

# Examination of the potential relationship between boring sponges and pea crabs and their effects on eastern oyster condition

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**ABSTRACT:** The eastern oyster *Crassostrea virginica* provides a number of ecosystem services and is an important commercial fishery species along the US East and Gulf Coasts. Oyster populations have declined dramatically due to overharvesting, habitat loss, and disease. As restoration efforts and aquaculture of oysters continue to increase throughout their range, it is important to consider the impacts of a number of potential oyster pests, including the boring sponge *Cliona* spp. and the pea crab *Zaops (Pinnotheres) ostreum*, on oyster populations. Both of these have been demonstrated to reduce oyster growth, condition, and in some instances, reproductive output. Boring sponges in particular are a major concern for oyster growers and managers. Our monitoring efforts have suggested that pea crabs might be more prevalent in sponge-infested oysters; we therefore conducted an observational study to determine if there was any relationship between pea crab prevalence and sponge presence, and to examine whether the presence of both pests had synergistic effects on oyster condition. At 2 very different sample sites, North Carolina and New Jersey, oysters with 1 pest (i.e. boring sponge) were significantly more likely to have the second pest (i.e. pea crab) than the background population. Furthermore, sponge presence negatively affected oyster condition in North Carolina only, while pea crabs significantly reduced condition at both locations. When sponges and pea crabs were present together, the effects on oyster condition were additive. This study provides further evidence that interactions between an individual and a fouling/pest organism can alter oyster susceptibility to other parasites.

**KEY WORDS:** *Crassostrea virginica* · *Cliona* spp. · *Zaops (Pinnotheres) ostreum* · Parasite · Condition

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## INTRODUCTION

A number of external factors can influence the strength of parasite–host interactions. In particular, factors that alter host condition and growth (Rainer & Mann 1992, Trussell et al. 2006), or adjust energy allocation by the host (Allen & Little 2011), can increase host susceptibility to parasites. These external factors can be environmental, such as temperature and salinity, which can either affect the host,

the parasite, or otherwise alter the interaction (Hall et al. 2013). Biotic interactions, such as predation and competition, can also negatively affect the parasite–host relationship by increasing host stress (Seppälä et al. 2004). In particular, the impacts of predator–prey interactions on host–parasite relationships have been extensively explored (Hassell & Anderson 1989, Hall et al. 2005, Cáceres et al. 2009). There has been little research, however, into the potential interaction between hosts and non-

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parasitic pests, and how these interactions might alter parasite–host relationships.

The eastern oyster *Crassostrea virginica* is a useful model organism to study how biotic interactions might structure parasite–host relationships (Malek & Byers 2016). In coastal environments, oysters are a foundation species that provide food for fishes, gastropods, and crustaceans (Johnson & Smee 2014), create habitat for juvenile fish species and other organisms (Wilberg et al. 2013), stabilize sediments and buffer shorelines (Wallis et al. 2015), and improve water quality (Ehrich & Harris 2015). Additionally, oysters are a valued commercial resource that historically supported coastal fisheries (Kirby & Linares 2004). Unfortunately, oyster populations have been declining due to overharvesting and disease, among other factors (Rothschild et al. 1994, Coen & Luckenbach 2000), to the point of ‘functional extinction’ in many areas within their range (Beck et al. 2011). Consequently, local, state, and federal agencies, as well as non-governmental organizations, are annually investing considerable money and effort to restore and manage oyster resources (Coen et al. 2007) and increase aquaculture production (Dumbauld et al. 2009). With the increasing demand for oyster restoration and population management, it is vital to understand factors that may be limiting their recovery.

Due to the economic importance of oysters, the effects of abiotic and biotic factors on recruitment, growth, and survival are relatively well understood (Baker & Mann 1992, Austin et al. 1993, Kennedy et al. 1996, Lenihan & Peterson 1998). While environmental parameters can influence the distribution of oysters (Mann et al. 2009, Munroe et al. 2017), biotic interactions such as predation and disease are major drivers of oyster populations (Powell et al. 2008, Poirier et al. 2017). However, oyster pests might also influence oyster population distribution. Specifically, the boring sponges of the genus *Cliona* can be particularly devastating to oysters. The sponges excavate into the shell matrix of oysters, and laying down new shell layers requires considerable energy (Palmer 1992). As a result, sponge-infected oysters exhibit reduced growth, and in large individuals, reduced condition (Carroll et al. 2015a), which can be problematic in aquaculture operations (Carver et al. 2010) and restoration efforts (Dunn et al. 2014). Further, since sponges reduce oyster condition (Carroll et al. 2015a), they may make individuals more vulnerable to other stressors and parasites (Volety et al. 2009) and possibly even predators (Speights & McCoy 2017). Oysters stressed by one pest might be more

susceptible to another, and the combined effects on the host could therefore be synergistic.

