Mitchell, Kenneth Anderson (1975) Habitat selection by hermit crabs. PhD thesis

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HABITAT SELECTION BY
HERMIT CRABS

Thesis

for the

Degree of Doctor of Philosophy

in the

University of Glasgow

by

Kenneth Anderson Mitchell, B.Sc. (Glasgow).

ACKNOWLEDGMENTS

This work was carried out during the tenure of the James Fleming Scholarship and the Robert Donaldson Scholarship, both from the University of Glasgow. I would like to thank Professor D.R. Newth for research facilities provided in the Department of Zoology, University of Glasgow, and also Dr. John D. Costlow for inviting me for a six month stay at Duke University Marine Laboratory, Beaufort, North Carolina. Financial support for this venture was provided by the Carnegie Trust for the Universities of Scotland, Duke University, and the University of Glasgow.

The research conducted in this thesis was greatly assisted by Dr. J.R. Cuthbert, who advised me on many occasions on the statistical nature of my work and who carried out any computer programming necessary in this thesis. At Beaufort, Dr. C.G. Bookhout showed me the technique of rearing crab larvae, and Dr. D.R. Colby offered helpful critical advice on my research there. To these people, and to many more in the Departments of Zoology and Statistics in the University of Glasgow, and at Duke University Marine Laboratory, I am very grateful.

This thesis was typed by Miss Elizabeth Watson of Larbert, and I wish to thank her for her efficiency in the preparation of this thesis.

Lastly, I wish to thank especially my supervisor, Mr. P.S. Meadows, who has been a constant source of encouragement and advice throughout my three years' research for this thesis.

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CONTENTS

GENERAL INTRODUCTION

"In my beginning is my end"

East Coker

T.S. ELIOT.

Hermit crabs are a loosely defined group of animals classified within the section Anomura, order Decapoda, class Crustacea. Their derivation from other Decapod groups is obscure, since fossil evidence is sparse and fragmentary (Glaessner, 1969), but it is at least clear that they do not represent a monophyletic stock (Macdonald, Pike and Williamson, 1957). At present, two superfamilies are acknowledged, the Coenobitoidea and the Paguroidea. The Coenobitoidea consists of the hermit crab families Coenobitidae, Pylochelidae and Diogenidae, together with the monospecific member of the family Lomisidae, which has no hermit crab characteristics (Pilgrim, 1965). The Paguroidea consists of two hermit crab families, the Paguridae and the Parapaguridae together with the stone crab family, the Lithodidae (Macdonald, Pike and Williamson, 1957; Saint Laurent, 1972).

Of the five acknowledged hermit crab families, only the Coenobitidae occupy a habitat peculiar to them. All members of this family spend their larval life in the sea but come on land after metamorphosis to their glaucothoe form (Reese, 1968). On land, adults are occasionally found far from shore (Grubb, 1970; Verrill, 1908), and at least two species are known to climb trees (Ball, 1972; Sprungman, 1972). One of these species has a peculiar behaviour pattern of scrambling down vertical walls of cliffs 60 metres high on the same day each year. At the bottom, they cover the beach in heaps until dusk, when they "spread out over the sand and suddenly begin a mass exchanging of shells and frenzied mating" (Sprungman, 1972 p60). Since the Coenobitidae only occur in tropical and subtropical regions of the world, however, this interesting family has not been studied in this thesis.

No work has been done in this thesis on two other hermit crab families, the Pylochelidae and the Parapaguridae, because of their inaccessibility. Only one paper has reported on the behaviour of a member of the Pylochelidae (Batham, 1970) and likewise the Parapaguridae (Hazlett, 1966a). Both these papers recorded that the animals were dredged at considerable depths (110 - 713 metres) and some members of the Parapaguridae are even known to occur at depths of 3,570 metres (Wolff, 1961).

The remaining two hermit crab families, the Paguridae and the Diogenidae, are the most numerous in terms of numbers of species. They have a worldwide distribution, but the Paguridae are more common in northern waters and the Diogenidae in tropical waters. In British seas, for example, Pike and Williamson (1959) recorded only 1 Diogenid to 9 Pagurid species, and in Northwestern North America, McLaughlin (1974) recorded 2 Diogenid to 31 Pagurid species. In the territory of Papua and New Guinea, however, 24 Diogenids to only 2 Pagurids have been noted (Ball and Haig, 1972), and a similar pattern of 11 Diogenids to 3 Pagurids has been recorded for Krusadai Island in the Gulf of Mannar, Sri Lanka (Raj, 1927).

The habitats of the Paguridae and Diogenidae are varied. They are found on all substrates and have a vertical range of over 800 metres (McLaughlin, 1974). Many of the species are intertidal or occur in shallow water, and it is in this region that tremendous intraspecific aggregations of hermit crabs occur (Hazlett, 1966b; McKay, 1945). Other species can be very rare, however, (Hazlett, 1966b). As yet, no systematic study has been performed on what determines the abundance of certain hermit crab species but useful hypotheses have been made. These hypotheses include: limitation of numbers of gastropod shells (Hazlett, 1970; Provenzano, 1960; Reese, 1969; Thomson, 1903), condition of water circulation (Hazlett, 1966b; Pike and Williamson, 1959; Wolf and Sandee, 1971), low salinity levels (Biggs and McDermott, 1973; Bookhout, 1964; Davenport, 1972; Roberts, 1971), high levels of predation (Brightwell, 1952; Eales, 1949; Hunt, 1925; Rae, 1967 a, b, c; Ross, 1971; Samuelsen, 1970a; Shoup, 1968) and parasitism (Nielsen, 1970; Pike, 1953; 1961; Samuelsen, 1970b).

In the present study, three Pagurid and one Diogenid species were used. These were Pagurus bernhardus (L.), Pagurus prideauxi Leach, Pagurus longicarpus Say and Clibanarius vittatus Bosc. The three Pagurid species, although in the same genus, are not closely related. This is because the genus Pagurus is now recognized to be polyphyletic, and evidence from larval and adult studies suggests that the three species arose from three separate groups (Forest and de Saint Laurent, 1967; Macdonald, Pike and Williamson, 1957; McLaughlin, 1974; Roberts, 1970).

The only British site studied in this thesis was the Firth of Clyde where P. bernhardus and P. prideauxi are abundant. Both species occur all round British coasts but P. bernhardus is usually the more common species. The distribution of P. bernhardus is from Iceland to the Mediterranean, whereas P. prideauxi is found from southern Norway to the Cape Verde Islands, (Pike and Williamson, 1959) and recently seems to have moved into the Red Sea from the Mediterranean (Lewinsohn, 1969). P. bernhardus has been studied at many sites in Europe (Brightwell, 1952; Davenport, 1972; Hazlett, 1968a; Markham, 1968; Ross, 1960; Samuelsen, 1970) but has not been studied in any detail in the Firth of Clyde (Elmhirst, 1945; Pike and Williamson, 1959). Similarly, research on P. prideauxi has been performed by Berner (1953) at Marseille, Fox (1965) at Plymouth, Ross (1971) at Naples and Samuelsen (1970) in Norway, but little is known of it in the Clyde (Pike and Williamson, 1959).

The American site studied in this thesis was Beaufort Harbor, North Carolina, where P. longicarpus and C. vittatus are abundant. These species have an overlapping distribution from North Carolina to the Gulf States but P. longicarpus occurs as far north as Massachusetts and C. vittatus extends at least as far south as the Rio Grande, and possibly to Brazil (Provenzano, 1959). P. longicarpus has been studied at Massachusetts by Allee (1945) and Fink (1941), and at Virginia by Roberts (1970; 1971a, b; 1972) while C. vittatus was studied in Curaçao and Florida by Hazlett (1966b; 1968b; 1970). The only joint study of the two species was done by Wright (1973) at Texas.

The main aims of this thesis are: (1) to compare the behaviour and ecology of hermit crabs in the particular habitats cited with previously described work on hermit crabs in other habitats, and (2) to discover new techniques for studying habitat selection by hermit crabs. The Firth of Clyde and Beaufort Harbor were both excellent sites for this work, not only because of the abundance of hermit crabs in these areas, but also because the hermit crabs were always collected in good condition and easily maintained in laboratory conditions. This is not the case at Texas, for example, where Brunenmeister (1972) had great difficulty keeping P. longicarpus alive in the laboratory, while Samuelsen (1970) found that at his Hillersholmen site, near Bergen, one quarter of P. bernhardus picked up by dredge had left their shells on the sea floor.

SECTION 1

HABITAT SELECTION BY
SUBLITTORAL BRITISH
HERMIT CRABS

"I should have been a pair of ragged claws
Scuttling across the floors of silent seas."

The Love Song of J. Alfred Prufrock.

T.S. ELIOT.

Introduction

The general distribution of British hermit crabs has been well studied by Pike and Williamson (1959) but few experiments on behaviour in relation to their distribution have been done to complement their work. The papers of Brightwell (1950 ; 1952), Elmhirst (1947) and Wilson (1949), for instance, are largely anecdotal and other behavioural work on species appearing in British waters has been performed in other countries and is hence of limited value in explaining British distributions.

The work undertaken in this section is exclusively on sublittoral Pagurus bernhardus (L.) and Pagurus prideauxi (Leach). This is because both species are readily obtainable at short notice from the University Marine Biological Station, Millport, Isle of Cumbrae. Other species which occur in the Clyde estuary such as Pagurus pubescens, Pagurus cuanensis, Anapagurus hyndmanni and Anapagurus chiroacanthus are either uncommon (Pike and Williamson, 1959) or in the case of Anapagurus laevis occur in very limited areas (personal communication, Mr. Finlayson, University Marine Station, Millport).

Mar. Behav. Physiol. 1973, Vol. 2, pp. 187–196
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Printed in Reading, England

An Analysis of Inter- and Intraspecific Aggregations in Two Sympatric Species of Hermit Crab (Decapoda, Anomura, Paguridae)

P. S. MEADOWS and K. A. MITCHELL

Department of Zoology, University of Glasgow, Glasgow, G12 8QQ

(*Received May 21, 1973*)

A series of experiments was conducted on the relationship between population density and spacing out in two sympatric species of crab, *Pagurus bernhardus* (L.) and *Pagurus prideauxi* Leach. A second series of experiments investigated the two species' aggressiveness and activity by observing the behaviour of pairs of animals.

In the first series of experiments, animals became more aggregated (Clarke and Evans' R) as the population density (p) was increased. The rate of aggregation (dR/dp) was greater when the species were mixed than when they were separate.

In the second series of experiments, activity, total encounters, and resolved encounters, were highest in paired *P. bernhardus*, lower in mixed pairs of the two species, and lowest in pairs of *P. prideauxi*. Larger individuals were more active than smaller ones in *P. bernhardus* and *P. prideauxi* pairs. In the mixed pairs, *P. bernhardus* were more active. Paired *P. bernhardus* were slightly more active than isolated *P. bernhardus* but this difference was not statistically significant. The activities of paired and isolated *P. prideauxi* were not significantly different. The distances between individuals in pairs were similar for all combinations.

The results are discussed in relation to the distribution of sympatric species.

INTRODUCTION

The distribution of many marine animals appears to be largely governed by behavioural recognition of their local habitat (Meadows and Campbell, 1972a,b). Mobile benthic invertebrates, for example, may select their habitats in response to light (Oviatt, 1969), to shelter (Cobb, 1971), or to sediment particle size and microbial flora (Meadows, 1964a,b), while the larvae of many sedentary invertebrates are highly selective in their choice of a settlement site (Crisp and Meadows, 1962; Knight-Jones, 1951).

The distinction between which of these many factors and their interactions determine habitat choice is particularly interesting when considering the local distribution of sympatric species, whose habitats may overlap in part or all of their geographical range (Bovbjerg, 1970; Teal, 1958). The present paper is concerned with interactions of this nature in two sympatric species of hermit crab, *Pagurus bernhardus* (L.) and *Pagurus prideauxi* Leach. It attempts to assess the possible effects that inter- and intraspecific encounters might have on local distribution, by analysing the behaviour of single species' and mixed species' groups of animals as population density is increased, and by describing the behaviour of single species' and mixed species' pairs.

MATERIALS AND METHODS

Animals were supplied by the University Marine Biological Station, Millport, and had been caught by dredge in about 30 m in the Firth of Clyde. The two species are sympatric in this area, often being caught in the same dredge haul (personal communication Mr. Williamson, U.M.B. Station, Millport; cf. discussion). *Pagurus bernhardus* used in the present investigation were dredged from Kames Bay, and *Pagurus prideauxi* from the "Wishing Well" off the east coast of Cumbrae. The Wishing Well is about 1 mile from Kames Bay. The animals were transported to the University of Glasgow and then maintained in aerated sea water tanks in a 10°C cold room, with a 12 h day 12 h night automatic light regime.

Two series of experiments were conducted. The first series analysed the influence of population density on aggregation. The second series analysed the activity and tactile encounters of pairs of animals.

The first series was conducted as follows. Three categories of animal were used: (i) small *P. bernhardus* occupying adult *Littorina* shells (length 1.4–2.6 cm), (ii) *P. prideauxi* in *Littorina* shells surrounded by the commensal coelenterate *Adamsia palliata* (length 1.7–2.9 cm), (iii) a 50/50 mixture of the two species. Length was measured from the front of the carapace to the back of the shell or sea anemone when the crab was withdrawn. This is an approximate measure of crab size, but was the only feasible method in the present investigation. The experimental procedure was the same for all three categories. A gravel sand mixture was placed into white fibreglass tanks (57 cm, 42 cm, 13 cm height) until the bottom was covered, and the tank was then filled with sea water. Animals were placed in the tanks at densities of 4, 7, 10, 12, 14, 20, 25 and 28 per tank. All tanks were aerated. Animals were fed at the end of each day's readings. One to four tanks were set up at a time because of space limitations. Light intensity at the water surface was c540 lux. Each of the points in Figure 1 represent one tank at one density. During the first twenty-four hours animals were very active and a number of encounters occurred. No measurements were taken during this period. Nearest neighbour distances were measured over days 2 to 6 (see Clarke and Evans, 1954; Edgar and Meadows, 1969 for method). Readings were always taken more than three hours apart. These data are presented in Figure 1.

The second series consisted of sixteen replicate experiments. In the first eight of these, a pair from each of the three categories (*P. bernhardus* + *P. bernhardus*, *P. prideauxi* + *P. prideauxi*, *P. bernhardus* + *P. prideauxi*) was placed into a small white plastic tank (35 cm, 18 cm, 9 cm height). In the second eight experiments an additional four tanks of the same size were used. Two contained an isolated *P. bernhardus*, and two an isolated *P. prideauxi*. The tanks were filled with sea water and the tank bottoms either left uncovered or covered with a layer of fine gravel. The presence or absence of gravel did not noticeably affect the behaviour of the animals. The light intensity at the water surface was c35 lux. All experiments were run for thirty minutes. At one-minute intervals each animal was classed as active (moving from place to place in the tank) or inactive (remaining in one position in the tank), and at two-minute intervals a note was taken of the distance between the two individuals (the pair distance) in the tanks containing a pair of animals. The times of all tactile encounters between pairs of animals were recorded and classified as resolved or unresolved: in resolved encounters only one crab moved away from the other crab after tactile contact; in unresolved encounters, either both crabs moved away from each other after tactile contact, or neither moved away. Tactile contact consisted of antennae touching, chelae touching, or chelae touching shell/anemone.

All experiments were conducted in the 12 hr day/12 hr night 10°C cold room. Readings were only taken during daylight hours.

RESULTS

The results of the first series of experiments are presented in Figure 1. The distances between individuals were analysed by Clarke and Evans' (1954) nearest neighbour method. At each population density, individuals are taken in turn and the distance to their nearest neighbour measured. The mean of these distances is the mean nearest neighbour distance ($\bar{r}_o$) for that population density. The mean expected nearest neighbour distance ($\bar{r}_e$) for the same population density is given by

$$\bar{r}_e = \frac{1}{2\sqrt{p}}$$

where p = population density. The ratio $\bar{r}_o/\bar{r}_e$ is defined as R, an estimate of

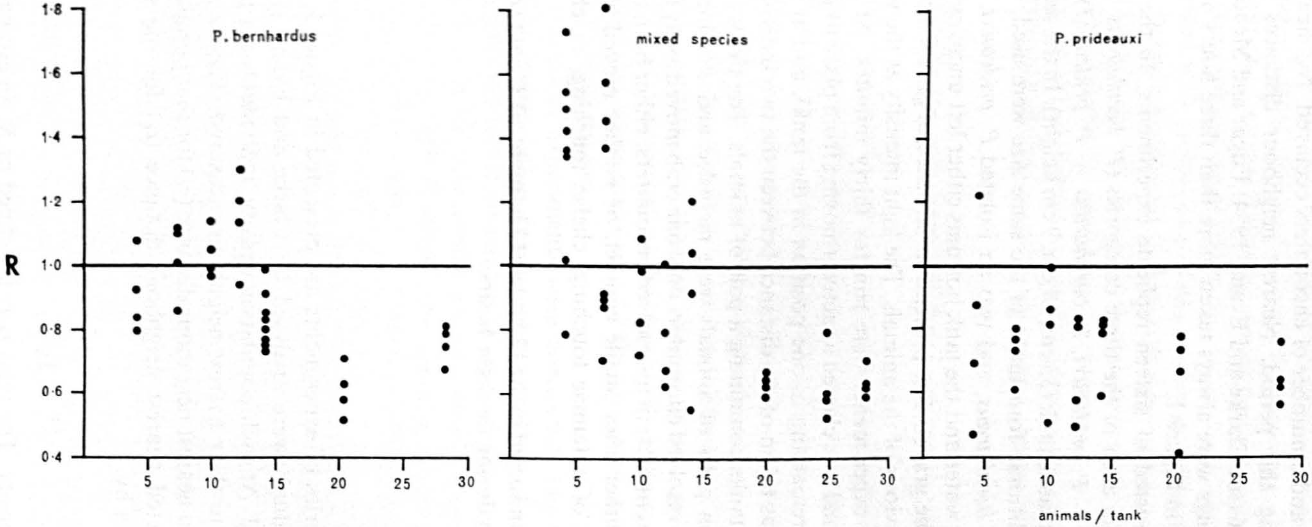

FIGURE 1 Effect of increasing population density on aggregation measured by Clarke and Evans' (1954) *R*. *P. bernhardus* $y = -0.01437x + 1.096$, $t = 3.583$, 30 df, $P < 0.002 > 0.001$, slope of line significantly different from zero. *P. prideauxi* $y = -0.00667x + 0.8134$, $t = 1.609$, 26 df, $P < 0.20 > 0.10$, slope of line not significantly different from zero. Mixed species $y = -0.03106x + 1.362$, $t = 6.005$, 38 df, $P < 0.001$, slope of line significantly different from zero. Comparison of *P. bernhardus* with *P. prideauxi*, $t = 1.336$, 56 df, $P < 0.20 > 0.10$, slopes not different. Comparison of *P. bernhardus* with mixed species, $t = 2.376$, 68 df, $P = 0.02$, slopes significantly different. Comparison of *P. prideauxi* with mixed species, $t = 3.336$, 64 df, $P < 0.01 > 0.001$, slopes significantly different.

the aggregation or dispersion of the population. If $R < 1$ the population is aggregated, if $R = 1$ the population is randomly distributed, if $R > 1$ the population is dispersed (spaced out). A more detailed account of the method is given in Edgar and Meadows (1969). R decreased with increased population density in all three categories of animals (Figure 1), indicating that in all three categories animals became more aggregated as the population density was increased. Regression lines were fitted to these data and then compared both with a line of zero slope and with each other. Significant differences were found between the regression lines of *P. bernhardus* and the mixed species when compared with the line of zero slope. The regression line of *P. prideauxi* was not significantly different from a line of zero slope. The regression lines of *P. prideauxi* and *P. bernhardus* were not significantly different from each other, but each was significantly different from the regression line of the mixed species (for statistical comparisons see Figure 1). The latter difference suggests that either one, or both, species change their behaviour when mixed with the other. The second series of experiments, in which pairs of animals were observed, was designed to examine this hypothesis. In it, the distance between individuals of a pair, their activity, and their encounters, were recorded over periods of 30 minutes.

There was no difference in the pair distances of *P. bernhardus* pairs, *P. prideauxi* pairs, or the mixed species pairs, when the data were assessed by an analysis of variance. In this analysis, categories of animals and experiments were classed as two factors with three and fifteen levels respectively, and the fifteen measurements of pair distances in each experiment as fifteen replicates in each cell. There was a very large variation in pair distances between experiments, and this was reflected in a highly significant first order interaction between the two factors ($P < 0.001$). A breakdown analysis of variance was considered but further inspection of the data showed that this would have yielded little of value.

There were very marked differences among the activities of the different categories of paired and isolated animals. Table I records these differences, and the mean sizes of the animals in the pairs. Wilcoxon's signed ranks test was applied to the activity data (Sokal and Rohlf, 1969). Two tailed criteria were used in the assessment of probability levels. *P. bernhardus* pairs were considerably more active than mixed pairs of *P. bernhardus* and *P. prideauxi* ($T_s = 100.5$, $n = 31, P < 0.01$) and than the *P. prideauxi* pairs ($T_s = 71.5, n = 31, P < 0.01$). The mixed pairs were slightly more active than *P. prideauxi* pairs ($T_s = 125.5$, $n = 28, P = 0.078$), and the paired *P. bernhardus* were slightly more active than isolated *P. bernhardus* ($T_s = 25, n = 14, P = 0.09$); neither of these two differences can be considered statistically significant by two tailed criteria. Paired *P. prideauxi* were not more active than isolated *P. prideauxi* ($T_s = 41, n = 13$, $P > 0.1$). In the *P. bernhardus* pairs and the *P. prideauxi* pairs, the larger

TABLE I

Size and activity of single species' and mixed species' pairs and of single *P. bernhardus* and *P. prideauxi*. Size was measured as maximum shell length to the nearest mm. Size differences were assessed by students' t with 30 degrees of freedom. Summed activities from sixteen 30-min experiments. The maximum activity score possible if all animals in a group were continuously active in each of the sixteen experiments would be 480. The statistical significance of the differences between the observed activities, 168 and 108, 87 and 47 and so on, was assessed by Wilcoxon's signed ranks test treating the sixteen experiments as blocks and the pairs of animals as treatments (for details see Sokal and Rohlf, 1969, p. 399).Two tailed criteria were adopted in all four tests.

	Paired		Paired		Paired		Single	Single
	P. bernhardus		*P. prideauxi*		*P. bernhardus* & *P. prideauxi*		*P. bernhardus*	*P. prideauxi*
Size (cm)	large	small	large	small				
(mean ± s.d.)	2.21 ± 0.35	1.83 ± 0.25	2.59 ± 0.34	2.09 ± 0.32	2.14 ± 0.45	2.63 ± 0.61	1.73 ± 0.31	2.37 ± 0.39
t	3.573		4.224		2.596		5.200	
P	<0.002 >0.001		<0.001		<0.02 >0.01		<0.001	
Activity	168	109	87	45	138	58	83	35
T_s	13.5		13		12		21	
n	15		12		15		15	
P	<0.01		0.042		<0.01		0.025	

individuals were more active than the smaller ones; however, in the mixed pairs *P. bernhardus* although smaller in size than *P. prideauxi* were more active: these differences were significant when assessed by Wilcoxon's signed ranks test (see Table I).

Encounters, like activities, differed among the categories of pairs. *P. bernhardus* pairs had a significantly higher number of encounters than either the mixed pairs or the *P. prideauxi* pairs, but the mixed pairs were not significantly higher than the *P. prideauxi* pairs. The ratio of resolved encounters to unresolved encounters differed significantly among the three categories. Resolved encounters were greatest in *P. bernhardus* pairs, less in mixed pairs, and least among *P. prideauxi* pairs. Large *P. bernhardus* had more resolved encounters than small *P. bernhardus* (43:12), but there was no difference between the large and small *P. prideauxi* (2:2), and between *P. bernhardus* and *P. prideauxi* (14:8). The statistical analysis of these results is given in Table II.

DISCUSSION

It is clear from the first series of experiments that *P. bernhardus* and *P. prideauxi* become more aggregated as the population density is increased (Figure 1), and that mixed species' populations do so more rapidly than single species' populations. In general an increase in aggregation with population density might seem unexpected, especially when one of the species, *P. bernhardus*, has stereotyped visual and tactile agonistic displays (Hazlett, 1968a, 1970) which do not decrease with increased population density (Hazlett, 1968b). However, aggregations of hermit crabs at fairly high population densities do occur in natural unrestrained populations (Mackay, 1947) and in populations under semi-natural conditions (Ball, 1968), while the freshwater crayfish, *Orconectes virilis*, also forms aggregations more readily at higher densities (Bovbjerg and Stephen, 1971).

The difference in the rate of aggregation of the mixed species' populations and the single species' populations implies a change in behaviour when one species is in the presence of the other. It was investigated in the second series of experiments by observing pairs of animals. No difference was detected between the pair distances of single species and mixed species pairs, but there were very pronounced differences in activity and encounters. Activity, total encounters and resolved encounters were highest in pairs of *P. bernhardus*, lower in the mixed species pairs, and lowest in pairs of *P. prideauxi* (cf. Hazlett, 1967, 1968b). Differences among activities in these three categories may be explained by the two species having different responses to illumination (unpublished observation K.A.M.), while the encounter differences observed could be explained by the conspecific shell swapping behaviour of *P. bernhardus*

TABLE II

Encounters in single species and mixed species pairs. For definition of resolved and unresolved encounters see Materials and Methods. There are more encounters in paired *P. bernhardus* (75) than in paired *P. prideauxi* (36) ($\chi^2 = 13.79$; 1 df; $P < 0.001$) or than in heterospecific pairs (43) ($\chi^2 = 8.68$; 1 df; $P < 0.01, > 0.001$), but there is no difference between the number of encounters of paired *P. prideauxi* and the heterospecific pairs ($\chi^2 = 0.585$; 1 df; $P < 0.5, > 0.3$). The ratio of resolved : unresolved encounters is greater in paired *P. bernhardus* (55:20) than in the heterospecific pairs (22:21) ($\chi^2 = 5.064$; 1 df; $P < 0.05, > 0.02$), and the ratio for the heterospecific pairs is greater than the ratio for paired *P. prideauxi* (4:32) ($\chi^2 = 12.32$; 1 df; $P < 0.001$). In conspecific pairs, large *P. bernhardus* win more resolved encounters than small *P. bernhardus* (43:12) ($\chi^2 = 17.47$; 1 df; $P < 0.001$), but there is no difference between the large and small *P. prideauxi* (2:2), or between the *P. bernhardus* and *P. prideauxi* in the heterospecific pairs (14:8) ($\chi^2 = 1.636$; 1 df; $P < 0.3, > 0.2$).

	Paired *P. bernhardus*			Paired *P. prideauxi*			Paired *P. bernhardus* & *P. prideauxi*		
	large	small	Total	large	small	Total			Total
Resolved encounters	43	12	55	2	2	4	14	8	22
Unresolved encounters	20		20	32		32	21		21
Total encounters			75			36			43

in contrast to *P. prideauxi* which rarely swaps either shells or anemones (Hazlett, 1967, 1968c). This explanation however, does not entirely explain the difference in aggregation between the mixed and single species' populations observed in the first series of experiments.

Nearest neighbour methods are usually preferable to χ^2 for analysing patterns of animal distribution under laboratory and field conditions, since they do not depend on choosing a suitable quadrat size (Edgar and Meadows, 1969). On the other hand, they only accurately measure the intensity, not the grain, of a spatial pattern (Pielou, 1969, p. 118–119), and so would not have detected the aggregations of hermit crabs in the corners of tanks that sometimes developed in the first series of experiments. Furthermore, they do not take account of the finite size of animals, since they are based on a consideration of point sources; in the present investigation nearest neighbour analyses were based on the nearest distance between animals or their shell or anemone.

In the Clyde Estuary *P. bernhardus* and *P. prideauxi* are sympatric, the former occurring on a fairly wide range of sediments from the intertidal zone to 70 m and sometimes to 140 m, and the latter on clean sandy sediments down to about 40 m (Henderson, 1887; Pike and Williamson, 1959). Little else is known of their localized distribution. However, it is clear that if populations or individuals of the two species meet, their behaviour is likely to change (Figure 1, Tables I, II) (Hazlett, 1967). Populations will space out more at low densities for example; while if animals become isolated from a group, they may be less active (Table I) (cf. Courchesne and Barlow, 1971) and as a result be less likely to explore their local environment.

The exact local distribution of the two species may well be dictated by interactions between increased aggregation at high population densities (Figure 1), intra- and interspecific encounters (Tables I, II), and a presumed habitat selection by recognition of specific attributes of the habitat itself (Bovbjerg, 1970; Teal, 1958). For example, two species of freshwater crayfish studied by Bovbjerg (1970) that were sympatric over part of their ranges showed patterns of habitat selection which were altered when the two species met (loc. cit. p. 231). One species was more aggressive than the other in interspecific encounters, and because of this was able to evict the latter from otherwise preferred rock crevices. These observations parallel the more aggressive behaviour of *P. bernhardus* compared with *P. prideauxi* (Tables I, II), and suggest that the local distribution of the hermit crabs might be changed in a similar manner.

Acknowledgements

We would like to thank Miss M. T. Emerson for her help in the preparation of the paper.

The data in Figure 1 form part of an honours thesis conducted by K.A.M. under the supervision of P.S.M., and the data in Tables I and II represent joint experiments by P.S.M. and K.A.M.

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Mar. Behav. Physiol. 1973, Vol. 2, pp. 229–236

Printed in Reading, England

Activities of Two British Species of *Pagurus* (Crustacea, Decapoda, Paguroidea)

K. A. MITCHELL

Department of Zoology, University of Glasgow, Glasgow, G12 8QQ

(*Received July 31, 1973*)

Two series of experiments were conducted to investigate the activities of two British species of hermit crab, *Pagurus bernhardus* (L.) and *Pagurus prideauxi* Leach. The first series showed that *P. bernhardus* was more active during day than night whereas the opposite was true of *P. prideauxi*. In the second series, conducted under periods of 24 hours constant illumination, the activity pattern of *P. bernhardus* persisted to a lesser degree, but *P. prideauxi* showed no activity pattern. Differences in activity were observed among individuals of the same species, and also between individuals kept in the laboratory for different lengths of time.

INTRODUCTION

Activity rhythms, although well studied in many decapods (Brown, 1961; Naylor and Atkinson, 1972; Naylor, Atkinson and Williams, 1971), are little known in hermit crabs. Only Ball (1968) has studied activity in hermit crabs in a controlled experimental manner. By recording changes in the dispersion of two Pacific species, *Pagurus samuelis* (Stimpson) and *Pagurus granosimanus* (Stimpson), he concluded that both species were more active in darkness than in light. This he related to their proximal retinal pigment migration which occurred under conditions of darkness.

Pigment migration cannot always be correlated with nocturnal activity, however, as *Pagurus longicarpus* Say is known to have light sensitive proximal retinal pigment (Nagabhushanam and Sarojini, 1964) yet has been observed to be less active during night than day (Fink, 1941). Thus, although Rabaud (1941) has recorded differences in eye structure between the two species under present study, *Pagurus bernhardus* (L.) and *Pagurus prideauxi* Leach, this is no guarantee that their activities will be different from each other, and hence the reason for the following experiments. Investigations were also carried out to extend the work done by Meadows and Mitchell (1973) on the activities of pairs of animals from these two species.

MATERIALS AND METHODS

All animals were supplied by the University Marine Biological Station, Millport, and kept under the same laboratory conditions as described by Meadows and Mitchell (1973). Two series of experiments were conducted. The first series analysed differences in the activities of the two species during two normal 12-hour day/12-hour night regimes. Differences among pairs of crabs and isolated crabs were also analysed. The second series analysed differences in the activities of the two species during two separate periods of 24 hours constant illumination, and also differences between individual crabs of the same species under the same circumstances.

