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HIGHLIGHTED STUDENT RESEARCH

Non-native parasite enhances susceptibility of host to native predators

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Abstract Parasites often alter host physiology and behavior, which can enhance predation risk for infected hosts. Higher consumption of parasitized prey can in turn lead to a less parasitized prey population (the healthy herd hypothesis). *Loxothylacus panopaei* is a non-native castrating barnacle parasite on the mud crab *Eurypanopeus depressus* along the Atlantic coast. Through prey choice mesocosm experiments and a field tethering experiment, we investigated whether the predatory crab *Callinectes sapidus* and other predators preferentially feed on *E. depressus* infected with *L. panopaei*. We found that *C. sapidus* preferentially consumed infected *E. depressus* 3 to 1 over visibly uninfected *E. depressus* in the mesocosm experiments. Similarly, infected *E. depressus* were consumed 1.2 to 1 over uninfected conspecifics in field tethering trials. We evaluated a mechanism behind this skewed prey choice, specifically whether *L. panopaei* affects *E. depressus* movement, making infected prey more vulnerable to predator attack. Counter to our expectations, infected *E. depressus* ran faster during laboratory trials than uninfected *E. depressus*, suggesting that quick movement may not decrease predation risk and seems instead to make the prey more vulnerable. Ultimately, the preferential consumption of *L. panopaei*-infected prey by *C. sapidus* highlights how interactions between organisms could affect where novel parasites are able to thrive.

Keywords Disease ecology · Host–parasite interactions · Predator–prey · Introduced species · Marine invertebrate · Rhizocephalan · Parasitism

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We found preferential consumption of native hosts infected by invasive parasites, highlighting how interactions between organisms can affect where novel parasites are able to establish and survive.

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Introduction

With the increase in the movement of species around the globe, through vectors such as shipping and aquaculture, new species interactions are forming, including infections by novel parasites and diseases (Mack et al. 2000; Levine and D'Antonio 2003). Invasive parasites, and more broadly emerging infectious diseases, can have devastating effects on new hosts, depressing host populations to low levels (Garner et al. 2006; Dunn and Hatcher 2015). This is likely due to the limited defenses of native populations against novel parasites, leaving the population largely vulnerable (Hatcher et al. 2012). However, native predators can help to limit the influence of invasive parasites on prey populations if they target parasitized prey.

Selective consumption of infected prey by predators can occur if infected hosts exhibit physiological or behavioral changes that increase their vulnerability (Peacock et al. 2014). For example, nematode-infected red grouse release more scent, leading to higher predation rates on infected individuals (Hudson et al. 1992). Theory suggests that predators should be able to limit disease transmission within populations (Hethcote et al. 2004; Wild et al. 2011; Chakraborty et al. 2015). For example, the 'healthy herd' hypothesis suggests that predators dampen disease transmission, particularly when predators selectively feed on

infected prey (Packer et al. 2003). However, preferential feeding on infected hosts does not always lead to decreased infection prevalence (Duffy 2007). For example, if predator avoidance behavior enhances host susceptibility, there can be increased prevalence even with strong preferential feeding on infected individuals (Duffy et al. 2011; Welch and Harwood 2011). Additionally, if the act of predation increases disease transmission by releasing infective stages into the environment (e.g., "predator spreader" hypothesis), then preferential predation on infected individuals can increase infection prevalence (Cáceres et al. 2009). While preferential feeding on infected hosts has been documented for a range of systems (Duffy et al. 2005, 2007; Cáceres et al. 2009; Krkosek et al. 2011), preferential feeding on native hosts infected by an invasive parasite has not been documented (Dunn et al. 2012).