An oyster parasite potentially impacted by the presence of the boring sponge is the pea crab *Zaops (Pinnotheres) ostreum*. The family Pinnotheridae contains numerous species of small, soft-bodied crabs that live in different hosts ranging from bivalves to echinoids (Grove & Woodin 1996). Pea crabs use the host for protection and food (Sandifer 1972), and typically enter the bivalve host during feeding processes and embed themselves in the gills, even entering early post-set individuals (Christensen & McDermott 1958, Byers et al. 2014). Their presence causes gill damage, and they might even consume small pieces of gill tissue, leading to reduced oyster condition and gonad development (Stauber 1945, O’Beirn & Walker 1999, Mercado-Silva 2005), which could affect population growth. While the prevalence of pea crabs varies across regions (Byers et al. 2014), initial observations in North Carolina (NC) intertidal reefs suggests that approximately 3% of oysters are infected (Hanke et al. 2015).

During surveys of local reefs in Masonboro Sound, NC, a much higher proportion of sponge-infested oysters were also colonized by pea crabs (J. M. Carroll pers. obs.), which suggested that oysters with one pest may be more susceptible to the other. However, the infection dynamics of pea crabs and boring sponges in oysters is unclear. Pea crabs may recruit to very small and typically younger oysters (Byers et al. 2014), although oysters that settle on sponge-infested substrates could rapidly become infected by sponge growth (Carver et al. 2010). Regardless, high prevalence of both species in the same individuals warrants examination of the relationship. Since both sponges and pea crabs negatively affect oysters, it is also possible that rather than acting independently, the effects of these stressors interact and have a more negative impact when both are present (Hall et al. 2013).

Biotic stressors (i.e. pests and parasites) may interact to make oysters more vulnerable and reduce health; therefore, we sought to determine whether the presence of an oyster pest (the boring sponge) affected the prevalence of an oyster parasite (the pea crab). Furthermore, we aimed to investigate the interaction between the pest and parasite on oyster condition. We hypothesized that oysters infected with sponges would have an increased prevalence of pea crabs and that there would be a synergistic effect on oyster condition when both sponges and pea crabs were present. We conducted field surveys in NC and New Jersey (NJ) to assess these interactions.

## MATERIALS AND METHODS

### Previous observations

During a sponge reproduction and recruitment study during the early summer of 2013 (see Stubler et al. 2017), sponge-infested oysters were harvested from intertidal oyster reefs at the University of North Carolina research lease in Hewletts Creek, Masonboro Sound, NC (34° 10' 35" N, 077° 50' 33" W). Tidal exposure of oysters at this site is ~3 h per tidal cycle (C. M. Finelli pers. obs.). Oysters were returned to the lab, measured, and dissected for condition index (CI) using shell weight (Rainer & Mann 1992). During dissections, the presence of pea crabs was noted. In total, we harvested 194 sponge-infested oysters, 22 of which also had a pea crab present in the mantle cavity. This pea crab prevalence (11.3%) was much higher than reported for nearby reefs (2–4% pea crab prevalence; Hanke et al. 2015). Additionally, CI for the sponge-infested oysters with pea crabs was significantly lower than the CI for sponge-infested oysters without pea crabs ( $t = -2.713$ ,  $p = 0.008$ ). Based on these findings, we designed an observational field survey in NC and NJ to determine the relationships and impacts of the pest and parasite.

### NC study

Oysters were hand collected by haphazardly tossing a 0.04 m<sup>2</sup> quadrat onto intertidal oyster reefs within the University of North Carolina Wilmington research lease located in Hewletts Creek, in Masonboro Sound, NC. The research lease is closed to fishing, thus any oyster removal from reefs is from scientific collections like those described here, and densities range from <200 to >700 oysters m<sup>-2</sup>, dependent on the reef (see Carroll et al. 2015b for more details on the study site). Oysters at this site exhibit high prevalence but low intensity of dermo (perkinsosis) (A. Wilbur pers. comm.). Quadrat collections occurred in 2013 (44), 2014 (52), and 2015 (20) during the month of July. All living oysters were excavated from the quadrats, returned to the lab, and frozen before analysis.

At the lab, all oysters from a sample were enumerated, measured for length and width, weighed, and visually inspected for boring sponge presence. All oysters were then dissected, and pea crab presence was noted. If present, pea crabs were removed and, starting in 2014, weighed to obtain wet weight. Oys-

ter tissues were placed into pre-weighed aluminum tins and dried at 70°C for 48 h. Since oysters were frozen and thawed, we were careful to quickly process oysters and placed thawing oysters with their cupped left valve down in an aluminum weigh-boat to minimize any potential loss of oyster liquor, which could lower whole wet weight, and calculated CI using the following formula:

$$CI = \frac{TDW}{WW - SW} \times 100 \quad (1)$$

where TDW is the tissue dry weight, and the difference between whole wet weight (WW) and dry shell weight (SW) is a proxy for internal shell volume (Rheault & Rice 1996). While we acknowledge that spongy shells are likely to be lighter, which could affect our calculations (Abbe & Albright 2003), this would artificially inflate our CI values, thereby making our estimates conservative. Any differences observed should be expected to be greater.

