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Use of the introduced bivalve, *Musculista senhousia*, by generalist parasites of native New Zealand bivalves

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Abstract Introduced species are often thought to do well because of an escape from natural enemies. However, once established, they can acquire a modest assemblage of enemies, including parasites, in their new range. Here we quantified prevalence and effects of infection with copepods (family Mycicolidae) and pea crabs (*Pinnotheres novaezelandiae*), in three mussel species, the non-native *Musculista senhousia*, and two native mussels, *Perna canaliculus* and *Xenostrobus pulex*, at Bucklands Beach, Auckland, New Zealand. Copepod prevalence was highest in *X. pulex* (17.9%), whereas pea crab prevalence was highest in *P. canaliculus* (33.6%). Both parasites infected *M. senhousia*, but at a much lower prevalence. Dry tissue weight was significantly lower in *P. canaliculus* infected with pea crabs. In addition, we experimentally investigated host

species selection by pea crabs. In an experimental apparatus, pea crabs showed a significant attraction to *P. canaliculus*, but not so for *X. pulex* or *M. senhousia*. When the mussels were presented in combination, pea crabs showed a weak attraction for *X. pulex*. Pea crab attraction to *M. senhousia* was not significant. It appears that the introduced *M. senhousia* largely escapes the detrimental effects of infection with either parasite species compared with native mussels occurring in sympatry.

Keywords non-native species; *Perna canaliculus*; *Xenostrobus pulex*; mussels; copepod; pea crab

1 INTRODUCTION

The impacts of marine biological invasions are now recognised as a global threat to native ecosystems and human economies (Cohen & Carlton 1998). The success of many introduced species is often explained by the Enemy Release Hypothesis (ERH), which states that non-native species escape their natural enemies, including parasites, upon introduction to a novel environment (Torchin et al. 2001, 2002; Keane & Crawley 2002). A different scenario is that non-native species are “empty habitats” when they arrive in a new area, awaiting colonisation by local parasites (Poulin & Mouillot 2003). Non-native species often acquire a new parasite assemblage from native organisms in the new environment over short periods of time (Bauer 1991; Barton 1997; Poulin & Mouillot 2003; Torchin & Mitchell 2004). The longer the non-native species is present, the more likely it is to accumulate enemies (Torchin & Mitchell 2004).

Because many parasites are specialists, often requiring multiple and sometimes specific intermediate hosts to complete their complex life cycles (Bauer 1991; Ruppert & Barnes 1994; Poulin & Mouillot 2003), specialist parasites present in native species are unlikely to switch host and establish in a non-native species (Torchin et al. 2002; Poulin & Mouillot 2003). In contrast, a native generalist

parasite that can make use of any one of several host species is more likely to adopt an introduced species as an alternative host (Bauer 1991; Barton 1997; Poulin & Mouillot 2003), which can result in an introduced species accumulating a modest assemblage of parasites in their new environment (Poulin & Mouillot 2003).

We investigated the use of an introduced host species by native parasites in the New Zealand intertidal zone. *Musculista senhousia* (Benson in Cantor, 1842), is a mytilid bivalve that has been established in New Zealand for approximately 30 years (Willan 1985; Taylor 1997). It was initially discovered in the Auckland region (Willan 1985; Creese et al. 1997), where it lives in sandy intertidal and shallow sub-tidal habitats (Creese et al. 1997). *Musculista senhousia* has established non-native populations in Australia, the western United States, and the Mediterranean Sea (Mastrototaro et al. 2003; Mistri 2003a, 2004a,b,c,d; Mistri et al. 2004). This bivalve is native to northeast Asia (Willan 1985; Inoue & Yamamuro 2000). A native New Zealand pea crab, *Pinnotheres novaezelandiae* (Filhol, 1886) and a copepod belonging to the family Myicolidae, have been found in *M. senhousia* (Miller 2007). Other bivalves have also been reported as hosts of *P. novaezelandiae*, including the natives *Austrovenus stutchburyi* (Wood, 1828), *Perna canaliculus* (Gmelin, 1791), *Mytilus galloprovincialis* (Lamarck, 1819), and the introduced *Crassostrea gigas* (Lamarck 1818) (McLay 1988; Stevens 1990a).

