



Shell dynamics and microhabitat selection by striped legged hermit crabs, *Clibanarius vittatus* (Bosc)

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Abstract

Hermit crabs respond to odors signaling potential shell availability by (1) withdrawing if they are in relatively large shells; (2) fleeing if the shells are ones they would occupy if given choices; (3) investigating if the shells occupied are relatively small. We used these behavioral responses as measures of shell fit to assess shell resources of *Clibanarius vittatus* (Bosc). From analysis of responses we conclude shell resources are dynamic. Behavioral tests suggest many crabs occupied relatively large shells in the spring and relatively small shells in the fall. Crabs in shells in which they would remain when presented with excess shells never comprised more than 30% of the population at any time of the year. Behavior of subpopulations of crabs from sand/mud and oyster reef habitats and crabs on land or in water at low tide was determined. In the fall, crabs whose behavior indicated they occupied relatively small shells for their size were found mainly in sand/mud habitats and remained in the water at low tide. Crabs whose behavior suggested shells they occupied that fit well were rare. The few that were found were found mainly in sand/mud habitats and were equally distributed on land and water. Crabs behaving as if shells were large for their size were found distributed evenly throughout oyster reef and sand/mud habitats and on both land and in water at low tide. Distributional results could not be explained by reduced mobility. Movement studies showed that even crabs in weighted shells should not be trapped by a receding tide. We postulate crab habitat choice is a behavioral adjustment that compensates for imperfect shell fit.

Keywords: Behavior; Habitat selection; Hermit crab; Shell resource assessment

1. Introduction

Literature on hermit crabs (Reviews, Hazlett, 1981a; Scully, 1983; Elwood &

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Neil, 1992) provides ample evidence and examples of the importance of gastropod shells to hermit crab biology. Shells, both the gastropod species and shell quality, are implicated in regulation of hermit crab populations (Review, Elwood & Neil, 1992). Similarly, shell characteristics by a variety of measures, and how shells fit crabs are implicated in hermit crab responses to environmental stress (Reese, 1969; Ball, 1972; Shumway, 1978; Young, 1978; Taylor, 1981), predation (Reese, 1969; Vance, 1972b; Bertness, 1981a, 1982), energy consumption (Herreid & Full, 1986a,b), fecundity (Childress, 1972; Fotheringham, 1976a; Bach et al., 1976; Bertness, 1981b) and copulatory success (Hazlett, 1989; Hazlett & Baron, 1989).

Intra- and interspecific competition for shells is reflected in reports of hermit crab behaviors associated with shell assessment (Reese, 196a, 1963; Hazlett, 1970; Elwood & Neil, 1992; Brown et al., 1993), exchange (see Hazlett, 1978, 1983) and acquisition (McClellan, 1983). Crabs respond to specific visual (1BPatridge, 1980; Hazlett, 1982; Orihuela et al., 1992; Diaz et al., 1995) and chemical cues (McLean, 1974; Hazlett & Herrnkind, 1980; Rittschof, 1980a,b; Mesce, 1982; Rittschof et al., 1992; Small & Thacker, 1994; Thacker, 1994). Chemical cues originate from two major sources of useable shells—dying gastropods (Brightwell, 1952; McClellan, 1974, 1975) and dying hermit crabs (Rittschof et al., 1992; Small & Thacker, 1994; Thacker, 1994). Cues from gastropods are enzymatically generated from muscle proteins (Rittschof, 1980b; Rittschof et al., 1990; Kratt & Rittschof, 1991). Cues from hermit crabs are found in the hemolymph (Rittschof et al., 1992; Thacker, 1994). Responses of crabs appear similar, but not identical, to both kinds of cues (Rittschof et al., 1992).