Invasive parasites are primed to enhance the vulnerability of their hosts to native predators. The naïve host theory suggests that novel infections can lead to the parasite overexploiting their new hosts (Cruz et al. 1985; Fassbinder-Orth et al. 2013; Lymbery et al. 2014), which can leave both host and parasite vulnerable to predators. In fact, for the invasive parasites with available comparative measures of pathogenic effects, 85% showed increased pathogenicity in naïve hosts (Lymbery et al. 2014). Pathogenicity can lead to disease behavior (e.g., lethargy) and increased vulnerability to predators. Even when the parasite has a shared coevolutionary history with the host, parasite range expansion into previously uninfected areas of the host range can lead to overexploitation of the naïve host population (Cudmore et al. 2010).

The United States Atlantic coast populations of the mud crab *Eurypanopeus depressus* are invaded by a castrating Rhizocephalan barnacle parasite, *Loxothylacus panopaei* (Reinhard and Reischman 1958; Kruse et al. 2011). Rhizocephalans often induce behavioral changes in their hosts, inducing movement of the host to risky positions to increase the spread of the parasite offspring (Hoeg 1995), and *L. panopaei* is known to decrease *E. depressus* feeding rates (O'Shaughnessy et al. 2014; Toscano et al. 2014). These behavioral alterations can also enhance predation risk in their hosts. *L. panopaei* is a native parasite of *E. depressus* in the Gulf of Mexico and was introduced to the Chesapeake Bay in the 1960s in association with oyster aquaculture (Van Engel et al. 1966). The parasite has since expanded its range north to Long Island, New York, and south to Cape Canaveral, Florida, and was first reported in Georgia in 2004/2005 (Kruse et al. 2007, 2011; Freeman et al. 2013; Eash-Loucks et al. 2014). *E. depressus* population density decreased following *L. panopaei* invasion in some regions (Andrews 1980; Eash-Loucks et al. 2014), and infection prevalence in the invaded range is markedly higher than that found in the native range (Hines et al. 1997; Kruse and Hare 2007). *E. depressus* utilizes oyster reefs as a refuge from predators (Meyer 1994; Hulathduwa et al. 2011), which include several fish and crab species (e.g., the blue crab *Callinectes sapidus*). In this study, we evaluate whether (A) the blue crab *C. sapidus* preferentially feeds on *E. depressus* infected with *L. panopaei*; (B) *E. depressus* infected with *L. panopaei* are more vulnerable to predation in the field; and (C) *L. panopaei* impedes *E. depressus* movement, possibly increasing the vulnerability of both host and parasite to predators.

Materials and methods

Collection techniques

For all experiments, we collected *E. depressus* and *C. sapidus* from Wassaw Sound, near Priests Landing, Savannah, GA (31°57′46.6″N, 81°00′47.9″W). We collected *C. sapidus* using small fish traps baited with frozen chicken. To collect *E. depressus* we collected oyster clumps at low tide and brought them back to the laboratory, where we removed mud and broke oyster clumps apart in a mesh basket to find *E. depressus*. We collected uninfected and infected *E. depressus* immediately prior to each experiment: 27–29 June 2012 and 16–19 July 2012 for experiment (A), 21 July and 6 August 2014 for experiment (B), and 7 February 2013 for experiment (C).

We considered a host 'infected' if it was bearing a mature externa (the external reproductive organ of the parasite), and considered it "uninfected' if it was non-externa bearing. There is an initial internal phase of infection, so some crabs labeled uninfected were likely internally infected with an incipient infection, making any difference found between uninfected and infected individuals in our study a likely conservative estimation of the parasite's effect. Throughout the manuscript we refer to a visibly uninfected *E. depressus* as an 'uninfected host' and an *E. depressus* visibly infected with *L. panopaei* as an 'infected host'. For all experiments, attempts were made to keep host size similar; however, the size differences between uninfected and infected hosts reflect those naturally observed in the field (Table 1; Gehman et al. 2016). Prior to each experiment, we kept infected and uninfected hosts in separate flow-through seawater tables to prevent parasite transmission.

Do predatory crabs preferentially consume infected hosts over uninfected hosts (mesocosm study)?