The objectives of this study were three-fold: (1) to quantify rates of infection by pea crabs and copepods as a function of shore height in *M. senhousia* and native mussels from a single locality—Bucklands Beach, Tamaki Estuary, Auckland, New Zealand; (2) to measure the impacts of pea crabs and copepods on their hosts by comparing bivalve dry tissue weight relative to shell size, and differences in shell dimensions between infected and uninfected individuals, in all three species; and (3) to determine whether native pea crabs show avoidance of, or attraction to, non-native versus native mussels.

MATERIALS AND METHODS

Collection of mussels took place on 19 and 20 August 2005, from an intertidal area between Bucklands Beach and Musick Point, Tamaki Estuary, Auckland, New Zealand (36°51'17.38''S 174°53'56.00''E). Four 100-m long transects were placed perpendicular to the water's edge. The position of the first transect

was determined by the presence of *M. senhousia*. Each successive transect was placed 100 m north of the previous one. Each transect was divided into four blocks, 10 m wide \square 25 m long, thus the upper-most block equated to the top 25 m of the shore (0–25 m), and the lowest block (75–100 m) was closest to the water's edge at low tide. This design provided four blocks per transect, a total of 16 blocks within the sampled area. Each of the three mussel species, *M. senhousia*, *P. canaliculus* and *Xenostrobus pulex* (Lamarck, 1819) present within each block was collected. A maximum of 100 individuals each of *M. senhousia*, *P. canaliculus*, and *X. pulex* were collected haphazardly within each block, and labelled correspondingly.

The mussels were taken to the laboratory where they were kept alive for up to 4 days, each species in a labelled plastic bag corresponding to transect and block of collection, in oxygenated sea water, until dissected; hence it was possible for pea crabs or copepods to switch between individuals of a species collected within a single block. Before dissection, each individual was weighed to the nearest 0.01 g, and length, width and depth of the shell were measured to the nearest 0.1 mm using vernier callipers. Dissections were carried out using a binocular microscope, with magnification ranging from 6.3 to 40 \times . Pea crabs and myicolid copepods associated with mussels were recorded. Pea crab carapace width (CW) was measured to the nearest 0.1 mm using vernier callipers. After being examined for parasites, the soft tissues of each individual mussel were placed in drying ovens at 65°C until constant dry weight was reached. Dry tissue weight (0.0001 g) was recorded for each mussel.

Regression analyses were carried out to investigate relationships between wet weight and shell length of mussel species, and between pea crab CW and host shell length (Steel & Torrie 1981). Chi-square tests were used to examine differences in parasite prevalence between native and non-native mussels (Steel & Torrie 1981). ANCOVAs (Statistica 7) were used to correct for shell length and test for any difference in dry weight or shell dimensions between individuals with and without either pea crab or copepod infection (Steel & Torrie 1981).

Pea crab host selection

Mytilus galloprovincialis were collected by hand from Taylors Mistake, Christchurch (43°35'4.52''S, 172°46'46.42''E) on 28 September 2006. They were transported to the laboratory where they were opened and any pea crabs present were removed. *Mytilus*

galloprovincialis was selected as the source host for pea crabs as it was not used in the following experiment. Previous research on pea crab host selection indicates that pea crabs show a preference for their original host species (Derby & Atema 1980; Stevens 1990b). Only male pea crabs were used, as previous research found only male pea crabs occurring in *M. senhousia* (Miller 2007). Also, female pea crabs do not leave their original host, usually growing too large to leave, thus their ability to move outside of a host is unknown (Soong 1997). A total of 27 male pea crabs were obtained from *M. galloprovincialis*. These were kept in the dark in small containers of well-aerated sea water, which was replaced daily. Pea crabs were not fed to avoid any inadvertent conditioning to a certain mussel species. *Perna canaliculus* and *X. pulex* were collected from Taylors Mistake, Christchurch, whereas *M. senhousia* was collected from Kaipara (36°29'37.43''S, 174°21'40.37''E) as it is not established in the South Island. Each bivalve species was held in separate containers of well-aerated sea water.

The choice chamber (dimensions: 6 cm high □ 37 cm □ 25 cm) was divided into four compartments by walls placed around a central chamber, all filled with well-aerated sea water. A small hole at the bottom edge of each side of the central chamber allowed water exchange between the central chamber and all compartments, and allowed the pea crabs to move from the central chamber into any compartment. Each compartment was sealed from adjacent compartments, so no mixing of water could take place directly between compartments, only with the central chamber.

