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ORIGINAL ARTICLE

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Shell choice in *Pagurus longicarpus* hermit crabs: does predation threat influence shell selection behavior?

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Abstract *Pagurus longicarpus* hermit crabs depend on empty gastropod shells for protection against predation. Hermit crabs avoid gastropod shells in which holes have been drilled by naticid gastropods, and hermit crabs forced to occupy drilled shells are more vulnerable to predation by green crabs, *Carcinus maenas*. In this study, we examined the effect of predator cues on *P. longicarpus* shell investigation behavior and shell choice. In paired laboratory shell choice trials, we examined hermit crab response to green crab chemical cues. We compared hermit crabs from two sites differing in the percentage of *Littorina littorea* shells with drill holes. The percentage of time hermit crabs spent occupying intact shells increased significantly in the presence of predator cues. The effect of predator cues on the amount of time hermit crabs spent investigating shells differed between individuals from the two sites. Predator effluent had a marginal effect on the proportion of hermit crabs initially choosing intact shells and within 15 min most hermit crabs in both treatments occupied intact shells due to shell switching. These results indicate that predation cues alter *P. longicarpus* shell choice behavior favoring intact shells, which provide greater protection. In summary, predation appears to be a key factor influencing hermit crab shell selection behavior.

Keywords Behavioral plasticity · Predation risk · Shell selection behavior

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Introduction

Hermit crabs occupy empty gastropod shells, and these shells act as shelters from biotic factors including predation (Kuhlmann 1992; Angel 2000), and abiotic factors such as desiccation (Taylor 1981; Brodie 1999) and osmotic stress (Shumway 1978; Pechenik et al. 2001). Particular gastropod shells are non-randomly chosen based on shell characteristics that optimally match requirements of individual hermit crabs (Reese 1963; Conover 1978; Brooks and Mariscal 1985; McClintock 1985; Cote et al. 1998). Shell choice occurs following shell investigation, which can vary depending on hermit crab condition and gastropod shell quality (Elwood and Stewart 1985; Elwood 1995; Elwood and Briffa 2001). These portable shell habitats are exchanged frequently for new shells as hermit crabs grow, thus shell choice behavior continues to be important throughout the lifetime of a hermit crab (Reese 1962; Hazlett 1981).

The Atlantic long-wristed hermit crab, *Pagurus longicarpus* (Say 1817), commonly occupies shells of the periwinkle, *Littorina littorea,* which are vacated following natural death or predation. Naticid gastropods kill *L. littorea* by drilling an access hole through the shell, and such drilled shells dominate the population of vacant shells available for *P. longicarpus* in some populations (Pechenik and Lewis 2000). Shell availability has long been known to influence hermit crab populations (Scully 1979, 1983; Blackstone 1985; Carlon and Ebersole 1995). Yet, despite scarcity of available shells, *P. longicarpus* avoids drilled or damaged shells to the point of sacrificing ideal shell thickness and size (McClintock 1985; Wilber 1990; Pechenik and Lewis 2000).

Predator-induced changes in prey behavior may have important implications for prey population dynamics and community interactions (Trussell et al. 2002). While behavioral plasticity in response to predator cues has been demonstrated for many species (Van Buskirk 2002; Relyea 2003), the impact of predator risk on hermit crab shell choice has not been addressed. Tropical hermit crabs gain protection from shell-crushing crab predators by

their preference for gastropod shells with protective structural traits, such as shell thickness and small aperture size (Bertness 1981; Bertness and Cunningham 1981). In the northeastern United States, the invasive green crab predator, *Carcinus maenas,* preys upon hermit crabs (Ropes 1968; Elner 1981). These predators use existing structural damage, including drill holes, to break open gastropod shells and gain access to hermit crab inhabitants (Pechenik et al. 2001). As a result, *P. longicarpus* hermit crabs inhabiting drilled gastropod shells are more vulnerable to green crab predation than hermit crabs occupying intact shells (Pechenik et al. 2001). Taken together, these studies suggest that hermit crabs would have an advantage if they were able to assess predation risks and alter their shell choice behavior to reduce vulnerability to potential predators.