In the first series of experiments, the experimental design was similar to that of the second series of experiments carried out by Meadows and Mitchell (1973) in that the temperature (10°C), water surface light intensity (c. 35 lux), plastic tanks (35 cm, 18 cm, 9 cm height), individual hermit crabs, classification of a crab as active or inactive at each minute and categories of crabs to each tank were all the same. Differences from the design of Meadows and Mitchell include: night readings by use of a weak red light as in Ball (1968), Hazlett (1968); the addition of two isolated crabs, one *P. bernhardus* and the other *P. prideauxi*, in two separate tanks for the complete duration of the 24 hours under study; regular 1½-hour intervals between each experiment; and observing the experimental animals for a period of 15 minutes instead of 30 minutes at a time.

The complete experiment, lasting 24 hours, was repeated two days later.

The second series of experiments consisted of observing the activities of seven *P. bernhardus* and seven *P. prideauxi* for 15 minutes every 1½ hours for a period of 24 hours in which an override switch was used to maintain constant illumination for this period. The experimental procedure involved measuring the activities of either the seven *P. bernhardus* in separate tanks, or the seven *P. prideauxi* in separate tanks, at each time. This was done over two days with a period of 12 hours light/12 hours dark between them. When the crabs were not being used in the experimental tanks, which were the same as in series 1, they were kept in seven stock tanks, one *P. bernhardus* and one *P. prideauxi* to each stock tank, so that a measure of a crab's individual activity over the experimental period could be obtained. After the experiments were over, the crabs were sexed and their size measured in terms of the length of the hard portion of the carapace as in Markham (1968).

RESULTS

The results of the day/night experiments carried out in series 1 are presented in Tables I and II.

TABLE I

P. bernhardus

Commencing time	0600	0730	0900	1030	1200	1330	1500	1630
Activity	49	59	60	32	41	50	34	33
Commencing time	1800	1930	2100	2230	2400	0130	0300	0430
Activity	27	20	8	6	12	11	24	21

TABLE II

P. prideauxi

Commencing time	0600	0730	0900	1030	1200	1330	1500	1600
Activity	10	11	29	20	14	36	21	15
Commencing time	1800	1930	2100	2230	2400	0130	0300	0430
Activity	39	25	36	27	27	29	45	33

Activity as recorded in these two tables is the total of all crabs tested at the particular time whether noted the first time or during the repeat. Comparison of *P. bernhardus* with *P. prideauxi* over the time intervals, 0600–1630, when the laboratory was illuminated, indicates a significant difference in their activities by carrying out the Wilcoxon two sample test ($P < 0.002$). A comparison of *P. bernhardus* from 1800–0430 (the times in which the laboratory was in darkness) with *P. prideauxi* from 1800–0430 shows a reversal of the day pattern. *P. prideauxi* is then more active than *P. bernhardus* ($P < 0.002$).

On comparing *P. bernhardus* day readings with their night counterpart readings 12 hours later, it can be seen that *P. bernhardus* is much more active during day, than night ($P < 0.002$) whereas *P. prideauxi*, on the other hand, is more active during night than day ($P = 0.02$). There is no significant difference between the total activity of *P. bernhardus* over 24 hours, and *P. prideauxi* over 24 hours under these conditions.

When series 2 data is arranged as in Table III, it is apparent that there are no significant differences between activities of large and small *P. bernhardus* or large and small *P. prideauxi* either during day or night. Differences between paired *P. bernhardus* and *P. prideauxi*, and differences between single *P. bernhardus* and single *P. prideauxi* are as expected, both during day and

TABLE III

Size and activity of single species "and mixed species" pairs and of single *P. bernhardus* and *P. prideauxi*. Size was measured as maximum shell length to the nearest mm. Size differences were assessed by students' *t* test with 30 degrees of freedom. Summed activities of 16 fifteen-min. experiments in light and 16 fifteen-min. experiments in dark. The statistical significance of the differences between the observed activities was assessed by the Wilcoxon signed ranks test

	P. bernhardus		*P. prideauxi*		Paired		Single	Single	Isolated	Isolated
	Large	Small	Large	Small	*P. bernhardus*	*P. prideauxi*	*P. bernhardus*	*P. prideauxi*	*P. bernhardus*	*P. prideauxi*
					In Light					
Size (cm) (mean ± s.d.)	1.99 ± 0.50	1.55 ± 0.18	2.58 ± 0.43	2.04 ± 0.34	1.69 ± 0.55	2.13 ± 0.57	1.96 ± 0.62	2.31 ± 0.41		
t	5.513		3.178		2.196		1.882			
P	< 0.001		< 0.01 > 0.001		< 0.05 > 0.02		< 0.10 > 0.05			
Activity	80	80	33	37	84	48	114	44	3	13
T_s	34		32		13		17		5	
N	12		12		15		16		6	
P	0.70		0.58		< 0.01 > 0.002		< 0.01 > 0.002		> 0.10	
					In Dark					
Size (cm) (mean ± s.d.)	2.16 ± 0.45	1.75 ± 0.51	2.59 ± 0.58	2.00 ± 0.41	1.82 ± 0.35	2.29 ± 0.58	1.73 ± 0.63	2.24 ± 0.46		
t	2.429		4.070		2.811		2.600			
P	< 0.05 > 0.02		< 0.001		< 0.01 > 0.001		< 0.02 > 0.01			
Activity	32	34	64	63	41	84	34	64	2	25
T_s	30.5		47.5		11		20.5		3.5	
N	13		14		16		14		12	
P	0.30		0.75		< 0.01 > 0.002		< 0.05 > 0.04		< 0.01	

night. A comparison of the isolated crabs with their appropriate single crab group shows a substantial drop in activity in all four groups ($P < 0.05$). This drop is more pronounced in *P. bernhardus* (114:3 and 34:2) than in *P. prideauxi* (44:13 and 64:25). It should be noted that, whereas up to 16 different crabs could be used in all other groups, only two *P. bernhardus* and two *P. prideauxi* were isolated during the series, and hence no standard deviations have been included in their size data.

The results of the second series of experiments are presented in Tables IV and V.

TABLE IV

P. bernhardus

Commencing time	0600	0730	0900	1030	1200	1330	1500	1630
Activity	45	47	53	57	54	47	63	51
Commencing time	1800	1930	2100	2230	2400	0130	0300	0430
Activity	51	48	42	54	43	43	52	45

TABLE V

P. prideauxi

Commencing time	0600	0730	0900	1030	1200	1330	1500	1630
Activity	16	19	22	25	13	15	18	18
Commencing time	1800	1930	2100	2230	2400	0130	0300	0430
Activity	18	10	12	19	18	18	17	20

Activity measurements in Tables IV and V are the total activity of the seven hermit crabs over 15 minutes for each time. A comparison of *P. bernhardus* from 0600–1630 with *P. prideauxi* 0600–1630 gives the same results as in the series 1 comparison of the two species for these time ranges. If *P. bernhardus* 1800–0430 is compared with *P. prideauxi* 1800–0430, however, an opposite result from series 1 is obtained ($P < 0.002$ by Wilcoxon two sample test). Thus, *P. bernhardus* has the same significantly greater activity than *P. prideauxi* whether during day or night hours when there is a period of 24 hours' constant illumination.

If the activity of *P. bernhardus* during day hours (0600–1630) is compared with its "night" hours activity (1800–0430) then there is some evidence for the hypothesis of an inbuilt diurnal rhythm of activity in this species. Its day activity is significantly greater than its "night" activity ($P = 0.05$ for a one-tailed test). There is no evidence for an inbuilt activity rhythm in *P. prideauxi*, however, as an opposite, though not significant, day/"night" pattern is shown to that of Table II.

The activities of each individual hermit crab over 24 hours' constant illumination is shown by Tables VI and VII.

TABLE VI

P. bernhardus

Sex	♂	♂	♂	♂	Berried ♀	Berried ♀	♀
Size (cm)	1.3	1.1	0.7	0.7	1.1	0.8	0.7
Day activity	58	80	38	68	81	34	58
"Night" activity	63	72	32	63	65	21	62

TABLE VII

P. prideauxi

Sex	♂	♂	♂	♂	♀	♀	Berried ♀
Size (cm)	1.4	1.2	1.2	1.2	1.2	1.2	1.0
Day activity	9	2	22	29	33	32	19
"Night" activity	4	4	16	20	41	19	28

It can be seen that activity does not seem to be directly related to either size or sex, with the exception of the berried *P. bernhardus* which have large differences between their total day and total "night" activities. More individuals would be needed, however, to establish this difference as statistically significant from non-berried individuals.

All statistical tests in series 2 were carried out by using Wilcoxon's two sample test and, unless otherwise stated, the probabilities obtained are from two-tailed tests.

DISCUSSION

The results of series 1 were, in part, predictable from the work done by Meadows and Mitchell (1973). They also found that *P. bernhardus* was significantly more active than *P. prideauxi* when there was illumination. There was no way of predicting the differences in activity during normal night hours, however, since all experiments done by Meadows and Mitchell were carried out during normal daylight hours. When these results are conjoined with those of series 2, it can be seen that there is some evidence of an inbuilt diurnal activity rhythm in *P. bernhardus*, but none for *P. prideauxi*. The differences in activities between crabs of the same species may indicate that some crabs are, by nature, errant, whereas others may prefer to keep to a particular known area.

The differences between activities in light and in darkness in series 1 by both species indicates that, like the two *Pagurus* species studied by Ball (1968), activity (in individual hermit crabs) is largely governed by presence or absence of light. Unlike Ball's study, however, one of the species in the present study, *P. bernhardus*, is much more active during day than night. This species has been shown to be unaffected in its behaviour by the presence of strong illumination (de Bruin and Crisp, 1958), but has no mechanism for dark adaptation (Bröcker, 1935). This is in keeping with the results obtained.

P. prideauxi's slight decrease in activity during night hours under illumination does not seem to be reconcilable with its significantly greater activity in darkness than in light. A possible explanation for this is that many crustaceans have a 24-hour cyclical migration of distal pigment regardless of illumination (see de Bruin and Crisp, 1957). If *P. prideauxi* was one of these crustaceans, it would mean that this species' eye pigment was in a less adapted state for illumination during "night" than day, when under 24-hours illumination, and hence activity would be reduced during night hours. This reduction in activity would at least be partially offset by the migration of proximal pigment which can occur in a matter of minutes in hermit crab species (Nagabhushanam and Sarojini, 1964, 1970) and thus the result would not be pronounced.

A comparison of the pairs of animals in series 1 with the pairs of animals in series 2 of Meadows and Mitchell (1973) is of interest because the same individual animals were used in both of the experiments but with contrasting results. The only probable differences which could account for this change in results are that Meadows and Mitchell observed the crabs for 30 minutes at a time, and that the crabs were only in the laboratory for a period of two weeks when tested by Meadows and Mitchell as opposed to six weeks' captivity in the present study. If a comparison of the total activity of each group is made by only including the total activity of the first 15 of the 30 minutes in the experiments done by Meadows and Mitchell, it is found by χ^2 that the activities of large *P. bernhardus* and large *P. prideauxi* have significantly decreased by being kept in the laboratory ($P < 0.05$), whereas the activities of single *P. bernhardus* and single *P. prideauxi* have significantly increased by being kept in the laboratory. All other activities have not significantly changed in any direction.

The significant increase in the activity shown by single *P. bernhardus* and single *P. prideauxi* may at first sight seem to negate the conclusion drawn by

Meadows and Mitchell that isolated animals are less likely to explore their local environment, but the results obtained from the *P. bernhardus* and the *P. prideauxi* which were kept isolated in separate tanks for 24 hours reinforce the conclusion.

Acknowledgements

I would like to thank Mr. P. S. Meadows for much helpful advice and criticism, and Miss M. T. Emerson for preparation of this paper.

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Criticism of Meadows and Mitchell (1973)

In the discussion of Meadows and Mitchell (1973) it was noted that two criticisms levied against the Clark and Evans (1954) approach to nearest neighbour analysis are that only the intensity of a spatial pattern is measured, and that no account of the size of animals is allowed. Since this paper was published, methods have been evolved to allow for these criticisms and a further criticism concerning unequal variances in the regressions performed has been noted. The methodology of this modified form of nearest neighbour analysis is discussed in detail in the next section, but it is worthwhile showing here how not taking account of crab size or unequal variances in regression analysis can affect the results of nearest neighbour analysis.

1. A comparison of least squares regression with weighted least squares regression

In Figure 1 of Meadows and Mitchell (1973) no account was taken of the effect of the variance of the value R as population density increased in the three different categories of animals tested. This means that too much account is placed on the values of R at low densities where the variances are high, and conversely too little account of the high densities with low variances. To modify this a weighted least squares regression was performed on each of the three categories by the following method.

The variance of R for each population density is first calculated from

$$\frac{\sigma^2}{\bar{r}_e^2}$$

where $\bar{r}_e$ is the expected mean nearest neighbour distance and σ^2 is its expected variance. (For information on how values of $\bar{r}_e$ and σ^2 were obtained see Clark and Evans (1954).) Let this value $= \lambda i$ where i defines population density.

The desired regression is

$$E\{R\} = \alpha + \beta t_i$$

where ti = number of crabs per tank at density i.

The parameter β is calculated from:

$$\beta = \frac{S_2 S_4 - S_1 S_3}{S_5 S_2 - S_3^2}$$

where $S_1 = \sum i \frac{(Ri)}{(\lambda i)}$

$$S_2 = \sum i \frac{(1)}{(\lambda i)}$$

$$S_3 = \sum i \frac{(ti)}{(\lambda i)}$$

$$S_4 = \sum i \frac{(Ri\ ti)}{(\lambda i)}$$

$$S_5 = \sum_i \frac{(ti^2)}{(\lambda i)}$$

and the constant α is calculated from :

$$\alpha = \frac{S_1 - S_3 \hat{\beta}}{S_2}$$

Example 1. P. bernhardus

Number of crabs per tank	R values
4	0.80; 0.93; 1.07; 0.82.
7	1.11; 0.86; 1.11; 1.01.
10	1.13; 0.97; 1.05; 0.99.
12	0.83; 1.13; 1.22; 0.94.
14	0.74; 0.75; 0.91; 0.73; 0.80; 0.83; 0.99; 0.70
20	0.57; 0.70; 0.63; 0.52; 0.83; 0.62; 0.90; 0.92
28	0.67; 0.80; 0.79; 0.74

$$\underline{E\{R\} = 1.075 - 0.01301t}.$$

Example 2. P. prideauxi

Number of crabs per tank	R values
4	1.22; 0.87; 0.69; 0.48.
7	0.80; 0.76; 0.73; 0.61.
10	0.99; 0.81; 0.86; 0.51.
12	0.58; 0.51; 0.81; 0.83.
14	0.82; 0.81; 0.59; 0.77.
20	0.66; 0.77; 0.73; 0.65.
28	0.62; 0.64; 0.56; 0.75.

$$\underline{E\{R\} = 0.806 - 0.00580t}$$

Example 3. Mixed Species

Number of crabs per tank	R values
4	1.34; 1.42; 1.36; 1.73; 1.01; 1.54; 0.78; 1.49
7	1.37; 0.89; 1.80; 1.57; 0.70; 1.45; 0.87; 0.90
10	0.82; 1.08; 0.98; 0.72.
12	0.67; 1.00; 0.78; 0.62.
14	1.20; 1.04; 0.55; 0.91.
20	0.65; 0.59; 0.62; 0.66.
25	0.58; 0.58; 0.52; 0.79.
28	0.59; 0.63; 0.69; 0.62

$$\underline{E\{R\} = 1.273 - 0.02699t}$$

A comparison of the regression slopes of Examples 1, 2 and 3 with a line of zero slope show the following results:

Example 1, $t = 4.157$, 30df, $P<0.001$;

Example 2, $t = 1.688$, 26df, $P<0.20, >0.10$;

Example 3, $t = 10.280$, 38df, $P<0.001$.

These significances are basically the same as those produced by ordinary least squares regression. A comparison of each pair of slopes shows the following results:

Example 1 with Example 2, $t = 1.551$, 56df, $P<0.20, >0.10$;

Example 1 with Example 3, $t = 3.390$, 68df, $P<0.001$;

Example 2 with Example 3, $t = 4.901$, 64df, $P<0.001$.

Once more these significances are similar to those produced by ordinary least squares.

It seems, then, that the conclusions drawn from the regressions performed in Meadows and Mitchell (1973, p.190) are only reinforced when the more statistically accurate weighted regressions are performed on the same data.

2. The effect of ignoring crab size on the interpretation of the results

In Meadows and Mitchell (1973) nearest neighbour distances were taken from the edge of one crab to the edge of its nearest neighbour, but it seems equally permissible to take the distances from the centres of the crabs. To find out what effect taking the distances from the centres would have on the regression slopes of R against population density, weighted regressions were carried out on the nearest neighbour distances of the centres of the crabs. It was assumed that each crab tested was 2.0 cm. in diameter. This is not strictly true as P. prideauxi tested were in general slightly larger than P. bernhardus and there was also individual intraspecific variation to some extent, but it is doubtful if these differences are enough to significantly alter the observed mean nearest neighbour distances even if the individual sizes of each crab tested were known and noted for each observation.

Example 1. P. bernhardus

Number of crabs per tank	R values
4	0.96; 1.09; 1.23; 0.98
7	1.31; 1.06; 1.31; 1.22.
10	1.38; 1.22; 1.30; 1.23.
12	1.09; 1.38; 1.48; 1.20.
14	1.03; 1.04; 1.20; 1.02; 1.09; 1.12; 1.27; 0.99
20	0.91; 1.04; 0.97; 0.86; 1.21; 0.96; 1.24; 1.26
28	1.08; 1.20; 1.19; 1.15

$$E\{R\} = 1.273 - 0.00521t$$

Example 2. P. prideauxi

Number of crabs per tank	R values
4	1.37; 1.02; 0.84; 0.63.
7	1.01; 0.96; 0.93; 0.81.
10	1.23; 1.05; 1.10; 1.09.
12	0.84; 0.77; 1.08; 1.09.
14	1.10; 1.09; 0.88; 1.06.
20	1.00; 1.11; 1.07; 0.99.
28	1.02; 1.03; 0.91; 1.15.

$$E\{R\} = 0.952 - 0.00320t$$

Example 3. Mixed Species

Number of crabs per tank	R values
4	1.49; 1.57; 1.51; 1.89; 1.17; 1.69; 0.86; 1.65
7	1.58; 1.09; 2.01; 1.77; 0.90; 1.65; 1.06; 1.10
10	1.06; 1.33; 1.23; 0.96.
12	0.93; 1.26; 1.04; 0.88.
14	1.48; 1.33; 0.83; 1.20.
20	0.99; 0.93; 0.96; 1.00.
25	0.96; 0.96; 0.90; 1.21.
28	0.99; 1.04; 1.10; 1.02.

$$\underline{E\{R\} = 1.311 - 0.01192t}$$

A comparison of the regression slopes of Examples 1, 2 and 3 with a line of zero slope show the following results:

Example 1, $t = 1.621$, 30df, $P < 0.20 > 0.10$;

Example 2, $t = 0.930$, 26df, $P < 0.40 > 0.30$;

Example 3, $t = 4.538$, 38 df, $P < 0.001$.

The t values of the slopes of the three examples are different from those obtained when the nearest neighbour distances were taken from the edge of each crab and this makes an important difference to the interpretation of P. bernhardus (Example 1). There is now no significant evidence that crabs aggregate as population density is increased.

A comparison of each pair of slopes shows the following results:

Example 1 with Example 2, t = 1.787, 56df, P<0.10>0.05;

Example 1 with Example 3, t = 1.618, 68df, P<0.20>0.10;

Example 2 with Example 3, t = 3.492, 64df, P<0.001.

The important difference in these comparisons from the comparisons made between the edge to edge nearest neighbour distances is that there is now no significant difference between the slopes of P. bernhardus (Example 1) and Mixed Species (Example 3).

In addition to the differences in the slopes of the regression lines caused by crab size there are differences in deciding whether or not a crab species is aggregated. Pagurus prideauxi, for example, which shows no significant effect in its R values when population density is altered either in edge to edge or centre to centre nearest neighbour distances, shows clear aggregation in one case and not in the other. 35 of the 36 edge to edge R values are less than 1.00, whereas only 11 of the 36 centre to centre R values are less than 1.

It can therefore be seen that the finite size of a crab such as sublittoral P. bernhardus or P. prideauxi can alter the interpretation of results obtained by nearest neighbour analysis when population densities are as high as those used in Meadows and Mitchell (1973).

SECTION 2

HABITAT SELECTION BY THE INTERTIDAL BRITISH HERMIT CRAB, *PAGURUS BERNHARDUS* (L.)

"The sea is the land's edge also, the granite
Into which it reaches, the beaches where it tosses
Its hints of earlier and other creation."

The Dry Salvages.

T.S. ELIOT.

Introduction

Pagurus bernhardus (L.) is the only common intertidal British hermit crab and is abundant on all coasts of Great Britain, Ireland and the Channel Islands (Bouvier, 1940; Pike and Williamson, 1959; Selbie, 1921). In the Clyde sea estuary this species is found on most rocky shores but is particularly abundant at Ardrossan beach (Lat. N 55° 38' Long. W 4° 49' - see photograph). For example, in the summer months as many as 200 can be found in a rock pool of less than 1 square metre area. Intertidal individuals of this species have certain advantages as experimental animals over sublittoral individuals. These advantages include a much greater tolerance to salinity variation (Davenport, 1972) and exact knowledge of the time and place of collection from the field. In addition, in distribution studies, the confines of an experimental tank resemble the limited surroundings of an intertidal rock pool much closer than the unconfined area of the sublittoral floor.

Shell selection studies are also easier to perform on intertidal rather than sublittoral P. bernhardus as intertidal gastropod shells are much more abundant and easier to collect. They are generally smaller as well and hence a greater number of shells can be offered in an experimental tank of limited size. Lastly, the shallow water in which hermit crabs are kept in the laboratory is similar to rock pool depths whereas sublittoral crabs are kept in depths which may make them behave in a different manner from their natural environment of depths up to 100 metres (Pike and Williamson, 1959).

For all the reasons outlined above, the remainder of the experiments conducted in Britain for this thesis was done on intertidal animals.

A MODIFICATION OF NEAREST NEIGHBOUR ANALYSIS FOR USE IN CLOSED CONTAINERS

Introduction

Nearest neighbour analysis (Clark and Evans, 1954) although extensively used in many fields of research, (Blackburn and Dennen, 1968; Claxton, 1963; Gleaves, 1973; Usherwood, 1972) depends on three assumptions which are rarely all fulfilled in practice. These assumptions are (1) that the area for investigation lies well within the total area covered by the entire population; (2) that the individual components of the population occupy an area that is small in regard to the sample area chosen for investigation; and (3) that the sample area should be uniform throughout. It is clear, therefore, that in any analysis in which any of the above three assumptions do not hold, a modified form of nearest neighbour analysis should really be applied. This is particularly true of the present study of distributions of hermit crabs in laboratory tanks where allowance must be made for (1) the closed container, (2) the size of each hermit crab, and (3) the known attraction of hermit crabs to the corners and edges of a tank (Hazlett, 1966; 1969). For these reasons the following experiments and computer simulations were conducted rather than a conventional Clark and Evans (1954) analysis.

Materials and Methods

Specimens of Pagurus bernhardus (L) in Littorina shells approximately 1 cm in diameter were collected from the intertidal zone of Ardrossan Beach, Firth of Clyde, during the summer months. They were taken to the University of Glasgow where they were kept in a 10°C constant temperature room equipped with a 12-hour day 12-hour night regime. Experimental tanks were of white fibreglass (57 cm, 42 cm, 13 cm height) with a gravel/sand mixture as substrate. No aeration was provided during the course of the experiments, and the animals were fed at the end of each day's readings. No readings were taken on the first day that crabs were put into a tank, as they were very active, exploring the contours of the tank.

(a) Rectangular tank

Crabs were placed in the tanks at densities of 7, 10, 14, 17, 20, 24 and 28 per tank. Readings were taken using a Perspex sheet the size of the tank, and which had been divided into 3 cm squares. The sheet was placed over the tank and the positions of the crabs in the tank were plotted on the Perspex using pieces of plasticine the same size as the crabs to mark their positions. The nearest neighbour distances (Clark and Evans, 1954) were measured by taking the distance between the centre of each crab and the centre of its nearest neighbour. The co-ordinates of each crab were then plotted using the system of notation in Figure 1. Six replicates were used for each density tested, and a gap of at least three hours was enforced before another reading was taken. This time interval was considered long enough to obtain a distribution independent from the previous reading.

(b) Circular tank

Only one circular tank was available at the time of the experiments so that the densities tested (12, 14, 17, 20, 25 and 28 crabs per tank) were done in sequential order, i.e. after six replicates of 12 per tank had been done, then six replicates of 14 per tank were conducted. Readings were taken with a sheet of Perspex which had a circle of 24.5cm. radius inscribed on it. This circle was placed over the tank and the nearest neighbours of each crab were measured as in the rectangular tank. The polar co-ordinates of each crab were then plotted and three hours were allowed to elapse before another reading was taken. No crab which had been in the laboratory for over three weeks was used as there is some evidence that continued presence of Pagurus bernhardus in the laboratory affects its behaviour (Mitchell, 1973).

Results

(a) Rectangular tank

The first part of the analysis consisted of testing the crabs' preferences for different parts of the tank. For this purpose, the tank was assumed to have three separate areas. These were the corners, the sides, and the middle of the tank. The corners consisted of a square of 3 cm side at each corner of the tank, while the sides were all the other areas 3 cm or less from the edge of the tank. The middle was judged to be the remaining area (see Figure 1). At each density the six replicate observations were superimposed and a standard χ^2 test was made to test where there was any change in the proportions of crabs falling on the three areas as the number of crabs per tank were altered (Table I). No significant effect of population density on the three areas was found.

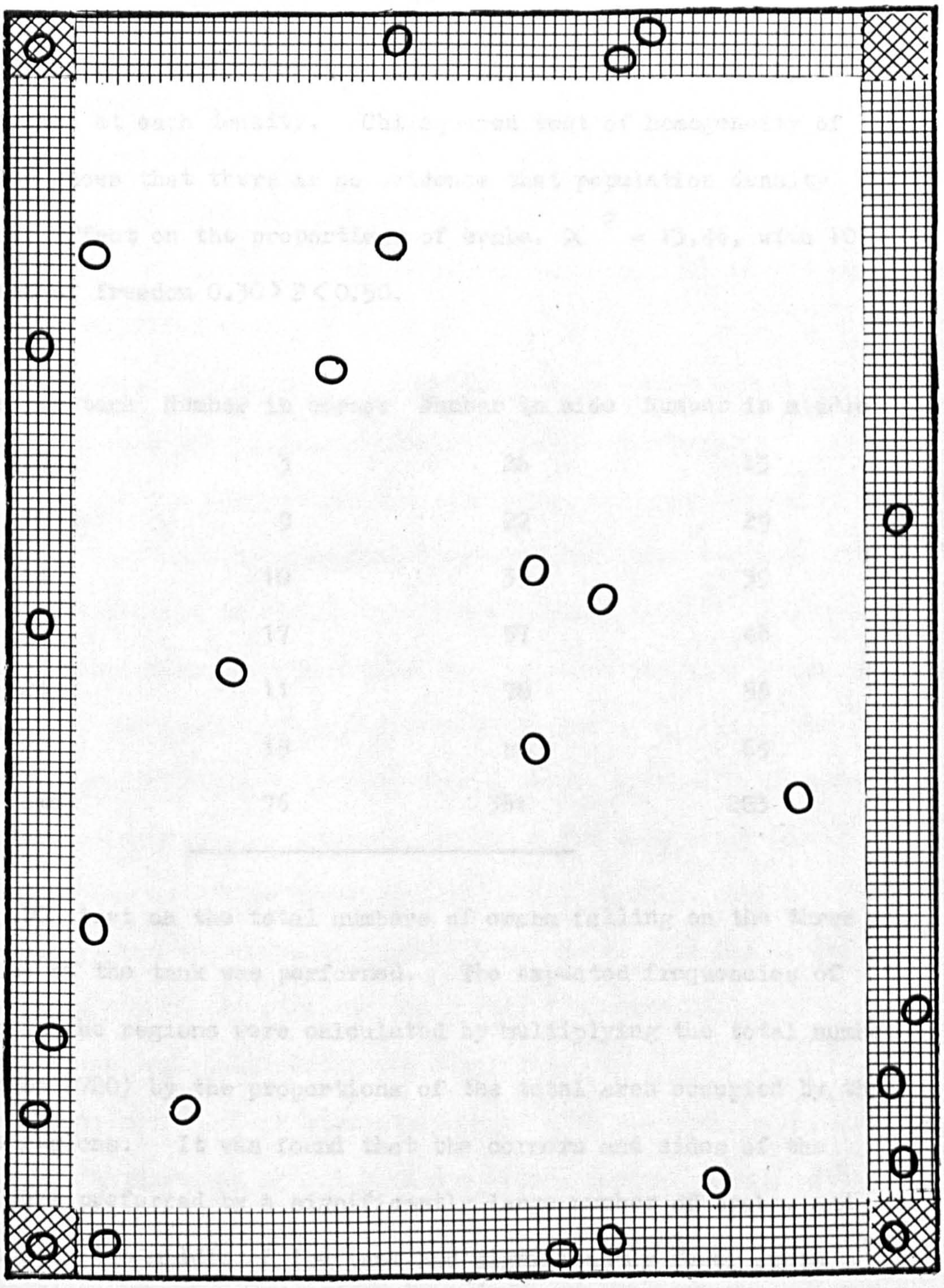

Figure 1. Distribution of 28 hermit crabs in 57 x 42 cm tank.

Key O = position of hermit crab

▨ = corner

⊞ = edge

☐ = middle

TABLE I

Number of crabs in each area of a rectangular tank. Six replicates were taken at each density. Chi squared test of homogeneity of results shows that there is no evidence that population density has any effect on the proportions of crabs. $\chi^2 = 13.46$, with 10 degrees of freedom $0.30 > P < 0.50$.

Crabs per tank	Number in corner	Number in side	Number in middle
7	3	26	13
10	9	22	29
14	10	35	39
20	17	57	46
24	11	78	55
28	15	88	65
Total	76	361	283

A χ^2 test on the total numbers of crabs falling on the three regions of the tank was performed. The expected frequencies of crabs in the regions were calculated by multiplying the total number of crabs (720) by the proportions of the total area occupied by the three regions. It was found that the corners and sides of the tank were preferred by a significantly large number of crabs, and conversely the middle of the tank had significantly fewer crabs than expected $(P < 0.01)$. No preference for any particular corner or a symmetric region of the tank was found, nor was there any evidence to reject the hypothesis that the distribution of crabs was uniform within each of the three separate regions. (A uniform distribution is defined mathematically in the context of this paper as in Grossman and Turner (1974, p341) and is <u>not</u> used in the sense of a regular distribution.

The second part of the analysis was the nearest neighbour analysis used by Clark and Evans (1954), but taking into account the different proportions of crabs in the three regions of the tank, and the size of the crabs.

To do this, the distribution of the average nearest neighbour distance between the crabs was simulated for each population density, under the assumptions that the crabs were positioning themselves uniformly and independently over the three regions, with proportions falling in each of the three regions equal to the observed proportions for that density. Account was also taken of the size of the crab. This was done by rejecting all iterations which produced overlaps of areas, once a circle of 1 cm diameter was drawn around each point. "Overlaps" can occur in reality during shell fighting or sexual behaviour, but shell fighting usually occurs only when two crabs first meet each other. It was never observed in any of the readings taken for this experiment. Similarly, no sexual behaviour was observed.

On completion of the simulation (i.e. when the average nearest neighbour distance was constant to the second decimal place), it was found that the simulated distributions were in each case well approximated by a normal distribution. The means and variances of these distributions were calculated, and the results are shown in Table II.

TABLE II

Results of the average nearest neighbour distance (x_i) observed for rectangular tank, compared with the simulated average nearest neighbour distances. x_i readings have been rearranged in increasing order for convenience of comparison at different densities.