Four different trials were conducted. Trial 1 used *M. senhousia* only, and 50 g of live *M. senhousia*, corresponding to approximately 50 mussels, were placed into each of two randomly chosen compartments, with the other two compartments left empty. After 1 h, 10 pea crabs were placed into the central chamber. They were given 1 h to enter a compartment. Pea crabs had three possible choices in this scenario: compartments containing *M. senhousia*, empty compartments, or remaining in the central chamber. After 1 h, all compartments were assessed and the presence of a pea crab in any particular compartment was considered a choice. Crabs moved by crawling during the experiment; therefore, the choice to remain in the central chamber was considered an active choice. This procedure was repeated five times, with the apparatus cleaned thoroughly with water between each trial, and

compartments containing 50 g of mussels chosen at random each time. Owing to the limited number of pea crabs available, they were haphazardly selected each time from the pool of available crabs.

The same procedure was repeated for *X. pulex* (trial 2), *P. canaliculus* (trial 3), and a combination of *P. canaliculus*, *X. pulex*, and *M. senhousia* (trial 4). Fifty-gram samples of each mussel species were placed separately, each in a different compartment, leaving one compartment empty. Individual mussel sizes were not measured, but were approximately 10 mm shell length for *M. senhousia* and *X. pulex*, and approximately 70 mm shell length for *P. canaliculus*. Pea crabs were allowed to choose between the four compartments. Each trial was repeated five times, resulting in a total of 50 choices for each of the four trials. Mussels were not dissected at the end of the experiment. Data were analysed using chi-square tests to examine differences in the number of times pea crabs made each possible choice within each trial. The null hypothesis was that the frequency of pea crabs in each compartment would be the same.

RESULTS

A total of 507 mussels, 173 *M. senhousia*, 116 *P. canaliculus*, and 218 *X. pulex*, were collected from Bucklands Beach. *Musculista senhousia* only occurred in two transects, and always at the lowest tidal height. *Perna canaliculus* was found most frequently in the low to mid-shore area, whereas *X. pulex* only occurred high in the intertidal (Table 1). A strong relationship between wet weight and shell length existed for all three species (*M. senhousia*, d.f. = 171, $r^2 = 0.93$, $P < 0.001$; *P. canaliculus*, d.f. = 113, $r^2 = 0.98$, $P < 0.001$; *X. pulex*, d.f. = 216, $r^2 = 0.92$, $P < 0.001$).

Highest copepod prevalence was observed in *X. pulex* (17.9%) (Table 2). Prevalence of copepods in *P. canaliculus* and *M. senhousia* was lower (0.9% and 1.7%, respectively) (Table 2). As mussel species were kept in separate tanks in the laboratory, no host species switching could have occurred before dissections. Thus overall copepod prevalence decreased down the shore at this site, although this pattern is likely related to shore position of preferred host species. Of 43 mussels harbouring copepods, only three (7%; two *X. pulex* and a single *P. canaliculus*) had multiple infections, each of two copepods per host.

There was no significant difference in dry weight between hosts with and without copepods after

Table 1 Prevalence of pea crabs and copepods found associated with *Musculista senhousia*, *Perna canaliculus*, and *Xenostrobus pulex* for each transect and block from Bucklands Beach, Tamaki Estuary, Auckland, New Zealand. A dash indicates no mussels were found in that block.

	Transect 1	Transect 2	Transect 3	Transect 4
Block 1, 0–25 m				
<i>M. senhousia</i>	–	–	–	–
<i>P. canaliculus</i>	–	–	–	–
<i>X. pulex</i>	12/100 copepods (12.0%)	–	–	3/27 copepods (11.1%)
Block 2, 25–50 m				
<i>M. senhousia</i>	–	–	–	–
<i>P. canaliculus</i>	3/15 pea crabs (20.0%)	–	3/14 pea crabs (21.4%)	–
<i>X. pulex</i>	–	–	–	13/91 copepods (14.3%)
Block 3, 50–75 m				
<i>M. senhousia</i>	–	–	–	–
<i>P. canaliculus</i>	4/14 pea crabs (28.6%)	12/27 pea crabs (44.4%)	17/47 pea crabs (36.2%)	–
<i>X. pulex</i>	–	–	–	1/47 copepod (2.0%)
Block 4, 75–100 m				
<i>M. senhousia</i>	1/100 pea crabs (1.0%) 3/100 copepods (3.0%)	1/73 pea crabs (1.4%)	–	–
<i>P. canaliculus</i>	–	–	0/2	–
<i>X. pulex</i>	–	–	–	–

Table 2 Pea crab, *Pinnotheres novaezelandiae*, and copepod, family Myicolidae, prevalence for *Musculista senhousia* ($n = 173$), *Perna canaliculus* ($n = 116$), and *Xenostrobus pulex* ($n = 218$) at Bucklands Beach, New Zealand.

