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ORIGINAL PAPER

Biotic resistance on muddy shores? Native epibiotic barnacles impose costs on non-native snails

Kiara R. Kattler · Hannah V. Watkins ·
Katrina-Nicole Perretta · Amanda R. Gray ·
Isabelle M. Côté

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Abstract Organisms that settle and grow on other organisms (i.e., epibionts) are often costly to their hosts in terms of locomotion, growth, and/or reproduction. Such costs can potentially result in biotic resistance against invasion when native epibionts colonise non-native hosts, but examples are rare. Here, we examine the extent to which native acorn barnacles *Balanus glandula* that grow on the non-native Japanese mud snail, *Batillaria attramentaria,* may offer biotic resistance against this invader. We conducted population surveys, mark-recapture experiments, and behavioural observations in British Columbia, Canada, to measure the effects of barnacles on the movement, growth, and recapture rate, a potential proxy of short-term survival, of mud snails. One-third of mud snails carried barnacles, the weight of which sometimes exceeded the weight of the mud snail carrying them. Barnacle presence, weight, and the ratio of barnacle to snail weight all decreased the probability that mud snails would move, which could have implications for the foraging success of mud snails carrying barnacles. The slopes of the relationship between shell weight and length were similar for mud snails with and without barnacles, suggesting a lack of effect on growth allometry. The probability of recapture was 36% higher for mud snails without barnacles in one of two trials (i.e., 68% probability of recapture for snails without barnacles vs 50% for snails with barnacles), which reflects weak evidence for a small detrimental effect on mud snails carrying barnacles. Overall, native barnacles appear to offer some, though weak, biotic resistance to invasive mud snails, providing new insight into the potential for ecosystems to resist invasions through epibiotic interactions.

Keywords Biotic invasions · Symbiosis · Parasitism · Japanese false cerith · Asian hornsnail

Introduction

Invasions can sometimes be curtailed by biotic resistance – a phenomenon whereby native species limit or reduce the performance and success of non-native species (Elton 1958; Levine et al. 2004). Biotic resistance is usually underpinned by competition or consumption (Kimbro et al. 2013; Alofs and Jackson 2014). Parasites and pathogens can also provide a source of biotic resistance to invasions. Indeed, the loss of enemies such as predators and parasites is often considered an important mechanism explaining the success of invading species (the 'enemy release

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K. R. Kattler (✉) · H. V. Watkins · K.-N. Perretta · A. R. Gray · I. M. Côté
Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada
e-mail: kiararkattler@gmail.com

hypothesis', Keane and Crawley 2002). Another type of ubiquitous interspecific interactions – epibiosis – is not usually considered as potentially important in biotic resistance but it perhaps should be.

Native and non-native epibionts are common in space-limited communities, where they can have positive, neutral, or negative effects on their hosts. In the ocean, many species of algae and invertebrates that require a solid substrate for settlement are found growing on benthic organisms (Wahl 1989). Epibionts can be advantageous to their hosts by camouflaging them, impairing chemical recognition by predators, increasing handling time or decreasing palatability, thus reducing predation on the hosts (Pitcher and Butler 1987; Wahl and Hay 1995; Laudien and Wahl 2004; Farren and Donovan 2007). Some epibionts, such as sponges on scallops, also limit establishment of other epibionts (Farren and Donovan 2007). However, there are sometimes significant costs to hosting epibionts, such as reductions in locomotion (Buschbaum and Reise 1999; Donovan et al. 2003), growth (Dittman and Robles 1991; Buschman and Saier 2001), and reproduction (Dittman and Robles 1991) of the host. In some cases, epibionts facilitate rather than inhibit further epibiotic settlement (Guttiérez and Palomo 2016). Mussels that are fouled with epibionts require greater attachment strength to prevent dislodgement due to hydrodynamic stress (Witman and Suchanek 1984; Dittman and Robles 1991), while colonised scallops develop larger adductor muscles to provide more strength in lift and swimming (Donovan et al. 2003). By imposing costs, native epibionts could provide some resistance against potential non-native hosts in a similar way as parasites can.

There is ample evidence of non-native epibionts imposing costs on their native bivalve hosts (e.g., Dijkstra and Nolan 2011; Eschweiler and Buschbaum 2011; Burgueño Sandoval et al. 2021). For example, non-native tunicates living on scallops interfere with scallop escape response (Dijkstra and Nolan 2011), non-native barnacles cause increased production of byssal threads by mussels to counteract increased drag (Burgueño Sandoval et al. 2021), and non-native oysters reduce growth, locomotion and reproduction of native periwinkles (Eschweiler and Buschbaum 2011). However, to our knowledge, there is no example to date of native species exerting potential biotic resistance as epibionts on non-native species.

