



A forced association between the slippersnail *Crepidula convexa* and the hermit crab *Pagurus longicarpus*?—possible influence from a third party

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Abstract

The suspension-feeding slippersnail *Crepidula convexa* is commonly associated with hermit crabs (*Pagurus longicarpus*) living in periwinkle shells (*Littorina littorea*) at our study site in Nahant, MA, USA. In 15 field surveys conducted at Nahant in 2000, 2001 and 2003, we found that (1) more than 61.8% of individuals of *C. convexa* resided on shells occupied by hermit crabs, as opposed to the shells of live periwinkles, empty periwinkle shells or other solid substrates; (2) an average of 8.3% of hermit crabs carried at least one individual of *C. convexa*; and (3) 39.1–75.0% of hermit crabs carrying *C. convexa* were carrying “large” individuals (snails with wet weight >10% of the weight of the periwinkle shells they occupied). However, it is unlikely that individuals of *C. convexa* seek out shells occupied by hermit crabs to colonize, and they showed no preference for empty periwinkle shells over other solid substrates in the laboratory. Moreover, in the laboratory the hermit crabs preferentially occupied intact shells bearing individuals of *C. convexa* only when the alternatives were shells that had been drilled by naticid snails. Thus, neither party preferentially associates with the other: rather, extensive predation by naticid snails on periwinkles at Nahant appears to limit the availability of suitable shells for the hermit crabs, forcing them to inhabit shells bearing “large” individuals of *C. convexa*. Individuals of *C. convexa* may benefit from this inadvertent association with hermit crabs: by facilitating snail dispersal, transport by hermit crabs should reduce the potential for inbreeding, an important consideration for a species that lacks free-living larvae in its life history.

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1. Introduction

The hermit crab *Pagurus longicarpus* lives in association with at least 30 other animals, most of which either attach to the gastropod shells occupied by the hermit crabs, burrow into those shells, or live freely in the shell's lumen (McDermott, 2001). The presence or absence of a particular symbiont in or on a given shell can affect the likelihood that a hermit crab will choose or reject that shell. For example, in experiments by Conover (1976), individuals of *P. longicarpus* preferentially occupied shells bearing the hydroid *Hydractinia echinata*, but rejected shells bearing the barnacle *Balanus amphitrite*. The crabs also rejected shells occupied by the gastropod *Crepidula plana*, which attaches to the shell's inner surface, and those occupied by large *Crepidula fornicata*, found on the outer surface (Conover, 1976).

Individuals of *P. longicarpus* are commonly associated with a third *Crepidula* species, *Crepidula convexa*; indeed, at our study sites at Nahant, MA and Wickford, RI, and in the Thimble Islands, CT (Shenk and Karlson, 1986), *C. convexa* is more common than both *C. fornicata* and *C. plana* on shells occupied by this hermit crab. The population implications of this association for individuals of *C. convexa* are substantial. Unlike *C. fornicata* and *C. plana*, which have a free-living larval stage in the life history, females of *C. convexa* brood their embryos under their shells so that offspring of *C. convexa* emerge as crawling juveniles (Franz and Hendler, 1970; Hendler and Franz, 1971). With no dispersive larval stage in the life history, an association with hermit crabs could provide an alternative means of dispersal for individuals of *C. convexa*. Surprisingly, the influence of *C. convexa* on shell selection by hermit crabs has not been previously reported.

We are interested in quantifying the degree of association between *P. longicarpus* and *C. convexa*, and exploring how the association comes about. If individuals of *C. convexa* are unlikely to seek out shells occupied by hermit crabs (Karlson and Sullivan, 1989), an alternative explanation for this association is required. Unlike individuals of *C. fornicata*, which can weigh as much as the shells they occupy (Conover, 1976), individuals of *C. convexa* rarely weigh as much as 30% of the empty shell's weight. Thus, the small size of adult *C. convexa* may make their presence or absence irrelevant to shell choice by hermit crabs. Alternatively, hermit crabs may deliberately select shells occupied by individuals of *C. convexa*, probably because the crabs can obtain certain benefits from being associated with the snails.

Another possibility is that neither hermit crabs nor individuals of *C. convexa* choose to live with their partners, and that the association between the two species is instead driven by outside factors. At our field site in Nahant, MA, individuals of *P. longicarpus* are rarely found living in the many periwinkle shells (*Littorina littorea*) that have been drilled by naticid snails (Pechenik and Lewis, 2000). Laboratory experiments have confirmed that the hermit crabs avoid drilled shells; in fact, they will choose intact shells that are much too small for them over drilled shells of appropriate size (Pechenik and Lewis, 2000). It is possible, then, that the association between hermit crabs and *C. convexa* at Nahant is largely driven by the high degree of predatory drilling activity at this site, leaving the hermit crabs with few alternatives in shell choice. If so, the increased dispersal potential for *C. convexa* is then essentially engineered, indirectly, by a third party.

In this study, we conducted 15 field surveys to determine the proportion of *P. longicarpus* associated with *C. convexa*, the size of the slippersnails relative to the size of the periwinkle shells occupied by the hermit crabs, and the abundance of the *C. convexa* snails residing on shells occupied by hermit crabs relative to the numbers living on other hard substrates. We also tested whether or not individuals of *P. longicarpus* discriminate against shells bearing *C. convexa*, and determined how the size of *C. convexa* snails or the condition of alternative shells affected the shell choices made by hermit crabs. We also asked whether individuals of *C. convexa* preferentially live on empty periwinkle shells.

2. Materials and methods

2.1. Field surveys at Nahant, MA

Fifteen field surveys were conducted during low tide in intertidal and subtidal areas at Nahant, MA over 3 years between May and October of 2000, 2001 and 2003. In 12 surveys, 260–2062 hermit crabs (*P. longicarpus*) were haphazardly collected to determine the proportion of hermit crabs carrying individuals of *C. convexa*. The habitats in which the hermit crabs were collected included both rocky shores and sand flats.