In this study, we investigated whether *P. longicarpus* hermit crabs respond to increased predation risk by modifying their shell choice behavior. In addition, since previous studies have demonstrated both morphological and behavioral differences among hermit crab populations (Benvenuto and Gherardi 2001), we compared *P. longicarpus* from two sites differing in drilled shell availability. In laboratory trials, individual crabs were presented with a choice of drilled versus intact *L. littorea* shells in the presence and absence of chemical cues from *C. maenas* predators.

Methods

Hermit crab collection and maintenance

P. longicarpus hermit crabs inhabiting *L. littorea* shells were collected from two sites along the Massachusetts coastline: Long Beach, Nahant (42°25.5′N, 70°55.1′W) and West Beach, Beverly (42°33.5′N, 70°52.8′'W) in May and June 2002. Although *L. littorea* represents the most common shell type inhabited by *P. longicarpus* at both sites, the two sites differ in the frequency of drilled *L. littorea* shells. Drilled shells represent up to 73% of all vacant *L. littorea* shells at Nahant (with some seasonal variation; Pechenik and Lewis 2000), while drilled shells represent only ~14% of all vacant *L. littorea* shells at the Beverly site (based on 100 vacant shells haphazardly collected on 8 May 2002). The predatory green crab, *C. maenas,* occurs at both sites (we were unable to locate sites with *P. longicarpus* but lacking *C. maenas*).

Approximately 100 hermit crabs were collected from each site on each of three collection dates, represented by blocks as described below. Ovigerous females (evident by the presence of egg masses) were not used for this study and were returned to their original location. Hermit crabs were maintained in 75.8-l (20-gallon) aquaria in Instant Ocean seawater (27–32 ppt salinity, ~22°C) at a density of ~60 hermit crabs per tank. Hermit crabs were held for 1 week prior to experimentation and were fed imitation crab meat (pollock).

Prior to the experiment, hermit crabs were removed from their shells by pulling them as gently as possible, and were then placed in individual 100 ml containers with seawater for 24 h. For this experiment, only intact individuals with both chelipeds and all legs (~90% of crabs extracted) were used since tactile cues are likely to be important for shell investigation and selection (Reese 1963; Scully 1986). Wet mass was measured for each crab, and optimal *L. littorea* shell size was determined using the equation developed for *P. longicarpus* (Angel 2000): log(shell aperture length in mm)=0.2623(log crab mass inmg)+0.4342

For each crab, two similarly-sized *L. littorea* shells, one with a natural drill hole and one intact, were identified: these shells were within 0.3 mm of the optimal aperture size. Before being used in experiments, shells were soaked in hydrogen peroxide for 15 min to remove organic residues, and then soaked in freshwater for 24 h. Only shells with no visible defects (other than drill holes) were used.

Experimental conditions

To investigate whether *P. longicarpus* shell choice behavior changed in the presence of predator cues, we conducted tests with each crab in both predator effluent (green crab-conditioned seawater) and normal seawater. Predator effluent was obtained by keeping six *C. maenas* collected from Beverly (weight range 1–16 g, mean=6.2 g) in 8.5 l Instant Ocean for 48–72 h. Green crabs were fed imitation crab meat (identical to hermit crab diet) until approximately 48 h before the experiment. Mechanisms for shell selection using sensory information have previously been explored in hermit crabs (Reese 1963; Hazlett 1981). Chemical cues may be used by hermit crabs for predation risk assessment (Hazlett 1996, 1997; Rittschof and Hazlett 1997), shell discrimination (Hazlett 1982), attraction to gastropod predation sites (McLean 1974; Rittschof 1980; Hazlett 1996, 1997), and attraction to dead conspecifics (Rittschof et al. 1992; Hazlett 1996). Based on these previous studies, we used seawater with green crab effluent as a predation threat in this experiment.

After 24 h of isolation, naked hermit crabs were each transferred to rectangular 8×12-cm opaque plastic arenas containing 120 ml predator effluent or control seawater. Each hermit crab was offered a drilled and an intact *L. littorea* shell, matched to individual crab wet mass as described above. Shells were approximately 8 cm apart, and the crab was placed equidistant from the two shells. Crabs were observed continuously for 15 min, during which behaviors were recorded using The Observer 3.0 software (Noldus Technology). For each crab, the following behaviors were recorded: the number of contacts with each shell type (drilled and intact), the duration of shell investigation (in seconds) for each shell type, and the number of times (and duration) a crab occupied each shell type. The experimental design was paired, such that each hermit crab (64 from Nahant, 59 from Beverly)

experienced predator effluent and control treatments in random order. Crabs were removed from their shells following each 24-h trial and again isolated for 24 h before starting the next treatment. Following behavioral observations, crabs remained in their arenas and final shell choice was recorded after 24 h.