The responses to chemical cues by one species of Diogenid crab, *Clibanarius vittatus* (Bosc) have been studied in relation to shell fit (Rittschof, 1980a; Rittschof et al., 1992; Katz & Rittschof, 1993). *Clibanarius vittatus* show one of three separate behaviors in response to stimulation with chemicals that cue shell availability (Rittschof et al., 1992). Crab responses are rapid and can be consistently and repeatedly evoked within a minute in a bucket bioassay (Rittschof et al., 1992; Katz & Rittschof, 1993). The response evoked depends at least in part upon shell fit (Katz & Rittschof, 1993). Crabs in shells that are too large withdraw and remain inactive in response to cues. Crabs in shells that fit flee the area. Crabs in shells that are too small show stereotyped shell assessment behavior.

Many studies report a relation between shell quality by some measure and behavior of *C. vittatus* upon stimulation with shell availability cues (Rittschof, 1980a; Gilchrist, 1982; Gilchrist & Abele, 1984; Rittschof et al., 1992; Katz & Rittschof, 1993). It is clear that assessment of shell resource quality includes variables like shell species, epibionts, damage, etc. (cf. Gilchrist, 1984). In the final analysis, crab behavioral response may be the best integrative measure of shell quality.

We decided to examine the shell resource of *C. vittatus* in a graded series of mud-sand and oyster reef habitats. We used the biological assay of chemically stimulated behavior to repeatedly, rapidly and nondestructively assess shell resources in *C. vittatus* in the field. The smallest *C. vittatus* in the study areas

occupy *Ilyanassa obsoleta* (Say) shells at least 1 cm in shell height. Shells of this size are easily discerned by experienced searchers in all habitats. Visual collection may have biased our estimates (Gilchrist, 1982; Gilchrist & Abele, 1984). However, our focus was questions that are relatively independent of sampling technique.

We wanted to examine the shell resource occupied by *C. vittatus* while minimizing the impact of sampling. Unlike most hermit crabs, *C. vittatus* occupy shells that are relatively large for the size of the crab. Most *C. vittatus* can withdraw totally out of sight into their shell (cf. Katz & Rittschof, 1993). Thus, the only ways to physically measure shell fit for *C. vittatus* are to destructively sample shells or to undertake the time-consuming and often fatal or physically damaging (to the crabs) approach of forcing crabs out of their shells. Both mechanisms require long-term removal of crabs from the habitat and loss of individuals or shells from the populations.

The goals of this study were: (1) to assess shell dynamics with respect to season in four spatially isolated populations of *C. vittatus*; and (2) to determine if shell fit is related to the microhabitat that crabs occupy. That crabs might utilize habitat differently because of shell quality has been reported by Gilchrist (1982) and Gilchrist & Abele (1984), who observed that crabs in damaged and otherwise low quality shells were more cryptic. We reason here, since shells are so important to so many aspects of hermit crab biology, one would expect that compensatory behavior based upon shell quality might have evolved. We found that shell dynamics are season and site specific and that each behavior class of crabs utilizes the habitat differently.

2. Materials and methods

2.1. Study sites

Four 100–150 m long by 10–20 m wide sites in the immediate vicinity of the Duke University Marine Laboratory were chosen. Sites had obvious populations of *C. vittatus* and were physically separated by at least 500 m and deep (5–10 m) water. Separated study areas were chosen to minimize probability sampling the same crabs as they move between sites. Movement between sites was possible, but presumably rare. In releases of over 1000 marked crabs from the NOAA beach site the year after this study was completed, we found one crab that moved from the beach to the marina site over the course of 2 months. Intertidal and immediate subtidal habitats varied at each site. The Beaufort bridge site (FINE SAND) was entirely fine sand with patches of scattered 2.5 to 10 cm dead oyster valves. The NOAA beach site (MOSTLY SAND) was $\approx 90\%$ fine sand and mud habitat with two 10 by 3 m patches of living *Crassostrea virginica* (Gmelin) and two 5–10 m patches of fringing *Spartina alterniflora* Loisel. The flounder pen site (OYSTERS AND SAND) was $\approx 70\%$ *Crassostrea virginica* and 30% fine sand and mud. The

marina site (MOSTLY OYSTERS) was 95% *Crassostrea virginica* and 5% fine sand.

