OPTIMISATION IN THE LIFE HISTORY OF THE HERMIT CRAB PAGURUS BERNHARDUS (L.)

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ABSTRACT

Aspects of the ecology of Pagurus bernhardus are examined and the strategies which enable this species to exploit two quite different habitats are determined. The area of shell selection is reviewed and mathematical indices of shell adequacy are rejected as biologically flawed. A subjective index is proposed to more accurately describe the quality of a hermit crab shell resource. Shell preference is considered to be an artificial phenomenon and shell selection is demonstrated to be an essentially random process. Shell-limitation is considered one of the most common problems facing all populations of hermit crabs, detrimentally affecting growth, fecundity, and longevity.

The reproductive cycle of Pagurus bernhardus is examined, and the period spent in the littoral zone is considered critical in the life history. Breeding is shown to occur only during the winter months in littoral populations, and is shown to require two interacting stimuli. Low temperatures affect egg production in the female, while reduced photoperiods affect breeding behaviour in the male. Gestation is shown to require some 43 days at temperatures of 8-10°C, and most females will produce two broods during a breeding season. Females are sexually mature in their first year and precocious breeding is seen as a vital strategy to overcome the restrictions of shell-limitation.

The monitoring of marked individuals indicates that Pagurus bernhardus is not territorial, and that the distribution of individuals on a shore is essentially random. The patterns of movement, the non-breeding interactions between individuals, and the residence times of these animals on a shore are suggested to be most strongly influenced by the quantity and quality of their shell contacts. Migration into the sublittoral is seen as an inevitable consequence of this behaviour.

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CHAPTER 1

INTRODUCTION

1.1 "SNAILS WITH CLAWS"

Hermit crabs are abundant and highly successful marine crustaceans, and have representatives on sea shores and in shallow coastal waters worldwide. The classification of the Crustacea is in much confusion (Schram, 1986) and technically the hermit crabs are placed in the decapod infra-order Anomala (McLaughlin, 1983a). The suggestion, however, that the name Anomura should be retained for this group because of its familiarity (McLaughlin and Holthius, 1985) is followed here.

Anomurans are characterised by having the last thoracic sternite free of the carapace, having the fifth (and sometimes the fourth as well) pereiopods reduced, and having the second antennae placed to the outside of the eyestalks (Ingle, 1980). Anomurans have a long fossil history and probably separated from the line which led to the more typical brachyuran crabs during the lower Jurassic period, some 200 million years ago (Glaessner, 1969). Along with the stone crabs (Lithodes spp. and Paralithodes spp.) hermit crabs are included within the super-family Paguroidea, one of four anomuran super-families, the others being the Lomidae (represented by the single species Lomis hirta - McLaughlin, 1983a), the Galatheoidea (the squat lobsters and porcelain crabs), and the Hippoidea (the mole crabs). Hermit crabs may have evolved from crevice-dwelling ancestors (which had progressively lost their abdominal calcification) attracted to the convenience of a more mobile shelter (McLaughlin, 1983b), and are most readily distinguished from other anomurans by the possession of a naked, unsegmented, and usually twisted abdomen, which is typically protected by an empty gastropod shell. The principal anatomical features of the hermit crab Pagurus bernhardus are illustrated in