Five surveys, 2 of them overlapping with the above 12, were also conducted to discover the sizes of *C. convexa* individuals relative to the sizes of the periwinkle shells (*L. littorea*) they occupied. We use the term “weight ratio” here to indicate relative size. “Weight ratio” refers to the total wet weights of all the snails on a given periwinkle shell relative to the wet weight of that shell, $\times 100\%$; 20 to 53 hermit crabs carrying individuals of *C. convexa* were collected in each of these surveys; the lengths of both the periwinkle shells and those of any associated individuals of *C. convexa* were measured with calipers to the nearest 0.01 mm. The “length” of a periwinkle shell refers to the distance from the apex to the farthest point on the aperture. The “shell length” of a *C. convexa* snail refers to the longest measurable length, since shells in this species grow linearly rather than spirally. The wet weights of both the periwinkle shells and the associated individuals of *C. convexa* were estimated, respectively, using the relationships between wet weight and shell length described below. These data allowed us to calculate the “weight ratios” (see also Section 2.2).

In the two surveys conducted in 2003, other hard substrates besides hermit crab shells were also searched at low tide for the presence of individuals of *C. convexa* to determine the extent to which the snails were primarily associated with hermit crabs. In each survey, we haphazardly collected hermit crabs, live periwinkles, and empty periwinkle shells for 30 min, noting the presence or absence of *C. convexa* snails and counting the number of snails on each periwinkle shell. We spent another 30 min examining numerous rocks, mussels, empty clamshells, and other hard substrates for the presence of individuals of *C. convexa*.

2.2. Determining the relationship between wet weight and shell length of field-collected individuals of *C. convexa* and empty periwinkle shells

Forty-two individuals of *C. convexa* and 91 intact, empty periwinkle shells were haphazardly collected from Nahant, MA in August 2003. Their shell lengths were measured

with calipers to the nearest 0.01 mm. After blotting away excess water, we weighed both the periwinkle shells and the snails to the nearest 10 mg. None of the periwinkle shells had any symbionts that could affect the wet weight. Shell lengths and wet weights were log transformed and the relationship between them was then determined by linear regression. The wet weights of the empty periwinkle shells and the *C. convexa* snails collected in field surveys, and the wet weights of those used in the experiments described below, were obtained from length measurements using these relationships.

2.3. General design of laboratory experiments

Empty periwinkle shells (*L. littorea*) and hermit crabs (*P. longicarpus*) in periwinkle shells (with and without *C. convexa* on them) were collected in the intertidal zone at Nahant, MA three times between June and October 2000. Hermit crabs were maintained in the laboratory on a diet of artificial crabmeat, while individuals of *C. convexa* were maintained in the laboratory on a mixture of the unicellular phytoplankton *Dunaliella tertiolecta* (clone DUN) and *Isochrysis galbana* (clone T-ISO). The intact periwinkle shells used in our experiments had no visible external damage and bore no symbionts other than individuals of *C. convexa*. The drilled shells used in our experiments had a single, circular hole drilled by a naticid snail (probably *Euspira heros* or *Neverita duplicata*; Pechenik and Lewis, 2000), but were otherwise undamaged.

In all shell selection experiments, each hermit crab was offered two shells of the same size, the size preferred by hermit crabs with a given wet weight (Angel, 2000). Hermit crab wet weight was determined by gently pulling a hermit crab from its shell, blotting away excess water, and weighing the crab to the nearest 10 mg (Angel, 2000; Pechenik and Lewis, 2000).

Seawater was collected from Nahant, forced through a 1- μ m cartridge filter, and aerated before use. All experiments were conducted at room temperature, about 23 °C.

Details of the different experiments are given below, and are summarized in Table 1. In these experiments, “large” *C. convexa* refers to *C. convexa* individuals with a “weight ratio” >10% and “small” *C. convexa* refers to *C. convexa* individuals with a “weight ratio” <2.5%. “Naked” hermit crabs are those that have been removed from their shells (Pechenik and Lewis, 2000; Pechenik et al., 2001).

2.4. Do “large” *C. convexa* affect shell selection by the hermit crabs?

Two experiments were conducted. In Experiment Ia, we tested 34 hermit crabs that were in intact periwinkle shells bearing “large” *C. convexa* when collected. The average wet weight of these “large” *C. convexa* (± 1 S.D.) was 240 ± 90 mg. Each crab, in its original shell, was placed in a $12.5 \times 8.5 \times 3$ cm container of translucent plastic filled with filtered seawater. The hermit crab was then offered another intact periwinkle shell of the same size, but which was not occupied by *C. convexa*. Over the next 24 h, the shells were examined periodically to determine hermit crab occupancy.

Experiment Ib was undertaken to exclude the possibility that hermit crabs will always switch to newly offered shells, which would confound the results of the previous experiment. Newly collected hermit crabs were used in this experiment to avoid the

Table 1
Summary of the experimental design for shell choice by *P. longicarpus*

Experiment	<i>N</i>	Experiment duration (h)	Shells offered	Weight ratio (mean \pm 1 S.D.)	Results
Ia	34	24	Shells with large <i>C. convexa</i> vs. shells without	20.5 \pm 7.6%	Fig. 4a
Ib	18	45	Shells with large <i>C. convexa</i> vs. shells without	18.3 \pm 7.0%	Fig. 4b
Ic	18	65	Shells originally bearing large <i>C. convexa</i> vs. shells without	NA	Fig. 4c
IIa	20	30	Shells with small <i>C. convexa</i> vs. shells without	1.3 \pm 0.6%	Fig. 5
IIb	18	30	Shells with small <i>C. convexa</i> vs. shells without	1.3 \pm 0.7%	
III	9	30	Shells with large <i>C. convexa</i> vs. drilled shells without	15.8 \pm 5.7%	Fig. 6

In each experiment, individual hermit crabs were allowed to choose between two shells of the same (preferred) size. The same hermit crabs were tested in Experiments Ib and Ic, 5 days apart. Different hermit crabs were used in each of the other experiments. All shells offered were undamaged except in Experiment III, in which one shell of each pair had been drilled by a naticid snail. The “weight ratio” for shells bearing individuals of the ectosymbiont *C. convexa* is the total wet weight of the snails living on a given periwinkle shell relative to the wet weight of that empty shell, $\times 100\%$. NA = not applicable.

possible influence of previous experience. Eighteen pairs of shells (one with and one without “large” *C. convexa*) from Experiment Ia were reused in Experiment Ib. This time, previously untested, naked hermit crabs were allowed to choose between the shells. The mean wet weight of the hermit crabs tested (± 1 S.D.) was 290 ± 190 mg. During the next 45 h, we examined the shells periodically to determine hermit crab occupancy.