To quantify the consumption of infected and uninfected *E. depressus* by predatory *C. sapidus*, we placed five

Table 1 Mean (SD) size of the uninfected *E. depressus* and *E. depressus* infected by *L. panopaei* that we offered to *C. sapidus* for consumption in the mesocosm experiment (A) and were tethered in the field (B) to test for the effect of parasite infection status on infected and uninfected host vulnerability to predators

	Infected host (mm)	Uninfected host (mm)
Mesocosm	9.78 (1.35)	7.78 (1.13)
Field	9.96 (1.04)	9.52 (1.08)

uninfected and five infected *E. depressus* hosts in a 19-L tank and exposed them to *C. sapidus*. For habitat, each tank contained a single layer of sun-bleached local oyster shell and its own separate delivery of flowing seawater which was kept at ~19 L/half hour throughout the trial. We allowed *E. depressus* to settle for half an hour and then placed a single *C. sapidus* predator (80–90 mm carapace width) in each tank. Light–dark cycles were set to 15 h of dark and 9 h of light. We ran each trial for 7 days and monitored them twice a day, once just prior to turning off the lights and once immediately after the lights turned on. For staging purposes, we conducted the full experiment twice, over two consecutive time blocks with ten replicate tanks in each block ($n = 20$ *C. sapidus* for the whole experiment).

At each monitoring point, we removed the predatory crabs from the tanks and placed them in a separate tank with seawater. We carefully examined the contents of each tank, removing each oyster shell one at a time to examine them for the presence of uninfected and infected hosts. We recorded the number of infected and uninfected hosts that were alive, dead, and missing, and removed the dead. We identified infected crabs by their externa, and although there is almost no chance that an infected crab could lose its externa during the experiment, if an externa was removed it would leave scarring and morphological alterations that we would have detected. We considered crabs consumed if they were missing. We considered crabs dead if they did not move in response to direct stimulus (only two crabs were recorded in this category over the course of the experiment). To keep the availability of uninfected and infected prey even across time, we brought the total number of available prey back to five uninfected and five infected hosts at each monitoring point (twice a day). After tabulating, we allowed the infected and uninfected hosts to acclimate for half an hour before returning the same predator to each tank. We quantified the cumulative number of infected and uninfected hosts consumed by each predator over the course of the full 7-day experiment.

We performed individual χ^2 tests on each replicate predator to compare the preference of each *C. sapidus* crab for uninfected or infected hosts. To determine whether predator preference was homogenous among replicates, we conducted an I^2 analysis, a more reliable modification of the χ^2 heterogeneity statistic (Higgins and Thompson 2002). The I^2 analysis describes the proportion of the variance in predator preference estimate that is driven by heterogeneity between individuals, allowing us to evaluate whether preference was consistent across individual predators (Higgins and Thompson 2002). The I^2 was relatively low across individuals in each time block and similar between each time block (time block one, $I^2 = 44$; time block two, $I^2 = 47$). Therefore, the two time blocks were combined together for an analysis to test the null hypothesis of no preference by predatory crabs for the infected or uninfected hosts. We used R 3.1.3 for this and all subsequent statistical analysis (R Development Core Team 2015).

Do predators preferentially consume infected hosts over uninfected hosts (field study)?

To evaluate whether infected hosts were preferentially consumed over uninfected hosts by a full suite of ambient predators in the field, we tethered uninfected and infected hosts to a 30.5-cm-long PVC pole with a 25.4-cm monofilament line. The tether line was then glued to the back of uninfected and infected hosts' carapace with Loclite® super glue (Fig. 1). Glue was allowed to dry for ~5 min. To assure that all host crabs were satisfactorily attached to their tethers, host crabs were kept for 24 h in the flow-through system prior to placement in the field.