Crabs per tank	Observed average nearest neighbour distances						Estimated mean	Estimated variance
7	12.85	14.28	14.57	15.42	16.14	16.85	12.48	9.29
10	8.10	9.80	11.10	13.60	13.60	16.00	10.18	4.09
14	9.35	9.92	10.00	10.07	10.86	10.86	8.19	1.65
17	7.29	7.41	8.41	8.53	8.59	8.71	7.05	0.99
20	6.15	6.45	6.50	7.15	7.35	7.55	6.42	0.72
24	5.42	6.41	6.42	6.46	6.67	6.75	5.68	0.42
28	5.93	6.00	6.04	6.25	6.39	6.39	5.24	0.31

Under the assumption that the crabs are positioned independently of one another, the quantity:

$$\frac{1}{\sqrt{6}} \sum \left(\frac{x_i - \theta}{\sigma} \right)$$

where θ = estimated expected nearest neighbour distance

σ^2 = estimated variance of nearest neighbour distances

will be normally distributed with zero mean and unit standard deviation for each density. (A multiplication by $\frac{1}{\sqrt{6}}$ is necessary in the above equation to convert a normal (0, 6) distribution, caused by summing the six replicates at each density, to the standard (0, 1) distribution given by most textbooks).

The values of the quantity at the seven population densities tested are shown in Table III.

TABLE III

Values of the quantity $\frac{1}{\sqrt{6}}\sum\left(\frac{x_i - \hat{\theta}}{\hat{\sigma}}\right)$ which measures degree of interaction of crabs with one another, and values of the degree of spacing out of the crabs. When $\frac{\bar{x}}{\hat{\theta}} < 1$, crabs are aggregated; when $\frac{\bar{x}}{\hat{\theta}} > 1$, crabs are spaced out. * = significant at 5% level. ** = significant at 1% level.

Crabs per tank	Values of $\frac{1}{\sqrt{6}}\sum\left(\frac{x_i - \hat{\theta}}{\hat{\sigma}}\right)$	Value of $\frac{\bar{x}}{\hat{\theta}}$
7	2.45*	1.20
10	2.24*	1.18
14	3.38**	1.24
17	2.67**	1.15
20	1.26	1.07
24	2.42*	1.11
28	4.05**	1.18

All the values are significantly large with the exception of the value for population density 20. There is therefore some evidence that the crabs do interact with one another in such a way as to increase their average separation over what would be expected from independence. As a measure of this degree of interaction, the

Clark and Evans (1954) statistic R was generalised. A new measure of interaction was thus defined as $\frac{\bar{x}}{\theta}$ for each density, where $\bar{x}$ was calculated from summing the observed mean nearest neighbour distances for each population density, and dividing by the number of replicates at that density. In the present paper

$$\bar{x} = \frac{\sum x_i}{6}$$

The values of this measure are also shown in Table III.

The relationship between this measure and population density was investigated using weighted regression techniques as in the Criticism of Meadows and Mitchell (1973), and no significant evidence was found of any change in interaction with density.

(b) Circular tank

As in the rectangular tank, the analysis was in two parts. The first part consisted of aggregating the angle measurements of the crabs at each population density to find if there was any departure from uniformity in angle measurements. Similarly, radius measurements were also aggregated at each population density so that a test of uniformity of radius measurements could be performed. A χ^2 analysis of 90^o, and, where samples were large enough, 20^o sectors of the tank revealed that there was no evidence at the 5% level of any departure from uniformity in the distribution of the angle measurements at densities 12, 14, 17, 20 and 25. At density 28, however, there was clear indication of departure from uniformity, some sectors of the tank being preferred over the other sectors (see Appendix 1).

The fact that there was no departure from uniformity in all but one density of crabs was taken to justify the assumption of angular symmetry upon which the later analysis depends, bearing in mind that the subsequent results for 28 crabs per tank would have to be interpreted with caution.

An analysis of the aggregated radius measurements at each density revealed a marked edge effect, if the edge was taken to be the outer 3 cm of the tank. For densities 14, 17, 25 and 18, there was no evidence to reject the hypothesis of uniformity of the points over the interior of the tank, but at densities 12 and 20 there was significant evidence at the 5% and 1% levels respectively of departures from uniformity over the interior. Departures from uniformity were tested by the Kolmogorov-Smirnov one sample test (see Appendix 2).

Since there was some evidence of a non-uniform distribution over the interior of the tank, an alternative analysis, not depending on this assumption, was adopted. As in the analysis for the rectangle, there was no evidence of a change in the proportion of crabs on the edge as density of crabs in the tank varied. The overall proportion of crabs on the edge was 0.43.

In the second part of the analysis, nearest neighbour analysis was carried out under the assumption that no particular sector of the tank was likely to have more or fewer crabs in it than any other sector, regardless of the size of sector. Under this assumption, the configuration of crabs in the tank can be regarded as resulting from a two-stage process. Firstly, n radius measurements $r_1 \ldots\ldots r_n$ are obtained by independent drawings from some unknown radius distribution p. Secondly, the n radii are paired off with n independent angles $\theta_1 \ldots\ldots \theta_n$, uniformly distributed over the circle to give the n coordinates $(r_1 \theta_1) \ldots (r_n \theta_n)$. The form of the radius distribution is not in general known, but given $r_1 \ldots r_n$, the positions of the points does not depend on p since technically $r_1 \ldots r_n$ are sufficient for p. In particular, for any given configuration of n crabs $(r_1\ \theta_1) \ldots (r_n\ \theta_n)$ the expected average nearest neighbour distance given $r_1 \ldots r_n$, does not depend on anything unknown, and can, in principle, be calculated. This was done by simulation for all configurations. Crab size was once more taken into account at this stage in the same way as in the rectangular tank case.

It was found from the simulations that the distribution of the average nearest neighbour distances is approximately normal in all cases. The corresponding variances for each mean nearest neighbour distance were obtained. Given this information:

$$\frac{x_i - \theta_i}{\sigma_i} \text{ approximates to the standard normal distribution}$$

where x_i = observed average nearest neighbour distance for a particular configuration

θ_i = corresponding estimated expected average nearest neighbour distance

σ_i = corresponding estimated standard deviation.

The six values of $\frac{x_i - \hat{\theta}_i}{\hat{\sigma}_i}$ for the different densities as shown in Table IV.

TABLE IV

Values of the quantity $\frac{x_i - \hat{\theta}_i}{\hat{\sigma}_i}$ which measures the degree of interaction of crabs with one another. If there was no interaction, there would be no significant differences between positive and negative signs. Values have been rearranged into increasing order for convenience.

Crabs per tank	Values of $\frac{x_i - \hat{\theta}_i}{\hat{\sigma}_i}$					
12	- .224	+.018	+ .043	+ .566	+ .971	+2.283
14	+ .034	+.431	+ .459	+ .704	+1.336	+2.482
17	- .287	-.007	+ .403	+ .444	+ .782	+1.814
20	- .912	+.174	+ .827	+ .892	+1.788	+3.634
25	-1.109	+.214	+1.017	+1.228	+1.233	+2.159
28	-1.244	-.165	+1.110	+1.316	+1.908	+2.124

It is unlikely that these are drawn from a standard normal distribution since there are, at each of the six densities of crabs per tank, more positive than negative signs. Moreover, in all but one density (17 per tank), there is at least one value which is significantly greater than expected at the 5% level in a N(0,1) distribution, and this value is always positive. This indicates that one of the assumptions made, either angular symmetry or independence should be rejected. It seems that independence is the reasonable assumption to reject in favour of the hypothesis that the crabs tend to space themselves out more than would be expected if they did not interact. This hypothesis seems to hold even for 28 crabs per tank. At this density the absence of interaction would produce a <u>smaller</u> average nearest neighbour distance than expected owing to the lack of angular symmetry.

The analogue of the Clark and Evans (1954) measure of concentration, $\frac{\bar{r}_A}{\bar{r}_E} = R$, was defined to be

$$\frac{1}{6} \sum \frac{x_i}{\theta_i}$$

for each density. These values are shown in Table V.

TABLE V

The measure of concentration of crabs per tank at different densities. If $\frac{1}{6} \sum \frac{x_i}{\theta_i} < 1$ crabs would be aggregated. $\frac{1}{6} \sum \frac{x_i}{\theta_i} > 1$ means that crabs are spaced out to a greater degree than expected from independent positioning.

Crabs per tank	$\frac{1}{6} \sum \frac{x_i}{\theta_i}$
12	1.132
14	1.156
17	1.079
20	1.090
25	1.078
28	1.076

It should be noted, however, that unlike the Clark and Evans' R, this measure cannot be readily interpreted in simple terms, as, while the expected value of this new function is 1 under independence, its properties are not clear under departures from independence. It should therefore be treated with caution as a measure of spacing and hence no weighted regression techniques were used to relate this measure to population density.

As a final exercise, the possibility that the observed average nearest neighbour distances have been increased by some constant, k, was investigated. This can be represented mathematically by the formula

$$x_i = \Theta_i + k + \varepsilon$$

where x_i and Θ_i are as before, k is some constant possibly dependent on density, and ε is an error with zero expected value and variance σ_i^2.

The constant, k, was estimated by the weighted least squares method for each density of crabs and the generalised likelihood ratio test for the equality of k for all densities was performed (see Appendix 3). It was found that there was no reason to reject the hypothesis of equality of k for all densities. The overall estimate of k is 0.454 cm. One way of viewing the crabs' interaction is therefore to say that they are on average about 0.5 cm further apart from one another than one would expect if they positioned themselves independently. This occurs irrespective of the population density range tested in these experiments, and since crab size has already been taken into account, cannot be accounted for by the radius of a crab being 0.5 cm.

Discussion

The results of both the rectangular and circular tank data show two very clear trends. One of these trends is the marked tendency for a crab to position itself near an edge. Animals can be congregated at the edges, however, and yet exhibit a different pattern than if they were positioning themselves there independently. A conventional Clark and Evans (1954) analysis is likely to give a misleading result under these circumstances, whereas the present analysis is able to separate out the effects of crabs independently orientating themselves to non-uniform parts of the physical environment and of genuine interaction between crabs.

This ability to separate interaction between animals from independent orientation to a non-uniform part of the physical environment may well be important in determining the interactions occurring among other groups of animals. Amongst research already published it could play a significant role in the analysis of Drosophila in a circular dish (Hay 1972, 1974), sticklebacks in pools (Black and Wootton 1970), and sublittoral hermit crabs in laboratory tanks (Meadows and Mitchell 1973).

The other clear trend shown in the results of the present paper is that there is a notable departure from independent positioning of crabs even after edge attractions and size of the animals have been taken into account. In addition, there is some evidence that the crabs used in the rectangular and circular tanks tended, on average, to space themselves out slightly more than expected from independent positioning, regardless of the density of crabs used in a tank. If a conventional Clark and Evans (1954) test had been applied to the present data then, although the effect of spacing out would have been apparent at all densities, there would have been a misleading impression of the effect of increasing density of crabs on the measure of spacing, R. This measure decreases as population density decreases - cf. Meadows and Mitchell (1973). The reason for this is probably once more because of the attraction to edges by the hermit crabs. As the number of hermit crabs round the perimeter increases, then the nearest neighbour distances of these hermit crabs will tend to decrease at a proportionately faster rate than that of Clark and Evans' (1954) $\bar{r}_E$. Hence the measure $R = \frac{\bar{R}_A}{R_E}$ will tend to become smaller at higher densities.

The ability of P. bernhardus to space out is no surprise in view of its documented agonistic repertoire (Hazlett 1968a, 1969). It is also no surprise to find that the degree of spacing out does not alter with density, as Hazlett (1968b), also studying P. bernhardus concluded that "with periods of adjustment (90 minute intervals), there were no marked increases in aggression as density increased". The advantages of spacing out have been discussed elsewhere in relation to aquatic invertebrates (Meadows and Campbell 1972, pp.311-331), but little is known of the advantages of the thigmotactic behaviour shown by P. bernhardus and other aquatic animals (Meadows and Campbell 1972, p.279). Little can therefore be said on the observed distributions of P. bernhardus in relation to its natural environment. For instance, it would be interesting to know if an aggressive crab would position itself in a preferred area next to an edge of a pool, or, alternatively, if it is only the submissive crabs which are attracted to the edges, since they would be less conspicuous and less liable to be attacked from any angle. Since nothing is known on the effect of predators on the spacing behaviour of P. bernhardus, or of their efficacy in limiting population density, these topics would also need to be studied for a more complete interpretation of the ecological significance of the laboratory distributions.

Summary

(1) A rectangular and a circular tank were used to investigate the distributions of intertidal Pagurus bernhardus (L.) at different population densities. In the rectangular tank, crabs preferred corners to edges while in both rectangular and circular tanks, edges were preferred to the middle of the tank. The proportions of crabs inhabiting these different areas did not change with population density.

(2) A nearest neighbour analysis was carried out on each distribution and each observed mean nearest neighbour distance was compared with an expected mean nearest neighbour distance for the same density. This expected distance was obtained from a computer simulation which assumed: (1) attractions towards preferred areas in the proportions observed in the laboratory; (2) independent positioning of crabs in relation to one another.

(3) In the rectangular tank, there was evidence that the hermit crabs spaced themselves out slightly greater than the expected simulated distance, and that this degree of spacing was not significantly affected by population density. A similar result

was obtained in the circular tank analysis in which the crabs spaced themselves on average 0.5 cm further apart than expected from independent positioning.

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THE EFFECT OF LIGHT
ON THE SPATIAL DISTRIBUTION
OF INTERTIDAL *PAGURUS BERNHARDUS*

Introduction

One of the areas of habitat selection in which little is known is the effect of light on the spacing out of mobile benthic invertebrates. This is in sharp contrast to the work done on the effects of light on planktonic animals (Meadows and Campbell, 1972 p280) and is surprising because many mobile benthic invertebrates have stereotyped visual aggressive displays which are thought to be concerned with spacing out (Bovbjerg, 1959, 1960; Hazlett, 1972). If this is indeed the case, spacing out behaviour would only occur in the presence of illumination. To test this hypothesis, the intertidal hermit crab Pagurus bernhardus was studied since its spacing out behaviour (see preceding paper, p19) and its aggressive displays (Hazlett 1968, 1969) have been documented under laboratory conditions.

Materials and Methods

The materials and methods used were similar to the circular tank part of the preceding paper (p21) except that readings were taken of crabs distributed first in the presence and then in the absence of illumination during 2000-2400 hours and that population densities of crabs were different. In the first series lights were off from 2400 to 0700 hours each day and readings were taken, one per night, at densities of 10, 13, 16 and 19 crabs per tank until six replicates at each density were obtained. This procedure was repeated in the second series of experiments, when readings of crabs distributed without illumination between 2000-2400 hours were taken. In this second series a perspex sheet was laid over the tank during normal daylight hours (1700-1900) and the distributions of the crabs were plotted immediately the lights were switched on between 2000 and 2400 hours to take the readings. This did not give the crabs enough time to move and hence break up their distribution during darkness. Once the distribution had been plotted, the lights were switched off again for the remainder of each night.

Results

The first part of the analysis was conducted as in the circular tank results of the previous paper (p28). In both the first and second series of experiments there was no evidence at the 5% significance level to suggest that the six aggregated angle measurements at each density departed from uniformity when tested by χ^2 analysis of 90° and, for densities 16 and 18, 20° sectors of the tank (see Appendix 1). There was also no evidence to suggest any significant departure at the 5% level from uniform radial distributions over the interior of the tank when the interior was defined as the first 21.5 cm radius of the tank (see Appendix 2). There was clear evidence of differences in radial distributions between the first and second series of experiments, however, as a significantly greater number of P. bernhardus was distributed on the edge area (the outer 3 cm of the tank) during illumination readings than in darkness readings. This is shown in Table I.

TABLE I

Proportions of P. bernhardus occupying different areas of the experimental tank in the presence and absence of illumination. There is no significant effect of population density on proportions of crabs occupying the two areas in either case ($\chi^2 = 3.58$ with illumination, $\chi^2 = 0.62$ without illumination), but there is a highly significant difference ($\chi^2 = 108.6$, 1df $P < 0.001$) between the total numbers of crabs inhabiting the two areas in the presence and absence of illumination. Six replicate experiments were performed at each population density.

	With Illumination		Without Illumination	
Number of crabs per tank	Number on edge	Number in interior	Number on edge	Number in interior
10	44	16	22	38
13	52	26	29	49
16	76	20	32	64
19	85	29	37	77
Total	257	91	120	228

A χ^2 test on the homogeneity of the proportions of edge: interior among the four different population densities tested showed no significant difference in either series. (With illumination, $\chi^2 = 3.58$, 3 d.f., without illumination $\chi^2 = 0.62$, 3 d.f.).

The nearest neighbour analyses were conducted by measuring the observed nearest neighbour distances to the nearest 0.5 cm and comparing the six observed mean nearest neighbour distances ($\bar{x}_i$) at each density with the expected mean nearest neighbour distances of crabs distributing themselves independently of each other (θ). Since the radial distributions in the interior of the tank were uniform the numbers of crabs in the edge and the interior shown in Table I were divided by 6 and rounded to the nearest whole number to obtain the expected number of crabs on the edge and interior at each density. Simulations consisting of 5000 iterations were then performed on points distributed independently of each other but occurring in the edge : interior ratios calculated from Table I. The effect of crab size was taken into consideration as in the previous paper by excluding those iterations which had nearest neighbour distances of less than 1 cm, which was the average diameter of a P. bernhardus. The mean nearest neighbour distance of the iterations not excluded by crab size was taken to be θ, and since there was no significant departure from a normal distribution in the simulated distances, the standard deviation, σ, was also obtained. Given this information, $\frac{\bar{x}_i - \theta}{\sigma}$ should approximate to the standard normal distribution if $\bar{x}_i$ in each case is obtained from crabs spacing themselves independently of each other. The values of $\frac{\bar{x}_i - \hat{\theta}}{\hat{\sigma}}$ are given in Table II for both series of experiments.

TABLE II

Values of the quantity $\frac{\bar{x} - \hat{\theta}}{\sigma}$ for P. bernhardus distributed in the presence and absence of illumination. The values have been rearranged from their temporal sequence into increasing numerical order for convenience. * = value is significant at 5% level.

With illumination

Crabs per tank	Values of $\frac{\bar{x}_i - \hat{\theta}}{\sigma}$					
10	-0.28	-0.13	+0.65	+0.65	+1.13	+1.37
13	-0.32	+0.73	+1.31	+1.66	+2.01*	+2.29*
16	-1.43	+0.01	+0.25	+0.61	+0.67	+2.60*
19	-1.70	-0.14	+0.40	+0.79	+1.47	+1.60

Without illumination

Crabs per tank	Values of $\frac{\bar{x}_i - \hat{\theta}}{\sigma}$					
10	-0.67	+0.26	+0.30	+0.66	+0.66	+0.97
13	-0.34	-0.16	-0.16	+0.26	+0.43	+2.08*
16	-1.87	-1.54	-0.52	+0.12	+0.12	+0.59
19	-2.23*	-1.04	+0.51	+0.96	+1.25	+1.48

There is some evidence to suggest a departure from normality in the readings taken with illumination since 18 of the 24 values are positive, and 3 of these 18 values are significant, but there is no evidence of departure from normality in the readings without illumination. These findings are further supported by a generalised likelihood ratio test on the significance of k in the formula

$$\bar{x}_i = \theta + k + \epsilon$$

where $\bar{x}_i$ and θ are as before, k is a constant and ϵ is an error with zero expected value and variance σ^2 (see Appendix 3).

In the first series, k was not found to be significantly different at any of the four densities and had an overall value of 0.65 cm. This was significantly different ($P < 0.05, > 0.01$) from the null hypothesis value of zero for k. The second series also showed no significant effect of population density on the value of k, but in this case, k was not significantly different from zero ($P > 0.20$). Finally, a comparison of the k's obtained in the two series yields a significant difference at the 5% level (see Appendix 3).

Discussion

Two main points of interest arise from the results of the two series of experiments. The first point is that P. bernhardus is visually attracted towards the edges of the experimental tank. The results of the previous paper (p29) had shown that P. bernhardus was attracted to edges, but this could have arisen from random movement about the tank until the crab was stopped by the edge of the tank.

The second point of interest is that P. bernhardus only seems to space out during conditions of illumination. A comparison of the constants "k" obtained in the present paper with the constant "k" obtained on p33 of the preceding paper indicates that there is no inherent spacing rhythm in P. bernhardus. There is no significant difference between the k value obtained in the first series of this paper (0.65 cm) and the k value obtained from readings taken between 0700 and 1900 in the preceding paper (0.46 cm). The k value obtained from crabs distributed in darkness (0.04 cm) is significantly different from both other k values calculated, however.

The ecological implications of this work are that P. bernhardus will tend to be found spaced out round edges of rock pools with steep edges during daylight hours. In contrast to this distribution, however, during darkness they will tend to be distributed independently of each other throughout the pool.

Summary

The spatial distributions of intertidal Pagurus bernhardus during normal hours of darkness in the laboratory were studied at different population densities with and without the presence of overhead illumination. With illumination P. bernhardus spaced out on average 0.66 cm more than expected from other P. bernhardus. In the absence of any illumination, however, the crabs did position themselves independently. No effect of population density on spacing behaviour was discovered either with or without illumination. There was a significant tendency for crabs to position themselves next to the

perimeter of the circular tank under all conditions, but this was much more obvious during illumination than without it. There is no evidence of any inherent spacing rhythms in this species.

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SHELL SELECTION IN THE HERMIT CRAB

PAGURUS BERNHARDUS

Introduction

It is well established that most hermit crab species need shells (Allee and Douglas, 1946; Brightwell, 1952; Reese, 1969), and that some shells are preferred to others (Grant and Ulmer, 1974; Mitchell in press; Orians and King, 1964) but little has been concluded about the importance of certain shell variables in determining which type of shell is preferred. Reese (1962) only considered shell weight as a variable against crab weight, while Hazlett (1970), Markham (1968) and Volker (1967) tried to compare shell weight and shell volume as variables against crab size but used inappropriate statistical techniques.

Vance (1972) used two measures of crab size and five measures of preferred shell size, and found the best correlation for three hermit crab species studied was between shell width and crab weight. He was careful to state, however (p.1066), that there was "no implicit assumption of a casual relationship between crab weight and preferred shell width". This is because shell variables are intercorrelated to such an extent that it is difficult to establish their effects by simple regression techniques. This criticism also applies to all other previous published work on shell selection and is probably at the source of the inconclusiveness of the role of certain shell variables in shell selection.

In the present study, the shell investigation behaviour of hermit crabs without their shells was studied to discover if this gave any clues as to what shell variables may be important in shell selection. Three often repeated sequences of behaviour were observed. These were (1) rolling the shell around the bottom of the aquarium (Hertz, 1933; Reese, 1962); (2) inserting its chelipeds or abdomen into the internal space of the shell (Reese, 1962), and (3) using its chelipeds as calipers to obtain a measure of the aperture width (Kinosita and Okajima, 1968). From these behavioural sequences it was suggested that the most important variables were (1) shell weight, (2) shell volume and (3) shell aperture width, and an attempt was made by using principal component analysis to separate their individual effects on shell selection by the intertidal hermit crab Pagurus bernhardus (L.).

Materials and Methods

Specimens of Pagurus bernhardus were taken from Ardrossan beach in the Clyde Estuary, and transported to the University of Glasgow where they were maintained in stock tanks in a 10°C cold room with a 12-h day, 12-h night automatic light regime. The empty shells used in the experiment had also been taken from Ardrossan beach at an earlier date. They consisted of 300 Littorina littorea (L.) and 300 Thais lapillus (L.). These two species are equally abundant at Ardrossan, and almost all P. bernhardus on the beach inhabit one or other of these species. Each of the 600 shells used for this experiment was numbered by waterproof ink (Magic Marker) for individual recognition by the experimenter, and then placed randomly with their apertures facing upwards a distance of 3 cm or more from the edges of an experimental tank 105 cm, 55 cm, 18 cm, height. This precaution was necessary as this species is known to favour the edges of tanks (Meadows and Mitchell, 1973).

Two P. bernhardus were taken from a stock tank, deprived of their shells by breaking the shells open mechanically, and put into the experimental tank. After 24h in the experimental tank, the crabs were taken out, removed from their shell by putting the shell next to a 60W light bulb, blotted dry of excess water, and weighed on a balance to the nearest 0.01 g. A note was taken of the labelled number of the shells which both crabs inhabited, and the shells were returned to the experimental tank. Two more P. bernhardus were then taken from a stock tank and the experiment was repeated until 50 shells had been chosen. The fact that some shells had been occupied by another hermit crab immediately prior to the repeats was not thought to influence the results as Jensen (1970) had found no evidence to suggest that previous occupation had any effect on shell choice for this species.

On completion of the Littorina/Thais choice experiment, the 300 Thais shells were taken out of the tank, leaving only the 300 Littorina shells in the tank. The experiment was then repeated as before until 25 Littorina shells had been selected. The 300 Littorina shells were then taken out and the 300 Thais put back into the tank. Once more the experimental procedure was repeated until 25 Thais shells had been selected.

During these experiments, no aeration or feeding was provided in the experimental tank, and no substrate was used, as these crabs are naturally found in rock pools on a grey background similar to that of the fibreglass experimental tank.

At the end of all the experiments, the 600 shells used in the experimental tank were put in an oven until completely dry. They were then weighed to the nearest 0.01 g and their aperture widths were measured to the nearest 0.01 cm. Finally, sand of particle size 3ϕ (phi) (125 μm) was used to measure the internal volume of each shell. This was done by filling the shell with sand, weighing the shell plus sand, subtracting the weight of the shell from it, and dividing the answer obtained by 1.5, which is the weight in g. of 1 ml of sand of size 3ϕ. This measure of volume was taken as accurate to the nearest 0.01 ml.

Results

Littorina/Thais choice experiment

The results of this experiment are presented in Table I. Since the standard errors of the Littorina variables were in all cases noticeably larger than the corresponding Thais variables, a modified form of the "t" test, the statistic d, was used to determine if the crab weights and shell parameters of the two shell species were significantly different from each other (Bailey, 1959, p.51). It was found that the volumes of Thais shells selected were significantly greater than those of Littorina shells selected, whereas the aperture widths of Littorina were significantly greater than those of Thais. No significant differences were observed between the means of the crab weights or shell weights of the two species. When the means of the Littorina and Thais shells selected were compared with the means of the 300 Littorina and 300 Thais used in the experiment, it was found that the Thais shells selected did not differ significantly from the population of 300 Thais shells in weight ($d = 1.68$, $P = 0.09$), volume ($d = 1.54$, $P = 0.12$), or aperture width ($d = 0.27$, $P = 0.79$). The Littorina shells selected were significantly smaller than the 300 Littorina shells in the three

TABLE I

Results of the crab weights and shell variables of the shells selected in the Littorina/Thais choice experiment. Twenty-five L. littorea and 25 T. lapillus were chosen. Table values are means ± standard errors for L. littorea and T. lapillus variables. the "d" values are those given from the formula of Bailey (1959, p.51) for comparing two means of unequal variances. Degrees of freedom and probability are represented by d.f. and P respectively.

Variable	L. littorea	T. lapillus	"d" value	d.f.	P
Crab weight	0.624 ± .0515	0.724 ± .0364	1.579	45	$<0.2, >0.1$
Shell weight	1.958 ± .2035	2.047 ± .1158	0.380	38	$<0.8, >0.7$
Shell volume	1.038 ± .0806	1.394 ± .0574	3.596	44	<0.001
Shell aperture width	0.826 ± .0200	0.763 ± .0141	2.571	43	$<0.02, >0.01$

variables measured ($d = 3.23$, $P < 0.001$), however. This is probably because no crabs of a large enough size were used so that large Littorina shells could be selected.

In view of the differences which were obtained when comparing the variables of the shell species, it was decided to perform a multiple regression of crab weights against shell weight (Morrison, 1967), volume and aperture width for Littorina, Thais, and the combined Littorina and Thais data. A likelihood ratio test on the null hypothesis of equality of all coefficients between the Littorina and Thais regressions could then be performed. The results of the multiple regressions are shown in Table II. To test for the equality of the regression lines of the two separate species, the following version of the standard likelihood ratio F test was used:

$$F = \frac{(R_{H_o} - R_{H_1})/4}{R_{H_1}/(m + n - 8)}$$

For interpretation of expressions see Table II.

If the null hypothesis holds, then the value F has an $F_{(4,42)}$ distribution. In this case, $F = 1.36$, which is well below the significant value at the 5% level. There is, therefore, no significant evidence of any difference between the two equations of Littorina and Thais.

It is important to realize at this stage that although a coefficient of a variable is not significant in the regression equation in Table III, this does not mean that it cannot play an important part in the selection of a shell. For instance, in the Littorina regression where no coefficient is significant, an F test on the hypothesis that the three coefficients of the shell variables are equal to zero yields a highly significant result ($F_{(3,21)} = 28.4$). The main problem with using a regression equation to distinguish the effects of the separate parameters is that there is a high correlation between shell weight, shell volume and shell aperture width which obscures their separate effects. To overcome

TABLE II

A list of symbols and expressions used in this paper to define shell selection by hermit crabs.

R_{H_o} = residual sum of squares for combined Littorina + Thais regression.

R_{H_1} = summed residual sums of squares for the two individual regressions of Littorina and Thais.

m = number of observations in the Littorina regression line.

n = number of observations in the Thais regression line.

F = variance-ratio value. Degrees of freedom are shown in brackets next to it.

Y = crab weight. $\bar{Y}$ = mean of crab weights.

W_i = shell weight. $\bar{W}$ = mean of shell weights.

V_i = shell volume. $\bar{V}$ = mean of shell volumes.

A_i = shell aperture width. $\bar{A}$ = mean of shell aperture widths.

x_1, x_2, x_3 = 1st, 2nd and 3rd principal components.

w_i = scaled shell weight. $\bar{w}$ = mean of scaled shell weights.

v_i = scaled shell volume. $\bar{v}$ = mean of scaled shell volumes.

a_i = scaled shell aperture width. $\bar{a}$ = mean of scaled shell aperture widths.

TABLE III

Results of the multiple regressions of crab weight (Y) against shell weight (W), shell volume (V), and shell aperture width (A). Standard deviations of the regression coefficients are given in brackets underneath. * = coefficient is significantly different from zero ($P < 0.05$).

Shell Species	Regression equation	Percentage of the variation in crab weight explained
Littorina	$Y_i-\bar{Y} = 0.0004(W_i-\bar{W}) + 0.095\,(V_i-\bar{V}) + 1.719(A_i-\bar{A})$ (.059) (.269) (1.102)	77.4%
Thais	$Y_i-\bar{Y} = -0.0605(W_i-\bar{W}) + 0.681^{*}(V_i-\bar{V}) + 0.349(A_i-\bar{A})$ (.056) (.135) (.605)	72.4%
Littorina + *Thais*	$Y_i-\bar{Y} = -0.0165(W_i-\bar{W}) + 0.419^{*}(V_i-\bar{V}) + 0.599(A_i-\bar{A})$ (.040) (.066) (.291)	73.5%

this difficulty, a change of variable can be made to the principal component variables. This in turn introduces a new problem, however, as arbitrary scale effects caused by the variables being measured in different units, may cause a distortion in the results. This problem was investigated by comparing the unscaled principal component variables of weight, volume and aperture width with principal component variables of the correlation matrix produced by dividing the variables by the square root of the sums of squares of their deviations from the mean. The results of the principal components of the Littorina and Thais shells are shown in Table IV (unscaled) and Table V (scaled). Regression equations of crab weight against these principal components (Morrison, 1967) are shown in Table VI.

TABLE IV

Principal components of the two species of shell in the Littorina/Thais choice experiment. No scaling has been performed on them.