A subset of dry oyster tissues was homogenized using a mortar and pestle and analyzed for tissue energy content using an IKA C1 benchtop calorimeter. In total, 95 oysters were used for calorimetry measurements: 25 that only had pea crabs, 24 that only had sponges, 18 that had both pests together, and 28 with neither. For each oyster, between 0.2 and 1 g of dried oyster tissue was placed into pre-weighed crucibles. Caloric density estimates for bombs were calibrated using 1 g benzoic acid (C<sub>6</sub>H<sub>5</sub>COOH) pellets with a known energy density of 26.460 kJ g<sup>-1</sup>. This method allows calculation of energy content per unit dry mass of oyster tissues, a proxy for lipid content and another measure of organism condition (McKinstry et al. 2013, Carroll et al. 2015a).

### NJ study

Oysters were collected monthly (July through November in 2013, and August through November in 2014) as part of an ongoing, long-term oyster survey from 9 subtidal oyster beds in Delaware Bay (Ashton-Alcox et al. 2017). Oyster density varies throughout the area surveyed, from approximately 15 m<sup>-2</sup> in the lower bay to approximately 248 m<sup>-2</sup> in the upper bay (see Ashton-Alcox et al. 2017 for more details). Seven beds where boring sponges are present were used for this study. Oysters were collected by dredge, and 20 oysters, i.e. 5 from each of 4 size classes (20–40, 41–60, 61–80, >80 mm), were retained from each bed each month for analysis. Oysters were returned to

the lab where they were immediately measured and weighed. CI was calculated as described for NC oysters. Pea crab presence was noted for each oyster in both years, and pea crab wet weight was recorded for the 2014 samples only. Sponge presence was assessed by visual inspection of dried, archived shells.

### Data analysis

To test if prevalence of pea crabs in sponge-infested oysters was greater than prevalence of pea crabs in oysters without sponges, we used a Pearson chi-squared test ( $2 \times 2$  contingency table). To determine the effects of sponges, pea crabs, and their interaction on oyster condition, we used a 2-way ANOVA with the presence/absence of either pea crabs or boring sponges as the treatment variable and CI as the response variable. We pooled data across all collections within each site to increase our sample size for analysis, particularly for the oysters with pea crabs and with both the pest and parasite. While we acknowledge monthly and annual variability in CI due to reproductive cycles and other factors (Kennedy & Battle 1964), pooling the data should increase the variability in our measurements and make any differences between groups less likely. By using this test, an interaction between pest treatments would be indicative of a synergistic effect on oyster condition, and no interaction suggests an additive effect. Each site (NC and NJ) was analyzed separately due to differences in sampling methods and tidal locations.

In addition, we sought to explore whether the size of oysters varied across different pest treatments using a 1-way Kruskal-Wallis test. The allometric relationships between shell sizes and dry tissue weight were compared for oysters with pea crabs, with sponges, and with no pests as another index of growth and condition (Pollack et al. 2011), which can be expressed as a power function (Dame 1972):

$$\text{LVL} = a\text{TDW}^b \quad (2)$$

where LVL is the left valve length (mm) and  $a$  and  $b$  are empirically derived coefficients. Parameter estimates were determined as above, and potential differences in the exponent  $b$  were determined using an ANOVA. Finally, we also investigated the relationship between oyster CI and oyster size for oysters with sponges and oysters with pea crabs using linear regressions.

CI is a measure of the amount of oyster body tissues relative to the amount of space available, which represents energy reserves and potential reproductive output. Since pea crabs reside within the mantle cavity and also take up space, we sought to determine if the observed lower CI of oysters with pea crabs present was a result of pea crabs merely reducing the amount of space that the oyster tissue could occupy. Thus, the weight of the pea crab was subtracted from the whole oyster wet weight, representing the amount of cavity space taken up by the pea crab, and CI was recalculated. Lastly, to test whether both pests affected the energy content of oyster tissue, a 2-way ANOVA with the presence/absence of each pest as the treatments and energy density ( $\text{kJ g}^{-1}$ ) as the response variable for NC oysters was used.

## RESULTS

### NC survey

In total, we collected 1216 oysters in 2013–2015. Across all years, 19.7% (240) of the oysters had clionid sponge infestation (Table 1). Overall, 4.0% (49) of oysters had pea crabs (Table 1), and 1.7% of the population sampled had both. Pea crabs were 3 times more prevalent in spongy oysters (9.6%; 21/240) than non-spongy oysters (3.0%; 28/976;  $\chi^2 = 17.2$ ,  $p < 0.001$ ). The presence of both boring sponges (2-way ANOVA,  $F_{1,1215} = 11.0$ ,  $p < 0.001$ ) and pea crabs ( $F_{1,1215} = 31.7$ ,  $p < 0.001$ ) significantly reduced oyster condition, but there was no significant interaction of sponge and pea crab on oyster condition ( $F_{1,1215} = 0.00002$ ,  $p = 0.99$ , Fig. 1A). ‘Healthy’ oysters, i.e. those with neither pest, had significantly higher CI than oysters with sponges alone, pea crabs alone, and both together ( $p < 0.001$  for all). Additionally, oysters with sponge alone had significantly higher CI than those with both pests ( $p < 0.001$ ), whereas there was no difference between sponges alone and pea crabs alone ( $p = 0.16$ ) or between pea crabs alone and both present ( $p = 0.09$ ; Fig. 1A).