2.2. Behavioral determination of shell fit

Shell fit was determined behaviorally using bucket assays (Rittschof et al., 1992; Katz & Rittschof, 1993). Stimulus odor was generated by incubating 3 g of foot muscle of *Polinices duplicatus* (Say) in 5 ml of unfiltered sea water for 30 to 90 min (Rittschof et al., 1992). Individual hermit crabs were categorized with respect to the responses they displayed within 60 s when exposed to chemical stimulus. Crabs were exposed in groups of 5 to 10. In monthly samples during the active season, crabs were categorized as investigators or noninvestigators. Investigators were crabs that displayed stereotyped shell grasping (=assessment sensu Elwood & Neil, 1992) behavior within the assay interval (Rittschof et al., 1992). Noninvestigators either remained withdrawn or were active, but did not display grasping behavior. Behavior of crabs was also categorized with respect to location within microhabitats, crab size, and shell species occupied. In these tests, crabs were observed in groups of 5 or less and each crab was categorized as an investigator, flier (crabs that became active upon chemical stimulation, but that did not display shell grasping) or withdrawer (crabs that pulled into their shells and did not come out during the 60 s assay interval).

2.3. Crab collection

Depending upon the question being asked, different numbers of crabs were collected and tested. Monthly data were based upon collections of 25 crabs from each site. These data were pooled to give a sample size of 100 crabs for each month. The number 25 was chosen because this number of crabs could be collected at each site, tested and released within an hour. Data collection was terminated in December because, although there were still a few crabs in all of the areas, 25 crabs could not be collected and tested within an hour at any of the sites.

For questions of behavior in relation to individual sites, a separate collection of 50 crabs was made at each site on a different day. These collections were made for three months beginning in June when 50 crabs could be collected and tested from each site within an hour of searching.

Beginning in July, every crab that could be collected in an hour was collected at low tide and tested in assays. Data from these collections were used to examine types of shells occupied in different habitats and to document changes in the size of populations at each site.

Questions of habitat choice and shell cue response behavior were asked in September, October and November. This time was chosen because it was after the breeding and larval release seasons. We postulated both sexual activity and reproductive state were complicating factors that would affect crab location in the habitat. Searches were begun on land one half hour before low tide and conducted in the water for the half hour past low tide; location in habitat (sand or

oysters on land or in water) was noted. In these studies, crabs were in captivity for ≈ 1 h before release on an incoming tide.

2.4. Shell species and size

Shells occupied by crabs were categorized by shell species and size (<3 cm or >3 cm shell aperture width). In August and September, when numbers of crabs in small shells were numerous, the shells crabs occupied were divided into three size classes: (1) small (<1 cm), (2) medium (>1 <3 cm), and (3) large (>3 cm) by aperture width (Kellogg, 1976).

2.5. Release recapture studies

We determined if crab mobility due to increased shell weight was a factor in determining distributions of crabs. Initial release experiments were performed with 20 to 50 of each behavior class. The experimental series culminated with a test using only crabs in the withdrawer behavior class. Withdrawers have the largest relative shell size. We determined mobility in relation to increase of total weight for withdrawers. For the experiment, 23 crabs collected on land at low tide and that responded as withdrawers upon chemical stimulation were used. Shells were drained of excess fluid and crab and shell together weighed to the nearest 1 g on a toploading balance. Total weight was increased by application of a layer of plaster of paris in a smooth coating over the shell. Weights were increased from not at all to 160% of the original total weight as determined after the plaster was firmly set. Crabs were then released at the center of Kirby-Smith Island sand flat (Rittschof et al., 1986). The sand flat is not *C. vittatus* habitat. Hermit crabs placed there routinely moved away in all directions. Crabs were marked with floats and allowed 2 h to move on an incoming tide. They were recaptured and the straight line distance they moved from the starting point determined.

3. Results

3.1. Shell fit in relation to time of year

Each month from May to November, 25 hermit crabs were captured at low tide from each of the four sites and assayed for responses to gastropod odor (Fig. 1). The percentage of investigating crabs ranged from a low of 15% in May to a high of 60% in October. Step increases in the percentage of investigating crabs in July and September were related to increases in the numbers of crabs occupying small shells (recruits) such as *I. obsoleta* and *Littoraria* (= *Littorina*) *irrorata*.