	Pea crab	Copepod
<i>Musculista senhousia</i>	2/173 (1.2%)	3/173 (1.7%)
<i>Perna canaliculus</i>	39/116 (33.6%)	1/116 (0.9%)
<i>Xenostrobus pulex</i>	0/218 (0.0%)	39/218 (17.9%)

Table 3 ANCOVA results of shell parameters and dry weight (all corrected for shell length) between infected and non-infected hosts (*Musculista senhousia*, *Perna canaliculus*, and *Xenostrobus pulex*) with copepods (family Myicolidae) and pea crabs (*Pinnotheres novaezelandiae*).

Species	d.f.	SS	MS	F	P
Copepod infection					
Dry weight					
<i>Musculista senhousia</i>	1, 170	0.0001	0.0001	2.01	0.16
<i>Perna canaliculus</i>	1, 112	0.12	0.12	1.68	0.19
<i>Xenostrobus pulex</i>	1, 215	0.00003	0.00003	0.91	0.34
Shell width					
<i>M. senhousia</i>	1, 170	0.0007	0.0007	0.006	0.94
<i>P. canaliculus</i>	1, 112	1.06	1.06	0.75	0.39
<i>X. pulex</i>	1, 215	0.04	0.04	0.16	0.69
Shell depth					
<i>M. senhousia</i>	1, 170	0.003	0.003	0.03	0.87
<i>P. canaliculus</i>	1, 112	1.91	1.91	1.34	0.25
<i>X. pulex</i>	1, 215	0.05	0.05	0.25	0.62
Pea crab infection					
<i>P. canaliculus</i>					
Dry weight	1, 112	0.318	0.318	4.57	0.03
Shell depth	1, 112	4.04	4.04	2.85	0.09
Shell width	1, 112	0.45	1.45	1.04	0.31

correcting for shell length, for any mussel species (ANCOVA, all $P > 0.16$) (Table 3). There were also no differences in shell width or depth between hosts with and without copepods, independent of shell length (ANCOVA, all $P > 0.25$). There was no significant difference in copepod prevalence between *M. senhousia* and *P. canaliculus* ($\chi^2 = 1.78$, d.f. = 1, $P > 0.05$). There was a significant difference in copepod prevalence between *X. pulex* and both of the other mussel species (*X. pulex* and *M. senhousia*: $\chi^2 = 16.35$, d.f. = 1, $P < 0.01$; *X. pulex* and *P. canaliculus*: $\chi^2 = 11.47$, d.f. = 1, $P < 0.01$), with *X. pulex* having a significantly greater copepod prevalence in both instances.

In general, pea crabs and copepods did not share hosts. Of those mussels infected with pea crabs, only one *P. canaliculus* also harboured a copepod. All pea crab infections were singletons. No pea crabs were recovered from *X. pulex* (Table 1). A total of 41 pea crabs were recovered from *M. senhousia* ($n = 2$) and *P. canaliculus* ($n = 39$). Pea crab prevalence differed between these two mussel species, and was significantly higher in the native *P. canaliculus* ($\chi^2 = 58.15$, d.f. = 1, $P < 0.001$) (Table 2). Pea crabs only occurred in mussels on the lower half of the shore, where hosts are submerged for much of the tidal cycle; therefore, pea crab prevalence increased with decreasing tidal height.

A strong positive relationship was observed between pea crab CW and host shell length (d.f. = 38, $r^2 = 0.58$, $P < 0.01$), i.e., larger pea crabs were associated with larger mussels, indicating indeterminate pea crab growth. Individual *P. canaliculus* harbouring pea crabs had a significantly lower mean dry weight than expected based on shell length (ANCOVA $P = 0.03$) (Table 3). There was an insufficient number of *M. senhousia* harbouring pea crabs ($n = 2$) to conduct a similar analysis. There was no significant difference in shell depth or width between individuals with or without pea crabs (ANCOVA, all $P > 0.09$) (Table 3).