Here, we present a potential example with the encrustation of native barnacles on non-native snails. The Japanese mud snail *Batillaria attramentaria* (also known as Japanese false cerith; hereafter, *Batillaria*) is native to the northwestern Pacific Ocean. It was introduced to the west coast of North America with oyster seed for aquaculture in the early part of the twentieth century (Byers 1999; Wonham and Carlton 2005), and currently ranges from Cortes Island, British Columbia, to the north, to at least San Diego, California, to the south (www.iNaturalist.org, 2023). Population explosions of *Batillaria* in California coincided with the decline of populations of a native mud snail (Byers 1999) and facilitated the establishment of several non-native species in Washington state (Wonham et al. 2005). In its native range, *Batillaria* is commonly found hosting little-cone limpets *Patelloida conulus*. The mobile limpets are thought to keep *Batillaria* shells free from encrusting barnacles and oysters (Noseworthy and Choi 2020). In the absence of a functionally similar limpet in eastern Pacific habitats invaded by *Batillaria*, we asked whether the common native barnacles *Balanus glandula*, which readily settle on *Batillaria*, might contribute to biotic resistance. Our study therefore explores if native barnacles impose one or more costs on the non-native mud snails upon which they settle. We examined the effects of native barnacles on mud snail movement, growth, and recapture rate, a proxy of short-term survival.

Materials and methods

Study site

We performed experiments and collected *Batillaria* at Blackie Spit (49°03′44.0"N 122°52′36.2"W), British Columbia, Canada, in June and July 2021. Blackie Spit is a sandy point that extends into Boundary Bay at the mouth of the Nicomekl River. The site is characterised by a wide, muddy intertidal area that stretches as a shallow slope from a saltmarsh to the soft-bottom subtidal. *Batillaria* was distributed across shallow ponds in the lower saltmarsh to the subtidal zone and was particularly abundant in areas with moist sand and mud (see also Swinbanks & Murray 1981). Another non-native snail, the eastern mud snail *Ilyanassa obsoleta*, on which we never observed barnacles, was also present but in much lower abundance than *Batillaria* (personal observations). Native snails that overlapped the distribution of *Batillaria* at our study site included the small (< 15 mm height) checkered periwinkle *Littorina scutulata*, which was always barnacle-free, and shells of dead wrinkled purple *Nucella lamellosa* (50–80 mm height), which occasionally hosted barnacles. The native barnacle *Balanus glandula* was abundant and occurred most frequently on rocks, driftwood, and live *Batillaria* snails (personal observations).

Population survey

To establish the proportion of mud snails hosting barnacles, we ran three transects perpendicular to the shore, extending from the edge of the saltmarsh to the water's edge at low tide. This stretch of habitat corresponds to the 'algal mat zone' (0.75 – 1 m above chart datum), which is covered by an almost continuous growth of cyanophyte mats, where *Batillaria* densities are highest (Swinbanks & Murray 1981). Transect length varied from 129 to 150 m. Every 3 m along each transect, we counted the total number of mud snails in a 20 cm × 20 cm quadrat as well as the number of mud snails with barnacles on their shells. Using calipers, we measured the length and noted the presence of barnacles on up to 10 mud snails chosen haphazardly in each quadrat.

Batillaria movement and length–weight allometry

To examine the potential locomotion cost imposed by native barnacles on mud snails, we measured the distance travelled by mud snails with and without barnacles in five ponds in the lower saltmarsh. These ponds were at similar intertidal heights, had abundant mud snails, and provided convenient, relocatable areas for this part of the study and the next (see below). We observed 12 mud snails, selected haphazardly, for 5 min each in each pond (60 snails total). Half of the mud snails were carrying at least one barnacle. We placed a wooden skewer near the posterior end of each mud snail's shell to mark its starting location. After 5 min, we placed another skewer near the posterior end of the mud snail's shell to mark its finishing location. We then recorded the distance between the two skewers for each mud snail. We were able to track four mud snails simultaneously per observation. We then collected each mud snail in an individually labelled plastic bag and froze the mud snails for later analysis.

