Heady Creek had the lowest predation rates despite an absence of seagrass, the highest predator densities, and the highest estimated consumption. However, scallop survival in the field did not appear affected by either seagrass abundance or predator density. Additionally, our estimates of field consumption based on lab experiments and field survey data was not related to either survival rates in the field or scallop densities. This study highlights the complexities associated with extrapolating laboratory results to the field but still provides important insights for scallop restoration.

Initially, we sought to estimate sites where scallop predation should be highest, based on mesocosm-derived consumption rates by abundant decapod crustacean predators and field-derived abundance and habitat data. When we considered all sites, our estimates for consumption were not correlated with either survival or scallop density. The lack of strong relationships reflects the difficulties in using lab experimental data to estimate interactions in complex, open field settings. Although we incorporated habitat complexity, our predator-specific consumption rates were almost certainly overestimated. While mesocosm experiments are widely used in ecology, consumption rates derived from them are likely to be overstated due to their lack of repeatability and realism (Kraufvelin, 1999), and may therefore differ greatly from the field (Ray-Culp et al., 1999). Particularly, mesocosm experiments may ignore interactions between predators, including antagonistic interactions (Griffen, 2006) and cascading effects (Grabowski et al., 2008), as well as intraguild interactions and cannibalism (Gerald, 2015). Additionally, only large, male crabs were used to calculate consumption rates (Carroll et al., 2015b), but all sizes and both sexes of crabs were used to estimate consumption. Most crabs in the survey were much smaller than those used in mesocosms, i.e., ~50% of mud crabs from our field surveys were < 10 mm in carapace width (CW), and most studies use mud crabs >20

mm for predation experiments (Tettelbach, 1986; Carroll et al., 2015b). However, other small xanthids (9–15 mm CW) will consume small bivalve prey (Kulp et al., 2011). Thus, while we included all crabs in our density numbers, the effective predator population size for consuming scallop prey is likely overestimated. Lastly, estimates based on mesocosm experiments may also ignore prey availability and prey choice. Several other species identified in suction surveys could be considered prey for our focal predators, including several other crustaceans, small gastropods, and other bivalves, as well as uncounted organisms such as worms, and even algal material and detritus. For example, while small (<40 mm) juvenile blue crabs may still feed on bivalve prey, they are also more opportunistic for other food resources at that size (Seitz et al., 2011). Therefore, there are several reasons why using mesocosms might lead to incorrect estimations of predation in the field, and any extrapolations should be made with extreme caution.

Another issue is that the mesocosm-derived data we used for this study focused specifically on seagrass – the preferred bay scallop habitat (Belding, 1910) – and unstructured bottoms. While seagrass is undoubtedly important for providing an attachment substrate and enhancing scallop abundances (Pohle et al., 1991; Irlandi et al., 1999), our results also add to growing evidence that other structured habitats may also be suitable alternatives (Carroll et al., 2010; Hernandez-Cordero and Seitz, 2014). For example, Heady Creek had the highest predator density (>200 crabs m⁻²) and no seagrass, yet it exhibited the highest scallop survival during tethering experiments, ~30% higher relative to the site with the highest seagrass density. There was considerable habitat complexity at this site, including 31% cover of the upright, branching macroalgae *C. fragile*, which has a similar refuge value as seagrass (Carroll et al., 2010), and a large bed of *C. formicata*, a gastropod that forms reproductive stacks, created a thick layer of complex shellfish bed habitat that is not normally considered for scallops.