Pea crab host selection

In trial 1, no significant difference was evident between the number of times *P. novaezelandiae* selected *M. senhousia* and the empty or central chambers. In trial 2, however, pea crabs chose the empty compartments significantly less often than the compartments housing *X. pulex* or the central chamber. In trial 3, pea crabs entered compartments with *P. canaliculus* significantly more frequently than the empty or central chambers. In trial 4, using a combination of all three mussel species, a significant difference was evident, with *X. pulex* and the central chamber being selected more frequently than expected by chance (Table 4).

DISCUSSION

The theory surrounding non-native species introductions and their release from natural enemies is still being developed. Much available evidence suggests that non-native species generally arrive in a new environment free from their natural parasites (Torchin et al. 2001, 2002; Colautti et al. 2004; Prenter et al. 2004; Torchin & Mitchell 2004). Once established in a new environment though, there is little to stop generalist parasites switching hosts and exploiting a non-native species (Bauer 1991). It has already been noted that infection with parasites can have marked effects on hosts and their communities (Mouritsen & Poulin 2002). Thus, if a native generalist parasite can switch host to exploit a non-native species, has detrimental effects on the host, and is prevalent, it may be able to slow the growth and reproduction of infected individuals, thus influencing the population structure and potentially reducing the impact on the community where it has been introduced (Mouritsen & Poulin 2002).

Copepods were the only parasite to be present in all three species studied at the single location of Bucklands Beach. No reports of copepods from *X.*

Table 4 Percentage of time the pea crab, *Pinnotheres novaezelandiae*, selected each mussel species in each trial; and chi-square tests examining differences in pea crab selection for each trial. Combination refers to when each mussel was presented in a single compartment within the same trial.

Trial no.	<i>Perna canaliculus</i>	<i>Xenostrobus pulex</i>	<i>Musculista senhousia</i>	Empty	Central	χ^2	d.f.	P
1. <i>M. senhousia</i>	–	–	40%	24%	36%	2.08	1	> 0.001
2. <i>X. pulex</i>	–	38%	–	12%	50%	11.32	1	< 0.001
3. <i>P. canaliculus</i>	56%	–	–	30%	14%	13.48	1	< 0.001
4. Combination	16%	30%	12%	12%	30%	8.60	3	< 0.050

pulex or *M. senhousia* have been published before and this is the first time this relationship has been reported from these hosts in New Zealand. The copepods found here were not identified to species level, but were assigned to the family Myicolidae, the same family as the copepod *Pseudomyicola spinosus*, which has been reported from other bivalves in New Zealand (Poulin et al. 2000). Copepods have previously been reported from *P. canaliculus* (Jones 1976; Jeffs et al. 1999; Hine & Diggles 2002). Although copepods are often assumed to feed on host tissue (Poulin et al. 2000), no reduction in tissue dry weight was evident in infected hosts. No difference in shell depth or width was observed, suggesting infection with copepods does not alter host tissue or shell growth. Because of low copepod prevalence, both *P. canaliculus* and *M. senhousia* may escape any potentially detrimental effects of copepods, compared with *X. pulex*. The relatively high prevalence in *X. pulex* suggests that it is the preferred host of copepods at Bucklands Beach.

Already known to exploit various bivalves in New Zealand (McLay 1988; Palmer 1995), the pea crab *P. novaezelandiae* was found associated with the native *P. canaliculus*, with the non-native *M. senhousia* being infected far less frequently, and *X. pulex* being uninfected. Pea crabs have been reported from *P. canaliculus* previously (Jones 1977; Hickman 1978; Baxter 1982; Hine & Jones 1989; Stevens 1990a,b, 1991; Jeffs et al. 1999). A significantly lower dry tissue weight was associated with the presence of *P. novaezelandiae* in *P. canaliculus*. The lower dry tissue weight in *P. canaliculus* suggests that pea crab infection decreases host tissue growth. A major implication of decreased host dry weight is that fecundity might also be reduced for any given host size, leading to a lowered potential for population growth and spread. Both O'Beirn & Walker (1999) and Bologna & Heck Jr. (2000) report decreased gonad condition in bivalve hosts infected with pea crabs.