In the laboratory, we used calipers to measure the maximum length, width and aperture diameter of each thawed mud snail. We counted and removed any barnacles and obtained the wet weight (to the nearest 0.001 g) of the mud snail and, when present, its barnacles. Finally, we crushed each mud snail's shell with a hammer to expose the posterior tissue and recorded the presence of trematode cercariae. The trematode parasite, *Cercaria batillariae,* which uses *Batillaria* as first intermediate host, was introduced to North America at the same time as its native host (Torchin et al. 2005). This parasite castrates the mud snails and causes them to grow larger (Miura et al. 2006). Trematode presence was noted as infection could confound effects of barnacles on mud snail behaviour and on length–weight allometry.

Mark-recapture study

Finally, we conducted two mark-recapture studies aimed at determining if hosting barnacles affects *Batillaria* recapture relative to snails that were free of barnacles. In the first study (18 June 2021), we haphazardly collected 10 mud snails with barnacles and 10 mud snails without in each of the five ponds used for behavioural observations (100 snails total). We used red nail polish (Sally Hanssen Insta-Dry, 'Rapid Red') to paint the posterior half of each snail and, after allowing 3–4 min for drying, placed the mud snails back into their original pond. Six days later, we revisited the ponds and recorded the number of marked mud snails remaining with and without barnacles. We repeated the mark-recapture study on 16 July 2021, expanding the marking to eight ponds (including four from the first study, giving the July experiment a total of 160 snails).

Analysis

For each component of the analysis, we used generalized linear mixed-effects models run in R (R Core Team 2021) with the package glmmTMB (Brooks et al. 2017). We chose the distribution and link function for each model according to the response variable type (i.e., negative binomial with log-link for overdispersed count data, hurdle-Gamma with logit- and log-links for continuous bounded data with 0 s, normal for continuous data not approaching a bound). In each model, we centered and scaled all continuous variables and accounted for sampling variation using random effects (i.e., transect for mud snail abundances, quadrat nested within transect for individual mud snail lengths and barnacles, and pond for mud snail movement, allometry, and recapture). When datasets had more than one outlier (i.e., extreme values with disproportionate leverage on the model), we conducted analyses with and without the outlying data, which yielded similar results in all cases. We therefore present the analysis with the clearest visual result in the text, and the alternative result for comparison in the online supplement.

We first examined the relationships between mud snail abundances and sizes with their location within the mudflat (i.e., their distance from the water's edge). In these models, we included a quadratic term of distance from the water's edge as the proportion of mud in sediment has been shown to peak approximately 100 m from the edge of the saltmarsh, coinciding with peak *Batillaria* abundance (Swinbanks & Murray 1981). For this analysis, we removed three quadrats that had 3–4 times more *Batillaria* than the average quadrat. We then tested whether the probability of a mud snail having one or more barnacles was related to it's location, size and the interaction between the two.

Next, we used hurdle models to determine whether there was an effect of barnacle presence on mud snail movement. The hurdle models contained two sub-models each: a logistic regression, to model the probability of a mud snail moving at all, and a Gamma-distributed regression, to model the distance moved *if* a mud snail moved at all. We chose this approach for two reasons. First, continuous positive data are generally modeled most appropriately with a Gamma distribution, but this distribution cannot handle zeros. Consequently, the hurdle model allows us to circumvent this limitation. Second, and more importantly, by modeling movement as two distinct processes (i.e., the presence or absence of mud snail movement and the total distance travelled), we can address two non-mutually exclusive but distinct mechanisms by which barnacles may be exerting biotic resistance on the mud snails (i.e., via total cessation vs some impairment of locomotion). We found only three mud snails that were parasitized with trematodes in the movement experiment. This low sample size prevented the inclusion of trematode parasites as a factor in the models, hence we removed these snails from the analysis. We conducted the analysis with and without outliers, i.e. snails that carried more than 2 g of barnacles, which represents > 2.5 SD above the mean barnacle weight carried. To examine potential size bias, we tested whether snails in the movement study were similar in length to those measured along transects at a similar intertidal height (> 100 m from the water). There was no detectable difference between the two groups (mean ± 1 SD, transects: 23.45 ± 5.70 mm, movement study: 24.37 ± 2.70, $t_{200.53} = -1.56$, $p = 0.12$).

We then ran a linear regression between the length and wet weight of mud snails (with barnacles removed), to determine if the presence of barnacles changed the slope of the length–weight relationship. We removed one small snail free of barnacles, which was only half of the weight of the nearest smallest, barnacle-free snail, from the analysis. Finally, we tested whether having one or more barnacles influenced the probability of recapture across two rounds of sampling. For all models, when the effects are not statistically significant but the effect sizes are biologically meaningful, we discuss the strength of evidence in support of an effect, following Muff et al. (2022; e.g., $0.05 < p < 0.1$ demonstrates 'weak support' for an effect).