During low tide, we secured the PVC poles at 0.5 m intervals within a mid-intertidal oyster reef at Priests Landing, near the collection site of the crabs. To account for the effect of location, we alternated uninfected and infected crabs systematically along the reef. We placed ~20 infected and 20 uninfected crabs in the field for each of five trials ($n = 93$ uninfected and $n = 95$ infected hosts), blocked by date. Each trial lasted ~12 h, starting on a late afternoon low tide and ending at the following low tide. Although tethering limited host movement, crabs were still able to move into the oyster reef to hide from predators (Fig. 1a and b). At collection we noted mortality, which was quantified by the loss of crabs, as well as recovery of crab remnants (Fig. 1d). We conducted trials on two adjacent reefs. The direction of the response was the same on each reef and our formal test of blocking by reef found no effect, so we pooled the results from the two reefs together for all statistical analysis. Because infected and uninfected crabs were of different sizes, we explicitly included size to test the effect of size on predation risk (Table 1). We fit a generalized linear mixed effects model with a binomial response (dead or alive), date of tethering trial as the random effect, and size and infection status and their interaction as fixed effects.

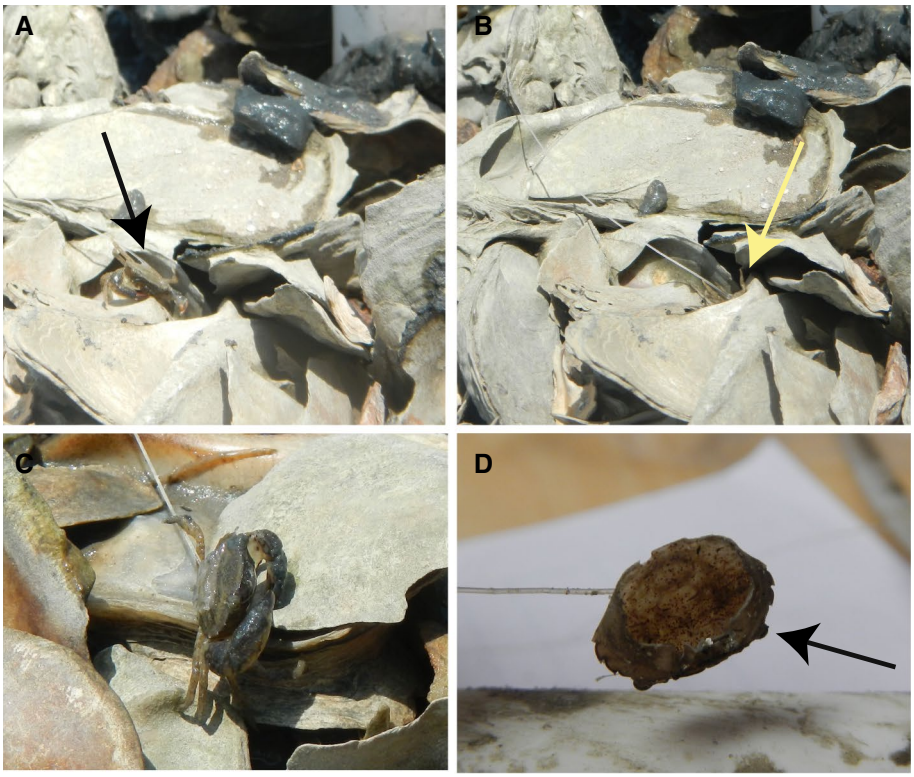

Fig. 1 *Eurypanopeus depressus* tethered in an oyster reef at Priest Landing, Savannah, GA, for a field predation trial. **a** An *E. depressus* on its tether moving across the oyster reef (*arrow*) **b** toward a crevice within an oyster clump to hide inside (*arrow*), demonstrating that *E. depressus* on the tethers were able to hide from predators. **c** A live *E. depressus* shortly after being placed in the field. **d** The empty carapace of a partially consumed *E. depressus* still on tether. The eyestalks (*arrow*) remain with the carapace, indicating that the crab did not molt

Do infected hosts move slower than uninfected hosts?