Shell Species	Principal components	Percentage contributions to the total variability of the x's
Littorina	$X_{1_i} = .94(W_i-\bar{W}) + .36(V_i-\bar{V}) + .09(A_i-\bar{A})$	97%
	$X_{2_i} = -.35(W_i-\bar{W}) + .92(V_i-\bar{V}) + .19(A_i-\bar{A})$	3%
	$X_{3_i} = -.02(W_i-\bar{W}) - .21(V_i-\bar{V}) + .98(A_i-\bar{A})$	0%
Thais	$X_{1_i} = .93(W_i-\bar{W}) + .36(V_i-\bar{V}) + .09(A_i-\bar{A})$	91%
	$X_{2_i} = -.37(W_i-\bar{W}) + .92(V_i-\bar{V}) + .125(A_i-\bar{A})$	9%
	$X_{3_i} = -.04(W_i-\bar{W}) - .015(V_i-\bar{V}) + .99(A_i-\bar{A})$	0%

TABLE V

Principal components of the two species of shell in the Littorina/ Thais choice experiment. Scaling was performed by dividing the shell parameters by the square root of the sums of squares of their deviations from the mean so that $w_i = \frac{W_i - \bar{W}}{4.980}$, $v_i = \frac{V_i - \bar{V}}{1.970}$ and $a_i = \frac{A_i - \bar{A}}{0.539}$ for Littorina and $w_i = \frac{W_i - \bar{W}}{2.839}$, $v_i = \frac{V_i - \bar{V}}{1.413}$ and $a_i = \frac{A_i - \bar{A}}{0.347}$ for Thais.

Shell Species	Principal components	Percentage contributions to the total variability of the x's
Littorina	$X_{1_i} = .56w_i + .58v_i + .59a_i$	94%
	$X_{2_i} = -.82w_i + .49v_i + .30a_i$	5%
	$X_{3_i} = -.11w_i - .70v_i + .75a_i$	1%
Thais	$X_{1_i} = .56w_i + .58v_i + .59a_i$	84%
	$X_{2_i} = -.81w_i + .55v_i + .22a_i$	11%
	$X_{3_i} = -.20w_i - .60v_i + .77a_i$	5%

TABLE VI

Regression equations of crab weight against scaled and unscaled principal components for *Littorina* and *Thais* in the *Littorina*/*Thais* choice experiment. Standard deviations of the regression coefficients are given in brackets underneath. * = coefficient is significantly different from zero ($P < 0.05$).

Shell Species		Regression equation	Percentage of the variation in crab weight explained
Littorina	Unscaled	$Y_i - \bar{Y} = .192^*X_{1_i} + .414^*X_{2_i} + 1.665X_{3_i}$	$X_1 = 65.43\%$
		(.0246) (.138) (1.127)	$X_2 = 9.67\%$
			$X_3 = 2.35\%$
	Scaled	$Y_i - \bar{Y} = .652^*X_{1_i} + .370\ X_{2_i} + .570X_{3_i}$	$X_1 = 75.3\%$
		(.078) (.337) (.775)	$X_2 = 0.6\%$
			$X_3 = 0.6\%$
Thais	Unscaled	$Y_i - \bar{Y} = .158^*X_{1_i} + .605^*X_{2_i} - .455X_{3_i}$	$X_1 = 28.9\%$
		(.034) (.1065) (.612)	$X_2 = 42.6\%$
			$X_3 = 0.7\%$
	Scaled	$Y_i - \bar{Y} = .390^*X_{1_i} + .642^*X_{2_i} - .636^*X_{3_i}$	$X_1 = 48.3\%$
		(.064) (.181) (.262)	$X_2 = 16.5\%$
			$X_3 = 7.7\%$

Littorina and *Thais* separately

The results of the selection of the 300 *Littorina* shells alone in the tank, and the 300 *Thais* shells under similar conditions are shown in Table VII.

TABLE VII

Results of the crab weights and shell variables of the shells selected in the experiments in which *Littorina* and *Thais* shells were offered separately. Twenty-five crabs were used in both conditions. Table values are means ± standard errors for *L. littorea* and *T. lapillus* variables. For other notations see Table I.

Variable	*L. littorea*	*T. lapillus*	"d" value	d.f.	P
Crab weight	0.692 ± .0456	0.686 ± .0732	0.074	42	>0.9
Shell weight	2.407 ± .2211	2.089 ± .1555	1.173	40	<0.3, >0.2
Shell volume	1.234 ± .0888	1.307 ± .0764	0.624	46	<0.6, >0.5
Shell aperture width	0.861 ± .0195	0.762 ± .0184	3.750	47	<0.001

Once again, the variances of the shell variables of *Littorina* are greater than those of *Thais*, and the shell aperture widths of *Littorina* are significantly greater than those of *Thais*. Unlike the choice experiment, there is no significant difference between the shell volumes of the two species, however. A comparison of the means of the Littorina and Thais shells selected, with the populations of 300 Littorina and 300 Thais shells showed no significant difference in weight (d = 1.43, P = 0.15), volume (d = 0.32, P = 0.75) or aperture width (d = 0.27, P = 0.79), for Thais shells. Littorina shells selected were significantly smaller in weight (d = 1.99, P = 0.046) and aperture width (d = 2.13, P = 0.034) but showed no significant difference in volume (d = 0.66, P = 0.51).

The multiple regressions of crab weight against shell weight, volume and aperture width are shown in Table VIII. Once more, a likelihood ratio test on the equality of all coefficients between the Littorina and Thais regressions showed no significant difference between the two equations ($F_{(4,42)} = 1.81$). In contrast to the choice situation, however, the Littorina regression line and the combined Littorina and Thais line show a marked decrease in the percentage of the variation in crab weight explained by the shell variables. This decrease is 20.2% in the case of Littorina and 14.6% in the case of the combined regression. A comparison of the two Thais lines also shows a drop in percentage of variation explained by the Thais alone line, but in this case the drop is only 4.3% from the percentage explained by the Thais choice line.

The principal components of both the unscaled and scaled Littorina and Thais shells selected in the absence of the other species of shell are shown in Tables IX and X respectively. In general, they show a similar situation to the principal components in the choice situation in both the magnitude of the parameters of the variable in the three components and in the percentage contributions of the three components to the total variability of

TABLE VIII

Results of the multiple regressions of crab weight (Y) against shell weight (W), shell volume (V), and shell aperture width (A), for Littorina alone, Thais alone and a combination of Littorina and Thais alone. Standard deviations of the regression coefficients are given in brackets underneath. * = coefficient is significantly different from zero ($P < 0.05$).

Shell Species	Regression equation	Percentage of the variation in crab weight explained
Littorina	$Y_i-\bar{Y} = \underset{(.073)}{-0.073\,(W_i-\bar{W})} + \underset{(.202)}{0.294\,(V_i-\bar{V})} + \underset{(.734)}{1.223\,(A_i-\bar{A})}$	57.2%
Thais	$Y_i-\bar{Y} = \underset{(.080)}{-0.062\,(W_i-\bar{W})} + \underset{(.225)}{0.384\,(V_i-\bar{V})} + \underset{(.832)}{2.205^*(A_i-\bar{A})}$	68.1%
Littorina + Thais	$Y_i-\bar{Y} = \underset{(.028)}{-0.122^*(W_i-\bar{W})} + \underset{(.064)}{0.498^*(V_i-\bar{V})} + \underset{(.218)}{1.298^*(A_i-\bar{A})}$	58.9%

the x's.

The regression equations of crab weight against the scaled and unscaled principal components of the Littorina alone and Thais alone shells selected are shown in Table XI. It is interesting to note that the percentage of the variation in crab weight explained by the X_2 principal component variable is greater than that explained by the X_1 principal component variable in the case of the unscaled Thais

TABLE IX

Principal components of the two species of shell in the _Littorina_ separate and _Thais_ separate experiments. No scaling has been performed on them.

Shell Species	Principal components	Percentage contributions to the total variability of the x's
Littorina	$X_{1_i} = .93\,(W_i-\bar{W}) + .35(V_i-\bar{V}) + .07(A_i-\bar{A})$	97.7%
	$X_{2_i} = -.35\,(W_i-\bar{W}) + .93(V_i-\bar{V}) + .13(A_i-\bar{A})$	2.1%
	$X_{3_i} = -.02\,(W_i-\bar{W}) - .15(V_i-\bar{V}) + .99(A_i-\bar{A})$	.2%
Thais	$X_{1_i} = .93\,(W_i-\bar{W}) + .36(V_i-\bar{V}) + .07(A_i-\bar{A})$	90.3%
	$X_{2_i} = -.36\,(W_i-\bar{W}) + .91(V_i-\bar{V}) + .18(A_i-\bar{A})$	9.3%
	$X_{3_i} = -.002(W_i-\bar{W}) + -.19(V_i-\bar{V}) + .98(A_i-\bar{A})$	.4%

regression. This is a similar result to the _Thais_ choice unscaled regression and is of interest because in both the _Thais_ choice and _Thais_ alone conditions, approximately 90% of the total variability was explained by the first principal component as opposed to only 9% explained by the second principal component.

TABLE X

Principal components of the two species of shell in the Littorina alone and Thais alone experiments. Scaling was performed by dividing the shell variables by the square roots of their sums of squares of their deviations from their means. This gave:

$w_i = \frac{W_i - \bar{W}}{5.435}$, $v_i = \frac{V_i - \bar{V}}{2.174}$ and $a_i = \frac{A_i - \bar{A}}{0.482}$ for Littorina and

$w_i = \frac{W_i - \bar{W}}{3.808}$, $v_i = \frac{V_i - \bar{V}}{1.871}$ and $a_i = \frac{A_i - \bar{A}}{0.448}$ for Thais

Shell Species	Principal components	Percentage contributions to the total variability of the x's
Littorina	$X_{1_i} = .58w_i + .58v_i + .57a_i$	91.9%
	$X_{2_i} = .59w_i + .19v_i - .79a_i$	5.2%
	$X_{3_i} = .57w_i - .79v_i + .24a_i$	2.9%
Thais	$X_{1_i} = .54w_i + .61v_i + .58a_i$	79.3%
	$X_{2_i} = -.81w_i + .19v_i + .56a_i$	14.8%
	$X_{3_i} = .23w_i - .77v_i + .59a_i$	5.9%

TABLE XI

Regression equations of crab weight against scaled and unscaled principal components for *Littorina* alone and *Thais* alone experiments. Standard deviations of the regression coefficients are given underneath. * = coefficient is significantly different from zero ($P < 0.05$).

Shell Species			Percentage of the variation in crab weight explained
Littorina	Unscaled	$Y_i - \bar{Y} = .107^*X_{1_i} + .366\,X_{2_i} + 1.105\,X_{3_i}$	X_1 = 40.5%
		$(.032) \quad (.212) \quad (.834)$	X_2 = 10.5%
			X_3 = 6.2%
	Scaled	$Y_i - \bar{Y} = .420^*X_{1_i} - .519\,X_{2_i} - .403\,X_{3_i}$	X_1 = 51.3%
		$(.110) \quad (.463) \quad (.620)$	X_2 = 4.3%
			X_3 = 1.6%
Thais	Unscaled	$Y_i - \bar{Y} = .235^*X_{1_i} + .764^*X_{2_i} + 2.091^*X_{3_i}$	X_1 = 28.16%
		$(.0545) \quad (.170) \quad (.847)$	X_2 = 30.66%
			X_3 = 9.27%
	Scaled	$Y_i - \bar{Y} = .881^*X_{1_i} + .877^*X_{1_i} - .030\,X_{3_i}$	X_1 = 57.431%
		$(.143) \quad (.331) \quad (.527)$	X_2 = 10.657%
			X_3 = 0.005%

Discussion

Before any conclusions can be drawn from the foregoing results it is necessary to decide whether the scaled or unscaled principal components analysis presents a clearer interpretation of shell selection. In both the scaled and unscaled cases, the large majority of the variability of the x's was explained by the first principal component, but whereas this first principal component explained the majority of variation in crab weight when a regression equation was calculated from the scaled analysis, this was not always the case in the unscaled analysis. It therefore would seem easier to look at the scaled analysis and interpret the first principal component as the main way in which P. bernhardus selects a shell. This principal component is, in fact, very easily interpreted as in all cases the weights attaching to w_i, v_i and a_i are almost equal to each other. In terms of relative importance of the three shell variables, this means that they all play an equal role in the selection of a shell along this component. This is not a full picture of the selection of a shell, however, as in both experiments the second principal component in the scaled analysis is also significant. Fortunately, this second principal component is similar in relative magnitudes of parameters in three out of the four conditions. (The exception is the Littorina separate condition, which explains far less of the variability of crab weight than any of the other three conditions.) This second principal component can therefore be interpreted to be a volume-aperture relative to weight idea. In boththe choice and separate experiments, the second principal component of Thais contributes a higher percentage to the total variability of the x's and explains a higher percentage of the variation in crab weight than Littorina. This could be caused by two explanations. Crabs could be more particular in choosing a Thais shell than a Littorina shell as far as the second principal component is concerned or alternatively it could be because there is more choice to exert along this direction in Thais shells than Littorina shells. The Littorina shells are therefore much better described by one linear relationship than the Thais shells.

It is interesting to observe the different conclusion that is obtained from the scaled principal components analysis regression compared with the conclusion obtained only by looking at the simple regression equations. In the simple regressions weight plays an almost negligible part but this is probably not because the crab does not consider weight when selecting a shell. The most probable explanation is that weight plays a positive role in the first principal component and a negative role in the second principal component and hence the two contrasting roles tend to cancel each other out in the multiple regression. This example shows the advantage of breaking the shell variables into their principal components over simple regression techniques.

Summary

Three shell variables were deemed to be important in the selection of a shell by the hermit crab Pagurus bernhardus (L.). These were the weight, volume and aperture width of a shell. Each of these variables was used in multiple regressions against crab weight for

25 *Thais lapillus* and 25 *Littorina littorea* shells chosen when both shell species were together in a tank, and for a further 25 *T. lapillus* and 25 *L. littorea* when the two shell species were separate. Principal component analysis was performed on the four groups of 25 shells selected, and multiple regression equations were calculated using the principal components as the new variables. It was found that crabs chose a shell of suitable general dimensions rather than solely on the basis of one shell variable. The advantages of using statistical techniques developed in this paper over previous approaches to shell selection are discussed.

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SECTION 3

HABITAT SELECTION BY TWO INTERTIDAL AMERICAN SPECIES OF HERMIT CRABS

"And what you thought you came for
Is only a shell, a husk of meaning
From which the purpose breaks only when it is fulfilled."

Little Gidding.

T.S. ELIOT.

Introduction

The Beaufort Harbor site, from which all hermit crabs used in this section were taken, has one major advantage over the British intertidal site of the previous section. This advantage is that whereas only one hermit crab species occurs at Ardrossan, two species, Pagurus longicarpus and Clibanarius vittatus, commonly occur at Beaufort. Interspecific competition between the two species for limited resources such as shells can therefore be studied. The two species occur in approximately equal numbers at Beaufort Harbor, but C. vittatus is more frequent in eel grass beds nearby, while P. longicarpus is more common on the mud flats of Bird Shoal, an island directly facing Beaufort.

C. vittatus grows to a much greater size than P. longicarpus and large specimens can occupy adult Busycon, Fasciolaria or Strombus shells. These large specimens, however, were not used in any of the experiments in this section.

AN ANALYSIS OF SHELL OCCUPATION BY TWO SYMPATRIC SPECIES OF HERMIT CRAB I. ECOLOGICAL FACTORS

To protect itself from its environment, a hermit crab must have a gastropod shell (Reese, 1969; Vance 1972a) and where numbers of gastropod shells are limited, there is evidence that this limitation reduces the number of hermit crabs an environment can support (Hazlett, 1970; Provenzano, 1960; Reese, 1969; Thomson, 1903). In addition to acting as a limiting factor, the type of shells present in any one place can also determine what size or species of hermit crab is present in that area. Reese (1969, p.346) states that "in Hawaii the availability of shells seems to limit the size of individuals in the population", while Markham (1968) found that occupation of small shells by the European hermit crab, *Pagurus bernhardus*, restricted the growth of these crabs. Examples of resource partitioning of hermit crab species on the basis of two different types of shell have also been studied. Grant and Ulmer (1974) and Wright (1973) both found that shells with *Hydractinia echinata* were preferred by one out of two sympatric species while Vance (1972b) showed that, of the three rocky intertidal species of the San Juan Islands, of Washington, one species preferred short, light shells whereas the other two species preferred comparatively taller and heavier shells.

In the present study experiments were performed on two species of hermit crabs *Pagurus longicarpus* and *Clibanarius vittatus* which were equally abundant in the intertidal zone at Beaufort Harbor, North Carolina. This area had no empty gastropod shells, thus suggesting that shells were a limiting factor in this area and that resource partitioning of the shells may explain the coexistence of the two hermit crab species. The experiments were designed to answer the following questions: (1) are shells a limiting factor in this area? (2) Does resource partitioning take place between P. longicarpus and C. vittatus? (3) If resource partitioning does take place, what factors maintain the partitioning?

Materials and Methods

All animals used in this experiment were taken from the intertidal zone of an area approximately 100 metres long at Beaufort Harbor, next to the Duke University Marine Laboratory dock. This area has a mixture of sand and mud as a substrate and has many living gastropods buried in it. All experiments were conducted during the summer months and no difficulty was encountered in obtaining specimens of either species of hermit crab in this area.

Three series of experiments were conducted. The first series tested the effect of shell limitation on the hermit crabs' occupation of shell, while the second tested the ability of one hermit crab species to obtain a preferred species of shell from the other hermit crab species. The third series of experiments tested the relation between substrate preference of both hermit crab species to the natural occurrence of two living gastropod species on different substrates.

1. Shell Selection

60 Pagurus longicarpus and 60 Clibanarius vittatus were collected in shallow water at low tide on the 14th of July, 1974. The species of shell which each crab inhabited was noted, and for each of these shells five empty shells of the same species were put into an experimental tank of 120 cm x 70 cm x 20 cm deep. This gave a total of 25 Nassarius vibex, 315 Ilyanassa obsoleta, 30 Urosalpinx cineria,

10 Thais haemastoma floridana, 200 Littorina irrorata and 20 Polinices duplicatus. All shells put into the tank had previously been collected in the nearby area. The ratio of gastropod shells occurring in nature was used rather than using equal numbers of different shell species so that an idea could be obtained of how a hermit crab would select a shell in nature if there was no competition from any other hermit crab for that species of shell.

After all the empty shells had been placed at random in the tank, three of the sixty P. longicarpus and three of the sixty C. vittatus were evicted from their shells by holding them over a glass plate under which there was a 100 watt light bulb. P. longicarpus came out by tugging on the minor cheliped side of its body, while C. vittatus climbed out onto my hand after about a minute of gentle heating. This method proved 100% successful and did not seem to harm the crabs in any way. After they were evicted, they were blotted dry of excess water, weighed and then placed in the experimental tank where they were left for 12 hours. It did not seem likely that any of the six crabs would choose the same shell, but to make the risk minimal, an effort was made not to put two crabs of less than 0.05g difference in the tank at the same time.

When the 12 hour period of shell selection had elapsed, the species of shell which each crab was inhabiting was noted and each crab was evicted from its shell and discarded from the experiment. The shells were then placed back in the tank ready for three more crabs of each species to be evicted from their "field" shell and placed in the tank for a 12 hour period. It was not thought likely that the shells chosen by the preceding crabs would have been made more or less attractive by their immediately previous inhabitation, as Jensen (1970) did not find this to be true when testing Pagurus bernhardus and there was no evidence to suggest that those crabs placed in the tank in the mornings selected shells any differently from those placed in the tank in the evenings, as diffuse artificial lighting was supplied during hours of normal darkness and no pronounced activity rhythms were apparent in either species.

No feeding, other than the detritus on the sand/mud substrate, was provided in the experimental tank, but in the stock tank, crabs were fed on pieces of meat from the blue crab, Callinectes.

2. Interspecific Shell Fights

Large specimens of P. longicarpus in I. obsoleta shells were collected from the Beaufort Harbor region, evicted from their shells, weighed and then returned to their shells. Crabs below 0.23g were rejected from the experiment as the results of the shell selection experiment showed that they may not prefer a Littorina irrorata shell to their home shell. C. vittatus inhabiting L. irrorata shells were then collected from the same area, evicted from their shells to check that none were below 0.23g, and then the first ten collected were given back their home shells. These ten C. vittatus, together with the first ten P. longicarpus found to be 0.23g or over, were then put into the experimental tank, this time with all the empty shells removed, and left for 24 hours. The crabs were then taken out of the tank and note was taken of which species of shell each crab was occupying.

The following day the experiment was repeated, this time using ten C. vittatus of 0.23g or over in I. obsoleta shells and ten P. longicarpus in L. irrorata shells. Owing to the lack of P. longicarpus found in L. irrorata shells in the field, five of the ten P. longicarpus used were given the choice of an L. irrorata shell taken at random and their I. obsoleta shell in which they were found. In four out of five cases the crabs went into the L. irrorata shell offered to it (the first L. irrorata shell was noticeably smaller in size than the I. obsoleta shell).

Substrate Selection

The substrate preference of P. longicarpus and C. vittatus for mud or sand was tested by dividing the experimental tank into halves by putting mud to a depth of approximately 2 cm on one half of the tank and coarse sand of an equal depth on the other half. The mud was taken from Bird Shoal, an island very near to Beaufort Harbor, and the sand was taken from Beaufort waterfront, directly across from the Bird Shoal collecting point. These sites were chosen because the former is abundant in living I. obsoleta, whereas the latter has many L. irrorata sticking to the reeds which grow in the sand. No live L. irrorata were found at the Bird Shoal site, however, nor was I. obsoleta found at Beaufort waterfront. A preference for one substrate over the other by P. longicarpus or C. vittatus would therefore limit its chance of finding shells commonly occurring on the less preferred substrate.

Three categories of experiments were performed on P. longicarpus and C. vittatus. These were: (i) isolated crabs; (ii) intraspecific groups of ten crabs; and (iii) interspecific groups of ten crabs of each species. These categories were used as there is evidence that hermit crab behavior is altered both by isolation (Courchesne and Barlow, 1971; Grant and Ulmer, 1974; Hazlet, 1966; Mitchell, 1973) and by the presence of another hermit crab species (Meadows and Mitchell, 1973).

The procedure for testing the first category was to put a hermit crab on the sand/mud partition, leave it isolated in the tank for five hours, then note which half of the tank it occupied. A minimum of five hours duration in the tank was chosen, as a hermit crab can be very active in a closed container until it has explored its surroundings. Its activity then drops off markedly. In the present situation this occurred at a maximum of five hours after being placed in the tank.

In addition to testing differences in the hermit crab species' preferences to mud and sand, it was decided to test if a hermit crab occupying a dark shell such as I. obsoleta was more likely to occur on mud than one inhabiting a white shell such as L. irrorata, or conversely if a crab inhabiting L. irrorata was more likely to occur on sand than mud. This was done by ensuring that half the crabs of both species tested occupied I. obsoleta and the other half occupied L. irrorata. Finally, after ten crabs of both species were tested, the sand and mud halves of the tank were reversed and another ten crabs of both species were tested in the same way as before. This reversal of substrates established a control for factors such as light which may have influenced the distribution of the crabs when they were in the tank.

The second category of experiments was performed in the same way as the first category, the only difference being that ten crabs of the one species were put into the tank at the same time. Similarly the third category was conducted as in the second category but this time ten crabs of both species were put into the tank at the same time.

Results

Shell Selection

The results of the field collection of 60 P. longicarpus and 60 C. vittatus are shown in Table I.

TABLE I

Field Collection: Number of gastropod shells occupied by each species of hermit crab.

Shell Species	P. longicarpus	C. vittatus
N. vibex	5	0
I. obsoleta	50	13
U. cineria	1	5
L. irrorata	3	37
T. haemastoma floridana	1	1
P. duplicatus	0	4

On analysis by the two tailed binomial test, the probability that there was no difference between the number of shells inhabited by P. longicarpus and C. vittatus was < 0.001 for both I. obsoleta and L. irrorata. Differences in the ratio of the two species occupying other shell species were not significant, or alternatively were not tested owing to the small sample size.

The results of the laboratory shell selection experiment for the same 60 crabs of both species are represented in Table II.

TABLE II

Laboratory Selection: Number of gastropod shells selected by each species of hermit crab.

Shell Species	P. longicarpus	C. vittatus
N. vibex	4	0
I. obsoleta	44	4
U. cineria	0	0
L. irrorata	12	18
T. haemastoma floridana	0	5
P. duplicatus	0	33

Significant differences in selection of shell species were obtained for I. obsoleta and P. duplicatus ($P < 0.001$). The only other species with large enough numbers selected to test hermit crab species preference was L. irrorata. No significant difference was recorded for this species of shell ($P = 0.36$).

There is therefore little doubt that resource partitioning of shells takes place both in the restricted selection conditions of the field, and in the unrestricted choice of shells in the laboratory. The partitioning which takes place in the field is not the same as that in the laboratory, however, as there is a significant increase in the number of *P. longicarpus* selecting *L. irrorata* in the laboratory over those occupying *L. irrorata* in the field ($P = 0.036$). Similarly with *C. vittatus*, there is a significant increase in the numbers selecting *P. duplicatus* in the laboratory ($P < 0.001$) but with an accompanying significant decrease in the numbers selecting *I. obsoleta* ($P = 0.05$) and *L. irrorata* ($P = 0.015$). The two tailed binomial test was again used to calculate all probabilities.

The influence of crab size on shell selection is shown in Figure 1. *P. longicarpus* shows a clear pattern in the laboratory selection of shells. As its size increases, so the species of shell which it prefers changes. Up to 0.04g it prefers *N. vibex*. From 0.05 - 0.15g it prefers *I. obsoleta*. There is then an indeterminate zone from 0.16 - 0.22g in which the crab may choose either *I. obsoleta* or *L. irrorata*. Finally, at 0.23g or greater, it prefers *L. irrorata*.

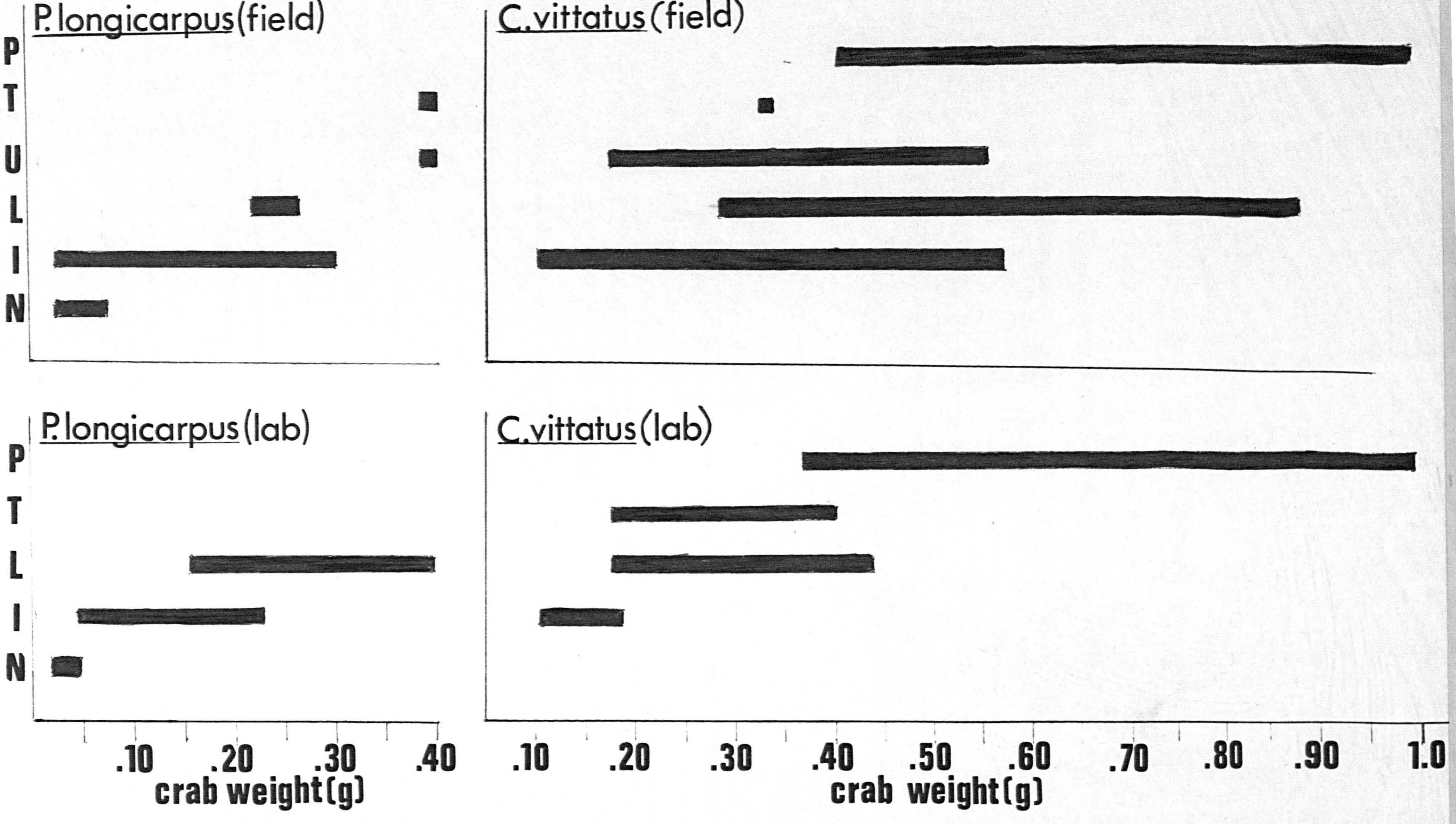
The weight ranges of *P. longicarpus* inhabiting different species of shell in the field are basically similar to that of the laboratory but with *I. obsoleta* making up for the lack of *L. irrorata* shells. Nevertheless a Mann Whitney U test shows that the weights of *P. longicarpus* in *L. irrorata* shells are significantly larger than those in *I. obsoleta*.

C. vittatus also shows a clear pattern in the laboratory. At a size range of 0.12 - 0.17g, *I. obsoleta* is preferred. At a weight of 0.19g, three shells can be chosen, however. These are *I. obsoleta*, *L. irrorata* and *T. haemastoma floridana*. From 0.19 - 0.37g, only the latter two species are selected, while at 0.38 - 0.44g, there is again an indeterminate zone where *L. irrorata*, *T. haemastoma floridana*

Figure 1: Effect of increasing weight of crab on shell species inhabitation. Black bars represent the weight range within which crabs inhabit a species of shell.

Abbreviations of shell species are:

P.	Polinices
T.	Thais
U.	Urosalpinx
L.	Littorina
I.	Ilyanassa
N.	Nassarius


P. longicarpus (field)
C. vittatus (field)
P. longicarpus (lab)
C. vittatus (lab)
P
T
U
L
I
N
.10
.20
.30
.40
.50
.60
.70
.80
.90
1.0
crab weight (g)

or P. duplicatus could be selected. At weights of 0.45g or greater, only P. duplicatus is selected. On applying a Mann Whitney U test to the crab weights in different species of shell, significant differences are obtained for all species except L. irrorata and T. haemastoma floridana. These two species seem to be interchangeable within their preferred range for C. vittatus but whereas L. irrorata shells were twenty times more common than T. haemastoma floridana in the experimental tank, they were only chosen 3.6 times more than them. A binomial test shows that a selection of 5:18 is significantly different from the expected ratio of 1:20 ($P = 0.002$). Hence there is reason to believe that C. vittatus prefers the general shape of T. haemastoma floridana to that of L. irrorata.

The field results of size of crab against species of shell show a similar though less clearly defined pattern. It is interesting to note that U. cineria, although occurring over a wide size range of crab in the field, is not selected at any size range in the laboratory.