Results

Distribution and prevalence of barnacles on *Batillaria*

We surveyed 142 quadrats and encountered 560 *Batillaria*, for 477 of which we recorded shell length. The number of *Batillaria* per quadrat ranged from zero to 46 (mean ± 1 SD: 3.9 ± 5.6 individuals per 400 cm^2) when considering all quadrats, and from zero to 11 (3.2 ± 2.7 individuals per 400 cm^2) when excluding the three outlier quadrats. Mud snail length ranged from 5 to 41 mm (mean ± 1 SD: 23.4 mm ± 6.3 mm, n = 477). Nearly one-third (32.9%, n = 184) of all *Batillaria* were carrying one or more barnacles.

Mud snail abundance peaked midway between the saltmarsh edge and water's edge (model with no outliers: *distance est.* $=0.20$, $P=0.009$, *distance*^{2} *est.* $=-0.25$, $P=0.001$, Fig. 1a; model with outliers: *distance est.* $=0.38$, $P<0.001$, *distance*^{2} *est.* $=-0.16$, $P=0.11$). Individual mud snail length was inversely related to mud snail abundance and was smallest midway between the saltmarsh and water (*distance est.* $=-0.45$, $p=0.26$, *distance*^{2} *est.* $=1.14$, $p=0.003$; Fig. 1b).

Larger mud snails were more likely to have one or more barnacles (*est.* $=1.08$, $P<0.001$), but neither distance from water (*est.* $=-0.06$, $P=0.79$), nor its interaction with mud snail length (*est.*: -0.13, $P=0.45$) predicted the probability of having a barnacle (Fig. 2).

Batillaria movement

The total weight of barnacles (Fig. 3) and the ratio of barnacle weight to mud snail weight (Figure S2) significantly reduced the probability that a