Table 1. Proportion (% , with sample size in parentheses) of oysters harvested in North Carolina ( $n = 1216$ ) and New Jersey ( $n = 1259$ ) with no pests (‘neither’), with either boring sponges or pea crabs only, and with both together

	Neither	Sponge	Pea crab	Both
North Carolina	78.0 (948)	18.0 (219)	2.3 (28)	1.7 (21)
New Jersey	51.4 (647)	38.6 (486)	4.7 (59)	5.3 (67)

Oysters were sampled across a wide size range (23.5–132.3 mm) from NC. Interestingly, size (shell height) significantly varied across the pest–parasite categories (Kruskal-Wallis,  $H_3 = 48.112$ ,  $p < 0.001$ ). Oysters with both pests were significantly larger than those without either pest (Dunn's  $Q = 2.893$ ,  $p < 0.05$ ), and similarly, oysters with sponges only were also significantly larger than those with neither (Dunn's  $Q = 6.293$ ,  $p < 0.05$ ). There were no other differences in size among categories (see Fig. A1 in the Appendix). When examining the allometric relationship between oysters with pea crabs ( $LVL = 91.32 \times TDW^{0.331}$ ;  $F_{1,48} = 91.784$ ,  $p < 0.0001$ ), oysters with sponges ( $LVL = 85.18 \times TDW^{0.314}$ ;  $F_{1,240} = 270.774$ ,  $p < 0.0001$ ), and oysters without pests ( $LVL = 87.84 \times TDW^{0.375}$ ;  $F_{1,975} = 2433.244$ ,  $p < 0.0001$ ), there was a significant difference in the exponent  $b$  across categories ( $F_{2,1263} = 5.415$ ,  $p = 0.005$ ). Post hoc analysis revealed that the exponent  $b$  was different between oysters with sponges and oysters without pests ( $p = 0.004$ ), with no other differences between the allometric relationships (Fig. 2). Interestingly, across all categories, there were negative relationships between oyster size and CI, although the oysters with no pests had the smallest negative slope and, overall, the regressions explained little (6–16%) of the variability (Table 2).

A total of 19 pea crabs (38% of pea crabs collected) were wet-weighted from the collected oysters. Each oyster that was infected only had a single pea crab. Weights ranged from 0.13 to 0.67 g, with a mean  $\pm$  SE of  $0.37 \pm 0.04$  g crab $^{-1}$ . Oyster condition without correcting for the weight of the pea crab for these 19 oysters was  $5.67 \pm 0.32$ , and when the weight of the pea crab was subtracted from the whole weight of the oyster, condition increased  $\sim 7\%$  to  $6.06 \pm 0.39$ , although these values were not significantly different ( $t = -0.8$ ,  $p = 0.4$ , Fig. 3A). This indicates that the lower CI observed in oysters with pea crabs is not simply due to the space occupied by the pea crab itself.

The energy content of oysters with neither pest was  $14.66 \pm 0.24$  kJ g $^{-1}$ , while the energy content of oysters with sponges was  $14.70 \pm 0.25$  kJ g $^{-1}$ , with pea crabs  $14.24 \pm 0.24$  kJ g $^{-1}$ , and with both  $13.73 \pm 0.28$  kJ g $^{-1}$ . There was no significant effect of sponge presence on energy content of homogenized oyster tissues (2-way ANOVA,  $F_{1,94} = 0.8$ ,  $p = 0.3$ ); however, pea crab presence significantly reduced energy density (2-way ANOVA,  $F_{1,94} = 7.5$ ,  $p = 0.007$ ; Fig. 4). There was no significant sponge $\times$ pea crab interaction ( $F_{1,94} = 1.2$ ,  $p = 0.3$ ).

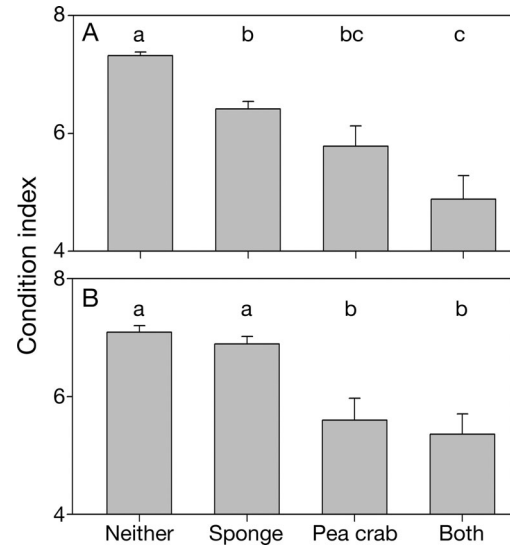


Fig. 1. Condition index of oysters harvested in (A) North Carolina and (B) New Jersey among the pest–parasite categories. Neither: neither sponge nor pea crab present; sponge: sponge only; pea crab: pea crab only; and both: both sponges and pea crabs present. Letters denote significant differences from a multiple comparisons test