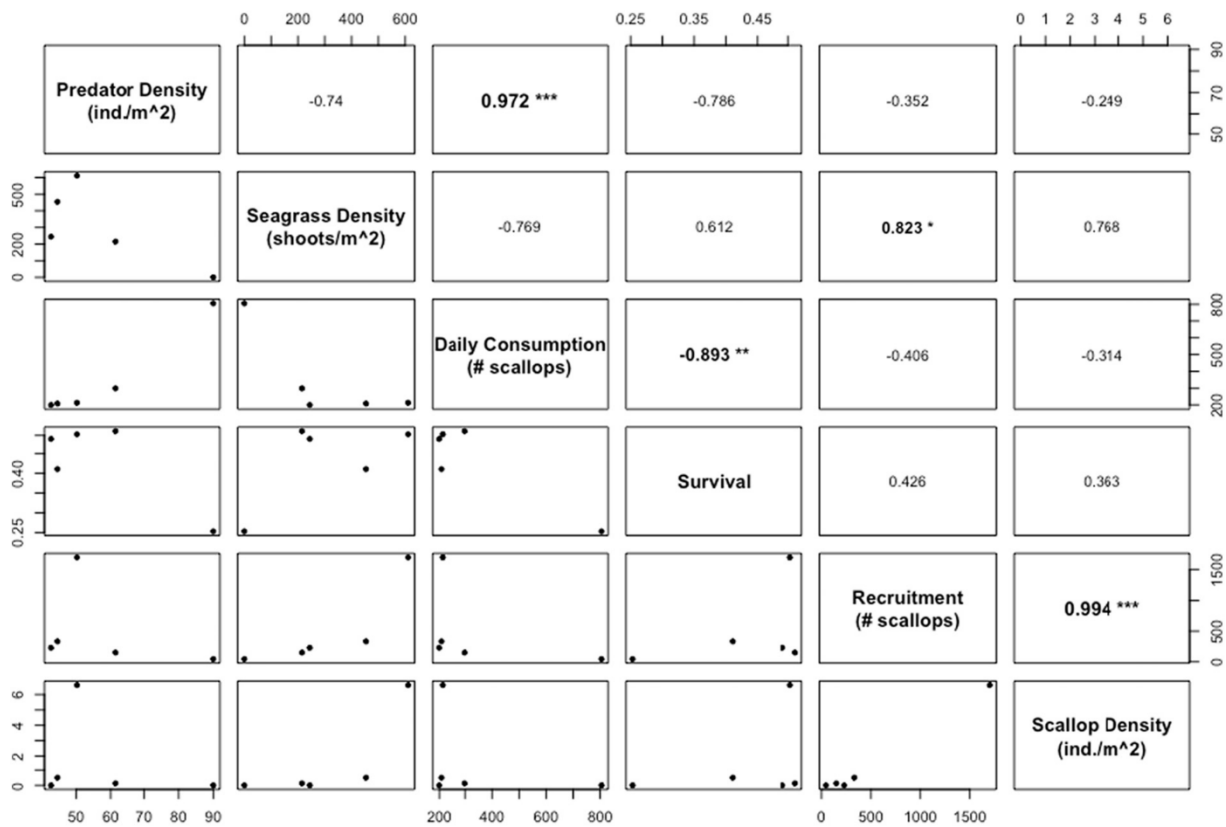


Fig. 5. Pearson correlation matrix plots showing relationships between predator density, seagrass density, estimated consumption, scallop survival, scallop recruitment, and scallop abundance for all sites except Heady Creek due to the confounding habitat complexity from both *Codium fragile* and *Crepidula fornicata*. Significant relationships are signified with bold font and an asterisk ($0.1 > \alpha > 0.05$), two asterisks ($0.05 > \alpha > 0.01$) or three asterisks ($\alpha < 0.01$).

Oyster shell habitats alter predator-prey interactions and increase prey survival (Grabowski, 2004; Grabowski et al., 2008), including for scallops (Macreadie et al., 2011; Hernandez Cordero and Seitz, 2014), and recently, *C. fornicata* habitat has been shown to reduce predator encounter rates with prey (Kulp, 2018) and increase prey survival (Mladinich, 2017). Therefore, the high complexity shellfish habitat provided by *C. fornicata* may provide many additional refuge opportunities for juvenile scallops, while also serving as an alternative food resources (Lindsey et al., 2006), leading to enhanced scallop survival. As previously mentioned, high predator densities at this site could lead to antagonistic interactions among predators, including changes in behavior and consumption (predation and cannibalism – Gherardi, 2015; emergent multiple predator effects – Griffen, 2006), reducing scallop predation. If Heady Creek was removed from the analysis, our estimates of consumption had strong, significant negative correlation with scallop survival, although it was driven primarily by 1 site. Regardless, when considering seagrass habitats and relatively unstructured bottom, our estimates for consumption may be more accurate. More research is needed to fully understand how to value the complexity of live *Crepidula* shell beds, as they are particularly understudied in their native range, and compare it to other habitats like submerged aquatic vegetation. Future experimentation should also attempt to tease apart the independent effects of shellfish habitat value from the predator interactions that are occurring within shellfish beds/reefs.