Interspecific Shell Fights

At the end of 24 hours, the 10 P. longicarpus and 10 C. vittatus still occupied the same species of shell as when they were first put into the tank. This was the case in both series of experiments. In the first series the 10 P. longicarpus were in a species of shell unsuitable for their size compared with the L. irrorata shells occupied by C. vittatus, whereas in the second series the opposite was true. It was assumed that if any shell swaps between species did occur in nature, it would be between individuals in a similar situation to those used in the experimental tank. Since no shell swaps did occur in the tank, it can be assumed with a fair degree of certainty that shell swaps between these two species at Beaufort rarely, if ever, occur in nature.

Substrate Selection

The results are presented in Tables III and IV.

TABLE III

Substrate selection of *Pagurus longicarpus*

Probabilities are calculated by the binomial test and are two tailed.

Category tested	Number on sand	Number on mud	Probability
Individually	5	15	.042
Grouped	3	17	.002
Mixed	4	16	.012

TABLE IV

Substrate selection of *Clibanarius vittatus*

Probabilities are calculated by the binomial test and are two tailed.

Category tested	Number on sand	Number on mud	Probability
Individually	8	12	.504
Grouped	11	9	.814
Mixed	11	9	.814

No significant differences were obtained for either species of crab inhabiting either species of shell against sand or mud when tested by a two tailed binomial test. The results were therefore pooled for each species of crab. Similarly, no significant difference was found between the results obtained before and those obtained after the sand/mud halves of the tank were reversed. These results were also pooled, so that the table shows only the results of the 20 crabs tested for each category in either species. Significant differences in preference of mud over sand were obtained in P. longicarpus regardless of what category was being tested, whereas C. vittatus had no preference in any category. To test whether presence or absence of the same or of the other hermit crab species had any effect on substrate choice, a chi-squared test of homogeneity was performed on the ratio of sand:mud for the three categories tested in both species. Neither P. longicarpus ($P < 0.80, > 0.70$) nor C. vittatus ($P < 0.70, > 0.50$) showed any significant change in preference in the three categories.

Discussion

The results of the shell selection experiment indicate that two major factors operate in determining shell inhabitation by both species of hermit crab in this area. The most obvious factor is that the species of shell which a hermit crab prefers is related to the size (weight) of the crab. In the laboratory there is a clear pattern of shell species inhabitation which is similar for both species of crab. That is, given a crab of a certain weight, it can be predicted which species of shell it will prefer compared with another species. Only in overlap zones (for example in C. vittatus from 0.38 - 0.44g) is there some doubt as to the preferred species. It still remains to be discovered, however, whether this apparent species preference is related to the dimensions or specific shape of the shell. This problem is the subject of a second paper on shell occupation of these species (in preparation).

The other major factor operating in determining shell inhabitation is the availability of certain shells. Evidently some species of shells are not available in the numbers that would allow every hermit crab to be in a preferred shell. If this had been the case then there would have been no significant differences between the number of shells each species picked up in the field and the numbers of shell species selected in the laboratory. It is worth noting, however, that the ratio of shell species found in the field agrees much closer to that found in the laboratory in the case of P. longicarpus than C. vittatus. Of the 60 crabs of each species tested, 40 C. vittatus chose a shell of a different species from the one they were inhabiting in the field compared with only 15 P. longicarpus changing shell species. This indicates that the finite number of shells in this area affects C. vittatus more than P. longicarpus.

The results of the interspecific shell fights experiment shows that C. vittatus did not obtain a preferred shell from P. longicarpus in the laboratory. Conversely, P. longicarpus was unable to obtain a preferred shell from C. vittatus. The former result is somewhat surprising in relation to the results of Wright (1973). Wright found that C. vittatus was able to obtain the shells of P. longicarpus even when P. longicarpus was the larger crab. The only instance he cited of C. vittatus not being able to do so was when P. longicarpus occupied a shell on which living Hydractinia echinata were present. No H. echinata were present on any of the shells used in the present experiment, however. Provenzano (1959) records a break in the distribution of P. longicarpus at Southern Florida, and also records differences in pigment and overall colour between Eastern Atlantic specimens and those from the west coast on Florida. From this evidence he divided them into subspecies and it may be that these subspecies have different behavioral as well as morphological properties. Provenzano (1959, p404) suspected this when he wrote "experiments in comparative behavior of morphologically similar and dissimilar members of the same genus might yield interesting results" in relation to P. longicarpus and Pagurus pollicaris. One other possibility is that P. longicarpus is in the middle of its geographical distribution at Beaufort, North Carolina, whereas C. vittatus is at the northern extremity of its distribution. In Texas where Wright worked, the opposite is the case. P. longicarpus is at the southern extremity of its distribution whereas C. vittatus has been reported as far south as Brazil (Provenzano, 1959). It may be that a species is more aggressive when it is in an environment which is better suited to its physiological needs.

The shell selection and aggression results help to explain most of the observed shell inhabitation of the two species of hermit crabs but do not entirely explain the small percentage of *P. longicarpus* occupying *L. irrorata* in the field. Approximately one in three of the *P. longicarpus* tested was large enough to occupy a *L. irrorata* shell compared with almost all the *C. vittatus* being large enough. This should therefore have given a *L. irrorata* species distribution of about 1:4 in favour of *C. vittatus*. The actual distribution, 3:37, is significantly above this ratio so that some factor other than chance seems to be responsible. This factor is probably the substrate preference of *P. longicarpus* for mud rather than sand. Since *C. vittatus* does not have this preference, a *C. vittatus* individual is much more likely to come across an empty *L. irrorata* shell than a *P. longicarpus* individual, assuming that *L. irrorata* shells are not washed far from the sand substrate on which they occur naturally.

This work was carried out at Duke University Marine Laboratory upon the invitation of Dr. John D. Costlow. It was partly financed by Duke University and the Carnegie Trust for the Universities of Scotland. Dr. D.R. Colby and Mr. P.S. Meadows offered statistical advice and critically reviewed the manuscript at varying stages of completion. I am most grateful to all concerned for their assistance.

Summary

Three series of experiments were conducted on *Pagurus longicarpus* and *Clibanarius vittatus* at Beaufort, North Carolina. The first series showed that the preferred species of shell by either species of crab is determined by the size of the crab and that certain species of shells are not available in preferred numbers for the hermit crab species. This affects *C. vittatus* more than *P. longicarpus*. The second series showed that shell fighting is not an important factor in determining which species occupies which kind of shell while the third series showed that a substrate preference for mud by *P. longicarpus* may limit it from obtaining a preferred species of shell that occurs naturally on sand.

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AN ANALYSIS OF SHELL OCCUPATION
BY TWO SYMPATRIC SPECIES OF
HERMIT CRAB II BEHAVIORAL FACTORS

Introduction

The relationship between a hermit crab and the shell it occupies can be studied in two different ways. One approach is ecological, in which the factors limiting shell availability to a hermit crab population are emphasised, while the alternative behavioral approach is concerned with preferences among available shells. Both these approaches have been adopted at Beaufort, North Carolina, to study two sympatric intertidal hermit crab species, *Pagurus longicarpus* and *Clibanarius vittatus.* The ecological approach was studied in Mitchell (1975) while the behavioral approach is studied in the present paper.

One of Mitchell's (1975) findings was that certain preferred shell species were not available in sufficient numbers for crabs of certain sizes, but no experiments were conducted to discover if these preferred shells were selected because of their structural or dimensional properties. This problem is investigated in the first set of experiments conducted in this paper. Mitchell (1975) also studied interspecific shell fighting which was not found to be an important factor in determining shell species occupation in the two hermit crab species. Possible reasons for this lack of interspecific shell fights are studied in the second set of experiments of this paper. Lastly, a substrate selection of mud over sand by *P. longicarpus* in this area was shown by Mitchell (1975) to limit this species to shells naturally occurring in or on mud. The third set of experiments in the present paper therefore investigates the flexibility of this substrate selection to environmental experience.

Materials and Methods

1. Shell Selection

1,200 empty shells were distributed randomly in a tank 198 × 78 × 11 cm. height. These shells consisted of the 600 used by Mitchell (1975) together with 300 *Littorina littorea* and 300 *Thais lapillus* brought from Scotland. Scottish shells were used to discover how the two hermit crab species would react to being given shell species not previously encountered by them.

Six *P. longicarpus* and six *C. vittatus* were removed from their shells as in Mitchell (1975) and placed in the experimental tank. After 24 hours they were taken from the tank, removed from their chosen shell, weighed and then discarded. The shells chosen were numbered in waterproof dye and returned to the tank. Numbering shells was not thought to influence shell choice (Reese 1963; Vance 1972a). A further six *P. longicarpus* were then put into the tank for 24 hours. This procedure was repeated until 90 crabs of each species had been tested. The 1,200 shells were then dried and individually numbered, after which their weights, internal volumes and aperture widths were measured to give measures of three variables known to be important in hermit crab shell selection (Hertz 1933; Kinosita and Okajima 1968; Reese 1962). Shell weights were measured to the nearest 0.01g, shell volumes to the nearest 0.01 ml and aperture widths to the nearest 0.01 cm. The method of obtaining shell volume was to pour dried mud or sand of 3 Ø (125 microns) into the shell until it was filled and then to divide the weight of sand in the shell by the specific gravity of the sand or mud (see Section 2, p52).

As a comparison with the 90 shells selected by the two species in the laboratory, 90 crabs of each species were collected from

Beaufort Harbor. These crabs were weighed, and the weights, internal volumes and shell aperture widths of their shells were measured.

2. Interspecific Agonistic Encounters

Two series of experiments were conducted. In the first series one C. vittatus in a Littorina irrorata shell and one P. longicarpus in an Ilyanassa obsoleta shell were put into an aluminium basin 20 cm. in diameter. Their activities and aggressive and fear displays were then observed over the first 15 minutes spent in the basin. Activity was measured by observing whether or not the crab was moving at the end of each minute, as in Meadows and Mitchell (1973) and Mitchell (1975). Aggressive displays were defined as in Hazlett (1972, p113) for C. vittatus, and as in Hazlett 1972, p117) for P. longicarpus, while fear displays were defined as in Courchesne and Barlow (1971, p34). This procedure was repeated fourteen times. For the second series, P. longicarpus in a L. irrorata shell encountered a C. vittatus in an I. obsoleta shell in the basin. As in Mitchell (1975), this meant that five P. longicarpus were given a L. irrorata shell in the laboratory, owing to the shortage of P. longicarpus occupying L. irrorata in the field. This reversed shell species to crab species situation was also repeated fourteen times.

Substrate Selection

Laboratory reared P. longicarpus were kept in a basin with a sand substrate for at least two months after metamorphosis from the glaucothoe stage. During this time they were fed on a variety of dead or decaying matter. An experimental tank 120 cm x 70 cm x 20 cm height with mud in one half and sand in the other half was used to test substrate preference as in Mitchell (1975). Two categories of experiments were performed. The first category consisted of testing 10 crabs individually by placing each one in turn on the sand/mud partition, leaving it for five hours in the tank, then noting which half of the tank it occupied. The second category tested a different set of 10 P. longicarpus placed in the tank at the same time and left for five hours then noting their positions. Both categories were repeated using different animals and reversing the sand and mud halves of the tank.

Results

1. Shell Selection

Multiple regressions of crab weight against shell weight, volume and aperture width were obtained for the 90 P. longicarpus and 90 C. vittatus tested in the laboratory. The results are shown in Table I. The coefficients of all three variables are significantly different from zero in the case of P. longicarpus, while C. vittatus shows the shell volume and aperture width coefficients to be significant. The slope and the multiple correlation coefficients of the P. longicarpus and C. vittatus lines are significantly different from each other. Owing to the highly significant difference in their crab weights ($P < 0.001$), however, these regression differences are not very meaningful, since the shells chosen were almost entirely from differently sized populations.

To discover if shell selection was influenced by some factor other than shell size, the optimum crab weight of each of the 1,200 shells

TABLE I

Multiple regressions of crab weight (C) against shell weight (W), shell volume (V) and shell aperture width (A) for P. longicarpus and C. vittatus when tested in the laboratory. Standard deviations of parameters are shown in brackets underneath. * = coefficient is significantly different from zero $(P < 0.05)$.

Species	Regression Equation	Percentage variation in crab weight explained
P. longicarpus	$C = 0.041^{*}W + 0.094^{*}V + 0.246^{*}A - 0.032$ (.016) (.036) (.072)	84.6%
C. vittatus	$C = 0.001\,W + 0.131^{*}V + 0.341^{*}A - 0.077$ (.012) (.026) (.115)	72.6%

was calculated for both crab species. This was done by taking each shell measurement and substituting it in the regression equations shown in Table I. Thus, a shell measuring 2g weight, 1 ml. volume and 0.50 cm. aperture width would have an optimum crab weight of $0.082 + 0.094 + 0.123 - 0.032$ g $= 0.267$ for P. longicarpus, and $0.002 + 0.131 + 0.171 - 0.077 = 0.227$ g for C. vittatus.

Histograms of the frequency of shell species occupation by crabs of different weight intervals were constructed for the 90 crabs of both species tested in the laboratory. These are shown in Figure 1 for P. longicarpus and Figure 2 for C. vittatus. Comparable histograms of the expected frequencies of shell species occupation were then constructed for both species. The expected frequency of shell species occupation (E) was calculated from

$$E = C \times \frac{n}{N}$$

where C = the number of crabs tested in a given size interval,

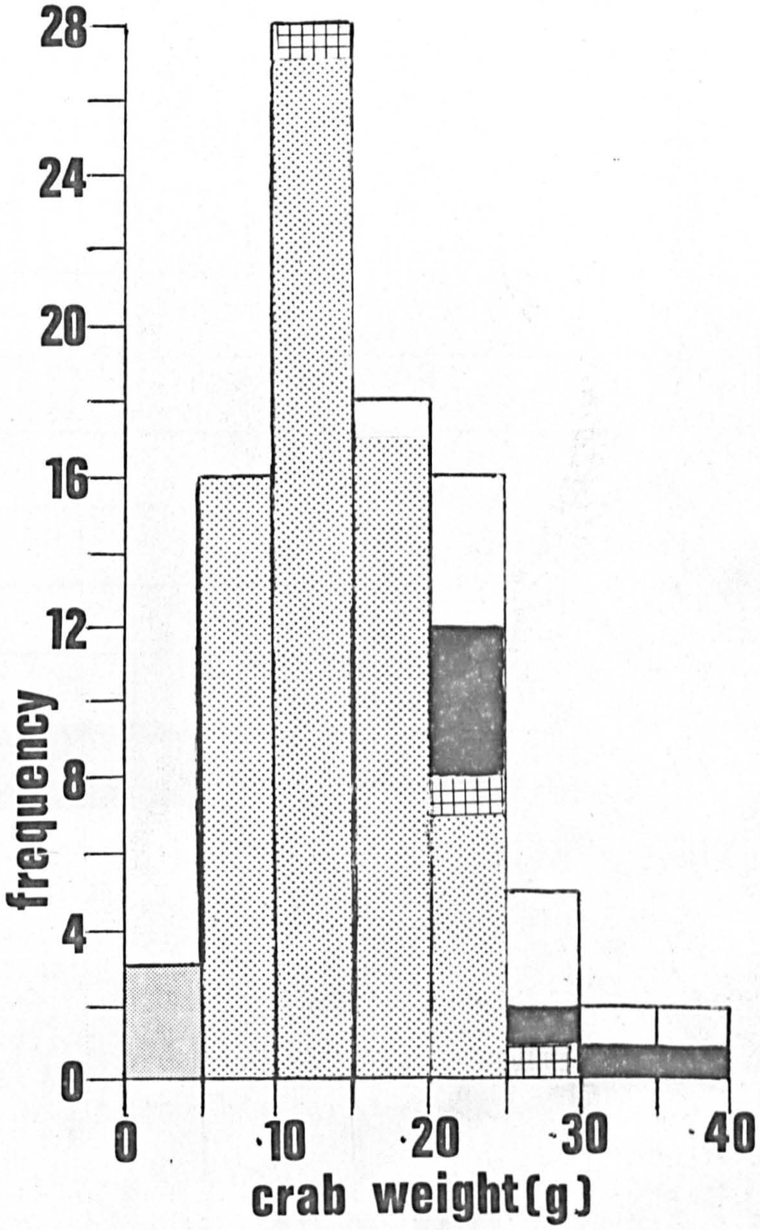

Figure 1. Histogram of the frequency of shell species occupation by *P. longicarpus* at different weights.

Key

▒ = *N. vibex*

░ = *I. obsoleta*

⊞ = *L. irrorata*

■ = *L. littorea*

□ = *T. lapillus*

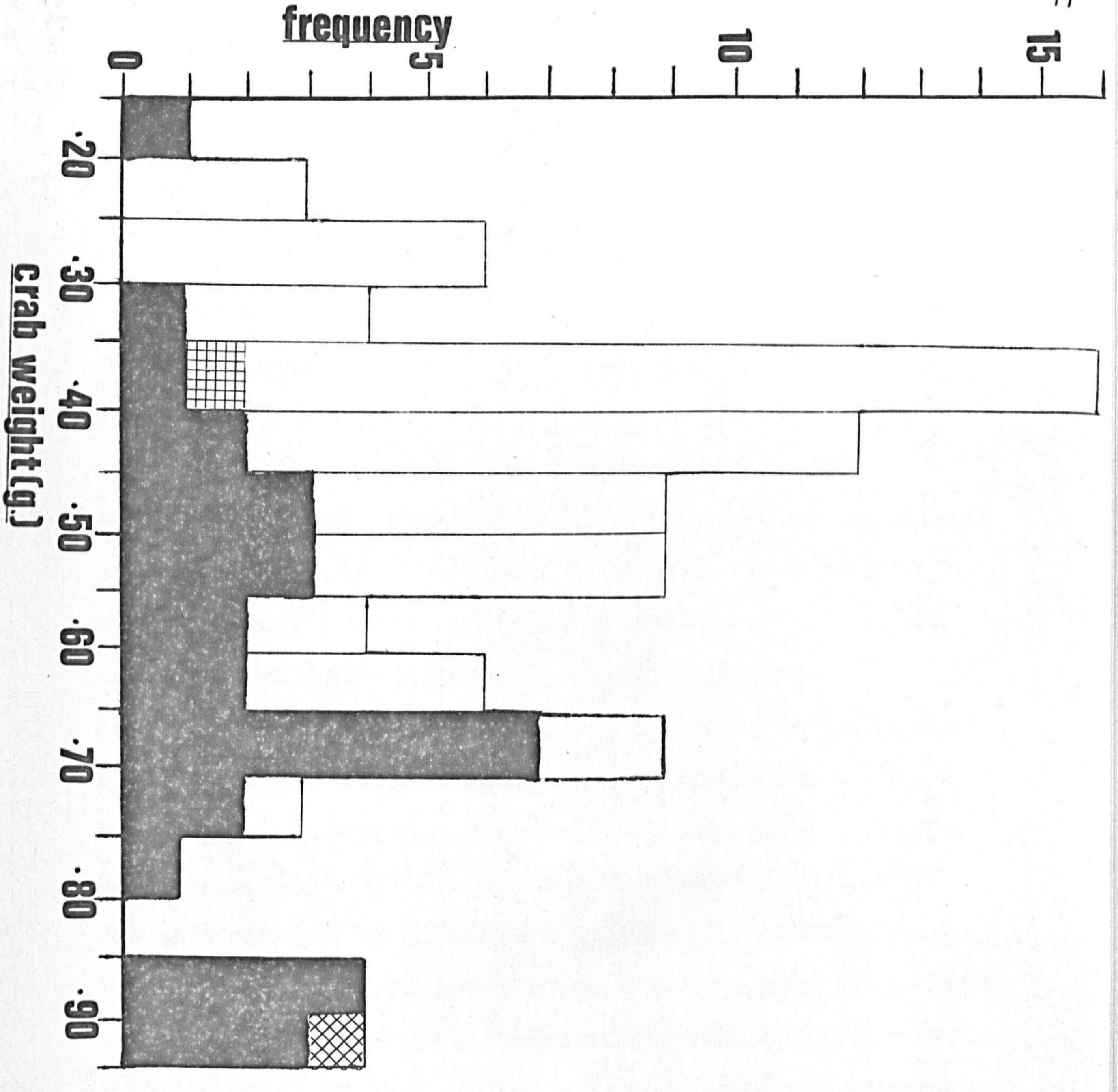

Figure 2. Histogram of the frequency of shell species occupation by *C. vittatus* at different weights.

Key

■ = *L. littorea*

□ = *T. lapillus*

⊞ = *L. irrorata*

⊠ = *P. duplicatus*

n = the number of shells of a particular species whose optimum crab weights occur in the same given size interval,

and N = total number of optimum weights of shells of all species within the given size interval.

The histograms of expected frequencies are shown in Figure 3 for P. longicarpus and Figure 4 for C. vittatus. Binomial tests were performed on the observed shell species occupation histogram, using the expected frequencies to obtain the expected ratios. In cases where a clearly significant difference between numbers of crabs occupying two species of shell were not obtained at any interval tested, a binomial test was performed on the group of comparisons of the two shells at all intervals. For example, in the P. longicarpus histograms, Littorina irrorata and Littorina littorea occur together at crab weights of 0.20 g. Binomial tests (Siegel 1956) of the following size intervals 0.20 - 0.25, 0.25 - 0.30, 0.30 - 0.35, 0.35 - 0.40 g reveal probabilities of 0.077, 0.423, 0.247 and 0.250 respectively in favour of L. littorea. A binomial test on the hypothesis that three probabilities of ≤ 0.250 can occur by chance out of four trials then gives a significant result ($P < 0.05$) so that it can be maintained that L. littorea is preferred by P. longicarpus over L. irrorata. The complete list of shell preferences given by binomial tests is shown in Table II.

Multiple regressions of crab weight against shell weight, volume and aperture width were performed for the 90 P. longicarpus and 90 C. vittatus collected in the field. These are shown in Table III. Both lines are significantly different from their corresponding laboratory regression lines shown in Table I. The multiple regression coefficient of C. vittatus is also significantly different from that

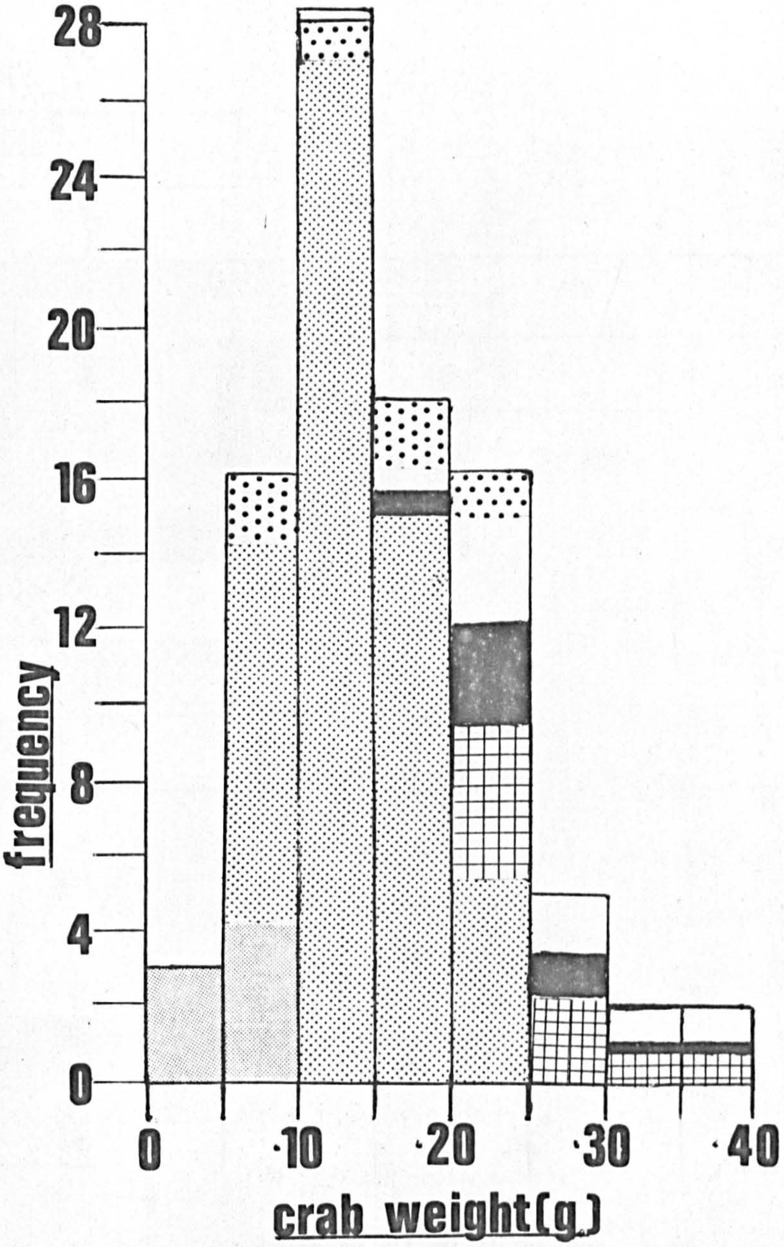

Figure 3. Histogram of the expected frequency of shell species occupation by *P. longicarpus* at different weights assuming no shell species preference.

Key ▓ = *N. vibex*
░ = *I. obsoleta*
⁘ = *U. cineria*
□ = *T. lapillus*
■ = *L. littorea*
⊞ = *L. irrorata*

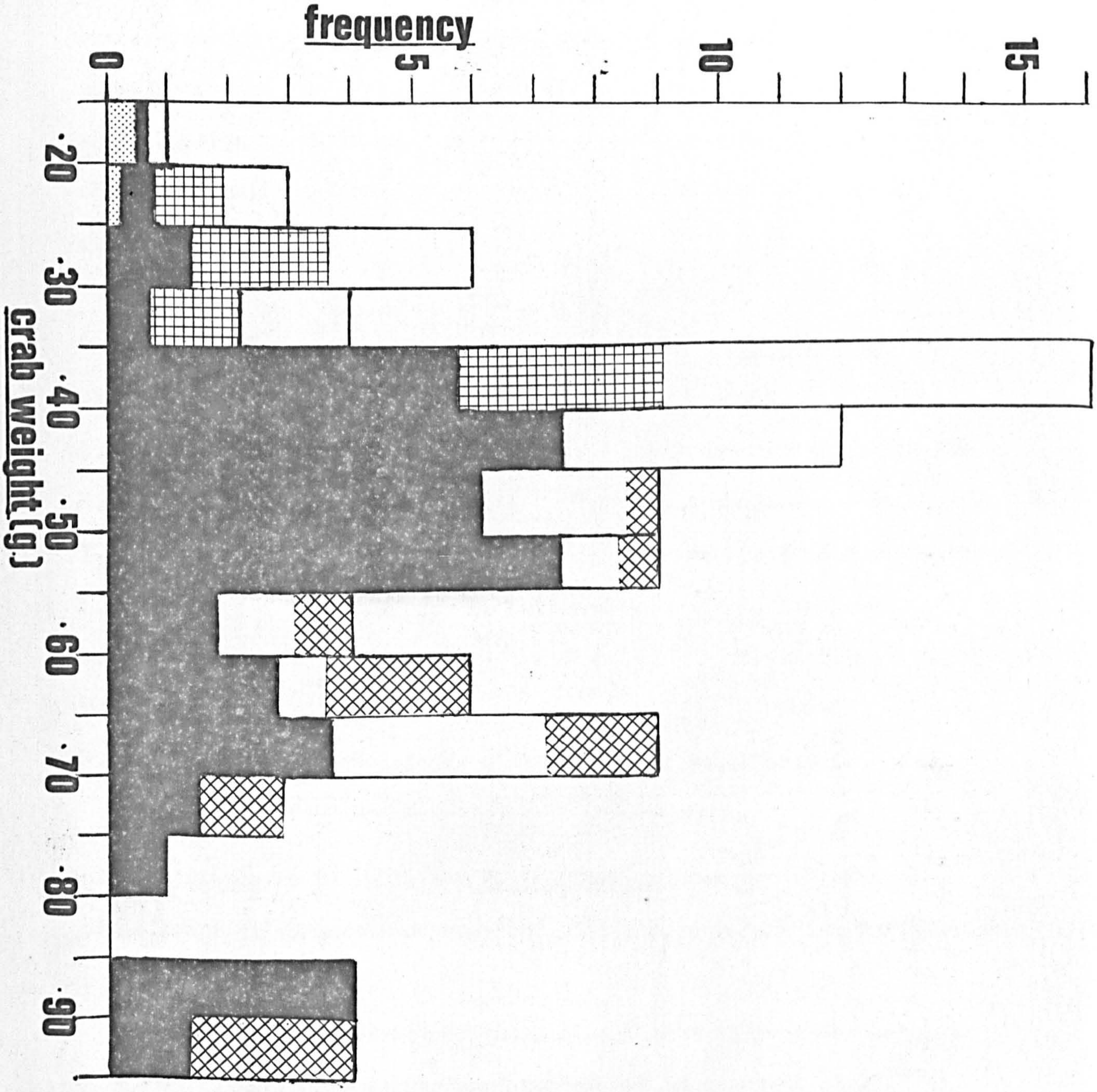

Figure 4. Histogram of the expected frequency of shell species occupation by C. vittatus at different weights assuming no shell species preference.

Key
▒ = I. obsoleta
■ = L. littorea
□ = T. lapillus
⊞ = L. irrorata
⊠ = P. duplicatus

TABLE II

Preferences of P. longicarpus and C. vittatus for different shell structures when shell size is controlled. Comparisons between two shell species in which one species has too few numbers to possibly obtain a significant result are ignored or listed as "no comparisons obtainable".

Shell Species	P. longicarpus	C. vittatus
	Preferred Shell Species	
N. vibex	I. obsoleta	No comparisons obtainable
U. cineria	I. obsoleta	No comparisons obtainable
I. obsoleta	None	No comparisons obtainable
L. irrorata	T. lapillus; L. littorea	T. lapillus
L. littorea	None	T. lapillus
T. lapillus	None	None
P. duplicatus	No comparisons obtainable	T. lapillus; L. littorea

of C. vittatus in Table I, but P. longicarpus does not show the same significant difference when compared with its corresponding multiple regression coefficient.