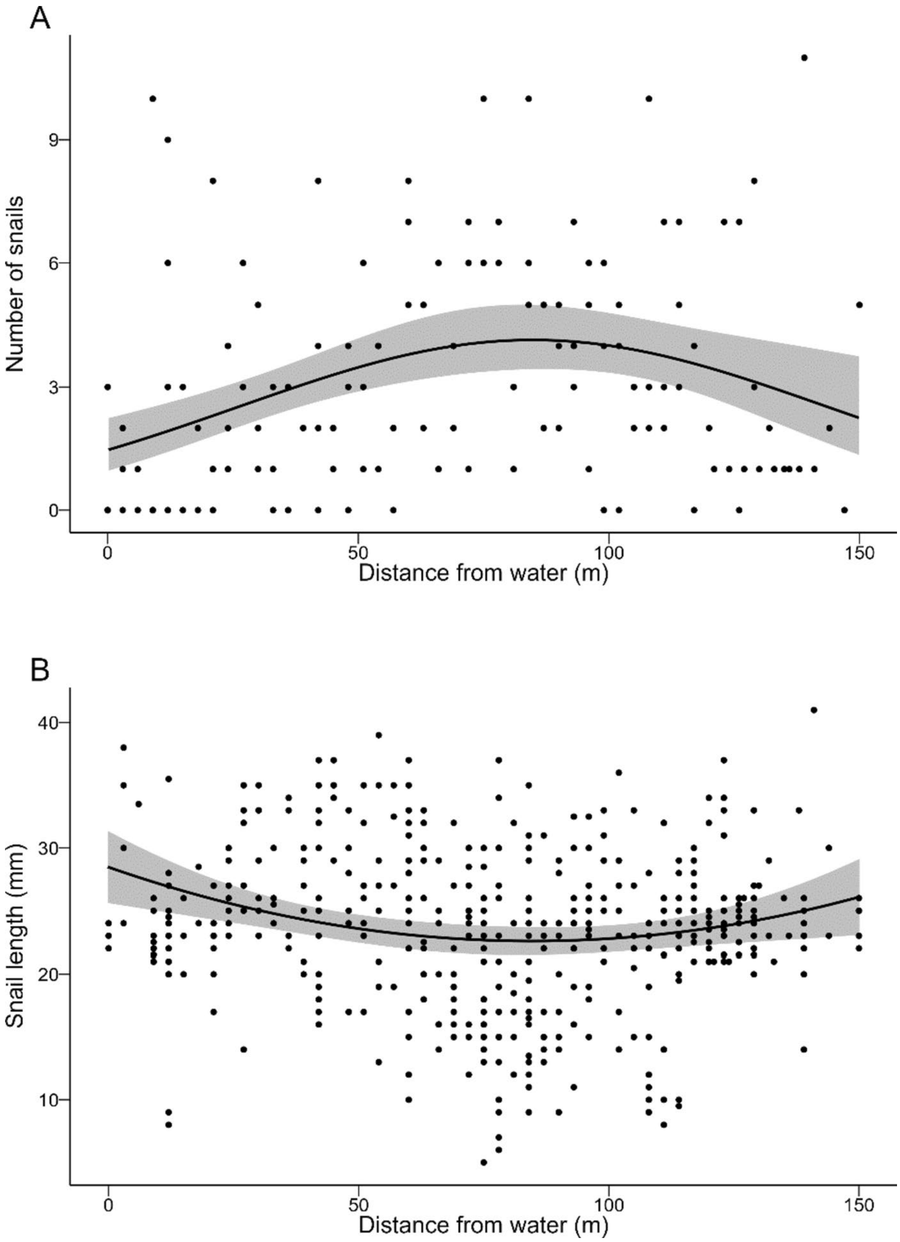

Fig. 1 Relationship between (**a**) mud snail *Batillaria attramentaria* abundance, and (**b**) mud snail length, and distance from the water at low tide. Lines represent mean model estimates and ribbons represent 95% confidence intervals. In (**a**), each point is an individual quadrat (n = 139 quadrats). In (**b**), each point is an individual mud snail (n = 477 individuals)

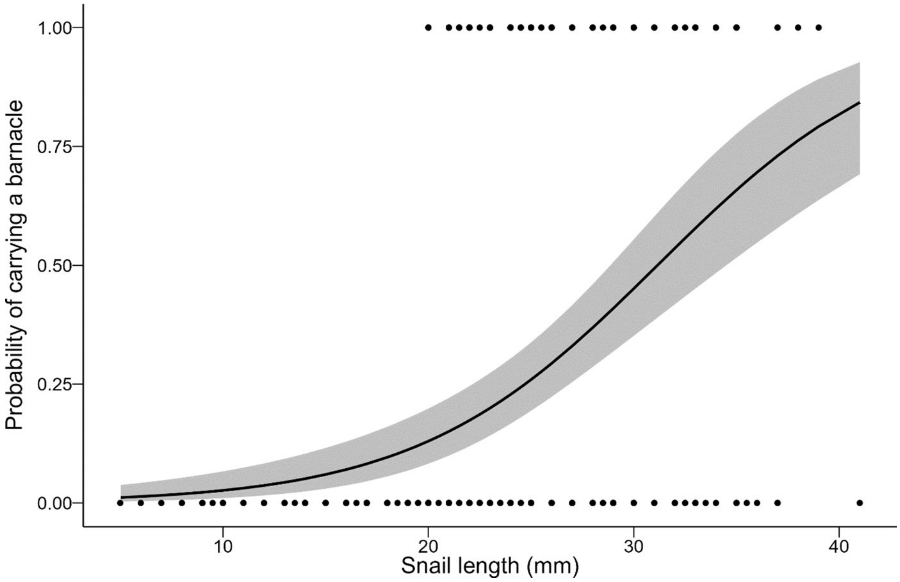

Fig. 2 Probability of a mud snail *Batillaria attramentaria* carrying one or more barnacles *Balanus glandula* in relation to snail length. The line represents mean model estimates and ribbon represents 95% confidence interval. Each point is an individual mud snail (n = 477 individuals)