Data analysis

We separately measured (in seconds) the duration of initial shell investigation by naked crabs and the duration of continued investigations by crabs already in shells. Latency to shell occupancy was calculated as the time it took for each naked crab to move into a shell. Total duration of shell occupancy in either shell was calculated as the sum of time each crab spent occupying either shell, and this was expressed as a percentage of the 15-min observation period. Intact shell occupancy was calculated as the percentage of the total shell occupancy duration that a crab spent in the intact shell. We also analyzed shell-switching, the number of times hermit crabs switched between the two shells. Finally, shell choice was examined by comparing the number of hermit crabs occupying intact versus drilled shells at three time points: initial (first shell occupied), at 15 min, and after 24 h. For the analysis of latency to shell occupancy, intact shell occupancy, and shell-switching behavior, hermit crabs remaining naked for the entire trial were excluded.

We compared shell investigation and occupancy behavior of hermit crabs between predator effluent and control treatments using paired *t*-tests to control for between-crab variability. To check for any block effects (three hermit crab collection dates) or site by predation treatment interactions, we also used repeated measures ANOVAs that included block, site, and predation treatment as a repeated measure. As there were no significant block effects, we removed blocks from the statistical model. Data were examined to check assumptions of each analysis. We report paired *t*-tests within sites when comparing the behavior of the same crabs with and without predator cues, and we report repeated measures ANOVAs when examining possible predator × site interactions. To account for the fact that naked crabs generally investigated only one shell before entering it (thus spending no time investigating the alternate shell from a naked state), investigation times of zero were eliminated: a repeated measures ANOVA was thus conducted on the subset of crabs that investigated the same shell in both predator effluent and control treatments.

To determine if predator effluent altered hermit crab shell choice, we used contingency table tests of heterogeneity to compare the proportion of crabs occupying intact versus drilled shells between treatments. All statistical analyses were conducted using Systat 10 (SPSS).

Results

Shell investigation

Overall, hermit crabs spent approximately twice as much time investigating intact shells as drilled shells (Fig. 1). Exposure to predator effluent did not significantly alter the total amount of time hermit crabs spent investigating drilled shells (Fig. 1; Beverly paired t=1.70, df=58, P=0.09; Nahant paired t=0.67, df=62, P=0.51). When investigating intact shells, hermit crabs from the two sites responded differently to predator effluent: Nahant hermit crabs spent more time investigating intact shells in the presence of predator effluent, whereas Beverly hermit crabs showed the opposite behavior (Fig. 1; repeated measures ANOVA predator × site interaction $F_{1,117}$=5.29, P=0.023).

We also partitioned shell investigation behavior into time spent by naked crabs investigating either shell type, and time spent in continued investigation by crabs already in shells. There was no effect of predator effluent on the time naked crabs spent investigating drilled or intact shells (Tables 1, 2). However, there was a significant predator × site interaction for naked crabs investigating drilled shells (Table 2); crabs from the Beverly site that were exposed to predator effluent spent more time investigating drilled shells (Table 1).

Shell occupancy

The percentage of the 15-min observation period that hermit crabs spent in either shell did not differ between predator effluent and control treatments (Fig. 2i, Beverly paired t=0.04, df=58, P=0.965; Nahant paired t=1.03, df=63, P=0.306). Interestingly, across both sites hermit crabs spent significantly more time in intact shells in the presence of predator effluent compared to control treatments (Fig. 2ii; repeated measures ANOVA, predation treatment $F_{1,82}$=10.18, P=0.002). This difference was