To discover the effect of these significant differences between field and laboratory regression lines on the adequacy of shell occupation in the field, the optimum crab weights of the 90 shells occupied by P. longicarpus in the field were calculated. Each of these optimum weights was then divided by the actual weight of the crab occupying the shell in the field to obtain a shell adequacy index. An index of 1 means that the crab is occupying a shell of its

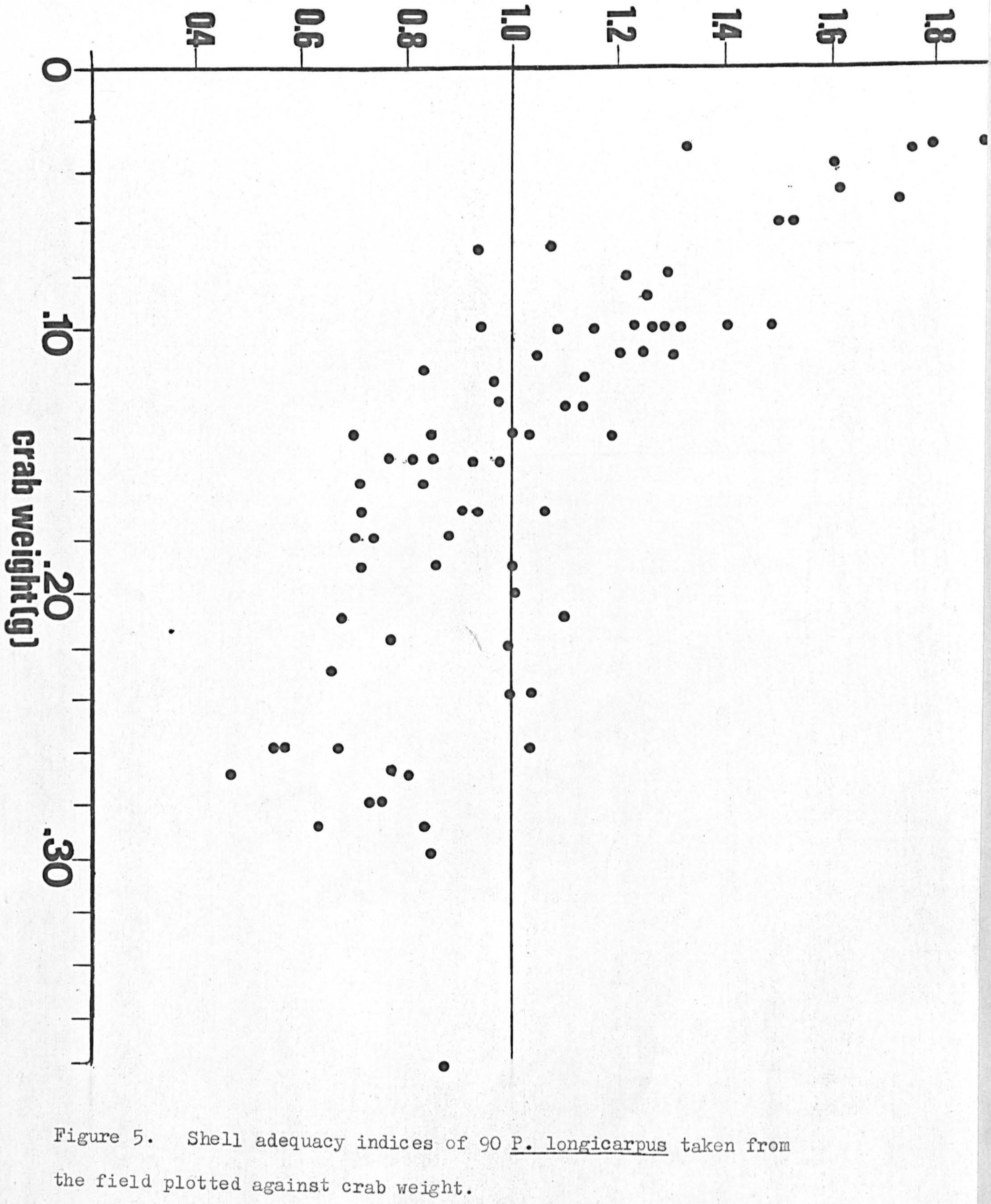

Figure 5. Shell adequacy indices of 90 P. longicarpus taken from the field plotted against crab weight.

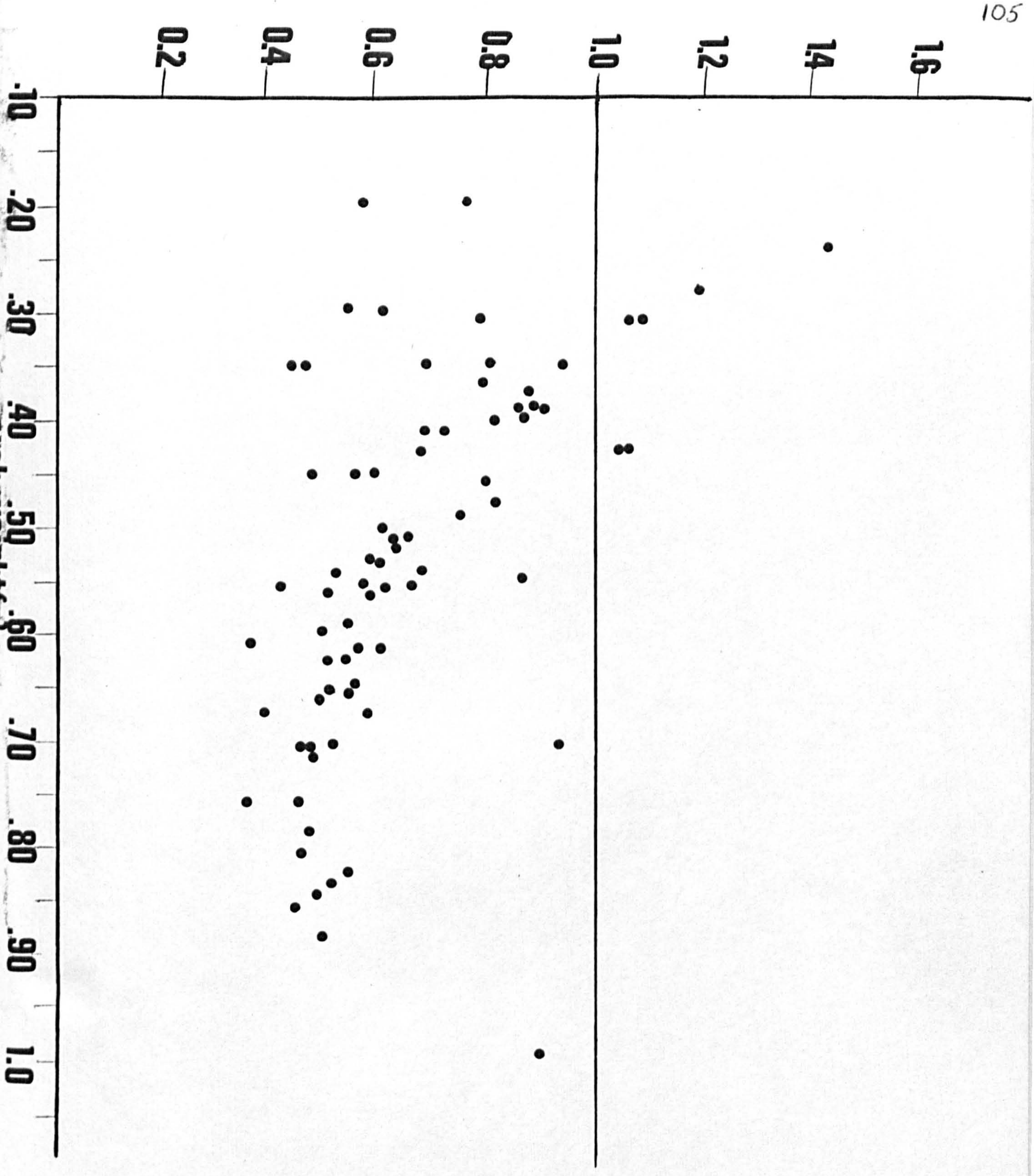

Figure 6. Shell adequacy indices of 90 C. vittatus taken from the field plotted against crab weight.

TABLE III

Multiple regressions of crab weight (C) against shell weight (W), shell volume (V) and shell aperture width (A) for P. longicarpus and C. vittatus collected from the field. Standard deviations of parameters are shown in brackets underneath. * = coefficient is significantly different from zero ($P < 0.05$).

		Percentage variation in crab weight explained
P. longicarpus	$C = 0.058^{*}W + 0.113^{*}V + 0.276^{*}A - 0.058$ $(.025) \quad (.056) \quad (.064)$	73.5%
C. vittatus	$C = 0.044\,W + 0.061\,V + 0.411^{*}A + 0.050$ $(.046) \quad (.084) \quad (.168)$	36.8%

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preferred size whereas an index of greater or less than 1 indicates a size of shell too great or too small, respectively, for the crab. The results are shown in Figure 5. A similar procedure was used to calculate the 90 shell adequacy indices of C. vittatus, and these are shown in Figure 6. Both figures show a similar downward trend in their shell adequacy indices as size of crab increases, but P. longicarpus shows a much greater tendency to occupy shells too large for them at low weights than does C. vittatus.

2. Interspecific Agonistic Encounters

The results of the activities of P. longicarpus and C. vittatus are shown in Table IV. P. longicarpus occupying L. irrorata shells are significantly less active than either P. longicarpus or C. vittatus in I. obsoleta shells. The C. vittatus occupying L. irrorata shells

TABLE IV

Summed activities of P. longicarpus and C. vittatus in the two series tested. The total possible activity score if all 15 crabs were continuously active for the fifteen minutes observed would be 225. Significances of results were obtained by either Wilcoxon matched pairs signed ranks test or, when two different groups of individuals were compared, by the Kolmogorov-Smirnov two sample test (Siegel, 1956). In both tests, two tailed criteria were used.

	P. longicarpus	C. vittatus	P
1st Series			
P. longicarpus (I) v. C. vittatus (L)	125	98	> 0.05
2nd Series			
P. longicarpus (L) v. C. vittatus (I)	66	132	< 0.01
P	$< 0.05, > 0.01$	> 0.05	

are also less active than either P. longicarpus or C. vittatus in I. obsoleta, but these differences are not significant.

The numbers of aggressive displays made by both species of crabs in both series are shown in Table V. P. longicarpus makes significantly more aggressive displays than C. vittatus regardless of shell occupation. Shell occupation also seems to make little difference to the numbers of aggressive displays made by either species.

The numbers of fear displays made by both crab species are shown in Table VI. No significant differences were obtained in any comparisons. The seemingly large differences shown in Table VI (42 : 13 and 15 : 32) were caused by only one crab being exceptionally dominant over another in each case, and not by the large majority of

TABLE V

Summed aggressive displays of P. longicarpus and C. vittatus in the two series tested. Significances were obtained by either the Wilcoxon matched pairs signed ranks test or, when two different groups of individuals were compared by the Kolmogorov-Smirnov two sample test (Siegel 1956). In both tests, two tailed criteria were used.

	P. longicarpus	C. vittatus	P
1st Series			
P. longicarpus (I) v C. Vittatus (L)	37	10	< 0.05, > 0.02
2nd Series			
P. longicarpus (L) v C. vittatus (I)	43	12	0.02
P	> 0.05	> 0.05	

TABLE VI

Summed fear displays of P. longicarpus and C. vittatus in the two series tested. Significances were obtained in the same manner as Table V.

	P. longicarpus	C. vittatus	P
1st Series			
P. longicarpus (I) v C. vittatus (L)	42	13	> 0.05
2nd Series			
P. longicarpus (L) v C. vittatus (I)	15	32	> 0.05
P	> 0.05	> 0.05	

crabs inhabiting I. obsoleta shells showing more fear displays than those inhabiting L. irrorata.

Substrate Selection

The number of crabs occupying the sand and mud halves of the tank five hours after being placed in it are shown in Table VII. There was no significant difference between the first results and those of the repeats when the sand and mud halves were reversed, so these results have been combined in both categories. There is no clear preference of one substrate in either category.

TABLE VII

Substrate selection of laboratory reared P. longicarpus. Probabilities are calculated by the binomial test and are two tailed (Siegel 1956).

Category tested	Number on sand	Number on mud	Probability
Individually	11	9	.814
Grouped	10	10	-

DISCUSSION

The shell selection results of P. longicarpus and C. vittatus show two clear trends. The most important of these is that a hermit crab's first priority in selecting a shell is shell size. Since both multiple regression lines in Table I show more than one shell variable parameter significant, it is doubtful if either P. longicarpus or C. vittatus selects a shell because of one particular size factor, but rather on the general shell size. Within a particular size range of shell, the two crab species tested showed shell species preferences, however, so that the general shape as well as the general size of the shell is also taken into account. It is interesting to note that the preferred general shape of a shell bears no relation to whether the crab species selecting it had previously encountered that species. P. longicarpus, for instance, preferred both Scottish species of shell to its native Littorina irrorata, and C. vittatus preferred Thais lapillus to any other shell species which overlapped its size range.

A comparison of Figures 1, 2, 3 and 4 with Figure 1 in Mitchell (1975) clearly shows that the shell preferences recorded in Mitchell (1975) were almost entirely based on size preferences. Only the preference of P. longicarpus for I. obsoleta rather than N. vibex or U. cineria can be shown to be a genuine species shape preference. Other "preferred" shells in Mitchell (1975) can be shown to be the only shell species occurring in the size range under study.

The comparisons of the sizes of shells occupied by crabs in the field and in the laboratory yield interesting results. P. longicarpus seems to inhabit shells which are too large for it at low weight ranges, while at higher weight ranges it occupies shells of either near optimum or smaller than optimum size. This means that in the field there are not enough small shells to house P. longicarpus of 0.03 - 0.11 g in optimum conditions. Presumably intraspecific shell competition exists for preferred shells in this size range, and from the results of Allee and Douglis (1946), Hazlett (1966 a, b; 1968) and Rossi (1971), a larger crab should usually be able to evict a smaller crab from its shell. This would mean that smaller crabs will end up in shells much too large for them while larger crabs of this range will be in shells only slightly too large for them. This is in fact the trend shown in Figure 5.

C. vittatus, unlike P. longicarpus, occupies few shells which are too large (Figure 6). From a weight of 0.43 g upwards, all shells occupied have an index of less than 1. This pattern of shell occupation is similar to the patterns obtained by Vance (1972b) at Lonesome Cove, in the San Juan Islands of Washington. Vance (1972b) attributes this pattern to shortage of large shells, and it is interesting to note that in Mitchell (1975) only the comparatively rare P. duplicatus shells were selected by C. vittatus at weights greater than 0.44 g.

The agonistic encounters of the two species show that P. longicarpus is more aggressive than C. vittatus. This does not necessarily mean that it is the dominant species, however, as there is no significant difference between the fear displays of the two species. A possible explanation of the differences obtained between aggressive and fear displays is that C. vittatus, which is generally the larger crab, ignores the aggressive displays made by P. longicarpus. This kind of behaviour has been noted already for C. vittatus in intraspecific encounters (Hazlett 1968). Shell species occupation did not seem to have any marked effect on agonistic behaviour in the populations of either species, but it did seem to have an effect on the activity of P. longicarpus. The possible adaptive significance of this behaviour is discussed in another paper (Section 3, paper 3).

The lack of a substrate preference in P. longicarpus when reared in the laboratory on a sand substrate shows that care should be exercised before stating that a species shows a substrate preference. Substrate preference in P. longicarpus seems to be controlled by previous experience rather than any innate behaviour. This may explain why P. longicarpus is found on sand substrates in other areas (Reese 1962), some of them only a few miles distant from the present sampling site (Neil Mercando, N.C. State University, personal communication). It may also explain the observation of Schijfsma (1935) that P. bernhardus is never found on mud, while Allen (1899), Samuelsen (1970) and Wolf and Sandee (1971) have found this species on all kinds of sediments.

Summary

Three series of experiments were conducted on Pagurus longicarpus and Clibanarius vittatus at Beaufort, North Carolina. The first series showed that a crab of either species selected a shell on the basis of the shell's size and shape. Previous experience of a shell species did not affect its preference. The second series showed that although P. longicarpus made more aggressive displays than C. vittatus, C. vittatus did not show greater fear behaviour than P. longicarpus. The third series demonstrated that a previously determined preference of P. longicarpus for mud over sand was capable of alteration by the crab's previous experience of substrate.

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SHELL FIGHTING BEHAVIOR IN THE HERMIT CRAB

CLIBANARIUS VITTATUS

One of the most striking aspects of hermit crab behavior is their aggressive interactions, and probably for this reason these interactions have been thoroughly described (Hazlett, 1966a,b,c, 1968a,b, 1969a,b, 1972; Reese, 1962; Rossi, 1971). The adaptations of this aggressive behavior has often been conjectural, however, and little is known of how much agonistic behavior in hermit crabs is related to shell fighting, spacing out, or competition for food, shelter, etc. Of the work done on the hermit *Clibanarius vittatus*, Hazlett, 1968a, showed that larger *C. vittatus* are more aggressive than smaller *C. vittatus*, while Hazlett, 1970, suggested that *C. vittatus* in large shells won more fights in intraspecific encounters than those in smaller shells. It therefore seemed of interest to observe the agonistic interactions of a large *C. vittatus* in a small shell against a small *C. vittatus* in a large shell. To give the work some ecological significance, the larger shell used was *Polinices duplicatus*, a relatively rare shell in the field which is preferred over the commonly occurring but smaller *Littorina irrorata* shell by all crabs over a certain size (Mitchell, 1975).

Materials and Methods

Clibanarius vittatus occupying *Littorina irrorata* shells were collected from the intertidal region of Duke University Marine Laboratory Dock, immediately prior to the experiments. Each *C. vittatus* collected was evicted from its shell as in Mitchell (1975), blotted dry of sea water and weighed. All animals weighing less than 0.45g were discarded at this stage, as they were judged too small to prefer a *Polinices duplicatus* shell to an *L. irrorata* shell (Mitchell, 1975). The first twenty crabs collected of 0.45g or over were divided into two groups of ten crabs each. The method of dividing them was to arbitrarily take two crabs and make the crab of smaller weight belong to group A and the heavier crab to group B. The rest of the eighteen crabs were arbitrarily chosen two at a time and again, for each pair, one was assigned to group A and one to group B depending on their weight differences. The crabs in group A and B were then put in separate finger bowls and each crab was given an empty Littorina irrorata shell. When all crabs had occupied the shell given (about three hours after the shells had been introduced to them), the first pair of crabs chosen were taken out of the finger bowls and placed in an aluminium basin of 20 cm diameter, with a sand/mud substrate 1 cm deep on the bottom. The agonistic behaviour and the activities of the two crabs were then observed for the next fifteen minutes. Agonistic behavior was noted as either aggressive displays (Hazlett, 1972, p.113), or fear behavior (Courchesne and Barlow, 1971). Activity was judged by whether or not the crab was moving at the end of each minute, as in Meadows and Mitchell (1973) and Mitchell (1973).

When fifteen minutes had elapsed, the crabs were taken out of the basin and put back into the finger bowls. The next pair of C. vittatus were observed in the basin in the same manner as the first pair. This procedure was continued until all ten pairs of crabs had been observed. At the end of this series of experiments, the crabs in group A were evicted from their shell and given a Polinices duplicatus shell in place of its previous L. irrorata shell. As a control, the individuals of group B were also evicted from their shell and given their home shell back. Crabs in both groups were immediately returned to their finger bowls after being evicted from their shell.

The following day, twenty-four hours after observing the crabs' behavior in the first experiment, the same pairs of crabs were observed again. These crabs were then discarded, and ten other pairs of crabs were chosen in the same way as before. This time, however, group A was given a _P. duplicatus_ shell instead of an _L. irrorata_ shell for the first set, and _vice versa_ for the second set of experiments. Otherwise the same procedure was maintained as in the previous ten pairs of crabs.

Results

A comparison of the number of aggressive displays made by _C. vittatus_ under the different conditions tested is shown in Table I.

TABLE I

Numbers of aggressive displays made by *C. vittatus* under different conditions. The statistical significance of the differences between the observed displays 52 and 69, 52 and 30 etc. was assessed by Wilcoxon's matched pairs signed ranks test, treating the ten experiments in each condition as blocks. Two tailed criteria were adopted in all tests.

Trial	Group A	Group B	P
1st *Littorina* (A) v *Littorina* (B)	52	69	0.05
2nd *Polinices* (A) v *Littorina* (B)	30	194	<0.01
P	> 0.05	> 0.05	
1st *Polinices* (A) v *Littorina* (B)	41	212	< 0.01
2nd *Littorina* (A) v *Littorina* (B)	53	104	<0.01
P	> 0.05	<0.05	
		>0.02	

Larger crabs made more aggressive displays than smaller ones under all four conditions, but the number of displays was greater when the larger crab confronted a *C. vittatus* in a *Polinices* shell than one in a *Littorina* shell. This was true regardless of previous experience. The number of aggressive displays made by the smaller crabs in group A, however, was not affected either by shell species occupation or previous experience.

The comparison of the fear reactions of *C. vittatus* in Table II show that the smaller crabs of group A made more fear reactions than their opponents under all four conditions, but the number of fear reactions a smaller crab made was decreased if it inhabited a *Polinices* rather than a *Littorina* shell. Previous experience did not affect this result. The number of fear reactions made by the crabs in group B was not affected by confrontation of a group A crab either in a *Polinices* or *Littorina* shell, nor did previous experience of their opponent significantly alter their fear behaviour.

TABLE II

Numbers of fear reactions of *C. vittatus* under different conditions. Statistical significance was assessed as in Table I.

Trial	Group A	Group B	P.
1st *Littorina* (A) v *Littorina* (B)	46	11	< 0.02, > 0.01
2nd *Polinices* (A) v *Littorina* (B)	27	6	< 0.01
P	< 0.05 > 0.02	> 0.05	
1st *Polinices* (A) v *Littorina* (B)	32	13	< 0.02
2nd *Littorina* (A) v *Littorina* (B)	45	5	< 0.01
P	< 0.05 > 0.02	> 0.05	

The activities of the crabs in groups A and B under the conditions tested are presented in Table III. Crabs in group A are less active when they occupy a Polinices than a Littorina shell. In one condition group B crabs are significantly more active than group A crabs in Polinices shells. In the other Polinices v Littorina condition, the group B crabs are also more active, but the difference just fails to be significant $(P > 0.05, < 0.10)$. There is no significant difference in the activities of the two groups, when they both occupy Littorina shells.

TABLE III

Activities of C. vittatus under different conditions. In each condition the maximum score possible if all ten crabs were continuously active for the 15 minutes observed would be 150. Statistical significance was assessed as in Table I.

Trial	Group A	Group B	P
1st Littorina (A) v Littorina (B)	115	122	> 0.05
2nd Polinices (A) v Littorina (B)	79	101	> 0.05
P	< 0.02 > 0.01	> 0.05	
1st Polinices (A) v Littorina (B)	59	101	< 0.01
2nd Littorina (A) v Littorina (B)	91	96	> 0.05
P	< 0.01	> 0.05	

To discover if the significant differences in aggressive and fear displays obtained in Tables I and II were the result of the different dimensions of the shells used, or if the differences in frequencies of displays were caused by crabs recognizing the structure of the preferred Polinices shell, multiple regressions of dominance against crab weight, shell weight and shell volume differences were carried out. Dominance was obtained from the formula:

D = (aggression of crab of group B - fear displays of
crab of group B) -
(aggression of crab of group A - fear displays of
crab of group A)

for any pair of hermit crabs tested.

The crab weight differences were calculated from the formula:

$$\frac{\text{crab weight of group B} - \text{crab weight of group A}}{\text{crab weight of group A}}$$

for each matched pair, and the shell weight and shell volume differences were calculated in a similar manner. The results are shown in Table IV.

TABLE IV

Regression of dominance (D) of crabs of group B over their paired opponents of group A against relative differences between crab weight (C), shell weight (W) and shell volume (V) pairs. For explanations of dominance and relative size difference calculations, see text. Standard deviations of the regression variable parameters are given in brackets underneath. * = regression co-efficient is significant ($P < 0.05$).

Condition tested	Regression equation	Percentage variability in D explained
Littorina (A) v *Littorina* (B)	$D = 18.55C^{*} + 0.32W - 2.02V$	33.51%
	(6.53) (5.66) (5.54)	
Polinices (A) v *Littorina* (B)	$D = 122.43C^{*} - 3.99W + 1.04V$	87.94%
	(13.22) (2.06) (2.93)	

Since there was no significant difference between the slope of the regression of the two *Littorina* (A) v *Littorina* (B) conditions, and there was also no significant difference between the slopes of the equations of the two *Polinices* (A) v *Littorina* (B) conditions, the results are pooled to form one *Littorina* (A) v *Littorina* (B) equation and one *Polinices* (A) v *Littorina* (B) equation.

Equations of dominance against absolute rather than relative size differences were also calculated. The equations were in both conditions very similar to the relative size difference equations but gave slightly poorer multiple correlation coefficients and hence are not included. There is a highly significant difference between the slope and the percentage variability of dominance explained by the two lines shown in Table IV.

Discussion

It is interesting to compare the results obtained in this paper with those of Hazlett, 1968a, on the same species. In Hazlett, 1968a, his conclusions were that larger crabs were more aggressive than smaller crabs and that interacting crabs were reacting to absolute rather than relative size differences. The results of the present paper support the former conclusion but show no evidence to support the latter conclusion. This may be because of the invalid statistical technique Hazlett used on his results (p.611). Instead of using a simple least squares fit to his data, he should have used a weighted least squares form of regression or alternatively some adaptation of logit analysis. Also of interest is the later work which Hazlett, 1970, performed on the same species. In this paper he concluded that "increasing the visual size of a crab's shell significantly increased the probability of a crab winning an encounter, as did increasing the weight of the shell". These conclusions are not supported by the present paper since the larger size and weight of a Polinices shell elicited significantly more aggressive displays and did not affect the number of fear displays made by its opponent in a Littorina shell. (The fewer number of fear displays exhibited by the smaller crabs in Littorina shells compared with Polinices shells may at first seem contrary to the above results, but was, in fact, caused by many of the smaller crabs completely withdrawing into their shells for several minutes at a time.)

A possible explanation of this difference in conclusions is that Hazlett used unnatural means to increase the visual size and the weight of a shell by attaching a plastic piece or a lead weight to it. In the present experiments, however, the visual size and the weight of the shell were increased by using a naturally occurring larger species of shell. Hence Hazlett's results may be interpreted as the crab's behavior to unnatural stimuli and the present results as their behavior to natural stimuli. In addition, Hazlett did not control for crab size which may also account for some difference in results.

The significant differences of the two multiple regression lines shown in Table IV indicate that C. vittatus can distinguish a Polinices shell from a Littorina shell, as the change in dominance recorded between the two conditions tested in the multiple regression equations is not caused by significant changes in the shell parameters. Larger C. vittatus in Littorina shells are not only more dominant but more predictably dominant depending on the size difference when confronted by a C. vittatus in a Polinices rather than in a Littorina shell. The smaller crab therefore either has to relinquish its Polinices shell to the larger crab (this occurred in three of the twenty encounters) or presumably allow the larger crab to acquire first choice of limited factors, such as food or shelter in the environment.

The activities results are interesting since they show larger crabs to be more active than smaller crabs only when the smaller crab occupies a Polinices shell. This is contrary to the activities of the hermit crabs Pagurus bernhardus and Pagurus prideauxi in which larger crabs were more active than smaller crabs when both groups occupied Littorina shells (Meadows and Mitchell, 1973). The differences observed in the activities of smaller C. vittatus in the two different species of shells occupied in the present paper could be caused by the smaller crab retracting into its shell for longer periods of time when in a Polinices than in a Littorina shell. There may be another factor operating, however, as another hermit crab species, Pagurus longicarpus, is also less active when in a preferred shell for its size (see Section 3, paper 2). An additional explanation for the observed differences in activity between C. vittatus in preferred and non-preferred shells is therefore that this species shows appetitive shell searching behavior until a preferred shell is found, after which a quiescent phase follows.

Summary

The aggressive behavior of large C. vittatus against small C. vittatus was investigated. Large C. vittatus were more aggressive and showed fewer fear reactions in all conditions tested. The degree of dominance of large over small C. vittatus was much more marked and more predictable when the smaller crab occupied a Polinices rather than a Littorina shell and the large crab occupied a Littorina shell in both conditions. Evidence is given to suggest that C. vittatus reacts more to the shape than the size dimensions of a Polinices shell, and that small crabs occupying a Polinices shell are less active than other crabs occupying a Littorina shell.

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SPACING OUT IN TWO
SYMPATRIC SPECIES OF
HERMIT CRABS

Introduction

When two hermit crabs meet, an aggressive encounter often ensues (Hazlett, 1966). In some species these encounters lead to one hermit crab becoming dominant over the other, and since hermit crabs have been known to recognize each other "individually" (Hazlett, 1969), this could result in the submissive crab keeping its distance from the dominant crab. In this way a spaced out distribution within a population can occur. Not all hermit crabs have a spaced out distribution, however. Aggregated distributions can occur through the effect of adverse environmental factors such as being exposed to water loss at low tide, by orientation towards other hermit crabs or towards factors of their local physical environment (Hazlett, 1966 p 122-123).

In the present study of spacing behaviour in Pagurus longicarpus and Clibanarius vittatus it has been shown that a dominance order exists for P. longicarpus (Allee and Douglis, 1945) but "individual" recognition has not been established. With the absence of strong environmental factors operating against adults of this species (personal observations) it can be predicted that P. longicarpus should have an independent or spaced out distribution. C. vittatus, in contrast, has strong environmental factors such as water loss at low tide operating against it (personal observations) and may therefore be thought to aggregate.

The following experiments were conducted to test the predictions made as to the two species intraspecific distribution patterns, and to discover how the two species space out with regard to each other.

Materials and Methods

Animals were taken from the intertidal zone of Beaufort Harbor, next to Duke University Marine Laboratory dock, during August and September, 1974. They were maintained in stock tanks with constant running water at about 20°C. Illumination in the form of diffuse artificial lighting was provided only during normal daylight hours.

Three series of experiments were conducted on the spacing behaviour of Pagurus longicarpus and Clibanarius vittatus at different population densities. The first series recorded P. longicarpus at densities of 7, 10, 14, 20 and 24 per tank, while the second series recorded C. vittatus at the same densities. The third recorded a 50/50 mixture of P. longicarpus and C. vittatus at densities of 10, 14, 20, 24 and 28 per tank.

The experimental tank used in the three series was circular with radius 27.5 cm. A sand/mud substrate 1 cm deep was used and the tank was filled to a depth of 8 cm with seawater taken from Beaufort Harbor. With the exception of using different animals, the conditions of each experiment were the same. These were that animals of the required species and density were put in the tank and left for 24 hours, following the practice of Meadows and Mitchell (1973) and Section 2 papers 1 and 2. They were then observed by placing a glass sheet with a circle of 27.5 cm radius inscribed on it over the tank and the polar co-ordinates of the positions of every hermit crab in the tank were recorded. This procedure was repeated at intervals of at least three hours until six readings at each density had been obtained in each series.

Results

1. Angular and Radial Measurements

χ^2 tests for angular symmetry were performed on the six replicates at each density for five categories of animals (see Appendix 1). These categories were (1) P. longicarpus by itself in the tank, (2) C. vittatus by itself in the tank, (3) P. longicarpus with C. vittatus in the tank, (4) C. vittatus with P. longicarpus in the tank, (5) C. vittatus and P. longicarpus together in the tank and treated as one population. Only in the fifth category was there significant evidence at the 5% level of departure from angular uniformity, and since 25 χ^2 tests were conducted overall, no strong importance was attached to this one result.

As in Section 2, paper 2, no departure from radial uniformity was observed at any density in any category tested (see Appendix 2 for details of method used) once the outer 3 cm of the tank was discounted. There were significantly different proportions of crabs occupying the outer 3 cm in different categories tested, however. This is shown in Table I. C. vittatus showed a significantly greater attraction towards this outer area than P. longicarpus both in the presence and absence of P. longicarpus. The proportions of C. vittatus occupying the outer : inner area were not significantly altered by population density, the overall ratio being 0.86 on the edge when separate from P. longicarpus, and 0.88 when with P. longicarpus in the tank. These ratios are not significantly different from each other when tested by χ^2. P. longicarpus, on the other hand, has not a homogenous proportion of numbers in the outer : inner areas when density is altered, nor is it unaffected by

TABLE I

A comparison of the numbers of P. longicarpus and C. vittatus falling in the outer : inner areas of the tank at different densities. The homogeneity of the proportions of outer : inner at each density is also shown for both species.

1. P. longicarpus and C. vittatus tested separately

	P. longicarpus		C. vittatus			
Density	Number in outer area	Number in inner area	Number in outer area	Number in inner area	χ^2	P
7	24	18	32	10	3.43	0.06
10	29	31	53	7	22.18	< 0.01
14	35	49	71	13	33.13	< 0.01
20	87	33	105	15	8.44	< 0.01
24	104	40	128	16	12.77	< 0.01
x^2	31.86		5.06			
P	< 0.01		0.28			

2. P. longicarpus and C. vittatus mixed in same tank

	P. longicarpus		C. vittatus			
Density	Number in outer area	Number in inner area	Number in outer area	Number in inner area	χ^2	P
5	11	19	26	4	15.86	< 0.01
7	8	34	39	3	46.42	< 0.01
10	20	40	53	7	38.09	< 0.01
12	17	55	67	5	71.43	< 0.01
14	11	73	69	15	80.28	< 0.01
x^2	11.72		5.53			
P	$< 0.02, > 0.01$		0.24			

the presence of C. vittatus. At each of the three comparable densities of 7, 10 and 14 crabs per tank, there are significantly fewer P. longicarpus in the outer area when C. vittatus is present than when it is absent in the tank.