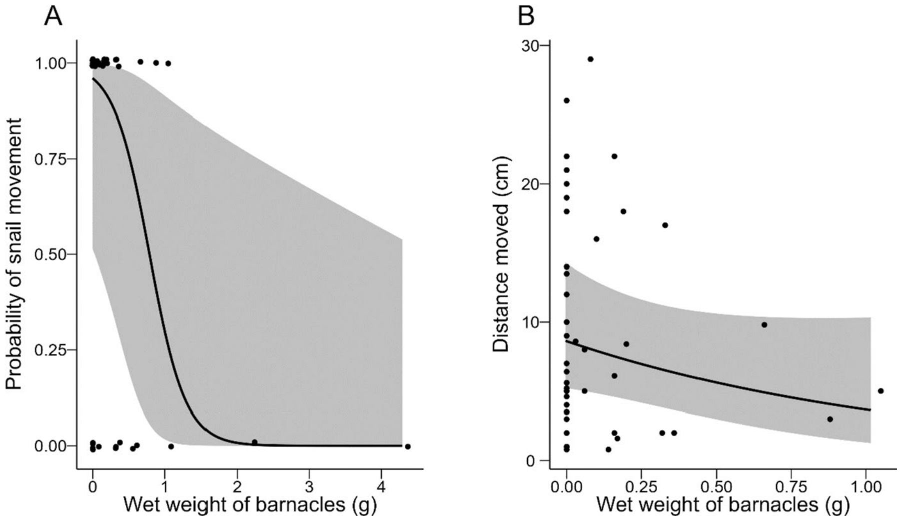

Fig. 3 Effect of native barnacles *Balanus glandula* (wet weight, g) on mud snail *Batillaria attramentaria* movement, measured as (**a**) the probability of any movement ($n = 57$) where 0 = no movement and 1 = movement, and (**b**) the distance moved (cm) in 5 min for those mud snails that moved ($n = 44$). The lines represent mean model estimates and ribbons represent 95% confidence intervals. The small points are individual observations

mud snail would move at all during the observation period (model with outliers: Table 1; model without outliers: Table S1), and there was weak evidence (sensu Muff et al. 2022; i.e., $0.5 < p < 0.1$) that the presence of any barnacles did the same (Table 1, Figure S1). However, there was little to no evidence that barnacles reduced the distance traveled of the mud snails that did move (Table 1). Individual mud snail length was not related to movement in any of the models (with outliers: Table 1; without outliers: Table S1).

Batillaria length–weight allometry

Mud snail shell weight was highly correlated with shell length (*est.* $= 0.13$, $P < 0.001$), but the slope of the relationship did not vary with whether a mud snail carried barnacles or not (*interaction est.* $= -0.02$, $P = 0.63$; Figure S3).

Mark-recapture

Across the two replicate experiments, we recaptured 40% of marked mud snails 6 days after release

Table 1 Results of hurdle models examining the effect of native barnacles *Balanus glandula* on non-native mud snail *Batillaria attramentaria* movement. The first submodel (i.e., the "hurdle" component of the overall model) examines whether a snail moves at all. If a snail passes this "hurdle" (i.e., if it moved), it is included in the second submodel, which examines the distance moved. In all models, 'Barnacles' refers to epibiont presence, and the parameter estimate is relative to movement in the absence of barnacle epibionts

Barnacle metric	Estimate	SE	*z*	*P*
Presence/absence of barnacles				
Movement versus no movement submodel				
Intercept	2.67	1.22	2.18	0.03
Barnacles	− 1.33	0.78	− 1.72	0.09
Snail length	− 0.66	0.51	− 1.29	0.20
Distance moved submodel				
Intercept	2.05	0.27	7.74	< 0.001
Barnacles	0.03	0.25	0.13	0.90
Snail length	− 0.13	0.14	− 0.91	0.36
Weight of barnacles carried				
Movement vs. no movement submodel				
Intercept	2.11	1.38	1.53	0.13
Barnacles	− 2.70	1.26	− 2.15	0.03
Snail length	− 0.84	0.59	− 1.43	0.15
Distance moved submodel				
Intercept	1.92	0.27	7.24	< 0.001
Barnacles	− 0.57	0.35	− 1.65	0.10
Snail length	− 0.15	0.14	− 1.02	0.31
Ratio of barnacle weight to snail weight				
Movement versus no movement submodel				
Intercept	1.95	1.13	1.73	0.08
Barnacles	− 2.03	0.93	− 2.18	0.03
Snail length	− 0.84	0.58	− 1.45	0.15
Distance moved submodel				
Intercept	1.94	0.26	7.52	< 0.001
Barnacles	− 0.49	0.32	− 1.56	0.12
Snail length	− 0.15	0.14	− 1.03	0.31

(59% in June and 30% in July). The probability of recapture was significantly higher in June than July (*est.* $= -1.54$, $p < 0.001$). There was weak evidence showing that the presence of barnacles reduced the probability of recapture (*est.* $= -0.75$, $P = 0.07$; Fig. 4), and there was no interaction between month of experiment and the presence or absence of epibiotic barnacles (*est.* $= 0.63$, $P = 0.23$).

Discussion

Epibiotic native barnacles were prevalent on invasive mud snails. One-third of mud snails hosted barnacles, the weight of which sometimes exceeded the weight of the mud snail carrying them. Mud snails that carried barnacles had a lower probability of moving compared to mud snails free of epibionts, although the distance covered by mud snails that did move was unaffected by the presence or weight of barnacles. There was no evidence that length–weight allometry of mud snails was affected by barnacle presence, but weak evidence for a higher probability of recapture for mud snails without barnacles, at least in our first mark-recapture experiment. Overall, native barnacles appear to offer some, though weak, biotic resistance to invasive mud snails.