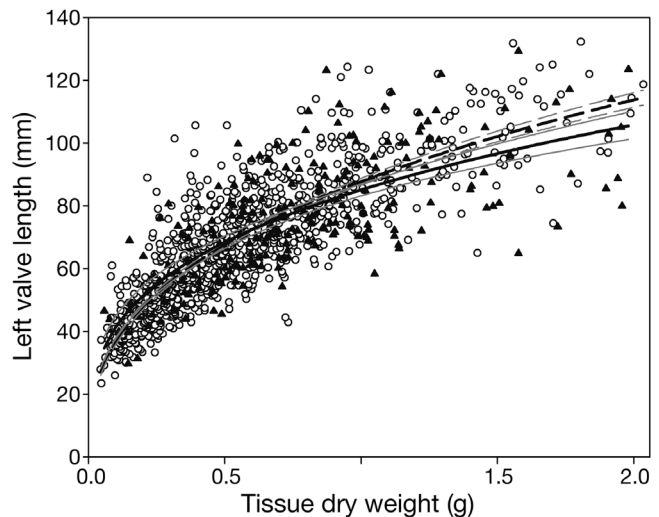


Fig. 2. Allometric relationship of oysters harvested from North Carolina with sponges (closed triangles, dashed lines) and without sponges (open circles, solid lines). Black lines (solid and dashed) represent the allometric relationships, whereas gray lines (solid and dashed) represent the 95% confidence intervals

### NJ survey

We collected a total of 1259 oysters during both surveys in 2013 ( $n = 630$ ) and 2014 ( $n = 629$ ) from NJ. Overall, 43.9% (553) of the oysters had sponge infestation (Table 1). The proportion of oysters with pea crabs was 10.0% (126) across both years (Table 1),

Table 2. Linear regression results illustrating the relationships between condition index (CI) and the left valve length (LVL) of North Carolina oysters in the different pest–parasite categories

	df	SS	MS	F	p
<b>Both pests</b>					
CI = 7.75 – (0.036 × LVL)					
R = 0.399, R <sup>2</sup> = 0.159					
Regression	1	8.989	8.989	3.598	0.073
Residual	19	47.466	2.498		
Total	20	56.455	2.823		
<b>Pea crabs only</b>					
CI = 7.854 – (0.029 × LVL)					
R = 0.409, R <sup>2</sup> = 0.167					
Regression	1	8.511	8.511	5.216	0.031
Residual	26	42.423	1.632		
Total	27	50.934	1.886		
<b>Sponges only</b>					
CI = 9.02 – (0.034 × LVL)					
R = 0.313, R <sup>2</sup> = 0.098					
Regression	1	88.601	88.601	23.666	<0.001
Residual	217	812.395	3.744		
Total	218	900.995	4.133		
<b>Neither pest</b>					
CI = 8.829 – (0.022 × LVL)					
R = 0.253, R <sup>2</sup> = 0.064					
Regression	1	194.071	194.071	64.498	<0.001
Residual	946	2846.474	3.009		
Total	947	3040.545	3.211		

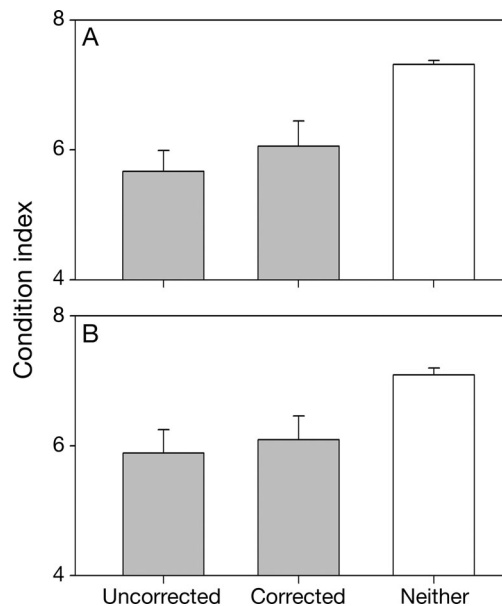


Fig. 3. Oyster condition index for oysters with pea crabs, either left uncorrected or corrected for the weight of the pea crab, as it takes up space within the shell. (A) North Carolina oysters, (B) New Jersey oysters. 'Neither' represents oysters with no pea crabs or sponges as a reference

and the proportion with both was 5.3% (67). Spongy oysters were more likely to have a pea crab (13.8%; 67/553) than non-spongy oysters (8.4%; 59/706;  $\chi^2 = 4.9$ ,  $p = 0.027$ ). Similar to NC, the presence of pea crabs significantly reduced oyster condition (2-way ANOVA,  $F_{1,1258} = 32.2$ ,  $p < 0.001$ ), and there was no significant interaction among sponge and pea crab ( $F_{1,1258} = 0.006$ ,  $p = 0.9$ ), but the presence of sponges alone did not significantly affect condition ( $F_{1,1258} = 0.7$ ,  $p = 0.4$ ). There was no significant difference in condition between 'healthy' oysters and those with boring sponges only ( $p = 0.420$ ), and both exhibited significantly higher CI than those with pea crabs only ( $p < 0.001$  for healthy and  $p = 0.004$  for sponge-only) and both present ( $p < 0.001$  for healthy and sponge-only). There was no significant difference between pea crabs only and both pests present ( $p = 0.6$ , Fig. 1B).