2.5. Distinguishing between the effect of *C. convexa* and the periwinkle shell it occupied on hermit crab shell selection

To exclude the possibility that hermit crabs were responding to subtle differences among the periwinkle shells used, rather than to the presence of “large” *C. convexa*, we performed an additional experiment (Experiment Ic). We allowed the same naked hermit crabs used in Experiment Ib to choose again between the same two shells, except that we first removed all the “large” *C. convexa* from the shells before re-offering them to the hermit crabs. This experiment was otherwise identical with Experiment Ib. Hermit crab occupancy was examined periodically over 65 h.

2.6. Does the presence of “small” *C. convexa* affect shell selection by the hermit crabs?

Two experiments were conducted. In Experiment IIa, 20 naked hermit crabs were each offered a shell bearing a “small” *C. convexa* and a snail-free shell of the same size. The mean wet weight of the hermit crabs (± 1 S.D.) was 370 ± 210 mg and the mean wet weight of the “small” *C. convexa* (± 1 S.D.) was 20 ± 10 mg (average shell length = 4.84 ± 0.95 mm, mean ± 1 S.D.). This experiment lasted 30 h.

Experiment IIb was a repeat of Experiment IIa, except that we used only 18 of the 20 pairs of shells used in Experiment IIa. The other two pairs of shells were not used because the “small” *C. convexa* on the shells died between the two experiments. Newly

collected hermit crabs were tested to avoid potentially confounding effects of prior experience in the laboratory.

2.7. Do hermit crabs distinguish between intact shells bearing “large” *C. convexa* and drilled shells?

In Experiment III, each of nine naked hermit crabs was allowed to choose between an intact shell bearing “large” *C. convexa* (see Section 2.3) and a naturally drilled shell of the same size. In the field, individuals of *C. convexa* were never found covering the holes drilled by naticid snails (personal observation). The average wet weight of the snails tested (± 1 S.D.) was 300 ± 90 mg. All shells offered were of ideal size for the hermit crabs tested, based on hermit crab wet weight (Angel, 2000). The mean wet weight of the hermit crabs (± 1 S.D.) was 260 ± 80 mg. We examined the shells periodically over the next 30 h to determine which ones the crabs occupied.

2.8. Do individuals of *C. convexa* seek empty periwinkle shells as substrata?

This experiment examined whether individuals of *C. convexa* preferentially occupy empty periwinkle shells and if they do, whether they distinguish between intact shells and drilled shells. The mean shell length of tested snails (± 1 S.D.) was 3.76 ± 0.87 mm ($N=20$). Each snail was put in the center of a glass dish filled with seawater to a depth of 15 mm. Two empty periwinkle shells of the same size—one intact and the other with a hole drilled by a naticid snail—and a small rock of the same size were placed in each dish such that each was at the same distance from the *C. convexa* individual at the beginning of the experiment. The glass dishes had an inner diameter of 105 mm. The periwinkle shells had a mean shell length (± 1 S.D.) of 23.33 ± 2.58 mm. The snails were fed with excess phytoplankton (*I. galbana*) every day and water was changed every other day. The locations

Table 2

The proportion of hermit crabs (*P. longicarpus*) carrying individuals of *C. convexa* in 12 surveys conducted at Nahant, MA between 2000 and 2003

Date of survey	Number of crabs collected	Percentage of crabs carrying <i>C. convexa</i>
20 June 2000	338	13.6%
7 July 2000	970	8.4%
21 July 2000	818	7.9%
28 July 2000	623	6.3%
10 August 2000	860	4.1%
1 October 2000	460	14.1%
18 October 2000	260	19.2%
24 July 2001	850	7.3%
27 July 2001	1509	4.2%
22 August 2001	2062	4.0%
8 June 2003	415	4.3%
15 August 2003	365	5.6%
	Total = 9530	Mean = 8.3%

of the *C. convexa* snails (on intact periwinkle shell, on drilled periwinkle shell, on rock, or on dish) were recorded every day for a week.

2.9. Statistical analysis

Data from all shell selection experiments were analyzed using χ^2 goodness of fit tests, with the Yates continuity correction (Zar, 1999).

3. Results

3.1. Results from field surveys

Of the 9530 hermit crabs examined in the 12 surveys over three summers, the percentage of hermit crabs carrying at least one individual of *C. convexa* averaged $8.3 \pm 4.9\%$ (± 1 S.D.; Table 2). In the seven surveys conducted in the year 2000, 78% of the 381 hermit crabs that carried *C. convexa* carried one snail, 20.2% carried two snails, 1.6% carried three snails, and 0.2% carried four snails. Of the 171 hermit crabs carrying *C.*