The high estimated consumption at the Heady Creek site relative to the actual survival of tethered scallops was likely driven by the high density of mud crabs, *D. sayi*, at this location. Overall, mud crabs were 3× to 100× more abundant than blue crabs, *C. sapidus*, the next most abundant predator, and 2 to 3 orders of magnitude greater than other crabs collected. While the per capita consumption rates of mud crabs are low relative to other, larger crab species (Carroll et al., 2015a), their

high abundances suggest a larger potential impact on prey populations (Rindone and Eggleston, 2011). We also predict that mud crabs are likely the most important scallop predator in this system – they have been identified as important consumers of small bivalves (Whetstone and Eversole, 1991; Streib et al., 1995; Ray-Culp et al., 1999; Kulp et al., 2011), including bay scallops (Tettelbach, 1986; Carroll et al., 2012), in multiple studies. When examining predation of small vs. large crabs, small mud crabs tend to be the dominant predators of other bivalves (Grabowski et al., 2008; O'Connor et al., 2008; Rindone and Eggleston, 2011; Johnson et al., 2014; Carroll et al., 2015a). Blue crabs are also considered important benthic predators in many systems (Eggleston et al., 1992; Seitz et al., 2001; Hovel and Lipcius, 2002), including of bay scallops (Bishop et al., 2005; Hernandez Cordero and Seitz, 2014). New York is near the northern edge of the blue crab range, so continued range expansion due to climate change may shift the balance of predators within this system (Rogers et al., 2018). At more northern locations, invasive green crabs, *C. maenas*, may be the most important scallop predators, although mud crabs were undoubtedly underestimated (Tettelbach, 1986). Identifying the dominant predators in a system may help inform restoration efforts, particularly those that practice seeding of juvenile individuals. In Connecticut, scallop size was the most important factor influencing survival across multiple seasons (Tettelbach, 1986), suggesting size thresholds might be useful for restoration. If mud crabs are currently the predator that can consume the most scallops in these estuaries, sizes of scallops that may be a refuge from mud crab predators (i.e. >30 mm shell height; Tettelbach, 1986; Streib et al., 1995) can be targeted in restoration efforts.

Scallop survival also was not correlated with seagrass density. The Bridge, a site with no seagrass and little other habitat complexity, experienced predation rates twice as high as the seagrass sites and had zero wild scallops observed in any survey. However, for the 4 sites with

seagrass, ranging from ~ 200 to >600 shoots m^{-2} , there was very little variation (41–50%) in scallop survival. Other studies have also observed negligible changes in predation rates with increasing seagrass complexity, particularly when confounded by increasing predator and prey densities (Mattila et al., 2008; Canion and Heck, 2009), suggesting a threshold response to seagrass at a very low density (Heck et al. 2003). Since seagrasses also provide suitable habitat refuge for numerous other species, including benthic decapods that are important mesopredators (Peterson, 1986; Orth and van Montfrans, 1987; Hovel, 2003), this may complicate any potential positive effects of seagrass. These results may fit in within the broader patterns of seagrass density-prey survival studies, although a bigger range of seagrass habitat, particularly at lower densities, would be required to fully test this pattern. The lack of pattern between seagrass and survival may also have important management implications. Specifically, seagrass presence per se is likely to dramatically increase prey survival compared to unstructured habitat, but beyond some low shoot density, increased habitat is unlikely to incur increased benefits to prey (Canion and Heck, 2009; Carroll et al., 2015a). Since seagrass density, at least at the ranges common in seagrass meadows along the US Atlantic coast (i.e. ~ 200 – 1000 shoots m^{-2} ; Fonseca and Bell, 1998; Greiner et al., 2013; Furman et al., 2017), and spatial configuration (Carroll and Peterson, 2013) may not be as critical for scallop survival, any site with any seagrass may be suitable for scallop restoration. Although they did not categorize seagrass density, Tettelbach et al. (2011) found a significant benefit of planting scallops in seagrass meadows when compared to unvegetated habitats for restoration. Therefore, efforts that focus on boosting seagrass cover may also aid in scallop restoration (Orth et al. 2020).