In NJ, a similar size range (23.6–121.9 mm) of oysters was sampled. A Kruskal-Wallis test revealed that differences among categories were greater than to be expected by chance ( $H_3 = 13.113$ ,  $p = 0.004$ ), although a Dunn's multiple comparison did not yield any significant differences among categories (see Fig. A1). When examining the allometric relationship between oys-

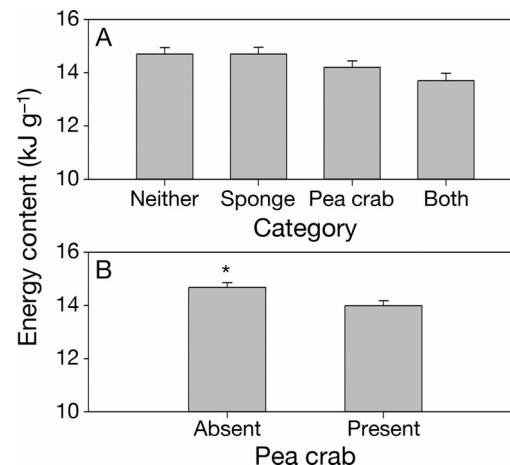


Fig. 4. Energy content of oysters collected from North Carolina: (A) among the 4 pest–parasite categories and (B) between just oysters with and without pea crabs. Asterisk denotes significant difference

ters with pea crabs ( $LVL = 69.08 \times TDW^{0.248}$ ;  $F_{1,82} = 108.36$ ,  $p < 0.0001$ ), oysters with sponges ( $LVL = 65.54 \times TDW^{0.297}$ ;  $F_{1,460} = 849.57$ ,  $p < 0.0001$ ), and oysters without pests ( $LVL = 66.42 \times TDW^{0.290}$ ;  $F_{1,654} = 1049.55$ ,  $p < 0.0001$ ), there was no significant difference in the exponent  $b$  across categories ( $F_{2,1200} = 1.544$ ,  $p = 0.214$ ). There were significant negative relationships between shell size and CI for both oysters with sponges and oysters with neither pest, although again, the regressions explained little (2–13%) of the variability (Table 3).

As in NC, condition was corrected for the presence of pea crabs when wet weights were available. Thirty-four pea crabs (27% of the total collected) were weighed from the NJ samples. Pea crab wet weights ranged from 0.2 to 1.7 g, with a mean of  $0.76 \pm 0.05$  g. CI for the 34 oysters before pea crab correction was  $5.89 \pm 0.36$ , and increased ~3% when corrected for pea crab weights to  $6.09 \pm 0.37$ . As with NC oysters, correcting for pea crabs did not significantly alter CI values ( $t = -0.4$ ,  $p = 0.7$ ; Fig. 3B), again indicating that the lower CI observed in oysters with pea crabs is not driven by reduced space for oyster tissues.

Table 3. Linear regression results illustrating the relationships between condition index (CI) and the left valve length (LVL) of New Jersey oysters in the different pest–parasite categories

	df	SS	MS	F	p
<b>Both pests</b>					
CI = $6.065 - (0.006 \times LVL)$					
R = 0.049, $R^2 = 0.002$					
Regression	1	0.351	0.351	0.0962	0.758
Residual	65	145.836	3.646		
Total	66	146.186	3.566		
<b>Pea crabs only</b>					
CI = $6.017 - (0.0001 \times LVL)$					
R = 0.0005, $R^2 = 3 \times 10^{-7}$					
N = 40					
Regression	1	$68 \times 10^{-6}$	$68 \times 10^{-6}$	$9.63 \times 10^{-6}$	0.998
Residual	57	268.353	7.062		
Total	58	268.354	6.881		
<b>Sponges only</b>					
CI = $9.23 - (0.032 \times LVL)$					
R = 0.145, $R^2 = 0.021$					
Regression	1	139.764	139.764	9.03	0.003
Residual	422	6531.657	15.478		
Total	423	6671.421	15.772		
<b>Neither pest</b>					
CI = $11.09 - (0.059 \times LVL)$					
R = 0.359, $R^2 = 0.129$					
Regression	1	604.252	604.252	89.869	<0.001
Residual	608	4087.998	6.724		
Total	609	4692.25	7.705		

## DISCUSSION

Both sponges and pea crabs impact oyster function, causing reduced CI that could have subsequent consequences for growth, reproductive output, and the ability to withstand additional stressors (O'Beirn & Walker 1999, Mercado-Silva 2005, Barnes et al. 2010, Carver et al. 2010, Carroll et al. 2015a). Despite slight differences in prevalence and impacts of the oyster pests at the 2 sites, the pattern was consistent, i.e. there was a tendency for oysters to have both pests when either was present, condition declined in the presence of pests, and impacts of the sponge and pea crab on oyster condition were additive. These patterns were similar despite the broad geographic range between the sample sites and differences in tidal distribution, i.e. intertidal in NC versus subtidal in NJ.