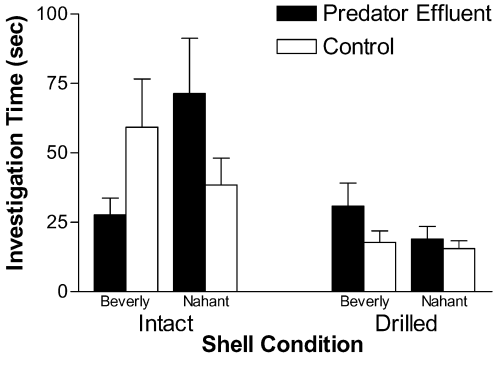

Fig. 1 Investigation times (s) by *P. longicarpus* hermit crabs of intact and drilled *L. littorea* shells in predator effluent versus control treatments during 15-minute observation periods. Means+1 SE are represented for hermit crabs from two different populations

Table 1 Comparison of *P. longicarpus* behavior between predator effluent and control treatments. Latency to occupy either of two *L. littorea* shells and the number of times hermit crabs switched between them was measured during 15-min observation periods for crabs from two sites. Shell investigation time by naked crabs and the duration of continued investigations by crabs already in shells were measured separately during the observation period

Behavior	Site	*n*	Predator effluent (mean±SE)	Control (mean±SE)
Latency (s)	Beverly	53	141.6±22.7	133.8±22.3
	Nahant	57	114.2±18.6	123.3±15.9
No. of switches in 5 min	Beverly	52	0.4±0.1	0.5±0.1
	Nahant	57	0.4±0.1	0.4±0.1
Shell investigation time (s)				
Drilled shell by naked crabs	Beverly	15	50.7±27.6	16.7±10.4
	Nahant	22	8.7±2.7	15.1±3.8
Intact shell by naked crabs	Beverly	14	9.1±3.1	64.9±59.3
	Nahant	21	52.6±41.4	8.3±3.1
Drilled shell by crabs in intact shell	Beverly	59	10.6±3.3	16.6±4.8
	Nahant	65	13.5±4.3	6.9±2.4
Intact shell by crabs in drilled shell	Beverly	59	19.9±6.1	36.2±10.9
	Nahant	65	31.7±8.9	30.6±9.5

Table 2 Statistical analysis of *P. longicarpus* behavior for naked hermit crabs initially investigating drilled or intact *L. littorea* shells, and for further investigation once crabs have entered either shell type. Reported *F* and *P*-values based on repeated measures ANOVAs for behavioral differences with and without predator cues (predator effect), differences between two sites, and interaction effects. For the naked crab investigations: *df*=1,35 drilled; *df*=1,33 intact; for all investigations from either shell type: *df* =1,122

Shell investigation of:	*F*	*P*
Drilled shell by naked crabs		
Predator effect	2.716	0.108
Site effect	1.992	0.167
Predator × site interaction	5.827	0.021*
Intact shell by naked crabs		
Predator effect	0.027	0.871
Site effect	0.035	0.853
Predator × site interaction	2.013	0.167
Drilled shell by crabs in intact shell		
Predator effect	0.005	0.945
Site effect	0.721	0.397
Predator × site interaction	3.153	0.078
Intact shell by crabs in drilled shell		
Predator effect	0.859	0.356
Site effect	0.097	0.755
Predator × site interaction	1.112	0.294