Some studies refer to pea crabs as symbiotic or having an obligate but not detrimental relationship with their host (Hine & Jones 1989; Stevens 1990a,b), although female pea crabs are widely seen as being parasitic (Baxter 1982; Bierbaum 1986; Haines et al. 1994; O'Beirn & Walker 1999; Bologna & Heck Jr. 2000). Studies on other pea crab-host systems show effects such as reduced filtering, damaged gills and palps, delayed gonad development and a reduction in the host's ability to feed itself (Yoo & Kajihara 1985; Haines et al. 1994; Tablado & Lopez Gappa 1995; Bologna & Heck Jr. 2000). These effects all

cause a reduction in energy available for host growth and reproduction. The results here provide additional evidence for a parasitic relationship between the pea crab, *P. novaezelandiae*, and its native host. Given the effects of pea crabs, uninfected individuals or populations with low pea crab prevalence incur a lower cost of parasitism. As females are recognised as parasitic (Baxter 1982; Bierbaum 1986; Haines et al. 1994; O'Beirn & Walker 1999; Bologna & Heck 2000), and only males were found in *M. senhousia* at very low prevalence, the introduced bivalve appears largely unaffected by this native generalist parasite. The lack of female pea crabs in *M. senhousia* also suggests it is not a preferred host of *P. novaezelandiae*.

Pea crab host selection

Pea crabs have been reported to use chemical cues to locate, identify and select hosts (Derby & Atema 1980; Stevens 1990b; Grove & Woodin 1996). The use of cues is of particular importance in species where males must locate females for reproduction (Grove & Woodin 1996). However, mussels were not dissected following the experiment, so it is unknown whether the prior presence of pea crabs in the test mussels could have influenced pea crab selection. Stevens (1990b) reports that *P. novaezelandiae* prefers returning to the natural host species from which it was originally removed. One of the populations of *P. novaezelandiae* investigated by Stevens (1990b) originally infected the blue mussel, *M. galloprovincialis*. In addition to being highly attracted to this species, these crabs also displayed a strong preference for the green-lipped mussel *P. canaliculus* (Stevens 1990b). In the present study, pea crabs were also obtained from blue mussels, and the same pattern as that reported by Stevens (1990b) occurred when the native mussel, *P. canaliculus*, was presented on its own.

When presented with all three mussel species simultaneously, native *P. canaliculus* and *X. pulex*, and introduced *M. senhousia*, *P. novaezelandiae* displayed a weak preference for *X. pulex*. This result is in direct contrast to results from Bucklands Beach, where no pea crabs were recovered from *X. pulex*. By contrast, when all mussels were presented individually, *P. canaliculus* was the only species consistently selected at a higher than expected rate, reflecting the pattern at Bucklands Beach, where pea crab prevalence was much higher in *P. canaliculus*. As *M. senhousia* was collected from a different area, it is possible that the pea crabs were not pre-adapted to this species.

Pea crabs showed a weak attraction to *X. pulex* when this species was presented by itself, and when all species were offered simultaneously. Considering the lack of infection in the field study, the experimental results suggest *P. novaezelandiae* may select *X. pulex* if encountered, but it is doubtful whether pea crabs venture high enough on the shore or encounter *X. pulex* for long enough to infect them in nature, as pea crabs tend to occur low in the intertidal (McLay 1988). As *X. pulex* is a small mussel, growth constraints would be imposed on any pea crabs using this species. *Xenostrobus pulex* has a short feeding time owing to its occurrence high in the intertidal, reducing food available for pea crabs, also possibly explaining why no pea crab infection was evident in the field study. To test whether the pattern observed here is an artefact of host species distribution, known hosts of *P. novaezelandiae* would have to be transferred to higher tidal heights and rates of pea crab infection examined at a later date.

There is often a positive relationship between pea crab size and host size (Pregenzer 1978; McLay 1988; Haines et al. 1994; Soong 1997), as was observed between *P. novaezelandiae* and its hosts at Bucklands Beach. A large host can be beneficial to a pea crab (i.e., fewer constraints on crab growth). *Pinnotheres novaezelandiae* is reported to feed on food particles collected by the host (McLay 1988), so a larger host potentially increases available food for the pea crab. *Perna canaliculus* was the largest host species offered in our study, although individual mussel size was not measured, only biomass. The advantages gained by pea crabs from selecting a large host may explain why *P. canaliculus* was the only species chosen significantly more often than expected when presented on its own, although to know if host size alone accounted for pea crab choice would require further testing.

Pinnotheres novaezelandiae occurred at a higher natural incidence in *P. canaliculus* compared with *M. senhousia*, even though both occur low in the intertidal. *Musculista senhousia* was not chosen more often than what would have been expected if pea crab selection was random. It is possible that infections of *M. senhousia* were chance encounters of the pea crabs with the introduced species, rather than an active selection in response to cues from this host. Therefore, the experimental results do not support active use of *M. senhousia* by *P. novaezelandiae*.

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