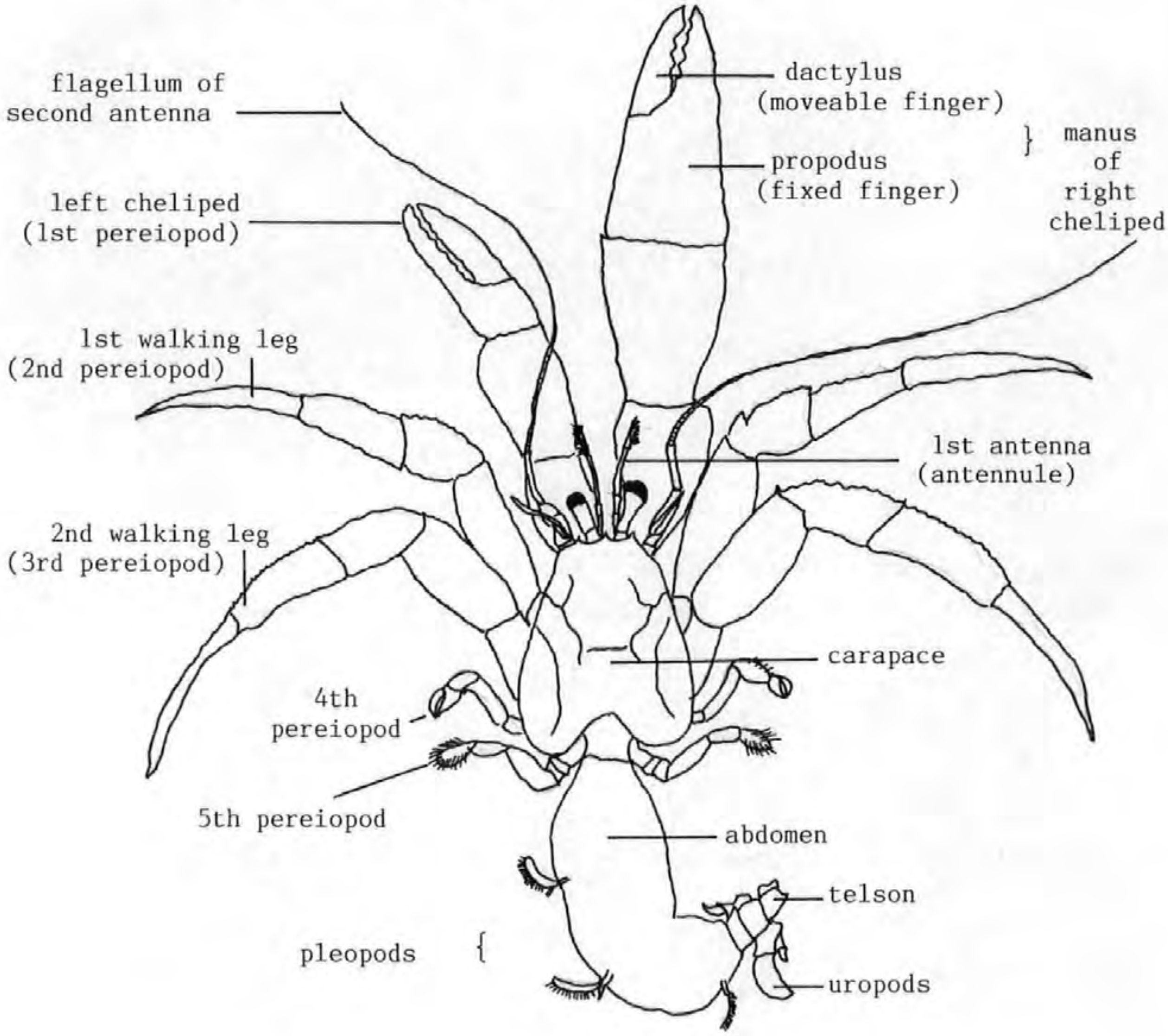
Figure 1.1.

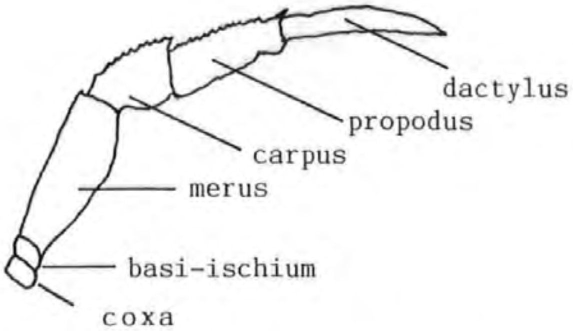
There are thought to be in excess of 800 species of hermit crab world-wide, belonging to some 86 genera in 6 families (Gordan,1956; Hazlett, 1981a). Although one tropical family (the Coenobitidae) with some 12 species is semi-terrestrial (termed "tree crabs"), all other hermit crabs are marine. Only 3 families are represented in N.E. Atlantic waters - the Diogenidae, the Paguridae, and the Parapaguridae - comprising some 40 species in 13 genera. Of these, the genus Pagurus not only contains the most local species (11 recorded - Ingle, 1985) but also contains in excess of 150 species world-wide (Garcia-Gomez, 1982). Pagurus bernhardus is the most common hermit crab recorded in British waters.

Hermits occur so commonly offshore in N.E. Atlantic waters that they have come to be recognised as members of a specific community - the boreal offshore gravel association (Jones, 1950) - characteristic of coarse deposits such as sand, gravel, stones, and shells at moderate depths. However, benthic studies with conventional grabs have provided little quantitative data on the distribution or abundance of hermit crabs (perhaps because these animals are so mobile) and, generally, their role in marine systems remains largely unexplored (Hazlett, 1981a). Hermit crabs are particularly conspicuous on shingle and gravel shores, especially where firm sand appears among the stones (Lewis, 1964), but are absent from the most wave-exposed coasts, particularly those composed of loose and shifting rocks (Reese, 1969). In sandy environments they tend to be restricted to the sublittoral. A study of a Swedish fjord population (Eriksson et al., 1975a, 1975b) has indicated that, given a choice, P.bernhardus prefers a hard substratum to one of sand. It has been suggested (Barrett,

Figure 1.1

SOME ANATOMICAL FEATURES OF PAGURUS BERNHARDUS
- after Jackson (1913).
(individual represented is male).





The segments of a crustacean appendage
- terminology from Warner (1977) and McLaughlin (1982).