* Significant at the 0.05 level

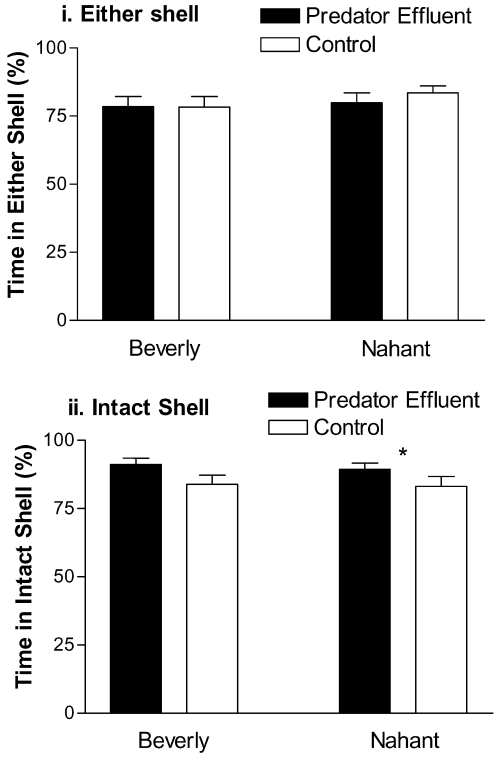

Fig. 2 Percentage time that *P. longicarpus* hermit crabs in predator effluent versus control treatments spent occupying *L. littorea* shells (does not include naked crabs). Means+1 SE are represented for hermit crabs from two different sites. *i* Percentage of 15-min observation time spent occupying either shell (Beverly *n*=59, Nahant *n*=64). *ii* Percentage time spent occupying intact shells out of total time spent in either shell (Beverly *n*=44, Nahant *n*=43). *Asterisks* indicate probability <0.05

most pronounced at the Nahant site (Beverly paired *t*=1.81, *df*=43, *P*=0.077; Nahant paired *t*=2.37, *df*=43, *P*=0.022).

There was no difference in the amount of time taken for hermit crabs to occupy either shell (latency) between the predator effluent and control treatments (Table 1; Beverly paired *t*=0.77, *df*=52, *P*=0.440, Nahant paired *t*=0.33, *df*=56, *P*=0.743). Once hermit crabs initially occupied a shell, we examined the number of times they switched to occupy the other shell, which ranged from zero to three, and was not affected by predator effluent at either site (Table 1; Beverly paired *t*=1.12, *df*=51, p=0.266 Nahant paired *t*=0.65, *df*=56, *p*=0.517).

Shell choice

More hermit crabs initially chose intact shells in the predator effluent compared to the control treatment; this difference was not statistically significant (data combined for both sites, 2×2 test of homogeneity, *G*=3.65, *df*=1, *P*=0.056). At the end of the 15-min observation period, a large percentage of hermit crabs in both treatments had moved into intact shells (Table 3). This percentage did not differ between the two treatments (2×2 test of homoge-

Table 3 Effect of predator effluent on the number of *P. longicarpus* hermit crabs occupying drilled or intact *L. littorea* shells, or remaining naked, at three different time points: initially (first shell occupied), at 15 min, and at 24 h

	Crabs in drilled shells	Crabs in intact shells	Naked crabs	% crabs in intact shells
Initial shell choice				
Predator effluent	49	65	9	57.02
Control	65	52	6	44.40
Shell choice at 15 min				
Predator effluent	15	98	10	86.73
Control	17	100	6	85.47
Shell choice at 24 h				
Predator effluent	7	116	0	94.31
Control	4	119	0	96.75

neity, G=0.076, df=1, P=0.783). After 24 h, nearly all hermit crabs occupied intact shells and again there was no difference between the two treatments (2×2 test of homogeneity, G=0.867, df=1, P=0.352).

Discussion

This study shows that effluent of the invasive predatory green crab, *C. maenas*, influences *P. longicarpus* assessment and choice of drilled versus intact *L. littorea* shells. We found that hermit crabs spent significantly more time occupying intact shells in the presence of predator effluent than they did in control treatments (Fig. 2ii), indicating that hermit crabs modify their shell selection behavior in the face of predation risk. Overall, hermit crabs spent less time investigating drilled shells than intact shells (Fig. 1), suggesting that drilled shells are relatively quickly identified and then avoided by hermit crabs. Previous studies have shown that *P. longicarpus* hermit crabs avoid shells with damage, including holes drilled by naticid gastropods, and prefer to occupy shells of suboptimal fit (McClintock 1985; Wilber 1990; Pechenik and Lewis 2000). *P. longicarpus* hermit crabs forced to occupy drilled shells are more vulnerable to predation, as *C. maenas* exploit drill holes to gain access to hermit crab inhabitants (Pechenik et al. 2001). Green crabs attack hermit crabs in drilled shells by enlarging the drill hole until they can remove the hermit crab from its shell. However, hermit crabs can survive attacks by predatory green crabs; in laboratory predation trials, 25% of hermit crabs in drilled shells remained alive after 24 h (Pechenik et al. 2001). Thus, hermit crab preference for intact shells may result from intense selection against hermit crabs occupying drilled shells.