Despite overall low bay scallop abundance across our study sites (<0.5 m^{-2} at 5 of the 6 sites) there was a strong, positive correlation with scallop spat settlement and scallop abundance. Multiple studies suggest that intense predation pressure common throughout the scallop's range may be responsible for low scallop abundance (Bologna and Heck, 1999; Bishop et al., 2005; Lefcheck et al. 2014; Fegley et al., 2009), and our current daily consumption estimates also suggests that the predator field may not be satiated by current scallop abundance. Such low densities are common throughout the range of bay scallops (Shumway and Parsons 2016, and references therein), which may, in part, hamper management and restoration efforts because low adult densities can limit fertilization success and subsequent recruitment (Leviton and Petersen, 1995; Tettelbach et al., 2013). However, larval recruitment is a critical driver of populations of numerous benthic organisms (Gaines and Roughgarden 1985; Menge et al., 2003), including bay scallops (Tettelbach et al., 2015), and our study suggests recruitment limitation in our study system. Therefore, efforts which seek to boost density via high density larval releases (Leverone et al. 2010), transplantation and protection by stockades (Fegley et al., 2009) or nets/cages (Arnold et al. 2005, Tettelbach et al., 2013), or by efforts to satiate the predator field by high density (~ 100 individuals m^{-2}) plantings of moderate sized (i.e. >30 mm shell height) individuals (Tettelbach et al., 2011), can help rebuild populations. Overall, the current study suggest that larval supply may be more important than habitat or predation for scallop density in this system, although future studies should incorporate more sites and use a stepwise, hierarchical approach to explore this relationship.

Overall, this study shows the potential limitations in trying to infer field conditions from lab experimentation which can lead to over- (i.e. Cormorant Point) and under-estimation (i.e. Heady Creek) of prey survival. Using mesocosm experiments and field surveys, the predator field in Shinnecock Bay appears to be unsatiated with respect to available scallop prey, potentially limiting population growth. However, our attempts to link site characteristics – habitat, predator density, estimated consumption, survival – to on-bottom scallop density remains elusive. Even when considering potential limitations, this study illustrates the importance of understanding the interplay between habitat complexity, predation, and prey density in prey survival and abundance, which can

have implications for population building in managed commercial species. Particularly, for seagrass-associated fauna, our results suggest that any amount of seagrass is likely to provide some benefit to scallops, but that alternative habitats including macroalgae (Carroll et al., 2010) and shellfish beds (Hernandez-Cordero et al. 2012) should be considered. Future research should target understudied, but useful, alternative habitats (macroalgae, *C. formicata* beds). Identification of the dominant predator in a particular system could also optimize restoration strategies, particularly seeding, which need to balance a trade-off between planting high densities at smaller sizes, saving time and money but risking high mortality, and planting lower numbers at larger sizes or offering protective devices, which may have higher overall survival but come with higher financial burden (Arnold et al. 2005, Fegley et al., 2009, Tettelbach and Smith 2009, Tettelbach et al., 2013, Schmitt et al. 2016). Given the large investments (US \$millions) in scallop and other shellfish restoration efforts, which may be hindered by high mortality, including due to predation, it is critical to not only explore issues related to habitat complexity and predation to inform these efforts, but to also test those findings in field conditions. Building better predictions of predation may allow smaller, local, and less well-funded efforts to be successful if appropriate sites can be identified. By selecting sites with a low predicted predation intensity, overall mortality may be reduced which can subsequently have a positive influence on restoration success.

Author contributions

JMC, BJP, STT and REK contributed to the conception of this study and experimental design. JMC, REK, LLJ and EM performed the experiments. JMC and REK analyzed the data. JMC and STT wrote the manuscript and all others contributed editorial advice.

Declaration of Competing Interest

The authors report no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2021.151663>.

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