Literature reports of boring sponge impacts on mollusks have been largely equivocal. Although some species might be negatively affected by boring sponge presence (Nollens et al. 2003, Stefaniak et al. 2005, Carroll et al. 2015a), a number of mollusks do not seem to be negatively affected by the presence of boring sponges, including various oysters (*Ostrea edulis*: Rosell et al. 1999; *Saccostrea commercialis*: Wesche et al. 1997; and *Striostrea margaritacea*: Schleyer 1991), scallops (*Chlamys islandica*: Barthel et al. 1994), abalone (*Haliotis iris*: Dunphy & Wells 2001; *H. tuberculata*: Clavier 1992), and gastropods (*Crepidula fornicata*: Le Cam & Viard 2011). Even within the eastern oyster, results have been mixed (Warburton 1958, Barnes et al. 2010, Dunn et al. 2014, Carroll et al. 2015a). In a comprehensive study using both field experiments and field surveys, Carroll et al. (2015a) demonstrated that while oyster growth was consistently reduced by the presence of sponges, the effects on condition were variable and depended on oyster size. In the present study, we demonstrated that the presence of sponges only negatively affected oyster condition in NC but not in NJ. This contributes to the indeterminate nature of the boring sponge–oyster relationship, since the effect of sponges and other fouling organisms is likely to be both size-

(Guenther et al. 2006, Carroll et al. 2015a) and location-specific (this study).

We explored the relationship between size and tissue weight and tissue condition for the oysters in our study as well. Interestingly, oysters in NC and NJ also showed different relationships. For NC oysters, we found a significant difference in the allometric relationships between oysters with and without sponges. There was also a significant negative relationship between size and condition for oysters with pea crabs and oysters with sponges, similar to Carroll et al. (2015a), and between size and condition for oysters with neither pest, although the slope was the smallest. In NJ, there were no differences in allometric relationships for oysters with or without sponges, and interestingly, there were significant negative relationships between size and CI for both spongy oysters and those with no pests, although in this case, the slope for oysters with no pests was more negative. Combined with the other results on condition, these findings further support our conclusion that the boring sponge–oyster relationship is site- or location-specific, and within particular locations, it is size-specific.

While the effects of clionaid sponges across the 2 sample locations were variable, pea crabs consistently negatively affected oyster condition. In fact, at both sites, the presence of pea crabs alone led to 21 % reduction in oyster condition, consistent with other studies of pea crabs and oysters (Mercado-Silva 2005, Byers et al. 2014, Hanke et al. 2015). While pea crabs take up space within the mantle cavity, our results suggest that this alone cannot explain the observed reduced condition. Rather, pea crabs reside in the oyster's mantle cavity for much of their life and cause significant damage to the gill tissue, palps, and gonads of their hosts (Stauber 1945, Sandoz & Hopkins 1947, O'Beirn & Walker 1999, Hanke et al. 2015), which likely contributes to reduced condition. This has been observed in other pea crab–bivalve relationships. The pea crab *Pinnotheres maculatus* causes a lower tissue condition, reproductive output, and growth in bay scallops *Argopecten irradians* (Kruczynski 1972, Bologna & Heck 2000) and blue mussels *Mytilus edulis* (Bierbaum & Shumway 1988). In New Zealand, a different species of pea crab, *P. novaezelandiae*, has been decreasing yield in the culturing of green-lipped mussels *Perna canaliculus* (Trottier et al. 2012). Thus, pea crabs, regardless of species, consistently have a negative impact on bivalves.

Interestingly, there were twice as many oysters with boring sponges in samples from NJ as there

were in samples from NC, as well as 2.5 times higher pea crab prevalence. The variability between sites regarding the pervasiveness of and effects by sponges and pea crabs is probably due to different tidal locations of reefs. Oysters were collected from subtidal reefs in NJ, and were thus submerged 100 % of the time, whereas oysters at our NC study site are exposed for ~3 h during every tidal cycle. The continued submergence likely led to increased sponge prevalence due to prolonged exposure potential to spreading (Stefaniak et al. 2005) and propagules (Stubler et al. 2017), and decreased stress on the sponge compared to intertidal locations (Volety et al. 2009). However, continual submergence may also help the oyster buffer against the effects of the sponge—subtidal oysters tend to be healthier than intertidal oysters, likely due to prolonged feeding ability (Diederich et al. 2015). Pea crabs are also more prevalent in subtidal oysters compared to intertidal oysters (O'Beirn & Walker 1999), likely also driven by flux of propagules and exposure time (Butman 1987, Byers et al. 2014). Thus, exposure to sponges and pea crab propagules could be driving intertidal–subtidal differences in prevalence to some extent. The magnitude of the differences in pea crab prevalence between spongy and non-spongy oysters was double in NC (~3 times) compared to NJ (~1.5 times), suggesting that the submersion period might play a role in this relationship. Regardless of the differences in prevalence between sites, the similarity in pest co-occurrence within each site is suggestive of some broader relationship between these 2 oyster pests.