3.2. Behavior in relation to site

Behavior assays showed apparent 3-fold variability among some sites with respect to number of investigating crabs in June, July and August. However, with

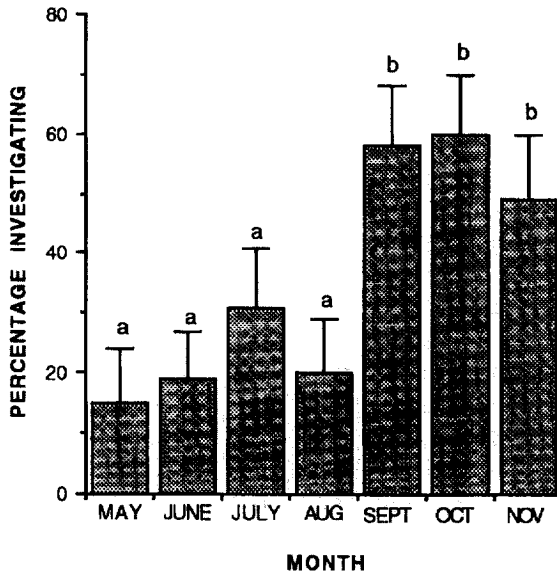


Fig. 1. Investigation behavior by crabs in relation to season. Each month 100 *C. vittatus* were collected haphazardly, 25 from each of four sites at low tide. Each site was searched systematically in the same pattern each month. Crabs were tested in bucket bioassays for investigation responses immediately after collection. Contingency analysis of the frequency of investigators showed the frequency of investigators changed significantly ($G = 92$, $p < <0.01$, 6 df). Percentages of investigators increased with recruitment pulses. Letters (a and b) above the bars indicate months that have similar frequencies. Error bars are confidence intervals for percentages.

sample sizes of 50 animals, contingency analysis yielded values between sites for each month that required acceptance of the null hypothesis that frequencies of responses at all sites were the same.

The question of variability of numbers of investigating crabs with size of crab was revisited in September, October and November. Every hermit crab that could be collected in an hour at each site was tested with odors to examine the relationship between behavior and size. Collected crabs were classified into two categories: (1) crabs in shells larger than a 3-cm diameter *P. duplicatus* shell, and (2) those in shells smaller than a 3-cm diameter *P. duplicatus* shell. In total, 448 crabs (317 large and 131 small) were tested and divided by response into those that investigated, withdrew, or fled (Table 1 a,b). Using these populations, we tested the hypothesis that large and small crabs were equally likely to display each behavior. The hypothesis was rejected for all three behaviors. Investigators were less frequently in large and more frequently in small shells (September–October $G = 16.5$, $p < 0.01$, 1 df; November $G = 15.9$, $p < 0.01$). Crabs that withdrew were more frequently in large than small shells (September–October $G = 57.2$,

Table 1a

The relation between size of shell and chemically stimulated behavior in crabs tested from September 16 to October 14, 1992. Large shells were those >3 cm in diameter

Category	Shell size					
	Large		Small		Totals	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	
Investigate	84	35	65	80	149	50
Withdraw	126	63	4	5	130	44
Flee	4	2	12	15	16	5
Total	214		81		295	

$p < 0.01$, 1 df; November $G = 33.5$, $p < 0.01$, 1 df). Crabs that fled were more frequently in small shells (September–October $G = 15.2$, $p < 0.01$, 1 df; November, no crabs in large shells fled).

3.3. Behavior in relation to habitat

The September and October shell fit data from hermit crabs that were analyzed for responses in relation to shell size were also analyzed in relation to microhabitat location. Crabs were categorized as found on land or in water. The null hypotheses tested were that each behavior class assorted to habitats at random. Predicted proportions were generated from distributional data and frequencies were tested by a goodness of fit test (Sokal & Rohlf, 1981). The data analysis grouped crabs so that the tests were independent of shell size (Table 2). Crabs that investigated were more likely to be found in water than on land ($G = 17.7$, $p < 0.01$, 1 df). Crabs that withdrew were distributed in the two habitats as if they were assorting randomly ($G = 2.48$, $p > 0.05$, 1 df). Crabs that fled were found significantly more frequently in water ($G = > 6.04$, $p < 0.01$, 1 df) than expected by chance.