2. Nearest Neighbour Analysis

Nearest neighbour analysis (Clark and Evans, 1954) was carried out on all five categories of crab and the modified form of analysis used in Section 2, paper 2 of this thesis was adopted in each case. Since the expected nearest neighbour distances obtained by simulation were normally distributed, the degree of aggregation or spacing out at each density was also calculated as in Section 2, paper 2 by the formula:

$$\bar{x}_i = \theta_i + k + \varepsilon_i \qquad \text{(see Appendix 3).}$$

where $\bar{x}_i$ = observed mean nearest neighbour distance

θ_i = expected mean nearest neighbour distance for crabs spacing out uniformly and independently of each other. This was obtained by simulation. Crab size (1 cm diameter) was taken into account as in Section 2, paper 2, as was edge attraction.

k = a constant possibly dependent on population density

ε_i = error function with zero mean and variance σ_i^2.

(i) P. longicarpus separate from C. vittatus

The results of $\bar{x}_i$, θ_i and σ_i^2 for each population density are shown in Table II. A generalised likelihood-ratio test on the equality of k for all densities gives a value of 0.130 which is well within the 5% limit of an F distribution with (4,25) degrees of freedom (Table III). The value obtained on the likelihoods-ratio

TABLE II

Observed mean nearest neighbour distances ($\bar{x}_i$), expected mean nearest neighbour distances (θ) and variances (σ^2) of *P. longicarpus* in the absence of *C. vittatus*. Readings have been arranged in increasing value for convenience.

Density of crabs per tank	$\bar{x}_i$ (cm)						θ	σ^2
7	7.36	11.14	11.93	13.43	14.14	16.14	12.62	7.44
10	8.05	8.90	8.95	9.20	10.80	10.95	9.93	3.12
14	5.50	6.36	6.43	7.21	9.07	10.21	8.00	1.42
20	5.13	5.73	5.75	5.78	6.20	6.70	6.15	0.65
24	4.38	4.46	5.44	5.94	6.02	6.15	5.46	0.41

test of k being different from zero is also not significantly greater than the 5% limit of an $F_{(1,29)}$ distribution. There is therefore no evidence to suggest that *P. longicarpus* by itself either aggregates or spaces out or that population density affects its spacing behaviour in any way.

(ii) *C. vittatus* separate from *P. longicarpus*

The results of $\bar{x}_i$, θ_i and σ_i^2 for each population density are shown in Table IV. The value of 0.541 obtained from a generalised likelihoods-ratio test on the equality of k is not significant for $F_{(4,25)}$ degrees of freedom (Table III) but the value of 50.23 for the test of k = 0 cm is very highly significant ($P < 0.01$) for an F

TABLE III

Values of the generalised likelihood-ratios tests on the equality of k over all densities, and on the significance of the overall values of k obtained. Under the null hypothesis k = 0. * = F value obtained is significantly different at 5% level from the expected F distribution of (4,25) degrees of freedom for equality of k, or (1,29) degrees of freedom for the hypothesis that k = 0.

Species tested	Condition	F value on the test of equality of k over all densities	F value on the test that k = 0 cm.	F value of comparison of species tested under the two different conditions
C. vittatus	P. longicarpus absent	0.54	50.23*	3.49
	P. longicarpus present	2.12	14.33*	
P. longicarpus	C. vittatus absent	0.13	1.36	1.15
	C. vittatus present	2.47	0.08	
C. vittatus and P. longicarpus	Treated as one population	1.38	0.01	

distribution with (1,29) degrees of freedom. The overall value of k obtained for all densities was - 1.36 cm so that C. vittatus can be said to space itself on average 1.36 cm less than expected under independent positioning, regardless of population density.

TABLE IV

Observed mean nearest neighbour distances ($\bar{x}_i$), expected mean nearest neighbour distances (θ), and variances of C. vittatus in the absence of P. longicarpus. Readings have been arranged in increasing value for convenience.

Density of crabs per tank	$\bar{x}_i$ (cm.)						θ	σ^2
7	8.79	9.21	11.50	13.21	15.07	17.14	12.55	9.07
10	6.35	6.60	7.75	8.15	9.15	10.00	9.31	3.75
14	4.18	4.60	4.89	5.61	6.32	7.57	7.36	1.22
20	3.55	4.08	4.13	4.53	5.05	5.80	6.39	0.78
24	2.81	3.65	3.81	4.52	4.66	5.44	5.80	0.58

(iii) P. longicarpus in the presence of C. vittatus

The results of $\bar{x}_i$, θ_i and σ_i^2 for each population density are shown in Table V, and the results of the generalised likelihoods-ratio tests on the equality and significance of k are given in Table III. Both F values are not significantly different at the 5% level, so that P. longicarpus seems to space itself independently of each other at all densities. A comparison of the value of k obtained over all densities with the value of k obtained in category (i) gives an $F_{(1,58)}$ value of 1.15 which is not significant. P. longicarpus is therefore unaffected in its intraspecific spacing behaviour by the presence or absence of C. vittatus at any density tested.

TABLE V

Values of the observed nearest neighbour distances ($\bar{x}_i$), expected nearest neighbour distances (θ) and variances (σ^2) of P. longicarpus in the presence of C. vittatus. Values have been arranged in increasing order for convenience.

Density of crabs per tank	$\bar{x}_i$ (cm.)						θ	σ^2
5	7.80	13.20	13.80	13.80	15.50	18.00	14.89	12.68
7	7.71	11.43	12.64	13.50	13.57	14.21	10.74	4.65
10	6.60	7.75	7.95	8.70	8.90	10.75	9.42	2.47
12	6.54	7.96	8.21	8.29	8.63	9.00	8.35	1.61
14	7.21	7.36	7.75	7.75	7.96	8.71	7.27	1.05

(iv) C. vittatus in the presence of P. longicarpus

The results of $\bar{x}_i$, θ_i and σ_i^2 for each population density are shown on Table VI and the results of the generalised likelihood-ratio tests on the equality and significance of k are given in Table III. The test on the equality of k gave a value of 2.123 which is not significant at the 5% level for $F_{(4,25)}$ degrees of freedom, but the value of 14.33 obtained on the test of $k = 0$ is highly significant for a $F_{(1,29)}$ distribution. The value of k over all densities was = 1.47 cm. This value is not significantly different from the k of C. vittatus separate from P. longicarpus. C. vittatus therefore spaces itself about 1.4 cm less than expected from independent positioning regardless of population density and the presence or absence of P. longicarpus.

TABLE VI

Values of the observed nearest neighbour distances ($\bar{x}_i$), expected nearest neighbour distances (θ), and variances (σ^2) of C. vittatus in the presence of P. longicarpus. Values have been arranged in increasing order for convenience.

Density of crabs per tank	$\bar{x}_i$ (cm.)						θ	σ^2
5	2.50	5.60	7.40	9.90	14.00	19.00	16.38	20.34
7	4.43	7.28	8.86	9.71	13.57	13.93	12.55	9.07
10	4.50	5.05	8.10	8.10	8.35	10.85	9.31	3.75
12	6.58	6.75	7.21	7.75	7.88	8.83	7.92	2.31
14	3.50	4.14	6.00	6.50	7.36	8.29	7.36	1.49

(v) P. longicarpus and C. vittatus taken together as one population

The results of $\bar{x}_i$, θ_i and σ_i^2 for each population density are shown in Table VII, and the results of the generalised likelihood-ratio tests on the equality and significance of k are given in Table III. The test on the equality of k gave a value of 1.380 which is not significant at the 5% level for an F distribution with (4,25) degrees of freedom. The test on the departure from zero of k gave a very small F value of less than 0.01 which is clearly not significant. It can therefore be said that the overall distribution of C. vittatus and P. longicarpus is not different from an independent distribution.

To discover if the distribution of the two species was independent of each other, the identity of the species which was the nearest neighbour of each crab was noted. Under independence, each

TABLE VII

Observed mean nearest neighbour distances ($\bar{x}_i$), expected mean nearest neighbour distances (θ) and variances (σ^2) of P. longicarpus and C. vittatus together and treated as one population. Readings have been arranged in increasing value for convenience.

Density of crabs per tank	$\bar{x}_i$ (cm.)						θ	σ^2
10	5.15	7.50	9.55	10.00	11.70	12.10	9.93	3.12
14	5.64	6.96	7.29	7.50	8.21	8.79	8.00	1.42
20	5.03	5.38	5.40	5.40	6.15	6.40	6.13	0.62
24	4.71	5.17	5.31	5.92	6.04	6.96	5.48	0.37
28	5.04	5.23	5.38	5.48	5.77	6.38	5.29	0.28

P. longicarpus should have been equally likely to have a C. vittatus as a P. longicarpus for its nearest neighbour. The same should also be true of C. vittatus. The results are shown in Table VIII. The hypothesis of interspecific independent positioning can be rejected with a strong degree of certainty at densities of 20, 24 and 28 per tank, but there is insufficient evidence to reject it at a density of 10 per tank. At a density of 14 per tank it can be rejected for C. vittatus but not for P. longicarpus.

As a final comparison, the nearest neighbour distances of C. vittatus to each P. longicarpus and P. longicarpus to each C. vittatus (see Figure 1 for illustration) were measured for each replicate at each density, and the mean distances are shown in Table IX. If a plus is given for each P. longicarpus to C. vittatus distance which is greater than the corresponding C. vittatus to

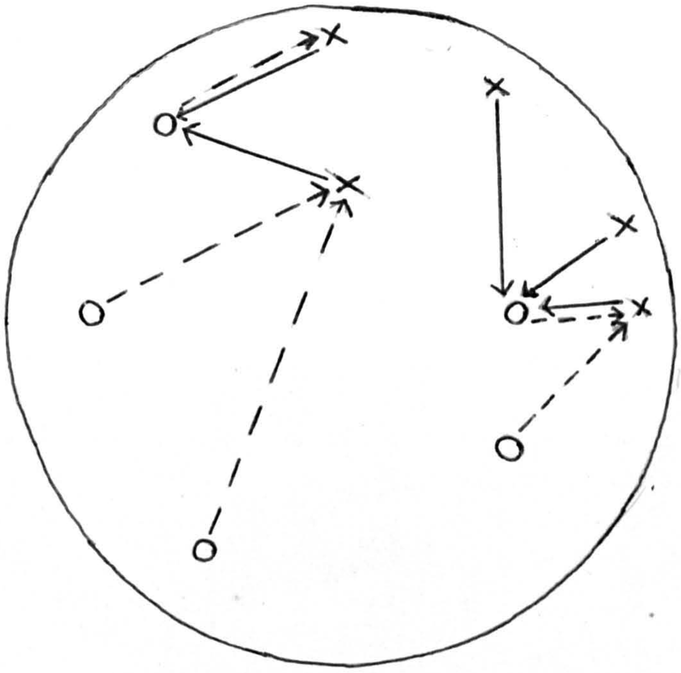

Figure 1. Nearest neighbour distances of 10 crabs in a circular tank.

Key

x = *C. vittatus* individual

O = *P. longicarpus* individual

——→ = Nearest neighbour distance of each *C. vittatus* individual to a *P. longicarpus* individual

- - → = Nearest neighbour distance of each *P. longicarpus* individual to a *C. vittatus* individual

TABLE VIII

A comparison of nearest neighbours in the 50/50 mixtures of <u>P. longicarpus</u> and <u>C. vittatus</u>.

1. <u>C. vittatus</u>

Density of crabs per tank	Number of <u>C. vittatus</u> nearest neighbours	Number of <u>P. longicarpus</u> nearest neighbours	χ^2	P
10	17	13	0.30	$< 0.75, > 0.50$
14	28	14	4.02	$< 0.05, > 0.25$
20	44	16	12.15	< 0.001
24	54	18	17.01	< 0.001
28	66	18	26.30	< 0.001

2. <u>P. longicarpus</u>

Density of crabs per tank	Number of <u>C. vittatus</u> nearest neighbours	Number of <u>P. longicarpus</u> nearest neighbours	χ^2	P
10	13	17	0.30	$< 0.75, > 0.50$
14	19	23	0.21	$< 0.75, > 0.50$
20	17	43	10.42	$< 0.005, > 0.001$
24	19	53	15.13	< 0.001
28	18	66	26.30	< 0.001

TABLE IX

Summed nearest neighbour distances of each P. longicarpus to C. vittatus and each C. vittatus to P. longicarpus at each density. Distances are measured in cm.

Density of crabs per tank		Summed nearest neighbour distances at each replicate					
10	P. longicarpus to C.vittatus	104.5	54.5	132.0	76.5	80.0	71.5
	C.vittatus to P. longicarpus	101.5	66.5	61.0	37.0	62.0	63.5
14	P. longicarpus to C. vittatus	84.5	156.5	105.0	130.5	102.0	77.0
	C. vittatus to P. longicarpus	67.0	105.0	74.0	95.5	83.0	82.5
20	P. longicarpus to C. vittatus	124.5	128.0	105.5	120.0	189.0	122.5
	C. vittatus to P. longicarpus	82.5	104.0	120.5	148.0	150.0	117.5
24	P. longicarpus to C. vittatus	167.0	138.0	172.5	133.0	165.5	123.5
	C. vittatus to P. longicarpus	127.5	121.5	107.0	106.0	156.5	114.0
28	P. longicarpus to C. vittatus	159.5	142.0	165.5	132.0	173.0	186.5
	C. vittatus to P. longicarpus	149.5	90.0	144.5	142.0	147.0	142.5

P. longicarpus distance at each replicate, then the total number of pluses at densities 10, 14, 20, 24 and 28 are 5, 5, 4, 6 and 5 respectively. Since these values are too small to test by χ^2 individually, they were lumped together and a χ^2 test was performed on the assumption that there was no difference between summed P. longicarpus to C. vittatus distances and summed C. vittatus to P. longicarpus distances. The χ^2 value of 13.33 obtained from this test was highly significant ($P < 0.01$). P. longicarpus therefore tends to space itself further from C. vittatus than C. vittatus spaces itself from P. longicarpus.

Discussion

The spacing out of the two species of hermit crabs in the three series of experiments shows a high degree of intraspecific similarity, and also shows modifications by P. longicarpus to the presence of C. vittatus in the tank. Neither P. longicarpus nor C. vittatus shows any difference in their degree of spacing out with regard to their own species when the other species is in the tank, but P. longicarpus is less likely to occupy the favoured edge area of the tank in the presence of C. vittatus. A P. longicarpus is also more likely to keep a greater distance from a C. vittatus than vice versa. This cannot be caused by an attraction towards a P. longicarpus by a C. vittatus, as Table VIII has shown that a C. vittatus shows a greater degree of attraction towards a member of its own species than towards P. longicarpus. In contrast to the behaviour of P. longicarpus, C. vittatus shows no difference in its ratio of individuals occupying the edge area of the tank at any density. This result suggests that C. vittatus is dominant over P. longicarpus, which supports the explanation given in the discussion of series 3, paper 2 (p111) regarding the two species interspecific agonistic encounters.

The aggregations of C. vittatus obtained in this paper seems typical of the genus Clibanarius. Hazlett (1966) observed that Clibanarius tricolor was very gregarious both in the field and in the laboratory at Curaçao and Hazlett (1970) also observed Clibanarius zebra to congregate under rocks at Hawaii. Another Clibanarius species observed to aggregate is C. digueti at Sonora, Mexico (Elaine Snyder, University of Arizona), while C. vittatus itself has been observed to aggregate in the field in Texas (Fotheringham, 1975). The spacing behaviour of Pagurus species is much more variable, however, probably due to the polyphyletic ancestry of this genus and the independent positioning of P. longicarpus is different from the distributions described for other Pagurus species (see General Discussion p149).

The ecological significance of the spacing behaviour of C. vittatus and P. longicarpus is that more intra- than interspecific encounters should occur in nature, thus helping to reduce competition between the two species. More intraspecific C. vittatus encounters than intraspecific P. longicarpus encounters should also occur, owing to the aggregation of C. vittatus. This may be helpful to C. vittatus in that it encourages shell swaps. C. vittatus occupies shells which are in general too small for it (Section 3, paper 2, figure 6) and therefore a high degree of shell swapping would tend to give a more uniform shell adequacy index throughout the population of C. vittatus than would otherwise occur. P. longicarpus in the weight ranges tested is not so poorly housed (Section 3, paper 2, figure 5) and shell swapping encounters are therefore not so important for the population.

Summary

Three series of experiments were conducted on the spacing behaviour of the hermit crab species Pagurus longicarpus and Clibanarius vittatus in a circular tank. In the first series, P. longicarpus individuals spaced themselves independently of each other at all densities tested, while in the second series C. vittatus spaced themselves approximately 1.4 cm less than expected from independent positioning at all densities. The third series showed that when the two species were mixed in equal numbers in the same tank their behaviour towards members of their own species remained unchanged. P. longicarpus, however, was less likely to occupy the favoured edge areas of the tank and kept a greater distance from C. vittatus individuals than C. vittatus kept from P. longicarpus individuals. Both species also tended to stay nearer members of their own species than members of the other species.

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GENERAL DISCUSSION

"These are only hints and guesses,
Hints followed by guesses."

The Dry Salvages

T.S. ELIOT.

Four main topics of habitat selection have been studied in this thesis. These are spacing behaviour, activities, shell occupation and aggressive behaviour. There is a certain amount of overlap among the four topics studied, since aggressive behaviour can influence shell occupation (Section 3, paper 3), and shell occupation can influence activity (Section 3, papers 2 and 3) but in other cases, care must be taken before a causal relation between any two topics can be assumed. Hazlett (1966b, c), for instance, thought that the number of aggressive encounters between hermit crabs should be directly proportional to the locomotor activity of the hermit crabs, but Courchesne and Barlow (1971) found that isolation decreased locomotor activity but increased aggressiveness. No relations are therefore made in this thesis between the effect of light on activity and spacing out in Pagurus bernhardus. It could be that reduced activity during darkness reduces encounters between individuals which in turn reduces the spacing out distances between individuals, but it may also be that P. bernhardus spaces out purely by visual displays. A safer approach in the light of this present evidence is to treat each of the topics separately and to suggest further experiments which could be performed to establish causal relationships between topics.

Spacing out experiments have been performed on all four hermit crab species studied, but the results of the sublittoral Pagurus bernhardus and Pagurus prideauxi experiments cannot be taken as statistically valid (see p16). The results of the experiments on intertidal P. bernhardus, P. longicarpus and C. vittatus are interesting both from a phylogenetic and a general distribution viewpoint.

At present, the spacing out behaviour of seven Pagurus species have been recorded (Ball, 1968; Hazlett, 1966b). Three of these species, P. bonairensis, P. pygmaeus and P. miamensis are in Group I of Forest and Saint Laurent's (1967) classification of the genus Pagurus. These three species are described as being "distributed contagiously" (Hazlett, 1966b p122). Group II of Forest and Saint Laurent's classification includes P. longicarpus which is the only Pagurus species studied which has an independent distribution. Group III includes the two species studied by Ball (1968) namely P. granosimanus and P. samuelis. They are described by Ball as being dispersed at night and clustered in tight groups during the day. A further group of Pagurus was proposed by McLaughlin (1974) and named the P. bernhardus group. P. bernhardus is the only studied species within this group, but Grant and Ulmer (1974) have also observed the closely related species P. acadianus which seems to have a spaced out distribution, a finding similar to that obtained on intertidal P. bernhardus in Section 2, paper 1 of this thesis. There is therefore some evidence to suggest that the spacing behaviour of members of the genus Pagurus is determined by phylogenetic factors, but more evidence is needed to certify this finding. The phylogenetic interest of the aggregating behaviour of C. vittatus is discussed in Section 3, paper 4.

The modifications made in Section 2, paper 1 to nearest neighbour analysis can have a wide variety of applications, some of which are discussed in that paper. In practice, it is rare for all three assumptions stated in the introduction to Section 2, paper 1 to be fulfilled in practice. One reason is that many distribution surveys have well defined boundaries. Examples of this are aphids on a leaf (Dixon, 1971), vesicles within axons (Usherwood and Rees, 1972) and geese on an island (Ewaschuk and Boag, 1972). In these studies the Clark and Evans (1954) nearest neighbour analysis should not have been used, since there could be no nearest neighbours outside the defined boundaries. This could have the effect of increasing observed nearest neighbour distances. Examples of disregarding the sizes of animals used are Stimson (1974) working on coral, and Sutherland (1970) working on limpets. The effect which size of animals may have on nearest neighbour analysis is discussed on page 76 of this thesis. Lastly, not all sample areas studied are uniform, and this is particularly true of field studies. Animals may be orientating towards some external factor which is not immediately obvious, and x^2 tests on uniformity of aggregated replicate measurements of the same area at different times should always be done to control for this criticism. An example in which this is not done is Rusch and Keith (1971). They studied the spacing out of grouse in an area of 2,560 acres, but no attempt was made to separate the attraction of grouse for different kinds of vegetation within that area from the spacing of one individual from another.

The activity studies performed in this thesis on P. bernhardus and P. prideauxi could have some relevance to their distribution in the Clyde. The differences observed in the reactions of sublittoral P. bernhardus and sublittoral P. prideauxi to the presence and absence of light may explain the differences in abundance of these two species at the Wishing Well, Isle of Cumbrae. Down to 15 metres, P. bernhardus is the more abundant species but at depths greater than 15 metres, P. prideauxi is more common (personal communication, J.G. Wilson, University of Glasgow). To establish if P. prideauxi stays at greater depths because it prefers darker habitats, and if P. bernhardus stays at shallower depths because it prefers more illuminated habitats, the direction of locomotory movement in response to light has to be considered. This has been done by Alverdes (1930) for P. bernhardus at Heligoland where he found that P. bernhardus was attracted to a single light source, and that even though some individuals later made excursions around the tank, their eyes were always directed to the light source. This evidence, coupled with the findings of Brocker (1935) that P. bernhardus has no mechanism for dark adaptation, suggests that light is the important factor in keeping this species in shallow depths. There is no evidence on the effect of light on P. prideauxi, however, so that it is not known if P. prideauxi prefers deeper waters or if it cannot compete with P. bernhardus in shallow waters.

Shell occupation has been studied in different ways depending on the species studied. At Ardrossan beach, gastropod shells are abundant for hermit crabs of all but the largest sizes at most times of the year, but only two shell species are common, whereas at Beaufort Harbor a few of only one species of shell, Terebra dislocata, were ever found empty during the six months of my stay, and there was a variety of gastropod species occupied by hermit crabs. For this reason, an ecological investigation of shell occupation at Beaufort seemed a reasonable undertaking whereas at Ardrossan there seemed little point in a short term investigation.

In the behavioural studies performed on crabs from Ardrossan and Beaufort, multiple regressions were performed on crab weight against shell weight, shell volume and shell aperture width. The two Beaufort species investigated showed that general size rather than one particular shell variable was important in shell selection but the P. bernhardus equations were not so clearly interpreted. This was the reason for using principal component analysis on the P. bernhardus data. Principal component analysis could also have been done on each shell species selected at Beaufort but this was not judged to be a worthwhile undertaking in the time available. Similarly a histogram of optimum shell sizes against crab weight (see Figures 3 and 4 of Section 3, paper 2) could have been included in Section 2, paper 3, but the results obtained were different from those of a repeat experiment. For this reason they are included in Appendix 4 together with the results of the repeat experiment.

The intraspecific aggressive behaviour of P. bernhardus, P. prideauxi and C. vittatus has been studied in this thesis. Each species showed the usual pattern of large individuals being dominant over smaller ones (Hazlett, 1966b, c; Rossi, 1971) but there were striking differences in the manner of intraspecific agonistic encounters. These differences have also been observed by Hazlett (1968a, c; 1972a) in some detail. The exact function of their agonistic behaviour is still not clear, however. Courchesne and Barlow (1971) suggested that aggressive behaviour in hermit crabs could be divided into two series. Series 1 components were characterised by being short in duration and not responsive to isolation while Series 2 consisted of long duration actions which were responsive to isolation. They then claimed that "Series 1 actions probably serve as visual displays that communicate the identity of the sender and that it is capable of behaving aggressively" (Courchesne and Barlow, 1971, p46) and that "these displays probably serve to keep the crabs spaced out, reducing the incidence of serious hostile interactions". Series 2 behaviour, on the other hand, "evidently contain the additional information that the sender intends to engage in serious aggressive behavior". This hypothesis of aggressive behaviour does not explain how *P. longicarpus* and *C. vittatus* which have well defined Series 1 behaviour patterns (Hazlett, 1972a) do not maintain spaced out distributions. It may be that each group of hermit crab species uses the same kind of aggressive displays to communicate different information. The *Clibanarius* group for instance would not use their Series 1 behaviour patterns to space out but rather to establish a dominance hierarchy (Hazlett, 1966b). The *Pagurus* Groups I and III (Forest and Saint Laurent, 1967) could also use their Series 1 patterns in this way (Hazlett, 1966b). *Pagurus longicarpus* is known to have different agonistic behaviour characteristics from the *Pagurus* Groups I and III species studied (Hazlett, 1972b). Movement in *P. longicarpus* is rapid, and jumping-hopping retreat is common whereas *P. miamensis*, *P. pygmaeus* and *P. marshi*, all of *Pagurus* Group I, and *P. samuelis* of Group III, are of moderate speed and during retreat no hopping or jumping occurs. Clearly, the agonistic behaviour of *Pagurus* Groups I and III species is much more inducive to individual recognition and aggregated distributions than the *P. longicarpus* type of behaviour. *P. longicarpus* therefore probably uses its aggressive signals to cover a wide area of sea bed than for any true dominance hierarchy by "individual" recognition.

Hazlett (1972) places the agonistic behaviour of *P. bernhardus* as intermediate between that of *P. miamensis* and its counterparts, and that of *P. longicarpus*. With this type of behaviour it is possible for P. bernhardus both to recognize each other "individually" (Hazlett, 1969) and to space out (Section 2, paper 1). It could be that only individuals of this group of hermit crabs behave according to the hypothesis of Courchesne and Barlow (1971) stated earlier in this discussion. Lastly, P. prideauxi's agonistic behaviour may be quite aberrant. Once beyond a certain size, they do not change shells and hence need not have a shell-fighting agonistic behaviour. Their intraspecific agonistic behaviour involves either a quick jumping-hopping away from each other (Hazlett, 1968b) or close tactile contact, often with no obviously resolved result (Meadows and Mitchell, 1973).

APPENDIX I

χ^2 Tests of Uniformity of Angular Measurements.

In Section 2 papers 1 and 2, and Section 3 paper 4, χ^2 tests were used on the aggregated angular measurements of six replicates at each population density. The method of conducting the χ^2 tests was first of all to divide the angular readings of all polar co-ordinates noted into 90° sectors (i.e. 1 - 90°, 91 - 180°, 181 - 270° and 271 - 360°). The expected numbers of crabs falling on each sector (E) under the assumption of a uniform distribution is $\frac{6n}{4}$ where n is the number of crabs per tank.

The standard χ^2 formula of

$$\chi^2 = \sum_{i=1}^{K} \frac{(O_i - E_i)^2}{E_i} \quad \text{(Siegel 1956 p43)}$$

is then used.

Example

The numbers of a 50/50 mixture of Pagurus longicarpus and Clibanarius vittatus in 90° sectors of a circular tank 27.5 cm radius are shown in Table I. (For experimental detail see Section 3 paper 4). For each χ^2 calculated there are 3 degrees of freedom.

Number of crabs per tank	1-90°	91-180°	181-270°	271-360°	Expected value	χ^2	P
10	11	18	19	12	15	3.33	$<0.50, >0.30$
14	17	25	13	29	21	7.62	$<0.10, >0.05$
20	19	28	30	43	30	9.80	$<0.05, >0.02$
24	38	30	43	33	36	2.72	$<0.50, >0.30$
28	33	42	37	56	42	7.19	$<0.10, >0.05$

The method of conducting χ^2 on 20° sectors of the tank was similar to above, but the expected values were then obtained by $\frac{6n}{18}$. If this value was less than 5 (i.e. if n < 15), it was deemed that x^2 analysis was not appropriate (Siegel, 1956).

APPENDIX 2

The use of the x^2 and the Kolmogorov-Smirnov One Sample Tests in Testing Homogeneity of Radial Measurements.

APPENDIX 2

The use of the χ^2 and the Kolmogorov-Smirnov One Sample Tests in Testing Homogeneity of Radial Measurements.

In the nearest neighbour analyses of the circular tanks in Section 2, papers 1 and 2, and in Section 3, paper 4, there was an obvious attraction of crabs to the outer 3 cm of the experimental tanks used. This attraction is easily tested by χ^2, since the expected number of crabs on the edge for six replicates at each density can be calculated by multiplying the total number of crabs tested at each density by the ratio of the "edge area" to the total area of the tank. The expected number of crabs in the interior of the tank is then obtained by subtracting the expected number on the edge from the total number of crabs tested.

Example

In Section 2, paper 2, it is given in Table I that the numbers of crabs on the edge of a 24.5 cm radius tank were 22, 29, 32 and 37 for densities 10, 13, 16 and 19 crabs per tank respectively when there was no illumination. The null hypothesis is that crabs are distributed uniformly and independently over the tank. The ratio of the edge area to the total area is obtained by:

$$\frac{\pi r^2 - \pi (r-3)^2}{\pi r^2} \quad \text{where } r = \text{radius of the tank.}$$

This expression simplifies to $\frac{r^2 - (r-3)^2}{r^2}$ which = 0.23 in this example.

The expected numbers on the edge for six replicates at 10, 13, 16 and 19 per tank are therefore:

13.80, 17.94, 22.08 and 26.22, and the expected numbers over the interior are 46.20, 60.06, 73.92 and 87.78 respectively. The χ^2 values with 1 d.f. for these densities are as follows.

Density	10	13	16	19
χ^2	5.48	8.08	5.21	5.23
P	<0.020 >0.010	<0.005 >0.001	<0.025 >0.020	<0.025 >0.020

There is therefore significant evidence to reject the null hypothesis that there is no attraction of crabs to the edges of the tank at all densities tested.

Once it has been shown that crabs occur in significantly greater numbers than expected at the edges of the tank, the next hypothesis to be tested is whether there is a uniform distribution of crabs over the interior of the tank. This is done by the Kolmogorov-Smirnov one sample test (Siegel, 1956 p47). For this test it is necessary to determine the largest deviation between the observed cumulative distribution under study, $S_n(x)$, and the theoretical cumulative distribution under the null hypothesis, $F_o(x)$. In the present studies, $S_n(x)$ is obtained from the aggregated radial measurements of the six replicates over the interior of the tank at any population density. $F_o(x)$ is obtained from the formula:

$$F_o(x) = \frac{R^2 - r_i^2}{R^2}$$

where R = the outer radius measurement of the interior of the tank and r_i = radius measurement varying from 0...... (R - 0.5) cm taken at 0.5 cm intervals.

Example

The radius measurements from 0 - 21.0 cm of intertidal P. bernhardus without illumination (see Section 2, paper 2) are given in Table I. To compare these with the theoretical cumulative distribution, $F_o(x)$ they must be divided by the total number of crabs occurring over the interior of the tank at each density. The observed cumulative distributions are shown in Table II, together with $F_o(x)$. The largest deviations between $S_n(x)$ and $F_o(x)$ are calculated for each density. These deviations (D) and their probabilities are as follows.

Density	10	13	16	19
D	.099	.153	.086	.037
P	> 0.20	< 0.20 > 0.15	> 0.20	> 0.20

There is therefore no evidence to suggest a departure from a uniform radius distribution over the interior of the tank at any density.

TABLE I

Number of P. bernhardus without illumination appearing at radius measurements of a circular tank, 24.5 cm. Only the interior (i.e. the first 21.5 cm of the tank) is given here since a significant edge attraction has already been shown.