Our results indicate that predator cues did not affect hermit crab shell switching behavior or the percentage of hermit crabs that occupied intact shells at 15 min or 24 h. This is consistent with previous research which has shown that *P. longicarpus* switch into preferred shells, even in the presence of other predators (Brooks and Mariscal 1985). Our results are also consistent with previous studies showing strong avoidance by *P. longicarpus* of drilled *L. littorea* shells (Pechenik and Lewis 2000).

Shell investigation behavior by hermit crabs varied between two sites. Predator cues increased the amount of time that Nahant hermit crabs spent investigating intact *L. littorea* shells, whereas the opposite occurred in Beverly hermit crabs (Fig. 1). One possible explanation for this is that these sites differ in the availability of intact shells. Among vacant *L. littorea* shells, intact shells are rare at Nahant (20–30%; Pechenik and Lewis 2000), while much more common (86%) at Beverly. As a result, *P. longicarpus* hermit crabs from Nahant are likely to have encountered few intact shells and therefore increased investigation of intact shells might be necessary to confirm shell condition. *P. longicarpus* from Beverly showed reduced investigation of intact shells when exposed to predator effluent, perhaps because predation threat reduces exploratory behavior in general. Interestingly, naked crabs from the Beverly site that were exposed to predator effluent spent more time investigating drilled shells (Table 1). This might be due to crabs with more limited experience with drilled shells taking longer to assess a shell before eventually accepting or rejecting it. An alternate explanation for the observed predator by site interaction might be a difference in the risk of predation by green crabs between sites.

Previous comparisons of hermit crabs from different populations have demonstrated both morphological and behavioral plasticity (Benvenuto and Gherardi 2001). Shell choice behavior of *P. longicarpus* from different populations differed in response to shell availability (Scully 1979). The different responses to predator threat observed in this study suggest that crabs from different *P. longicarpus* sites may differ in their motivation to find optimal shells, perhaps influenced by their prior experience with the disadvantages of occupying drilled shells.

These results suggest that predation threats may be a key determinant of hermit crab shell investigation and choice behavior. The green crab *C. maenas* has likely been an important predator of hermit crabs throughout the Atlantic rocky intertidal in Europe, and in the United States as well, following its multiple introductions over the past 150 years (Grosholz and Ruiz 1996). Despite the brevity of their local co-occurrence, our data show that *P. longicarpus* hermit crabs recognize chemical cues from *C. maenas* effluent and modify their shell investigation behavior in response. Future studies might further inves-

tigate *P. longicarpus* response to *C. maenas* or other crab predators by exploring how differences in hermit crab early experience with predators and shell availability affect shell choice behaviors.

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References

Angel JE (2000) Effects of shell fit on the biology of the hermit crab *Pagurus longicarpus* (Say). J Exp Mar Biol Ecol 243:169–184

Benvenuto C, Gherardi F (2001) Population structure and shell use in the hermit crab, *Clibanarius erythropus*: a comparison between Mediterranean and Atlantic shores. J Mar Biol Assoc UK 81:77–84

Bertness MD (1981) Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. Ecology 62:411–425

Bertness MD, Cunningham CW (1981) Crab shell-crushing predation and gastropod architectural defense. J Exp Mar Biol Ecol 50:213–230

Blackstone NW (1985) The effects of shell size and shape on growth and form in the hermit crab *Pagurus longicarpus*. Biol Bull 168:75–90

Brodie R (1999) Ontogeny of shell-related behaviors and transition to land in the terrestrial hermit crab *Coenobita compressus* H. Milne Edwards. J Exp Mar Biol Ecol 241:67–80

Brooks WR, Mariscal RN (1985) Shell entry and shell selection of hydroid-colonized shells by three species of hermit crabs from the northern Gulf of Mexico. Biol Bull 168:1–17

Carlon DB, Ebersole JP (1995) Life-history variation among three temperate hermit crabs: the importance of size in reproductive strategies. Biol Bull 188:329–337

Conover MR (1978) The importance of various shell characteristics to the shell-selection behavior of hermit crabs. J Exp Mar Biol Ecol 32:131–142

Cote IM, Reverdy B, Cooke PK (1998) Less choosy or different preference? Impact of hypoxia on hermit crab shell assessment and selection. Anim Behav 56:867–873