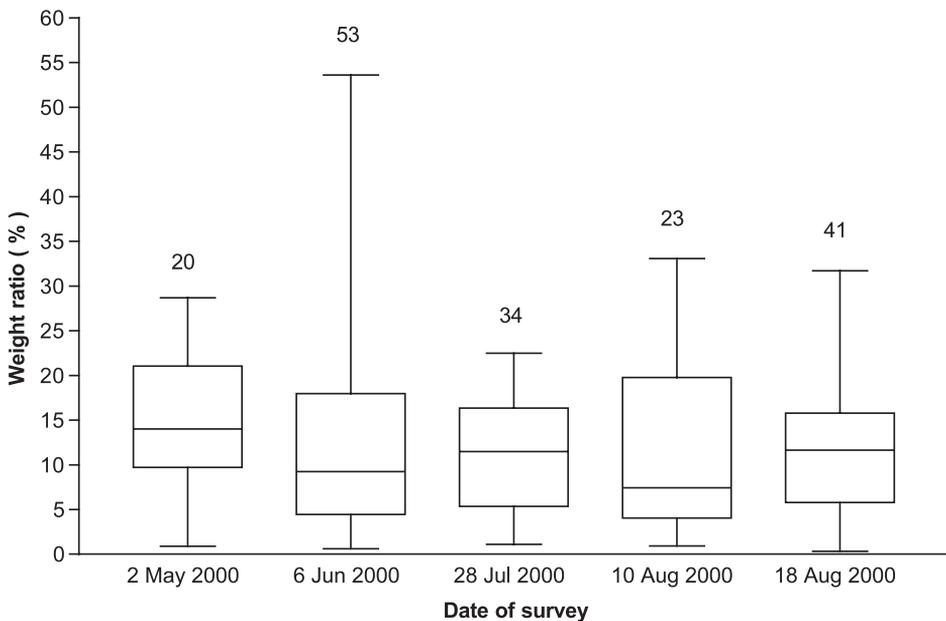


Fig. 1. Results of five surveys undertaken to discover the size of *C. convexa* snails relative to the sizes of the periwinkle shells they occupied at Nahant, MA. All shells examined contained hermit crabs (*P. longicarpus*) at the time of collection. “Weight ratio” refers to the total wet weight of all the snails on a periwinkle shell relative to the wet weight of that shell, $\times 100\%$. This is a box and whiskers graph. The upper edge of each box represents 75% percentile and the lower edge of each box represents 25% percentile. The horizontal line in the box is the median. The upper end of the whisker is the maximum and the lower end of the whisker is the minimum. The number above each box indicates sample size.

Table 3

Results of surveys conducted at Nahant, MA (a) on 8 June 2003 and (b) on 15 August 2003

	Shells occupied by hermit crabs	Live periwinkles	Empty periwinkle shells	Other hard substrates
<i>a</i>				
Total number examined	415	1245	46	NA
Number of <i>C. convexa</i> snails on this specific substrate	20	2	0	1
<i>b</i>				
Total number examined	365	833	169	NA
Number of <i>C. convexa</i> snails on this specific substrate	21	3	3	7

In each survey, we haphazardly collected *P. longicarpus*, *L. littorea*, and empty shells of *L. littorea* for 30 min and then spent 30 min examining other hard substrates for the presence of the snail *C. convexa*. NA=not applicable: different substrates varied substantially in surface area so that the total number examined is not informative.

convexa that were examined in five of the seven surveys in 2000, 39.1–75.0% bore “large” snails (Fig. 1).

Eighty-seven percent of the *C. convexa* snails collected on 8 June 2003 and 61.8% of those collected on 15 August 2003 were found on shells occupied by hermit crabs (Table 3).

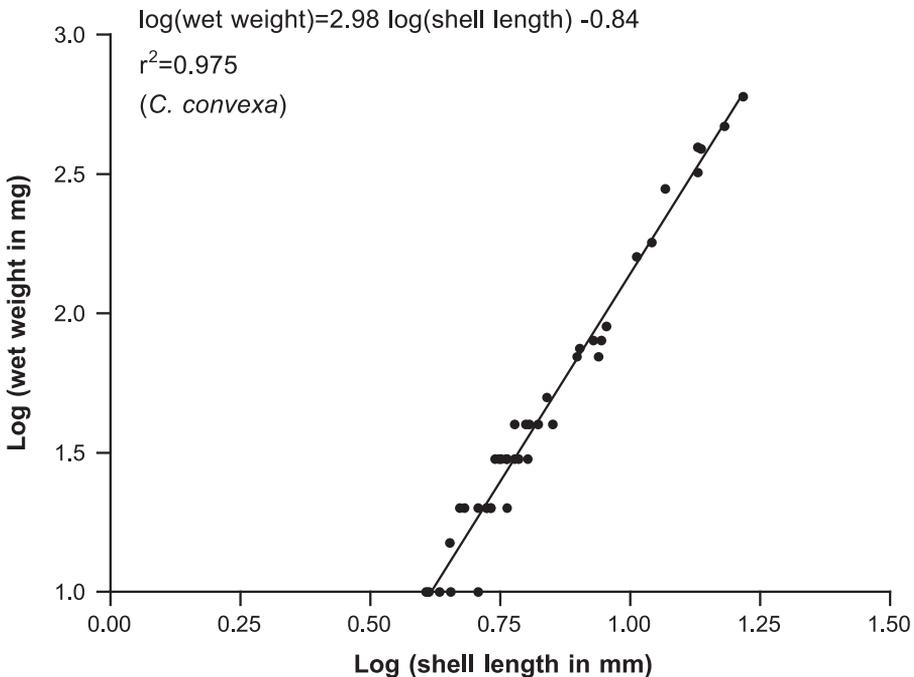


Fig. 2. The relationship between shell length and wet weight of 42 individuals of *C. convexa* collected from Nahant, MA in August 2003.

On average, only 0.26% of the live periwinkles inspected and 0.89% of the empty periwinkle shells inspected carried *C. convexa* snails, as opposed to 5.05% of shells occupied by hermit crabs. During the two 30 min searches for *C. convexa* on rocks and other hard substrates in the area from which we collected hermit crabs, periwinkles, and empty shells, only one and seven snails were found on these other substrates, compared to a mean of 20.5 snails on hermit crab-occupied shells.

3.2. Relationship between wet weight and shell length of field-collected *C. convexa* and empty periwinkle shells

There was a linear relationship between log (*C. convexa* wet weight) and log (*C. convexa* shell length) (test for zero slope: $F_{1,40} = 1534$; $p < 0.0001$; Fig. 2). There was also a linear relationship between log (periwinkle shell wet weight) and log (periwinkle shell length) (test for zero slope: $F_{1,89} = 1804$; $p < 0.0001$; Fig. 3).