To test whether infected hosts were slower than uninfected hosts, as a possible factor contributing to differential consumption, we conducted movement experiments in the laboratory. We quantified the time for a crab to move down an exposed runway to the end. To induce linear movement by each crab we created a standardized exposed runway, composed of a PVC tube cut in half lengthwise (diameter = 7.6 cm), which was submerged into artificial seawater in a container. To examine whether exposure distance altered movement, we ran two separate movement experiments, differing only in the length of the runway available. Thus, for the first trial, the runway was 220 mm from the center point to either end and for the second trial the runway was 94 mm. For all experimental runs, we hand-placed a single individual in the middle of the runway and recorded its movements and the time it took to reach the end of the runway with a camera suspended above the tank. Placing the crabs by hand on the runway served as an acute predator simulation. We ran 20 uninfected and 16 infected hosts along the long runway, and 19 uninfected hosts and 10 infected hosts individually along the short runway. To minimize the risk of exposing uninfected hosts to parasite larvae, for each trial we first ran uninfected hosts and then ran infected hosts. We analyzed each runway length experiment separately using an ANOVA, testing the effect of infection status on speed (mm/s) for each experiment.

Results

Do predatory crabs preferentially consume infected hosts over uninfected hosts (mesocosm study)?

Predatory crabs consumed three times as many infected hosts on average than uninfected hosts (Fig. 2, $\chi^2 = 33.3$, $p \ll 0.001$, $I^2 = 47.2$). Every one of the *C. sapidus*

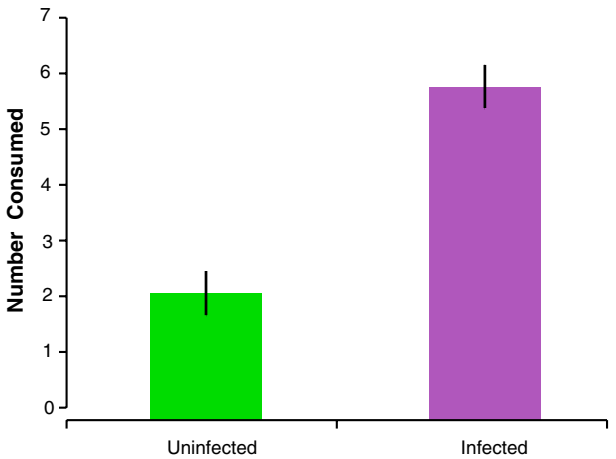

Fig. 2 The average number of uninfected and infected *E. depressus* consumed by each predatory *C. sapidus* ($n = 20$) over a weeklong mesocosm trial. The *error bars* depict 1 SE. The diet of each *C. sapidus* averaged 75% (±1.7 SD) *E. depressus* infected with *L. panopaei*

individuals consumed more infected *E. depressus* than uninfected, with the diet of each *C. sapidus* averaging 75% *E. depressus* infected with *L. panopaei* (±1.7 SD). Overall, 120 infected hosts were consumed through the course of this experiment, whereas only 36 uninfected crabs were consumed.

Do predators preferentially consume the infected hosts over the uninfected host (field study)?

The odds of mortality for an infected host was significantly higher over a single high tide cycle than for uninfected hosts (Fig. 3, $\beta = 0.85$, odds ratio $= 2.34$, $p = 0.02$). The interaction between host size and infection status was non-significant ($\beta = 0.01$, $p = 0.97$) and so it was removed from the analysis. Across both treatments, smaller host crabs were less likely to survive a single high tide cycle, and the odds of mortality decreased 58% for every 1.1 mm increase in carapace width (Fig. 3, $\beta = -0.55$, odds ratio $= 0.58$, $p = 0.002$). Overall, 72 infected hosts and 60 uninfected hosts were consumed during the tethering trials.