In late October and November, crabs were collected at low tide and their behavior analyzed in relation to shell size as well as to whether they were found in oyster reefs, or on sand substrata. The null hypothesis tested was each behavior

Table 1b

The relation between size of shell and chemically stimulated behavior of crabs tested in early November

Category	Shell size					
	Large		Small		Totals	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Investigate	37	36	35	70	72	42
Withdraw	66	64	5	10	71	46
Flee	0	0	10	20	10	7
Totals	103		50		153	

Table 2

The relation between size of shell, location in the habitat at low tide and chemically stimulated behavior in crabs tested from September 16 to October 14. Large shells were those >3 cm in diameter

Category	Shell size					
	Large		Small		Totals	
	Water	Land	Water	Land	Water	Land
Investigate	56	39	60	5	116	44
Withdraw	65	66	2	2	67	68
Flee	4	0	10	2	14	2
Totals	125	105	72	9	197	114

class assorted to habitats at random. Predicted proportions were generated from distributional data and frequencies were tested by a goodness of fit test. In this test, a total of 153 crabs were collected (Table 3). Of the three behaviors, crabs that investigated assorted at random in the two habitats ($G = 0.01$, $p > 0.02$, 1 df) as did crabs that withdrew ($G = 1.55$, $p > 0.02$, 1 df). Crabs that fled were more likely to be found on sand than in oysters ($G = 6.38$, $p < 0.01$, 1 df). Thus, crabs with large shells were found throughout the habitat at low tide. No large crabs with good shell fit were found. Small crabs with good shell fit were found in the water on sand bottoms. Finally, crabs that investigated were found primarily in the water in both oyster reef and sand habitats.

3.4. Mobility and behavior class

Mobility of all behavior classes of crabs was determined by recapture of marked crabs released at the center of a 100+ m diameter sand flat. In three initial experiments crabs were recaptured 12 h after release on an incoming tide (one tidal cycle); 6 h after release on an incoming tide; and 3 h after release at high tide. Even after 3 h, recapture of all behavior classes was low ($\approx 30\%$). Most crabs recaptured were found in *C. vittatus* habitat over 100 m from the site of release. We shortened the time interval to 2 h in the final release experiment with hourly

Table 3

The relation between size of shell, location on sand or in oyster reefs at low tide and chemically stimulated behavior in crabs tested from October 29 to November 4, 1992. Large shells were those >3 cm in diameter

Category	Shell size					
	Large		Small		Totals	
	Oyster	Sand	Oyster	Sand	Oyster	Sand
Investigate	24	13	18	17	42	30
Withdraw	45	21	2	3	47	24
Flee	0	0	2	8	2	8
Totals	69	34	22	28	91	62

checks of movement of withdrawer class crabs captured on land at low tide. Shells of most crabs were weighted and crabs marked with floats.

We asked the question, does shell weight decrease movement sufficiently to explain why crabs are frequently found in the intertidal zone at low tide. In the test, we released 23 crabs trapped on land at low tide and that withdrew upon chemical stimulation after increasing the weight of some of their shells with plaster of paris. Approximately 40% of the variability in movement was explained by shell weight. One crab moved less than 9 m (Fig. 2) in 2 h. The weight of the shell of this crab was over twice the original weight. Five other crabs moved less than 20 m. Mobilities of all but one crab were such that they could traverse the width of the study sites as the tide receded. We conclude that trapping of crabs on land as the tide recedes is not due to reduced mobility.