3.3. The effect of “large” *C. convexa* on shell selection by the hermit crabs

In Experiment Ia (Table 1), 30 out of 34 hermit crabs switched from their initial shells bearing “large” *C. convexa* to shells of the same size bearing no *C. convexa*,

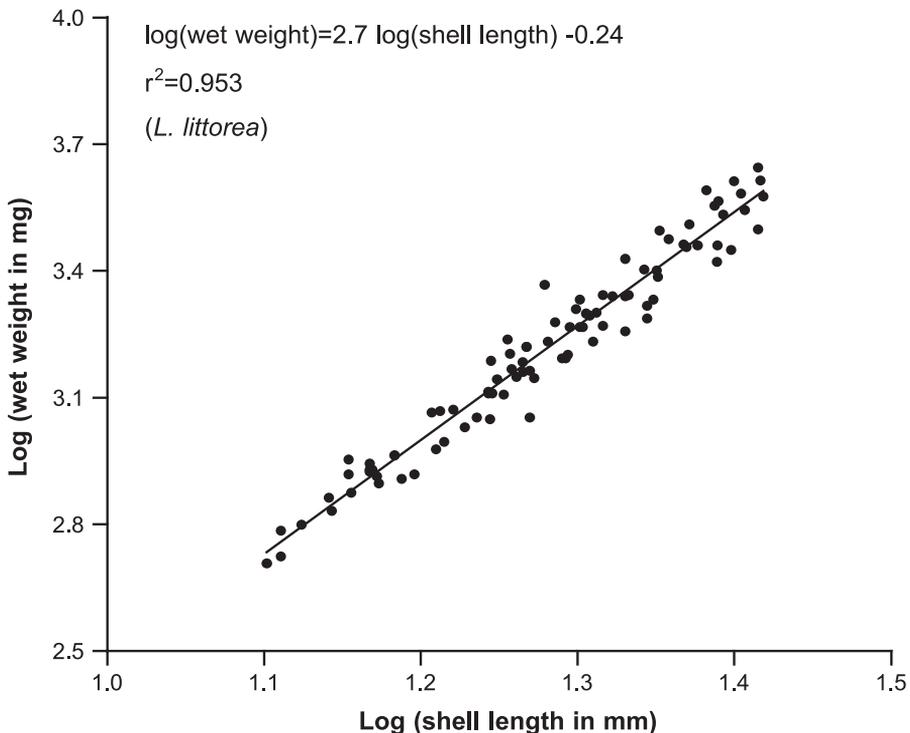
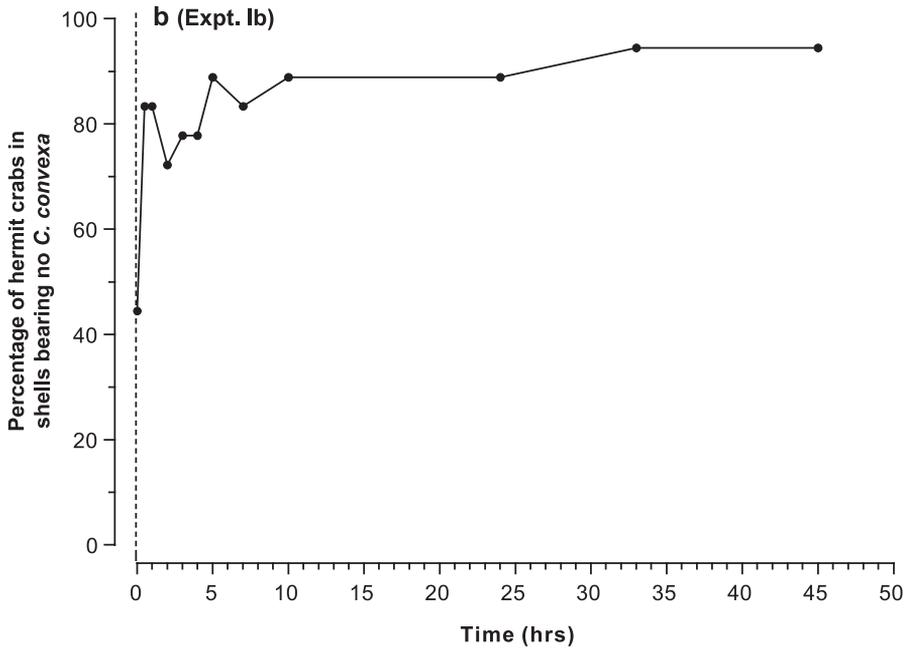
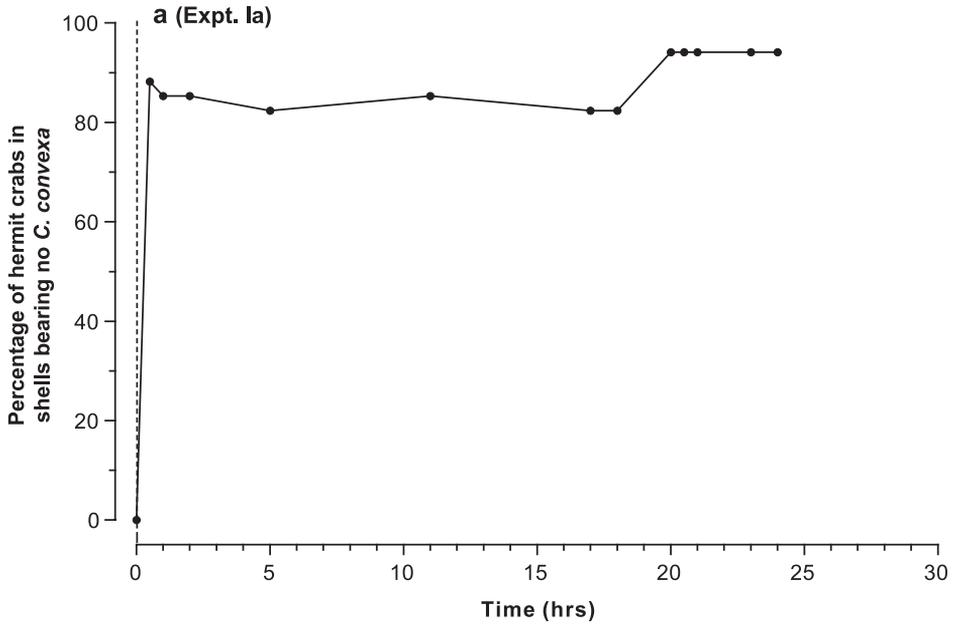