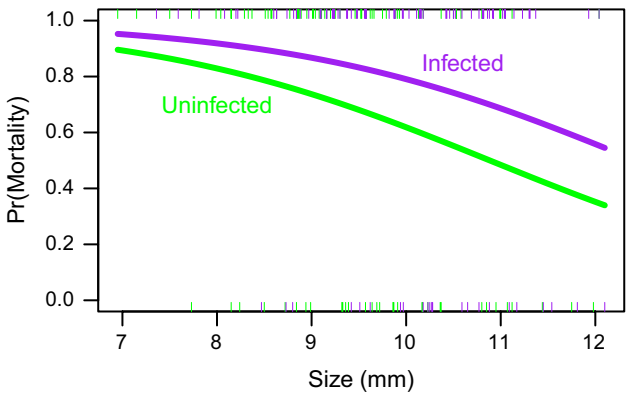

Fig. 3 The probability of mortality over a single high tide cycle for uninfected *E. depressus* and *E. depressus* infected with *L. panopaei,* when tethered on an oyster reef. *Probability curves* represent the results from a logistic regression on survival as a function of crab size, and *rug marks* along the *x*-axis indicate the spread of data across size

Do infected hosts move slower than uninfected hosts?

Regardless of the runway length, infected hosts moved approximately twice as fast to the end of the PVC tube than uninfected hosts in both experiments (long runway, $F = 8.5$, $df = 1$, MS $= 1323$, $p = 0.006$, short runway, $F = 14.9$, $df = 1$, MS $= 2565$, $p = 0.001$, Fig. 4).

Discussion

Parasitic infection by *L. panopaei* enhanced predator consumption of *E. depressus* by up to 3-fold in mesocosms (Fig. 2) and 1.2-fold in the field (Fig. 3). Counter to our hypothesis, the enhanced consumption of infected hosts was not due to slower movement. We had surmised that either increased drag from the externa on the infected crab's abdomen or infection-induced lethargy would slow the infected host. Rather, our experiment designed to isolate this behavioral mechanism showed that infected crabs moved twice as fast (Fig. 4), yet were still more vulnerable to predators. Thus, heightened vulnerability to consumption of infected hosts occurs in spite of, or because of, faster movement. Indeed, it is possible that quick movement could increase the visibility of prey (Hemmi and Pfeil 2010), or stimulate other sensory cues (e.g., mechanosensory; Schwalbe et al. 2012) of the prey to their predators.

The high consumptive pressure on infected hosts suggests the healthy herd mechanism could be acting within this system. Evaluated at a mechanistic level, infected crabs are being differentially removed from the environment by predators over their uninfected counterparts (Fig. 2). However, across estuaries there is a positive relationship between predator abundance and infection prevalence based on extensive field surveys (Gehman et al. 2016), which superficially might lead to the opposite conclusion (i.e., that predators preferentially consume uninfected hosts). Given the preferential consumption of infected individuals that we document, this positive association at a large scale must be driven by other mechanisms. *Loxothylacus panopaei* needs a living host to brood viable parasite

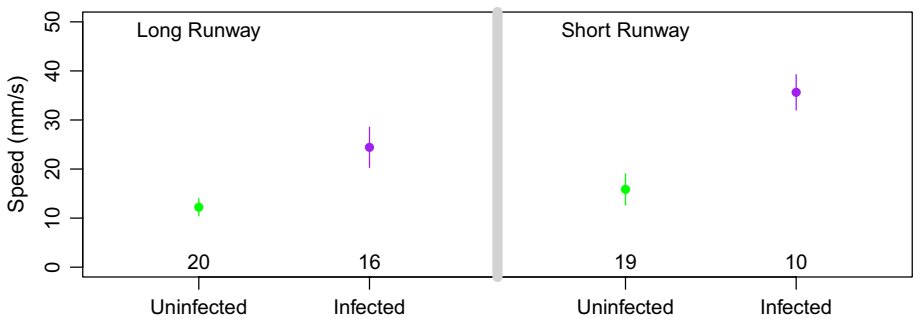

Fig. 4 Speed of uninfected *E. depressus* and infected *E. depressus* running 220 mm (long runway) and 94 mm (short runway) along a PVC tube. *Error bars* are standard errors and the number of replicates in each study is listed along the *x*-axis