3.5. Changes in shell resource

The dramatic change in quality of the shell resource between August and September (Fig. 1) prompted more detailed study of shell occupancy during those

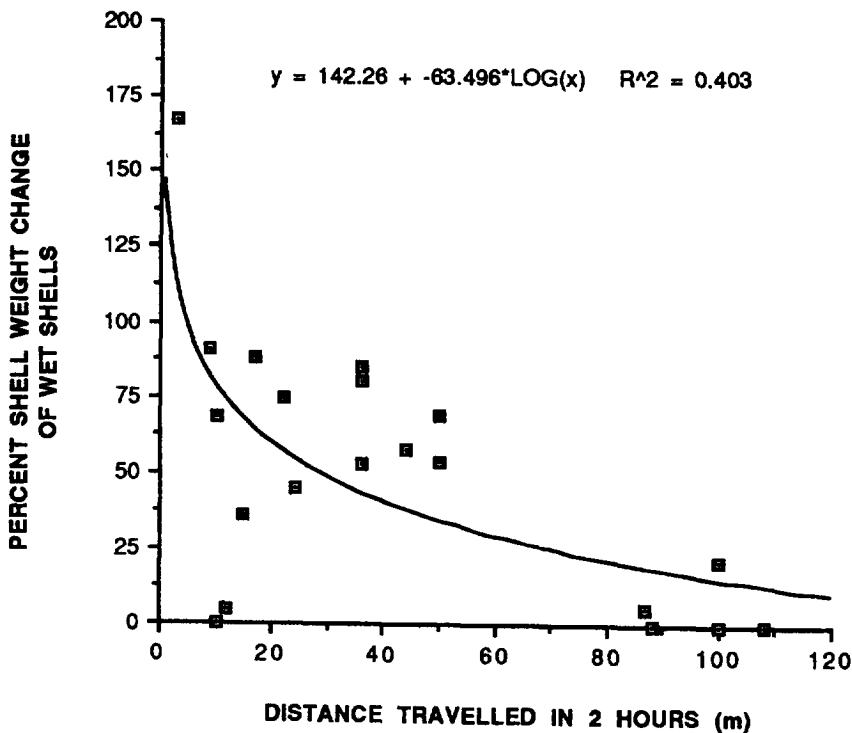


Fig. 2. Mobility of crabs in shells with increased weight. Each square represents the distance travelled by a *C. vittatus* that responded to chemical stimulation as a withdrawer. After the test, plaster of paris was added to each shell to increase its weight. The weight presented is the weight of the shell at the end of the 2-h interval.

Table 4
Frequencies of small, medium, and large shells occupied by *C. vittatus* in August and September

Shell size	August	September	Change	% Change
Large				
<i>Busycon</i> spp.	125	128	3	+2
<i>Fasciolaria</i>	70	42	-28	-40
Total	195	170	-25	-13
Percentage large	48	60		
Medium				
<i>Polinices</i> sp.	40	29	-11	-27
<i>Urosalpinx simplex</i>	35	26	-9	-25
Total	75	55	-20	-26
Percentage medium	18	19		
Small				
<i>Littoraria</i> sp.	82	48	-34	-43
<i>Ilyanassa</i> sp.	56	7	-49	-86
Total	138	55	-83	-60
Percentage small	34	20		
Grand totals	408	280	-128	-31

intervals. Another change in shell occupancy also occurred between August and September samples (Table 4). Although search times and personnel were the same, 30% fewer crabs were collected in September. When categorized by size, frequencies of shells occupied were different for the two months ($G = 44.4$, $p < 0.01$, 4 df). Crabs in larger shells were equally represented in both months, but those in smaller shells were underrepresented in the September collection.

Because shell occupancy frequencies changed dramatically between August and September, and the changes were most dramatic in small shell occupancy, we examined data on frequencies of crabs in *I. obsoleta* shells at the four sites for July, August, and September. Although there were dramatic decreases in the total numbers of crabs collected at the NOAA beach site in August, there were minor changes in crab totals at the other three sites. Contingency analysis showed frequencies of crabs occupying *I. obsoleta* shells (10–12% of total) were similar in July and August ($G = 1.0$, $p > 0.2$, 1 df). In September there were dramatic decreases ($\approx 50\%$) in numbers of crabs collected at the bridge and pen sites and little change in numbers at the NOAA beach and marina sites (Table 5). However, contingency analysis showed that proportions of crabs occupying *I. obsoleta* shells (3% of total) were dramatically reduced in September ($G = 17.2$, $p < 0.01$, 2 df). Because every shell seen was gathered and checked for crabs, we are confident that there were no empty shells and no evidence that small shells were being destroyed at this time. Empty shells were encountered in collections only in May, June and late November.