Fig. 3. The relationship between shell length and wet weight of intact, empty periwinkle shells (*L. littorea*) based on 91 shells collected from Nahant, MA in August 2003.

and did so within only 30 min after the experiment started (Fig. 4a). The percentage of hermit crabs found in shells without *C. convexa* stayed high during the rest of the experiment and stabilized by 20 h, at 94.1% (Fig. 4a). We therefore chose 24 h results



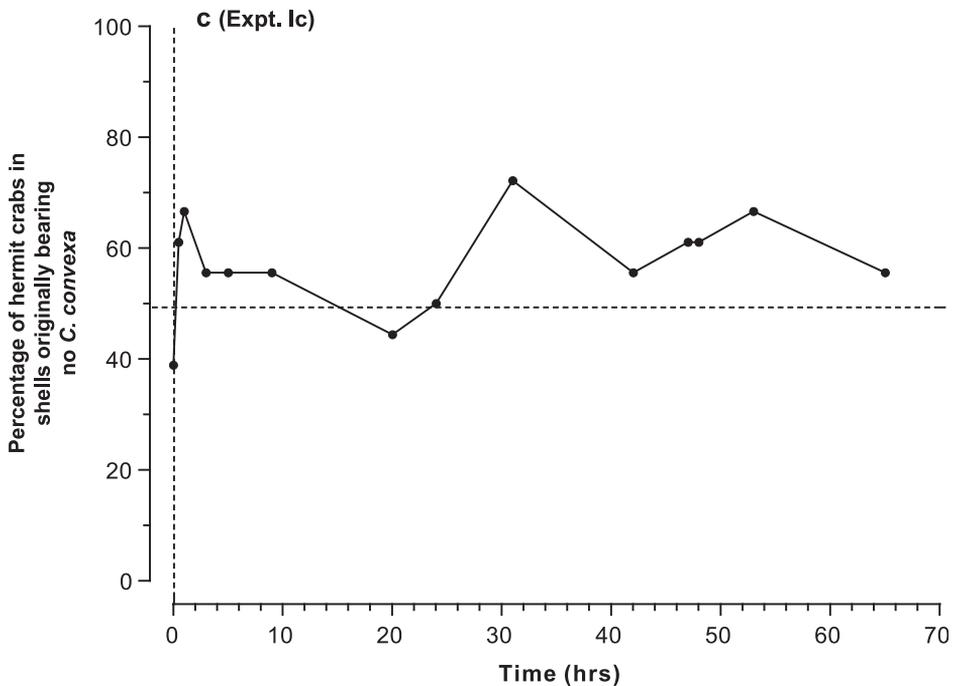


Fig. 4. Influence of “large” *C. convexa* on shell selection by the hermit crab *P. longicarpus*. (a) Each of 34 hermit crabs was given a choice between an intact shell bearing “large” *C. convexa* and an intact shell of the same size that bore no *C. convexa*. At the start of this experiment, the hermit crabs occupied shells bearing “large” *C. convexa*. (b) Each of 18 hermit crabs was given a choice between an intact shell bearing “large” *C. convexa* and an intact shell of the same size that bore no *C. convexa*. This experiment differed from that shown in (a) in that the hermit crabs were naked (i.e., without shells) at the beginning of the experiment. (c) Shell choices made by the same 18 naked hermit crabs (*P. longicarpus*) that were tested in Experiment Ib (b). This time they were re-offered the same pair of shells but only after the “large” *C. convexa* had been removed from one member of each pair.

for all statistical analyses: the hermit crabs in this experiment showed a significant tendency to switch out of shells bearing “large” *C. convexa* ($\chi^2=24.7$, $df=1$, $p<0.001$).

In Experiment Ib (Table 1), the naked hermit crabs initially moved into whichever shells they encountered first, so that about half the hermit crabs initially occupied shells bearing “large” *C. convexa*, while the other half initially occupied shells without *C. convexa* (Fig. 4b). The time hermit crabs took to find and enter the first shell varied from 9 s to 5 min. Within the next 30 min, however, most of the hermit crabs that initially occupied shells with “large” *C. convexa* switched to shells without *C. convexa* (Fig. 4b). By 24 h, significantly more hermit crabs ($N=16$) occupied shells without *C. convexa* than those with “large” *C. convexa* ($N=2$; $\chi^2=9.4$, $df=1$, $0.001 < p < 0.005$). Since the shells tested in this experiment had also been used in Experiment Ia, the hermit crabs’ apparent preference for shells without *C. convexa* in Experiment Ia did not simply reflect any tendency of hermit crabs to occupy newly offered shells.

3.4. Distinguishing between the effect of *C. convexa* and the periwinkle shell it occupied on hermit crab shell selection

In Experiment Ic (Table 1), the hermit crabs showed no significant preference for either of the two shells once the “large” *C. convexa* were removed (Fig. 4c). χ^2 values of all 14 observations at various times throughout the experiment ranged from 0.06 to 2.72 and p values of results from different time points were all >0.05 . Therefore, the shell choices documented in Experiments Ia and Ib must reflect the presence or absence of “large” *C. convexa*, rather than any subtle differences in the characteristics of the periwinkle shells themselves.

3.5. The effect of “small” *C. convexa* on shell selection by the hermit crabs

Results from Experiments IIa and IIb were nearly identical, so the data were pooled for statistical analysis (Zar, 1999). Hermit crabs did not discriminate between shells bearing “small” *C. convexa* and shells without *C. convexa* ($\chi^2=0.03$, $df=1$, $0.75 < p < 0.90$ for 24 h result). Data from Experiment IIa (Table 1) are shown in Fig. 5.