Larger mud snails were more likely to be carrying barnacles than smaller snails. This is a recurrent pattern among marine epibiont hosts. For example, the occurrence of epibiotic barnacles increases with carapace size in native cancrid crabs on the east and west coasts of North America (Key et al. 1997; McGaw 2006). Large hosts are usually older, so they have had a longer exposure to potential epibiont settlement (e.g., Dick et al. 1998), they offer a larger

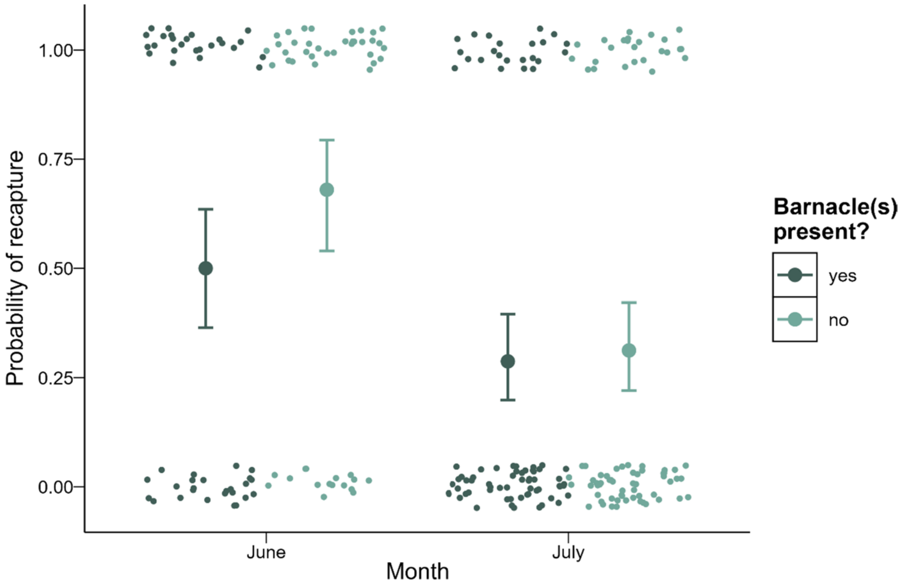

Fig. 4 Probability of recapture of marked mud snails *Batillaria attramentaria* across two sampling events. Large points and error bars represent model-estimated means and 95% confidence intervals. Each smaller point is an individual mud snail and points are jittered to assist with readability (zeros represent mud snails not recaptured and ones represent recaptured mud snails; $n = 260$ individuals)

target, and in the case of crabs, they also moult less frequently (Abelló et al. 1990; Gili et al 1993). The association between mud snail size and the presence of barnacles suggests that *Batillaria* possesses few, if any, defense mechanisms against epibionts in the invaded range, unlike some host species that can prevent epibiont establishment through chemical, physical or behavioural means (Wahl 1989). Moreover, there appears to be no ecological equivalent in the eastern Pacific to epibiotic little-cone limpets, which have been shown to keep their native *Batillaria* hosts free of encrusting barnacles through grazing (Morton 1980; Noseworthy and Choi 2020).

Native epibiotic barnacles had a small but negative effect on mud snail locomotion. Reduced locomotion by organisms hosting epibionts has often been recorded (e.g., Buschbaum and Reise 1999; Dijkstra and Nolan 2011; Eschweiler and Buschbaum 2011). Here, we reveal a more nuanced effect. While the probability of a snail moving when it had no barnacles was 96%, this declined to 50% when the snails had only 0.8 g of barnacles on them and to below 1% with 1.9 g of barnacles; however, there was no effect of barnacles on the distance travelled by mud snails that did move. Snails that did not move carried, on average, a weight of barnacles that was more than six times heavier than that of snails that did move, and snails became more likely to remain still (i.e., probability > 50%) when the weight of the barnacles they carried was 75% of own weight (Figure S2). Impaired movement of mud snails, which continuously scrape diatomaceous biofilm on the bottom when underwater (Whitlatch and Obrebski 1980), could potentially lead to reduced foraging success of snails with barnacles. In other marine mollusks, decreased locomotion as a result of various factors, such as tidal action, altered temperature or presence of predators, was associated with decreased foraging activity (Premo and Tyler 2013; Leung et al. 2015; Domenici et al. 2017; Taylor et al. 2017).