Table 5
Occupation of *Ilyanassa obsoleta* shells by *Clibanarius vittatus* in July, August, and September

Site	July		August		September	
	# I.o.	Total	# I.o.	Total	# I.o.	Total
FINE SAND (Beaufort bridge site)	34	170	26	139	6	65
MOSTLY SAND (NOAA beach site)	7	341	10	57	1	67
OYSTERS AND SAND (Flounder pen site)	30	143	13	170	2	91
MOSTLY OYSTERS (Marina site)	0	79	2	66	0	64
Totals	71	733	51	432	9	287

4. Discussion

Shell availability is a major force in structuring hermit crab populations (Childress, 1972; Vance, 1972a,b; Kellogg, 1976; Fotheringham, 1976b; Bertness, 1982). In the present study, chemically stimulated behavior was used to rapidly and nondestructively assess shell resources in four spatially separated populations of *C. vittatus*. The goals were to describe shell resources through the active season and to determine if there were relationships between chemically stimulated behavior and microhabitat choice.

The data show that the quality of the shell resource is dynamic. Seasonally, shells are too small in the early fall when populations are at their yearly maximum in the post settlement interval and too large in late spring and early summer when crab populations are at a yearly low. Shells are too small for small, rapidly growing crabs and too large for larger, slowly growing crabs. Availability of intermediate sized shells appears to be a bottleneck. Shell fit is directly related to crab location within the habitat.

Independent of season, smaller crabs are more likely to occupy shells that are too small. Larger crabs are more likely to occupy shells that are too large. A likely hypothesis is the availability of intermediate sized shells (such as *P. duplicatus*) limits transition of crabs from smaller shells such as *I. obsoleta* and *Littoraria irrorata* to larger shells such as *Fasciolaria hunteria* and *Busycon* spp. Although intermediate sized *Busycon* and *Fasciolaria* spp. shells should be available, their occurrence is rare. Thus, *P. duplicatus* is the only common gastropod species that is of intermediate size. Its availability is further limited through its use by the common subtidal hermit crab *Pagurus pollicaris*. *P. duplicatus* is the preferred shell (sensu, Elwood & Neil, 1992) of *Pagurus pollicaris* (McLean, 1975; Hazlett, 1980). *Pollicaris pollicaris* does not directly exchange shells with *C. vittatus* (Hazlett, 1980). *Pollicaris pollicaris* moves more quickly and is more agile than *C. vittatus* and may locate and flee with *P. duplicatus* shells before *C. vittatus* can respond. *Pollicaris pollicaris* occupying *P. duplicatus* shells may flee from encoun-

ters with *C. vittatus*. Thus, interspecific competition for intermediate sized shells may limit this class of shell resource for *C. vittatus* populations.

Clibanarius vittatus in optimal shells are those that flee upon chemical stimulation (Katz & Rittschof, 1993). Fleeing crabs are a low percentage of the population throughout the active season. Fleers reached a maximum (28%) in the month after recruitment. At this time, many crabs were in the correct size range for the variety of small shells available. Shell fit in larger crabs is improved at this time also. The increase in numbers of large crabs with optimal shells may be due to crab growth or changes in crab shell selection parameters with the end of the breeding season. Fleers were observed to occupy all of the five major types of shells. This suggests *C. vittatus* can achieve optimal shell fit in a variety of shells.

It would be informative to test other hermit crabs reported to preferentially occupy specific shells such as pagurids (Elwood & Neil, 1992) and coenobitids (Herreid & Full, 1986a) for their behavioral responses with respect to shell species occupied. Both groups are known to respond to shell cues (pagurids: McClean, 1975; Rittschof, 1980a; Gilchrist, 1982; Rittschof et al., 1992; coenobitids: Thacker, 1994; Small & Thacker, 1994). There is at least one report for each group (Rittschof, 1980a; Thacker, 1994) that shell fit is related to investigation behavior.