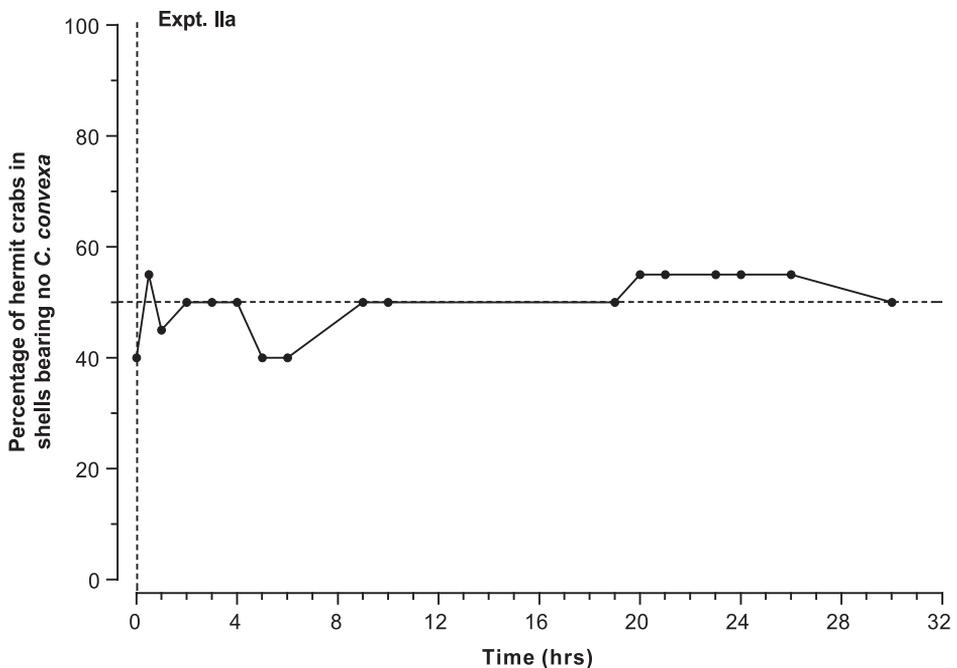


Fig. 5. Influence of “small” *C. convexa* on shell selection by the hermit crab *P. longicarpus*. Each of 20 naked hermit crabs was given a choice between an intact shell bearing a “small” *C. convexa* and an intact shell of the same size but bearing no *C. convexa*.

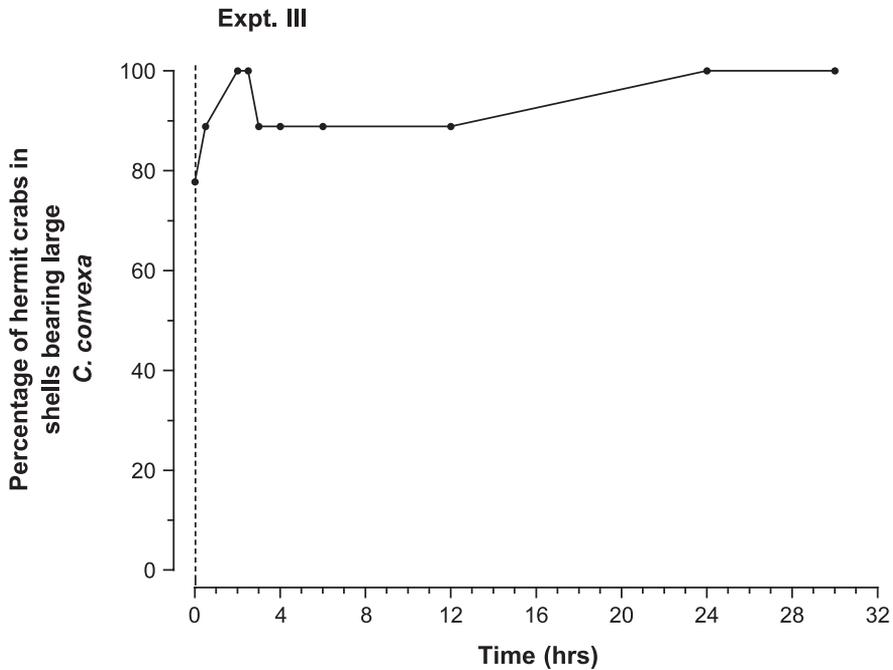


Fig. 6. The effect of drill holes on the discrimination by the hermit crab *P. longicarpus* between shells with and without “large” *C. convexa*. Each of nine hermit crabs was offered two shells of the same size. One shell was intact and bore “large” *C. convexa*, while the other shell bore no *C. convexa* and had been drilled by a naticid snail.

3.6. Hermit crab choice between intact shells bearing “large” *C. convexa* and drilled shells

Despite their dramatic avoidance of shells bearing “large” *C. convexa* (see Section 3.3), the hermit crabs significantly preferred such shells to drilled shells of the same size (Fig. 6). Within half an hour, all but one hermit crab were found in shells with “large” *C. convexa*, and by 24 h, all nine hermit crabs were found in shells with “large” *C. convexa* ($\chi^2 = 7.1$, $df = 1$, $0.005 < p < 0.01$).

3.7. Lack of preference of *C. convexa* individuals for empty periwinkle shells

By the end of the first day, only 2 individuals of *C. convexa* were found on the rock and 18 were found on the dish walls. None were found on the periwinkle shells. The same result was seen every day after that until the end of the experiment on day 7.