When both sponges and pea crabs were present in the same oyster, the lowest condition values were observed. This supported our initial expectation, although statistical analysis revealed that the combined effects of each biotic stressor were additive and not synergistic. Studies have demonstrated that the effects of co-infections by multiple species on an individual host are driven by whether the pest species stimulate or suppress the host response (Malek & Byers 2017). Thus, while there appears to be some relationship between the sponge and pea crab, at least in terms of increased prevalence, the 2 pests are not having an interactive impact on oyster condition. Although there was no synergistic interaction between the 2 oyster pests in this study, having reduced condition can affect an individual oyster's ability to withstand other environmental stressors (Rainer & Mann 1992). Pests and parasites may also interact with environmental conditions to drive host responses (Malek & Byers 2017). In our study, it appears as



though oysters in NC, which are intertidal, exhibit different responses to sponges than those in NJ that are subtidally distributed. Therefore, additional stressors, either environmental factors like exposure or temperature or biotic factors like parasites and predators, are likely to exacerbate the reduced condition of infested oysters.

It is possible that the presence of one of these oyster pests makes individual oysters more attractive or susceptible to other pests. For example, settlement cues are pervasive in the environment and are used by a number of marine benthic species (Pawlik 1992). The cues pea crabs or sponges use to settle are unclear, but it is possible that an oyster already bored by the sponge or inhabited by a pea crab will give off different cues than one that is not already stressed (e.g. alarm cues; Hay 2009), or that the sponge or crab itself is producing some cue that attracts the other pest species. If not cue-mediated, a stressed oyster might gape wider and/or longer to maximize energy acquisition (Lombardi et al. 2013). By increasing the size of the gape and amount of time spent agape, exposure to pea crab recruitment is likely to increase. Both of these potential explanations are unfortunately beyond the scope of this study; however, they warrant further investigation.

Finally, the literature suggests that pea crabs tend to prefer oyster spat and otherwise small oysters, and the percent prevalence of pea crabs declines with increasing size and age of oysters (Christensen & McDermott 1958, Byers et al. 2014). Further, Christensen & McDermott (1958) suggested that large oysters might have the ability to shed pea crabs. This presumably comes at some energy cost; however, if a large oyster is dealing with another stressor, such as a boring sponge, it might have less energy available to reject a pea crab. While our results did not indicate that sponge-infested oysters had lower energy, it is likely that they have some finite amount of energy and invest it in shell maintenance (Carroll et al. 2015a), rather than in rejecting pea crabs. We unfortunately did not explore oyster spat specifically, and in our study, oysters with both pests tended to be largest, so it is possible that sponges reduce pea crab rejection. Yet, it is likely that some combination of mechanisms—tidal location and inundation, settlement cues, gape width and period, and available energy to deal with stressors, among others—are contributing to the patterns observed in our study.

In conclusion, we found that subtidal oysters in NJ were minimally affected by boring sponge presence, in contrast to intertidal oysters in NC, where oysters experienced significantly reduced condition. Pea

crabs, however, had a significant negative effect on both oyster populations, and the presence of both pests together was additive. This research adds to the growing evidence of biotic interactions between species potentially affecting rates of parasitism. Further research should be conducted to determine the mechanism driving the observed patterns, as well as investigations into how exposure to sponges and/or pea crabs affects the interaction between oysters and other pests and parasites, including polydorid polychaete worms, dermo, and *Haplosporidium nelsoni*, among others. Additionally, more research should be conducted on other species afflicted by these pests and parasites.

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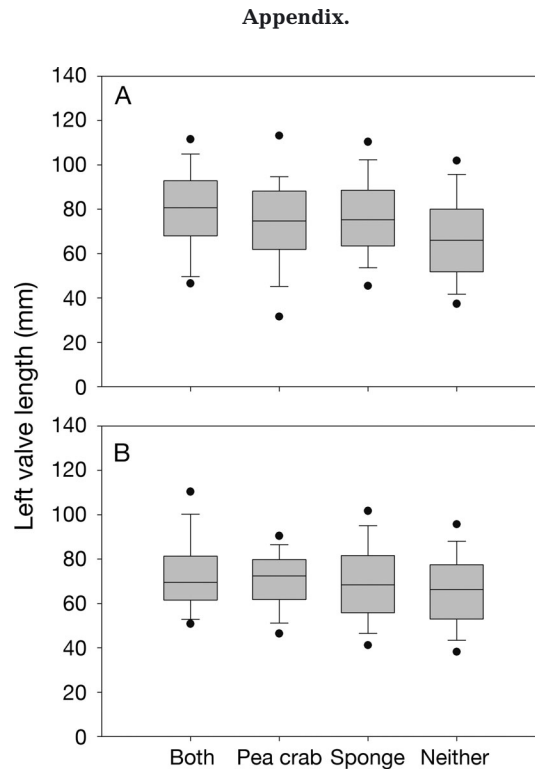


Fig. A1. Left valve length of oysters harvested in (A) North Carolina and (B) New Jersey, among the pest-parasite categories. Both: both sponges and pea crabs present; pea crab: pea crab only; sponge: sponge only; neither: neither sponge nor pea crab present. Box: 25th to 75th percentiles; line within box: median; whiskers: 10th and 90th percentiles; points: 5th and 95th percentiles

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