propagules (Hoeg 1995), so the predator spreader hypothesis is unlikely to be driving the pattern. Instead, the predator and prey, which both have pelagic larval stages, could be positively associated with a third environmental variable (e.g., ocean currents). Alternatively, the positive association between the predatory crab and its prey at a regional scale could indicate that *C. sapidus* move to areas within the estuary with higher infection prevalence to take advantage of easy prey items (Sih 1982; Wieters et al. 2008).

The removal of visibly infected individuals may do more than just remove infectious individuals. Infected, and therefore castrated, hosts likely compete with uninfected hosts for refuge (Hulathduwa et al. 2011), and although infected host feeding rates are lower than their uninfected counterparts (O'Shaughnessy et al. 2014; Toscano et al. 2014), they still likely compete for food resources. Thus, removal of infected individuals may reduce the parasite pressure on the remaining uninfected hosts and reallocate the remaining refuge and food resources to uninfected hosts. Alternatively, on a long-term scale, consumption of easy to consume infected crabs could lead to increased predator populations, suppressing the equilibrium values for the remaining host population (Noonburg and Byers 2005).

Prey size is an important factor for prey survival, with many prey reaching a refuge from predators at larger sizes (e.g., McLennan et al. 2004). In our study, host carapace width significantly increased host survival and had a similar positive effect on infected and uninfected hosts (Fig. 3). However, for any given carapace width, infected crabs had higher mortality than uninfected crabs (Fig. 3), a trend that holds across all carapace widths as signified by the non-significant interaction of infection status and carapace width. In some prey species, larger size confers a size refuge from predation (Paine 1976). This is likely to play a lesser role here since many of its predators are an order of magnitude bigger than even the largest *E. depressus*. However, size determines dominance in many crab species (Somers and Nel 1998; Shervette and Perry 2004) and refuge dominance is important for crab survival (Beck 1995; Shervette and Perry 2004; Hulathduwa et al. 2011). Therefore, increased survival with size suggests that larger *E. depressus,* regardless of infection status, are able to dominate refuge use over their smaller counterparts.

The predator used in our mesocosm trials, the blue crab *C. sapidus,* is a prodigious predator, and this is not the first time it has been implicated in biological resistance to invasion. *C. sapidus* preferentially consumes *Carcinus maenus*, the invasive European green crab, and high predation rates have likely inhibited the southern spread of *C. maenus* (deRivera et al. 2005). The preferential feeding on infected *E. depressus* by *C. sapidus* we found in this study suggests that this predator has the potential to provide a biotic defense against this invasive parasite. Specifically, the preferential feeding on *L. panopaei*-infected *E. depressus* by *C. sapidus* suggests that the predators could be able to help limit the spread of this invasive parasite. *L. panopaei* infection prevalence varies substantially along the Atlantic coastline (Hines et al. 1997; Kruse et al. 2007, 2011; Freeman et al. 2013), and variation in predation pressure between sites could affect infection prevalence. In this era of increased biological invasions that in turn increase novel species interactions (Mack et al. 2000; Levine and D'Antonio 2003), there is a great need to identify how novel species will interact with the community they are invading. The results from this project help to highlight the importance of understanding how interactions between organisms, such as predation, can influence the prevalence and abundance of novel parasites.

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Author contribution statement AMG and JEB conceived and designed the experiments and wrote the manuscript; AMG conducted the experiments and analyzed the data.

Compliance with ethical standards

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

Conflict of interest The authors declare that they have no conflict of interest.

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