4. Discussion

A clear association between the snail *C. convexa* and the hermit crab *P. longicarpus* was seen in the 15 field surveys conducted at Nahant, MA. An average of 8.3% of the

hermit crabs collected (almost 20% in one survey) carried *C. convexa* snails. Most individuals of *C. convexa* found in the two surveys in 2003 were associated with hermit crabs. Karlson and Shenk (1983) found similar results with *C. fornicata* in their survey in Delaware Bay, DE—*C. fornicata* was significantly more prevalent on hermit crab (*Pagurus pollicaris*) occupied shells than on live or empty shells of *Busycon carica*. They also found that in the Thimble Islands, CT, *C. convexa*, *C. fornicata* and *C. plana* used hermit crab-occupied gastropod shells as their major substrata, with *C. convexa* being more commonly associated with the hermit crab *P. longicarpus* than with *P. pollicaris* (Shenk and Karlson, 1986). In our data, at least 39% of the *C. convexa* individuals collected on hermit crab (*P. longicarpus*) occupied shells were “large” (i.e., with a “weight ratio” >10%).

In marked contrast to the expectations based on the clear association of the snails and the crabs found in our field surveys, the hermit crabs tested in our laboratory experiments avoided shells with “large” *C. convexa* in favor of shells without snail symbionts. This apparent discrimination was not caused by the order in which the shells were offered or by any subtle differences among the periwinkle shells used, but rather directly by the presence of the “large” *C. convexa* (Fig. 4a–c). As with the individuals of *P. longicarpus* tested in our study, individuals of the hermit crab *P. pollicaris* rejected shells bearing individuals of *C. fornicata* when the snails weighed as much as the shell, but did not discriminate between shells with and without *C. fornicata* as long as the snail weighed less than 15% of the shell’s weight (Conover, 1976). This discrimination against large symbionts by *P. longicarpus* may reflect the increased energetic costs associated with carrying more weight: the terrestrial hermit crab *Coenobita compressus* consumed 50% more oxygen when carrying a shell than when living without a shell (Herreid and Full, 1986). Heavy shells might also decrease the locomotory ability of hermit crabs (Conover, 1976). Individuals of *P. longicarpus* may also avoid shells bearing “large” individuals of *C. convexa* because such symbionts probably alter the shell’s center of gravity (Conover, 1978). Individuals of *P. pollicaris* apparently value balance over protection from octopuses in determining where on their shells to place the sea anemone *Calliactis tricolor* (Brooks, 1989). Additional studies will be needed to distinguish between the relative importance of additional weight and altered center of gravity on shell choice by the hermit crab *P. longicarpus*.

In short, our laboratory results suggest that hermit crabs should not be found occupying shells with “large” individuals of *C. convexa* in the field, which was not the case (Fig. 1). Possibly the association begins when individuals of *C. convexa* are small: individuals of *P. longicarpus* did not discriminate between shells with and without “small” *C. convexa* (Fig. 5). However, this would not explain the observed association between hermit crabs and “large” individuals of *C. convexa* in the field, because once snails grew to a “large” size, the associated hermit crabs would clearly switch shells if more suitable shells were available. It is also unlikely that “large” individuals of *C. convexa* deliberately promote an association with hermit crabs (Karlson and Sullivan, 1989). In a field experiment (Karlson and Cariolou, 1982), individuals of *C. convexa* colonized shells of *Ilyanassa obsoleta* at comparable rates whether the shells were available for colonization by the hermit crab *P. longicarpus* or whether the shell apertures had been plugged. In the laboratory, *P. longicarpus* preys readily on *C. convexa*, so association with the hermit

crabs may increase predation risk for the snails. In our experiments, individuals of *C. convexa* did not preferentially occupy empty periwinkle shells, which hermit crabs could later move into, over other hard substrata. There might not be many empty periwinkle shells to colonize anyway, where there are sizable hermit crab populations, even if the snails did prefer to occupy them. Again, such behavior could not explain the observed distribution of *C. convexa* at our field site: hermit crabs would quickly switch to new shells once the current shells acquired a “large” individual of *C. convexa*.

It seems that neither member of the association goes out of its way to form the association, and one member of the association—the hermit crab—in fact preferentially avoids the association when the other member is of substantial size and weight. The association between the two species at Nahant must instead reflect the low availability of suitable shells that do not bear individuals of *C. convexa*. A large proportion of the empty periwinkle shells at our field site (up to 73% of all empty shells collected) exhibit conspicuous holes formed by naticid snails (Pechenik and Lewis, 2000; Pechenik et al., 2001). In our experiment, the hermit crabs consistently chose shells with “large” *C. convexa* over shells with drill holes. Thus, naticid snail predation upon periwinkles may be promoting, indirectly, a close relationship between hermit crabs and individuals of *C. convexa* at this field site.

The selective pressures against the occupancy of drilled shells by hermit crabs include increased vulnerability to decapod predators (e.g., the green crab, *Carcinus maenas*), increased ease of eviction by conspecifics, and increased susceptibility to low-salinity stress (Pechenik et al., 2001). The higher energetic and locomotory costs associated with occupying a shell bearing “large” *C. convexa* are apparently minor in comparison with the selective disadvantages of occupying a drilled shell. In consequence, large individuals of *C. convexa* at the Nahant field site may obtain benefits from their association with hermit crabs (e.g., increased dispersal potential, better feeding opportunities, and protection from burial—Hendler and Franz, 1971; Stachowitsch, 1980) that they do not obtain at field sites offering a greater availability of high quantity shells. However, they might also encounter higher predation risk when associated with the hermit crabs, since the hermit crabs prey readily on the snails (personal observation). Therefore, the overall outcome of this association with hermit crabs for the snails is still unclear.

The presumably increased dispersal potential of *C. convexa* that is mediated at this site by its association with hermit crabs may have important population-level genetic consequences, considering that this species lacks dispersive larvae (Hendler and Franz, 1971); in particular, hermit crab-mediated transport of the snails may decrease the likelihood that close relatives encounter each other as adults and, therefore, may decrease the potential for inbreeding in this population. This will be the subject of a future report.

Our results may have implications for the evolution of symbiotic relationships. Symbiotic relationships are usually brought about by the deliberate behavior of at least one of the members of the association (e.g., Allee et al., 1949; Ross, 1971). A well recognized association such as the one we report here between hermit crabs and individuals of the snail *C. convexa*, in which neither party prefers to live with the other and which is instead apparently promoted by the actions of a third party, is certainly rare; in fact, we believe that such an influence by a third party has not been previously reported.

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