Elner RW (1981) Diet of green crab *Carcinus maenas* (L.) from Port Herbert, southwestern Nova Scotia. J Shellfish Res 1:89–94

Elwood RW (1995) Motivational change during resource assessment by hermit crabs. J Exp Mar Biol Ecol 193:41–55

Elwood RW, Briffa M (2001) Information gathering and communication during agonistic encounters: a case study of hermit crabs. Adv Study Behav 30:53–97

Elwood RW, Stewart A (1985) The timing of decisions during shell investigation by the hermit crab, *Pagurus bernhardus*. Anim Behav 33:620–627

Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced species: lessons from the multiple invasions of the European green crab. Biol Conserv 78:59-66

Hazlett BA (1981) The behavioral ecology of hermit crabs. Annu Rev Ecol Syst 12:1–22

Hazlett BA (1982) Chemical induction of visual orientation in the hermit crab *Clibanarius vittatus*. Anim Behav 30:1259–1260

Hazlett BA (1996) Organisation of hermit crab behaviour: responses to multiple chemical inputs. Behaviour 133:619–642

Hazlett BA (1997) The organisation of behaviour in hermit crabs: responses to variation in stimulus strength. Behaviour 134:59–70

Kuhlmann ML (1992) Behavioral avoidance of predation in an intertidal hermit crab. J Exp Mar Biol Ecol 157:143–158

McClintock TS (1985) Effects of shell condition and size upon the shell choice behavior of a hermit crab. J Exp Mar Biol Ecol 88:271–285

McLean RB (1974) Direct shell acquisition by hermit crabs from gastropods. Experientia 30:206–208

Pechenik JA, Lewis S (2000) Avoidance of drilled gastropod shells by the hermit crab *Pagurus longicarpus* at Nahant, Massachusetts. J Exp Mar Biol Ecol 253:17–32

Pechenik JA, Hsieh J, Owara S, Wong P, Marshall D, Untersee S, Li W (2001) Factors selecting for avoidance of drilled shells by the hermit crab *Pagurus longicarpus*. J Exp Mar Biol Ecol 262:75–89

Reese ES (1962) Shell selection behaviour of hermit crabs. Anim Behav 10:347–360

Reese ES (1963) The behavioral mechanisms underlying shell selection by hermit crabs. Behaviour 21:78–126

Relyea RA (2003) How prey respond to combined predators: A review and an empirical test. Ecology 84:1827–1839

Rittschof D (1980) Chemical attraction of hermit crabs and other attendants to simulated gastropod predation sites. J Chem Ecol 6:103–118

Rittschof D, Hazlett BA (1997) Behavioural responses of hermit crabs to shell cues, predator haemolymph, and body odour. J Mar Biol Assoc UK 77:737–751

Rittschof D, Tsai DW, Massey PG, Blanco L, Kueber GL Jr, Haas RJ (1992) Chemical mediation of behavior in hermit crabs alarm and aggregation cues. J Chem Ecol 18:959–984

Ropes JW (1968) The feeding habits of the green crab, *Carcinus maenas* (L.). Fish Bull 67:183–203

Scully EP (1979) The effects of gastropod shell availability and the habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. J Exp Mar Biol Ecol 37:139–152

Scully EP (1983) The effects of shell availability on intraspecific competition in experimental populations of the hermit crab *Pagurus longicarpus*. J Exp Mar Biol Ecol 71:221–236

Scully EP (1986) Shell investigation behavior of the intertidal hermit crab *Pagurus longicarpus*. J Crustac Biol 6:749–756

Shumway SE (1978) Osmotic balance and respiration in hermit crab, *Pagurus bernhardus*, exposed to fluctuating salinities. J Mar Biol Assoc UK 58:869–876

Taylor PR (1981) Hermit crab fitness: the effect of shell condition and behavioral adaptations on environmental resistance. J Exp Mar Biol Ecol 52:205–218

Trussell GC, Ewanchuk PJ, Bertness MD (2002) Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecol Lett 5:241–245

Van Buskirk J (2002) Phenotypic lability and the evolution of predator-induced plasticity in tadpoles. Evolution 56:361–370

Wilber TPJ (1990) Influence of size species and damage on shell selection by the hermit crab *Pagurus longicarpus*. Mar Biol 104:31–40