Radius Measurement	Density of crabs per tank			
	10	13	16	19
21.0	2	6	2	1
20.5	2	2	6	2
20.0	1	2	2	6
19.5	2	4	4	3
19.0	2	1	1	2
18.5	3	1	5	5
18.0	3	4	3	3
17.5	1	4	3	2
17.0	2	1	2	2
16.5	1	1	0	6
16.0	0	2	2	4
15.5	0	2	0	2
15.0	2	1	2	2
14.5	0	2	4	3
14.0	0	0	3	2
13.5	1	1	1	2
13.0	3	0	5	4
12.5	2	1	2	1
12.0	0	3	2	3
11.5	0	1	0	1
11.0	1	0	2	1
10.5	2	0	3	1
10.0	2	0	1	2
9.5	0	1	2	1
9.0	2	0	1	2
8.5	1	3	0	1
8.0	0	0	1	0
7.5	0	1	0	4
7.0	0	1	0	1
6.5	0	0	1	2
≤6.0	3	4	4	6

TABLE II

Observed cumulative distributions obtained by dividing the values of Table I by the total number of crabs occurring at each density, and the theoretical cumulative distribution $F_o(x)$ obtained from area measurements of the tank.

Radius Measurement	Density of crabs per tank				
	10	13	16	19	$F_o(x)$
21.0	.053	.122	.031	.013	.046
20.5	.105	.163	.125	.039	.087
20.0	.132	.204	.156	.117	.135
19.5	.184	.286	.219	.156	.177
19.0	.236	.306	.234	.182	.219
18.5	.315	.327	.313	.247	.260
18.0	.395	.408	.359	.286	.299
17.5	.421	.490	.406	.312	.337
17.0	.474	.510	.438	.338	.375
16.5	.500	.531	.438	.416	.411
16.0	.500	.571	.469	.468	.446
15.5	.500	.612	.469	.494	.480
15.0	.553	.633	.500	.519	.513
14.5	.553	.673	.563	.558	.545
14.0	.553	.673	.609	.584	.576
13.5	.579	.694	.625	.610	.606
13.0	.658	.694	.703	.662	.634
12.5	.711	.714	.734	.675	.662
12.0	.711	.776	.766	.714	.688
11.5	.711	.796	.766	.727	.714
11.0	.737	.796	.797	.740	.738
10.5	.789	.796	.844	.753	.761
10.0	.842	.796	.859	.779	.784
9.5	.842	.816	.891	.792	.805
9.0	.895	.816	.906	.818	.825
8.5	.921	.878	.906	.831	.844
8.0	.921	.878	.906	.831	.862
7.5	.921	.898	.906	.883	.878
7.0	.921	.918	.922	.896	.894
6.5	.921	.918	.938	.922	.909
≦6.0	1.000	1.000	1.000	1.000	1.000

APPENDIX 3

Applications of generalised likelihood-ratio tests to nearest neighbour analysis.

The generalised likelihood-ratio test is discussed statistically in some detail by Silvey (1970) but it is worthwhile showing here how the general model of the linear hypothesis (Silvey, 1970 p183) is adapted to test the equality of k in the model given on pages 33, 45 and 134 of this thesis.

The assumptions are that the mean, θ, has been altered by a constant k, leaving the variance unaltered.

This is:

$$\bar{x}_i = \theta_i + k + \epsilon_i \quad \text{where the variance of } \epsilon_i = \sigma_i^2. \qquad (1)$$

(i = any number between 1 and n, where n is the number of observations performed.)

Formula (1) can thus be rewritten as: $\bar{x}_i - \theta_i = k + \epsilon_i$. This version of formula (1) is then transformed by dividing by σ_i^2 so that ordinary least squares techniques can be used to calculate k. The division by σ_i^2 gives:

$$\frac{\bar{x}_i - \theta_i}{\sigma_i^2} = \frac{1}{\sigma_i^2} k + \text{error} \qquad (2).$$

k is then estimated by:

$$k = \sum_{i=1}^{n} \frac{(x_i - \theta_i)}{\sigma_i^2} \Big/ \sum_{i=1}^{n} \frac{1}{\sigma_i^2} \qquad (3).$$

The residual sums of squares is obtained from the formula:

$$R = \sum_{i=1}^{n} \frac{(x_i - \theta_i - k)^2}{\sigma_i^2} \qquad (4).$$

Formula (3) is applied to each density to work out estimates of k at each density of crabs per tank tested. A generalised likelihood ratio test is then used to test for the equality of k over all densities tested. To perform this test, the following quantities must be obtained:

R_o = the sum of expressions (4) for each density separately

R_1 = the application of expression (4) when all observations at each density are taken together to give an overall value of k.

The desired test statistic is then

$$\frac{R_1 - R_o}{R_o} \cdot \frac{r(s - 1)}{(r - 1)} \qquad (5).$$

where r = number of different densities tested,

s = number of observations at each density.

This statistic is distributed as F (r - 1, r(s - 1) when the hypothesis holds.

Example

The following readings are those taken on intertidal Pagurus bernhardus with illumination in Section 2, paper 2 of this thesis.

Number of crabs per tank	$\bar{x}_i$ readings						θ	σ^2
10	8.35	8.60	9.90	9.90	10.70	11.10	8.81	2.79
13	6.96	8.25	8.96	9.38	9.81	10.15	7.35	1.50
16	4.69	6.06	6.29	6.63	6.69	8.53	6.05	0.90
19	4.32	5.52	5.94	6.24	6.76	6.86	5.63	0.59

These values are used in formula (3) to obtain a value of k for each density. The values of k are 0.945, 1.57, 0.53 and 0.31 cm for densities of 10, 13, 16 and 19 crabs per tank respectively. These values of k are used in formula (4) to obtain a value for R_o. R_o was calculated to be 23.19.

A value for k for all 24 observations is then calculated by formula (3). This value is 0.66 cm. It is then used in formula (4) to obtain a value for R_1. R_1 was calculated to be 27.79.

The above valued are substituted in formula (5) as follows:

$$\frac{27.79 - 23.19}{23.19} \cdot \frac{4(5)}{3}$$

$= 1.32.$ This value is not significant at the 5% level for an F distribution with 3, 20 degrees of freedom. There is therefore no evidence to reject the hypothesis that k is constant for the four densities of crabs tested.

To test if the value of k obtained for all densities is significantly different from zero, the following formula is used:

$$\frac{R_2 - R_1}{R_1} \cdot (rs - 1) \qquad (6)$$

where $R_2 = \sum_{i=1}^{n} \frac{(x_i - \theta_i)^2}{\sigma_i^2}$, and R_1, r and s are defined as before.

This formula is distributed as F (1, rs - 1) degrees of freedom when the null hypothesis of k = 0 holds. Any value greater than the value of F (1, rs - 1) at P = 0.05 is taken to mean that the null hypothesis should be rejected.

Example

The value of R_2 obtained for intertidal P. bernhardus with illumination in Section 2, paper 2 of this thesis is 47.44. On substituting this value and the other values previously used in formula (5), into formula (6), the following result is obtained.

$$\frac{36.72 - 27.79}{27.79} \cdot 23$$

$= 7.39$. This value is greater than the F value of $F_{(1,23)}$ at the 5% significance level so the null hypothesis of $k = 0$ is rejected. P. bernhardus therefore spaces out significantly more than expected from independent positioning.

Finally to test the likelihood that the values of k obtained in two different populations are the same, the following version of the generalised likelihood ratio test is used.

Let n = number of observations in one population

m = number of observations in the other population

R_n = residual sum of squares of population with n observations

R_m = residual sum of squares of population with m observations.

Then $$\frac{R_1 - R_0}{R_0} (n + m - 2) \ldots (7)$$ is distributed as $F_{(1,\ n + m - 2)}$ degrees of freedom

where R_1 = residual sum of squares over all (i.e. n + m) observations, with k defined from formula (3) with the summations taken over n + m observations and $R_o = R_n + R_m$.

Example

It is wished to compare the k obtained from intertidal P. bernhardus with illumination of Section 2, paper 1 with the k of intertidal P. bernhardus with illumination in Section 2, paper 2. It is known that $n = 24$, $m = 36$, $R_n = 27.79$ and $R_m = 32.92$. R_1 was calculated to be 61.86. The appropriate values were substituted in formula (7).

$$\frac{61.86 - (27.79 + 32.92)}{(27.79 + 32.92)} . \; 58 = 1.10.$$

This value is well below the significant value of F for (1,58) degrees of freedom, so there is no evidence to suggest that the two populations of hermit crabs are spacing themselves out differently.

APPENDIX 4

A Further Analysis of Shell Selection in the Hermit Crab, *Pagurus bernhardus*

It was at first intended to compare the numbers of Littorina and Thais selected in the Littorina/Thais choice experiment of Section 2, paper 3 with the expected numbers of these two shell species which would be selected if there was no preference for either species at any crab weight interval (see Section 3, paper 2 for the method of calculating expected shell numbers for different crab weight intervals). A sensitive method of testing shell species selection would be by an adaptation of a generalised likelihood-ratio test, but even a crude analysis by χ^2 shows that the two shell species were not selected without preference.

Crab weight interval	Number of Littorina selected	Number of Thais selected	Expected Number of Littorina selected	Expected Number of Thais selected	χ^2
0.19 - 0.45	7	3	5.0	5.0	1.6
0.46 - 0.65	8	5	5.2	7.8	3.4
0.66 - 0.85	3	12	6.6	8.4	3.5
0.85 - 1.26	6	5	7.6	3.4	1.1
					9.6

The value of χ^2 obtained from summing the χ^2 values for the four intervals is significantly different from an expected χ^2 value with 4 degrees of freedom. ($\chi^2 = 9.6$ $P < 0.05, > 0.02$). There is no clear preference shown for one shell species over the other through all four intervals, however. Littorina shells seem to be preferred by crabs of less than 0.65 g but Thais shells seem to be preferred by crabs greater than 0.65 g.

In view of this slightly surprising result, the experiment was repeated using the same materials and methods as previously used in Section 2, paper 3. In this repeat, 37 Thais shells and 13 Littorina shells were chosen. The multiple regression equations of the shell variables against crab weight are shown below.

Shell Species	Regression equation	Percentage of the variation in crab weight explained
Littorina	$Y_i-\bar{Y} = 0.026\ (W_i-\bar{W}) + 0.957^*\ (V_i-\bar{V}) - 1.614\ (A_i-\bar{A})$	88.9%
	$(.062)\qquad(.288)\qquad(1.382)$	
Thais	$Y_i-\bar{Y} = 0.203^*(W_i-\bar{W}) + 0.256^*(V_i-\bar{V}) + 0.063\ (A_i-\bar{A})$	68.2%
	$(.094)\qquad(.123)\qquad(.775)$	
Littorina + Thais	$Y_i-\bar{Y} = 0.062\ (W_i-\bar{W}) + 0.366^*(V_i-\bar{V}) + 0.392\ (A_i-\bar{A})$	75.8%
	$(.049)\qquad(.091)\qquad(.424)$	

There is no significant evidence of any difference between the equations of Littorina and of Thais in the above table when the two lines were tested by the formula given on page 54 of this thesis. Furthermore, the combined Littorina + Thais equation given above is not significantly different from the combined Littorina + Thais equation given on page 56 of this thesis. The regression equation for the combined Littorina + Thais sample used on page 56 plus the repeat combined Littorina + Thais sample is: $Y_i-\bar{Y} = 0.023(W_i-\bar{W}) + 0.372(V_i-\bar{V}) + 0.590(A_i-\bar{A})$, with 74.2% of the variation in crab weight being explained by this equation.

The results of the expected number of Littorina and Thais shells of optimum crab weight at different intervals and the actual numbers of Littorina and Thais shells selected at these intervals in the repeat experiment are shown below.

Crab weight interval	Number of *Littorina* selected	Number of *Thais* selected	Expected Number of *Littorina* selected	Expected Number of *Thais* selected	χ^2
0.19 - 0.45	0	12	5.8	6.2	11.2
0.46 - 0.65	4	11	5.9	9.1	1.0
0.66 - 0.85	3	6	4.0	5.0	0.5
0.86 - 1.26	6	8	9.8	4.2	4.9

There is a significant preference for *Thais* over *Littorina* at crab weight intervals 0.19 - 0.45 g and 0.86 - 1.26 g ($\chi^2 = 4.9$, 1 d.f., $P < 0.05$). Since there was no significant difference between the combined regressions of the *Littorina*/*Thais* choice experiment and its repeat, a Fisher exact probability test was conducted on the numbers of *Littorina* and *Thais* shells selected in the choice experiment and the repeat. It was found that there was a highly significant difference ($P < 0.01$) between the numbers of *Littorina* and *Thais* chosen in the 0.19 - 0.45 g weight range but the other three weight ranges tested (0.46 - 0.65, 0.66 - 0.85, 0.86 - 1.26 g) showed no significant difference in the numbers of *Littorina* and *Thais* chosen.

To try to account for the differences between the shells selected in the *Littorina*/*Thais* choice experiment and its repeat, regression equations of log shell weight against log shell volume, log shell weight against log shell aperture width, and log shell volume against log shell aperture width were calculated for the 600 shells used in the experiment. Logarithmic data was used in preference to basic data since the logarithmic regressions gave consistently better correlations. The shells selected in the *Littorina*/*Thais* choice experiment were then plotted on graphs of the three regression lines, and the total numbers of these shell co-ordinates above and below each of the regression lines were recorded. The co-ordinates of the shell variables of the repeat experiment were similarly plotted and a note was again taken of the numbers above and below each regression line. The results are shown below.

	Littorina/Thais choice experiment		Repeat	
Regression line	Number of shell co-ordinates above line	Number of shell co-ordinates below line	Number of shell co-ordinates above line	Number of shell co-ordinates below line
Log weight against log volume	29	21	41	9
Log weight against log shell aperture width	26	24	28	22
Log volume against log shell aperture width	24	26	16	34

None of the numbers of shell co-ordinates appearing above and below the line significantly different from an expected 25/25 distribution in the <u>Littorina/Thais</u> choice experiment, but the number of shell co-ordinates appearing above the log weight against log volume line is highly significantly different from expected in the repeat. (χ^2 = 20.48, 1 d.f., $P < 0.001$). The number appearing below the log volume against log shell aperture width is also significantly greater than expected (χ^2 = 6.48, 1 d.f., $P < 0.025, > 0.010$). <u>P. bernhardus</u> in the repeat experiment therefore seems to be selecting shells of a low weight and aperture width in relation to volume, compared with the general population of 600 shells. This is particularly true of crabs less than 0.46 g since all 12 crabs of 0.46 g showed low weights and aperture widths in relation to volume. The shell species selection differences therefore seem to be caused by dimensional differences in the shell variables. Thais shells in general have a higher volume in relation to weight and aperture widths (see Figures 1 and 2) than Littorina while Littorina shells have higher aperture widths in relation to weight than Thais (see Figure 3).

This still does not explain why P. bernhardus selected shells of different relative dimensions in the Littorina/Thais choice experiment and in the repeat, however. The only explanation I can conceive for this change in selection is related to the male to female ratio of the population. Pike (1961) found a striking difference in the the sex ratio of P. bernhardus at different sizes in the month of June. He did not examine specimens at other months, but I noticed a much greater number of females in the repeat sample, taken from Ardrossan in February, than in the Littorina/Thais choice sample taken the previous April. Unfortunately no exact note was taken of which crabs were male and which were female in either sample, but this would be an interesting line to follow.

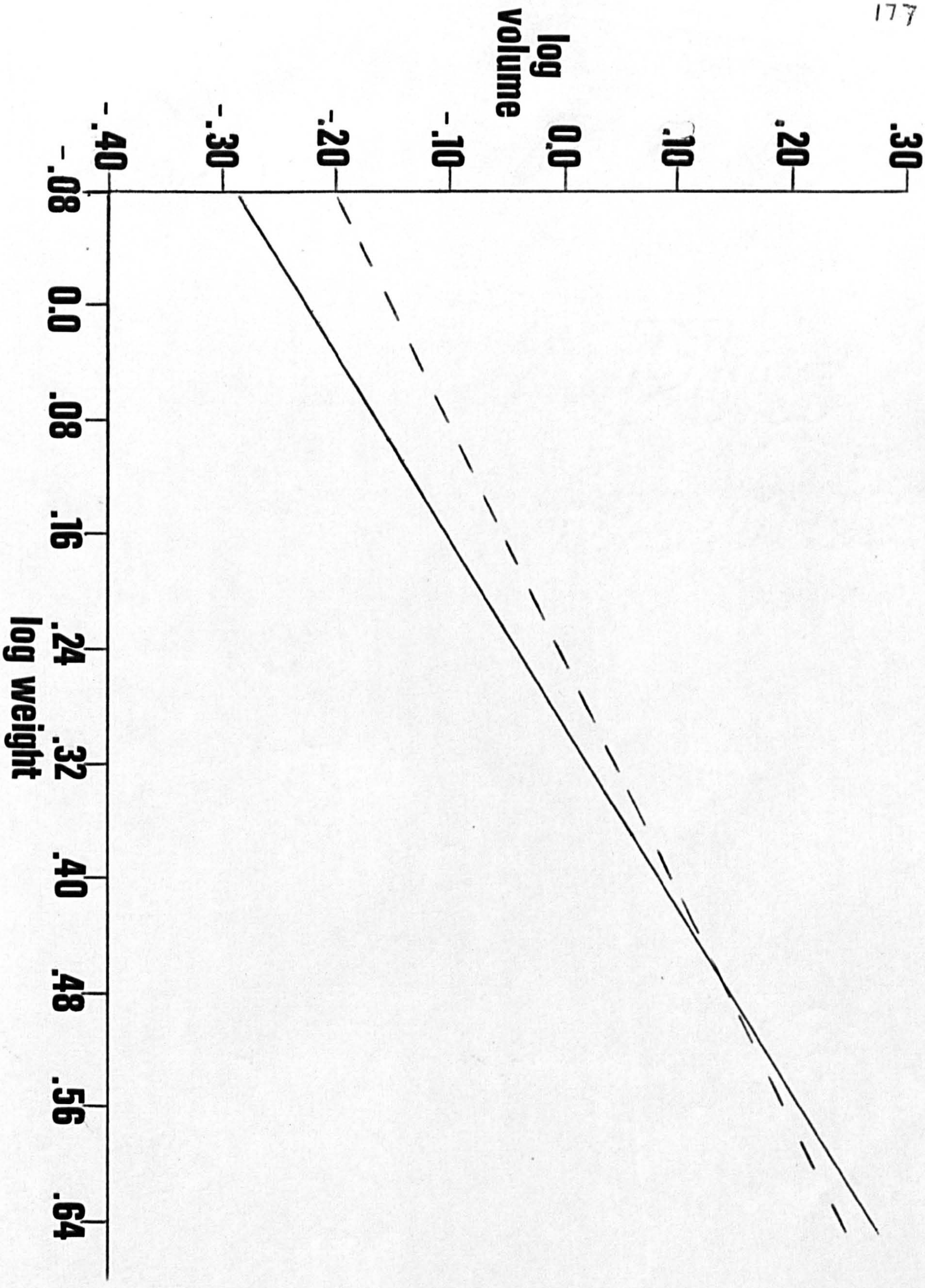

Figure 1. Regressions of 300 L. littorea and 300 T. lapillus weights against volumes. Slopes of lines are significantly different from each other ($P < 0.01$). The logarithmic relationship between these two shell variables is presented because it gives a better relationship than untransformed data.

—— = L. littorea

- - - = T. lapillus

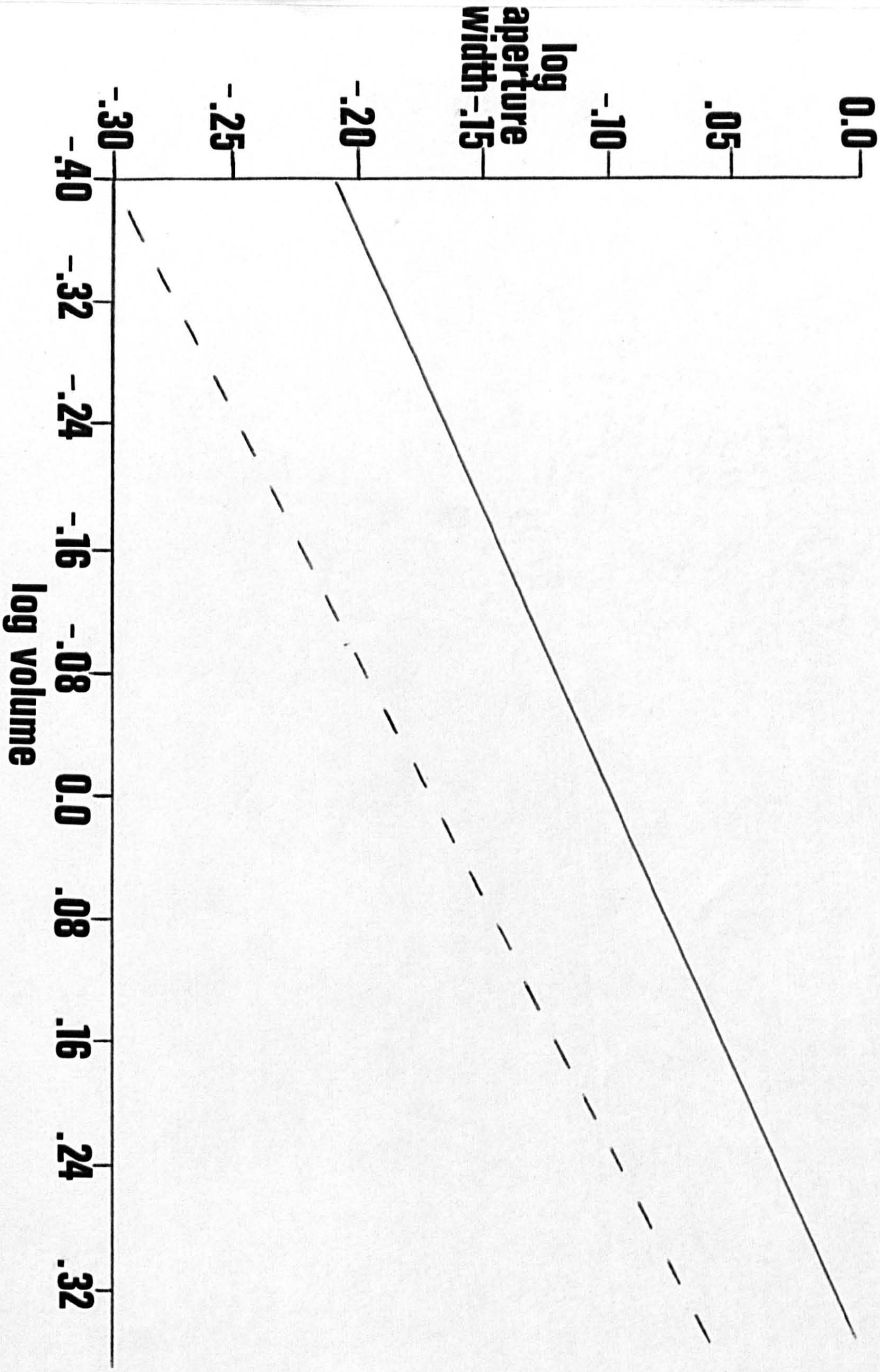

Figure 2. Regressions of 300 <u>L. littorea</u> and 300 <u>T. lapillus</u> volumes against aperture widths. Slopes of lines are significantly different from each other ($P < 0.01$). The logarithmic relationship between these two shell variables is presented because it gives a better relationship than untransformed data.

—— = <u>L. littorea</u>

- - - = <u>T. lapillus</u>

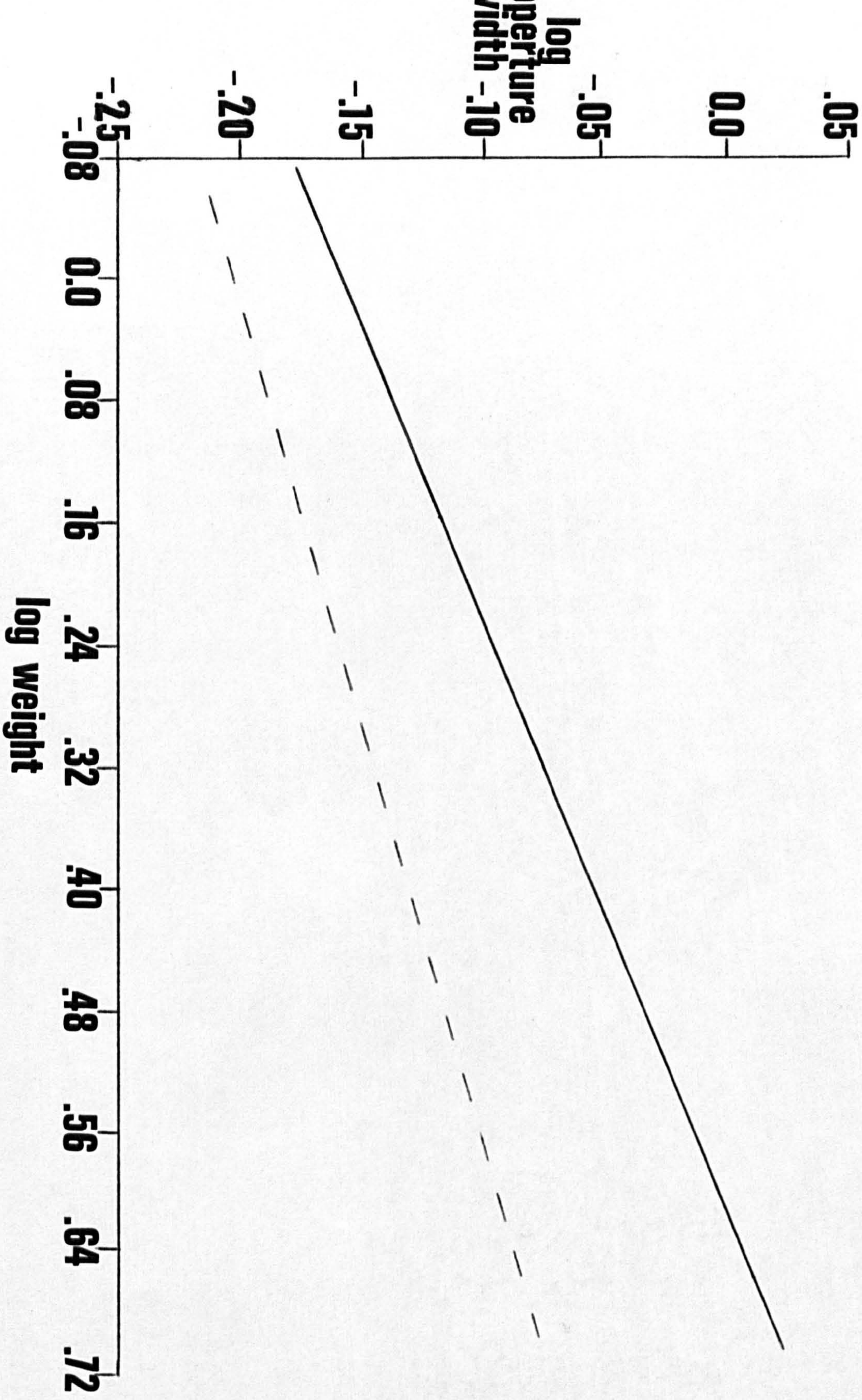

Figure 3. Regressions of 300 L. littorea and 300 T. lapillus weights against aperture widths. Slopes of lines significantly different from each other ($P < 0.01$). The logarithmic relationship between these two shell variables is presented because it gives a better relationship than untransformed data.

——— = L. littorea

- - - = T. lapillus

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SUMMARY

1. Experiments on habitat selection were conducted on three categories of hermit crabs. These were: (1) the sublittoral British hermit crabs, Pagurus bernhardus and Pagurus prideauxi; (2) the intertidal British hermit crab, Pagurus bernhardus; and (3) two species of intertidal hermit crab from the east coast of the U.S.A., Pagurus longicarpus and Clibanarius vittatus.

2. Pairs of sublittoral Pagurus bernhardus and Pagurus prideauxi were found to react inter- and intraspecifically. Total aggressive encounters were highest in paired P. bernhardus, lower in mixed pairs of the two species, and lowest in pairs of P. prideauxi. Their spacing out behaviour was also investigated but the conclusions drawn from conventional nearest neighbour analysis were found to be statistically invalid.

3. The activities of sublittoral P. bernhardus and P. prideauxi were altered on prolonged duration in the laboratory. In paired experiments, larger individuals were more active than smaller ones of the same species when the crabs had been kept in the laboratory for two weeks; however there was no significant difference after six weeks.

4. Isolated sublittoral P. bernhardus and P. prideauxi were in all cases less active than their paired counterparts.

5. Sublittoral P. bernhardus shows a distinct increase in locomotor activity in response to continual illumination compared with continual darkness. The opposite was true of P. prideauxi, however.

6. The spacing out behaviour of the intertidal P. bernhardus during daylight hours was investigated using a modified form of nearest neighbour analysis to take into account the size of the crabs and their attractions to the edges of the closed containers. In both rectangular and circular tanks, they were found to space out on average about 0.5 cm further apart from each other than expected from independent positioning. The expected distributions were obtained by computer simulations of crabs occupying the same proportions of different areas of the tanks as was observed in the laboratory. Population density did not affect either the proportions of crabs inhabiting different areas of tanks or the degree of spacing out of the crabs.

7. The spacing out of intertidal P. bernhardus was also studied during normal hours of darkness in a circular tank in the laboratory, using similar techniques as above. With illumination, P. bernhardus spaced out on average 0.66 cm more than expected from each other, but in the absence of illumination they positioned themselves independently. No effect of population density on spacing behaviour was discovered with or without illumination. There was a significant

tendency for crabs to position themselves next to the perimeter of the tank under all conditions, but this was much more obvious during illumination than without it. There was no evidence of any inherent spacing rhythms in this species.

8. The relative importance of three shell variables in the selection of a shell by intertidal P. bernhardus was investigated by techniques of principal component analysis and multiple regression. Two shell species, Littorina littorea and Thais lapillus, were used and it was found that for both shell species, P. bernhardus chose a shell of suitable general dimensions rather than solely on the basis of shell weight or volume or aperture width. In the case of T. lapillus, however, they made an additional discrimination between shells which have a high volume and aperture width in relation to a low weight.

9. The shell occupation of P. longicarpus and C. vittatus was studied at Beaufort, North Carolina. The ecological factors found to be important were the sizes of the crabs and the relative abundance of certain shell species. The lack of numbers of some shell species affected C. vittatus more than P. longicarpus. However, a substrate preference for mud over sand by P. longicarpus may limit this species from obtaining a preferred species of shell which naturally occurs on sand.

10. The behavioural factors important in shell occupation at Beaufort are the dimensions and structure of shell species. Both crab species are capable of discriminating between shell species structures and

different sizes of the same species of shell. Previous experience of a shell species did not affest these preferences. Previous experience of substrate was capable of altering the preference of mud over sand by *P. longicarpus*, however.

11. The interspecific agonistic behaviour of *P. longicarpus* and *C. vittatus* was investigated. No shell swaps were observed under any conditions but *P. longicarpus* made more aggressive displays than *C. vittatus*. No difference was observed in the number of fear displays between the two species.

12. The intraspecific agonistic behaviour of *C. vittatus* was studied. Large *C. vittatus* were more aggressive and showed fewer fear reactions than smaller ones in all conditions tested. The degree of dominance of large over small *C. vittatus* was much more marked and more predictable when the smaller crab occupied a *Polinices* rather than a *Littorina* shell, the large crab occupying a *Littorina* shell in both conditions. *C. vittatus* reacts more to the shape than the size dimensions of a *Polinices* shell.

13. The spacing behaviour of *P. longicarpus* and *C. vittatus* was studied at different densities with and without the presence of the other species. *P. longicarpus* spaced itself independently, whereas *C. vittatus* was aggregated under all conditions. The spatial distribution of *C. vittatus* was unaffected by *P. longicarpus*, but *P. longicarpus* tended to keep to the middle rather than the edges of the tank when in the presence of *C. vittatus*. The average nearest neighbour distances of *P. longicarpus* to *C. vittatus* were

consistently higher than those of C. vittatus to P. longicarpus. C. vittatus is therefore dominant over P. longicarpus and can thus obtain preferred habitats when in competion with P. longicarpus.