Loss of locomotion, and associated potential loss of feeding opportunities, can have consequences for growth and/or survival of fouled hosts (e.g., Dittman and Robles 1991; Farren and Donovan 2007; Eschweiler and Buschbaum 2011). We saw no evidence that hosting a barnacle influenced the growth trajectory of mud snails. Such a result might be expected for filter-feeding hosts that do not rely on locomotion to obtain food (e.g., scallops: Donovan et al. 2003; mussels: Buschbaum and Saier 2001; Garner and Litvaitis 2013), but it is unexpected for a deposit-feeder such as *Batillaria* (Whitlatch and Obrebski 1980; Byers 2000). For instance, surface-grazing periwinkles have significantly lighter tissue dry-weight when fouled by oysters than when free of these epibionts (Eschweiler and Buschbaum 2011). It is possible that we might have found a similar effect by considering dry weight instead of wet weight.

We did find weak evidence that mud snails carrying barnacles had a lower recapture probability than those that did not host barnacles, at least in our first mark-recapture experiment. We must interpret this result cautiously. There could be several causes for a failure to recapture a marked snail, including loss of the mark, emigration out of the pond, burial in the substrate, and natural mortality. We believe that loss of mark was uncommon since all resighted snails had intact marks, with no evidence of peeling paint. Emigration is possible, although we searched for marked snails beyond the pond edges to mitigate this issue. Mud snails bury headfirst in the substrate to avoid desiccation (Swinbanks & Murray 1981), but we did not notice this behaviour in the experimental ponds, which had water 5–12 cm deep through June and July. We therefore cautiously conclude that recapture rates might reflect natural mortality to some extent. If this is so, our results mirror those of several other studies of epibiont-carrying mollusks (e.g., Dittman and Robles 1991; Buschbaum and Reise 1999; Farren and Donovan 2007), although we could not identify the source of mortality and hence the mechanism(s) underpinning this potential effect. The recapture rate for all mud snails was significantly lower in July than in June, which might be ascribed at least in part to the extreme heatwave ('the dome') that occurred between 25 June and 1 July 2021 throughout British Columbia (Climate Canada 2022) and resulted in lower water levels and warmer water in the ponds during the second experiment (personal observations).

While we have focused on the effects of native epibionts on non-native hosts, the reciprocal effect is rarely considered (Creed et al. 2022). There is evidence that barnacles prefer to settle on rocky substrate than on biotic hosts such as mussels (Bell et al. 2015). There is also evidence that barnacles settled on mussels ingest a lower quality of food (i.e., lower polyunsaturated fatty acids, lower delta N values) than when settled on rock as a result of competition between epibiont and host (Puccinelli and McQuaid 2021) – an interaction that is unlikely to exist between native barnacles and *Batillaria* in our system. However, *Batillaria* shells provide a hard settlement surface, which is in limited supply in the muddy intertidal area of Crescent Beach. But although these settlement 'patches' (i.e., snail shells) can be relatively long-lived (i.e., up to 10 years, Behrens Yamada 1982), they are small and unstable in wave action (IMC, personal observations). It seems likely that acorn barnacles that settle on mud snails would fare more poorly than those that settle on rock (Bell et al. 2015).

In the framework proposed by Creed et al. (2022) to understand the potential impacts of invasions on native symbionts, the *Batillaria*–barnacle association appears to align with the path to 'native symbiont resistance'. *Batillaria* is a competent host for acorn barnacles, native symbionts have a negative effect on invader fitness, and the invading host exhibits little or no spread in the new habitat (Creed et al. 2022). However, our results suggest a weak interaction strength between native barnacles and invasive *Batillaria*. As such, barnacles are unlikely to provide very strong biotic resistance to mud snails. Other factors appear to be more important in limiting *Batillaria* populations. For example, in Elkhorn Slough, California, where densities of *Batillaria* were phenomenally high for decades, a sudden decline was ascribed to a combination of increased crab predation, water temperature and restoration of natural tidal exchange (Wasson et al. 2020). The lack of rapid spread of *Batillaria* beyond introduction locations is also likely related to its lack of a dispersive pelagic larval stage (Behrens Yamada 1982). Nevertheless, we have documented some negative effects of native barnacles on proxies of *Batillaria* fitness, providing a rare example of the potential for ecosystems to resist invasions, however mildly, through epibiotic interactions.

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Data availability The raw data and code are available at https://github.com/hannahvwatkins/snails-and-barnacles.

Declarations

Competing interests The authors have disclosed no competing interests.

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