Location in the microhabitat appears related to shell fit and is not due to decreased mobility of crabs with large shells. Our studies of movement of marked crabs confirmed those of Hazlett (1981b). Even the smallest size classes of crabs were capable of rapid long-distance movements. Our studies with crabs classified as withdrawers show most crabs remaining on land at low tide are capable of moving the width of the intertidal zone even with weighted shells. To prevent being trapped on land at low tide, crabs would have to move less than 20 m in their usual habitats in the same time interval. Thus, crab distribution cannot be explained by restricted mobility.

If choice of microhabitat by the crabs is a behavioral adaptation related to shell fit, why might the choices be adaptive? A combination of physiological, behavioral and ecological processes might be involved. Crabs in relatively small shells (investigators) are more frequently found subtidally. Crabs in shells that are too small have been shown to be more vulnerable to desiccation (Young, 1978; Taylor, 1981), and predation (Reese, 1969; Vance, 1972a,b; Bertness, 1981a, 1982). Desiccation and thermal stress are likely explanations for the selective forces that make staying in the water adaptive for crabs in shells that are too small.

Fleeing crabs, those occupying shells they would choose in free access experiments, occupy sand habitats. Crabs in optimal shells are more resistant to predation (Vance, 1972a,b) and energetically best suited to locomotion (Herreid & Full, 1986a,b). Fleeing crabs frequent sand habitats and are likely to be exposed at high tide. One explanation for the adaptive advantage to fleers of staying on sand substrates is they would be less vulnerable to being trapped and forced into trading shells by either crabs in shells that were too large or too small (Hadfield, pers. comm.). *Clibanarius vittatus* do not engage in shell fights and trading when on land.

Crabs in relatively large shells distributed at random in all habitats. Bertness

(1981b) showed crabs in large shells expend energy for growth. Crabs in shells too large would be resistant to desiccation and thermal stress as well as predation. Movement would require relatively more energy because of the overly large shell. Reduced movement could free up energy for growth. Although crabs that moved to habitats where they normally do not occur leave rapidly, these same crabs moved minimally within acceptable habitat as evidenced by their location on land at low tide. Reduced movement could free up energy for growth.

The relation between behaviorally determined shell fit and other shell acquisition behaviors, such as shell fighting [Hazlett, 1969, 1972a,b, 1981a (Review); Elwood & Neil, 1992], has not been studied directly. However, crabs in shells that are too large move to smaller shells given free access to empty shells (Katz & Rittschof, 1993). Similarly, crabs in shells that are too small are much more likely to engage in shell fighting and trading (Hazlett, 1978).

The study sites contained varying frequencies of crabs in shells that ranged in size from small, occupying adult *I. obsoleta* shells, to large, occupying medium sized *B. carica* shells. As some of the crabs occupying *I. obsoleta* shells are sexually mature, it appears that the smaller size classes of *C. vittatus* occupy a different habitat. Similarly, the August vs. September data indicate rapid decreases in numbers of crabs with changes in shell occupation, and increasing numbers of crabs in shells that are too small. There are two obvious explanations for the observations: (1) crabs are experiencing high levels of predation by shell destroying predators; (2) crabs in shells that fit poorly move to unstudied habitats where the likelihood of acquiring shells in the correct size range is higher. Because we saw no evidence of increased predation (recently broken shells or empty shells), our data are consistent with the hypothesis that crabs are moving to habitats that we did not study. These movements could be seasonal and unrelated to shell fit, or could be in response to shell fit. It is clear from the work of Wilber & Herrnkind (1984) that there are areas such as *S. alterniflora* habitat where large numbers of gastropod shells such as *L. irrorata* become available through predation. Since gastropods can respond to the odor of intact marsh cord grass *S. alterniflora* (Duval et al., 1995), it is possible that hermit crabs in poor fitting shells could have evolved an attraction to snail habitat where they could trade in their outgrown *I. obsoleta* shells for *L. irrorata* shells, the next larger shell in the series. Future studies will test these hypotheses.

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