1974) that the possession of a shell may provide hermit crabs with a survival advantage in exposed sandy environments since the shell can be rolled about by wave action without damage to the crab within - thus providing them with access to habitats that might be denied other types of crab. Littoral populations are most usually associated with rock pools - particularly those from about mid-shore level downwards - though numbers of hermit crabs in any area may vary enormously, both from place to place and from season to season (e.g. Pike and Williamson, 1959; Southward and Southward, 1977; Perkins, 1985).

P.bernhardus has been recorded from all parts of the coasts of Britain and Ireland, though its range extends from Iceland, the Faeroes, the Murman Sea and Norway north of the Arctic Circle, via the waters of Sweden and Denmark to Spain, Portugal, and the Mediterranean (Selbie, 1921). Although most commonly associated with the littoral zone and shallow coastal waters, P.bernhardus has a bathymetric range to at least 500m (Selbie, 1921).

The total number of species of hermit crab represented in British waters is difficult to estimate since identifications of these animals are often automatically ascribed to P.bernhardus (Biological Records Centre - personal communication). A figure of 10-15 species altogether is, however, suggested in the literature (Table 1.1). Since many records of this species use the generic name "Eupagurus", a discussion of the nomenclature of the common European hermit crab is presented in Appendix I.

Hermit crabs have such an intimate and immediately recongnisable association with borrowed gastropod shells that they have been described as members of a "shell-dwelling guild" in behavioural studies (Vance, 1972b). Indeed, it is thought that such a structure is so important to an animal with a naked and

Table 1.1

SPECIES OF HERMIT CRAB RECORDED FROM BRITISH WATERS

(* recorded as present)

	BATTERY ROCKS	CORNISH BIOLOGICAL RECORDS UNIT	"BRITISH INSHORE WATERS" Crothers & Crothers (1983)	SEVERN ESTUARY Boyden et al. (1977)	CLYDE SEA AREA Allen (1967)	ISLE OF MAN Bruce et al. (1963)	MILFORD HAVEN & SOUTH PEMBROKESHIRE Crothers (1966)	CLYDE SEA, ISLE OF MAN & CHANNEL ISLANDS Pike & Williamson (1959)	ENGLISH CHANNEL Marine Biological Association (1957) (also Southward & Southward, 1977)	COAST OF IRELAND Selbie (1921)	COAST OF CORNWALL Clark (1909)
Pagurus (=*Eupagurus*) *bernhardus* (L.)	•	•	•	•	•	•	•	•	•	•	•
P. cuanensis Bell	•	•	•	•	•	•		•	•	•	•
P. prideaux (=*P. prideauxi*) Leach		•	•		•	•	•	•	•	•	•
P. forbesii (=*P. sculptimanus*) Bell		•			•			•	•	•	•
P. carneus Pocock					•					•	
P. pubescens Krøyer			•		•	•		•		•	
P. excavatus (=*P. variabilis*) (Herbst)					•					•	
Anapagurus laevis (Bell)		•	•		•	•	•	•	•	•	•
A. hyndmanni (Bell)	•	•	•	•	•	•	•	•	•	•	•
A. chiroacanthus (Lilljeborg)		•	•		•	•		•		•	
Cestopagurus (=*Catapaguroides*) *timidus* (Roux)		•			•			•			
Parapagurus pilosimanus Smith					•					•	
Nematopagurus longicornis Milne Edwards & Bouvier					•					•	
Diogenes pugilator (=*D. varians*) (Roux)		•	•		•			•	•	•	•
Clibanarius erythropus (=*C. misanthropus*) (Latreille)	•	•			•				•		

vulnerable abdomen that few aspects of hermit crab behaviour will be unaffected by the shell carrying habit (Hazlett, 1966). A shell fulfils a multitude of functions to these animals. It offers protection from predators (Ross, 1960; Reese, 1969; Vance, 1972a), from mechanical abrasion by a rough substrate (Bollay, 1964), from temperature fluctuations (Reese, 1969), from water loss if the animal is exposed on an open surface at low tide (Herreid, 1969), and from salinity stress (Shumway, 1978; Davenport et al., 1980). A female will also protect her eggs within the safety of her shell during their gestation. In fact, the adaptations which hermit crabs have evolved associated with shell-use enable them to exploit the intertidal habitat particularly successfully - they can avoid extreme conditions by creating microhabitats within their shells, and yet they are sufficiently mobile to be able to move to a new area if conditions become intolerable. A shell literally provides them with "... all the advantages of a burrow without any of its restrictions" (Reese, 1969: p. 353).

The use of a gastropod shell incidently makes hermit crabs amongst the easiest of invertebrates to identify on the shore ("snails with claws" - Andrew, aged 7!), yet, paradoxically, also makes this group one of the most difficult to study in detail. The animals must usually be removed from their shells before identification to species can be confirmed, or before the individuals can be sexed or their reproductive states determined. This is probably the principle reason why so much is still to be learned about this group of crabs.

1.2 THE CONTRIBUTION OF THIS WORK TO HERMIT CRAB RESEARCH.

The curious association between hermits and borrowed gastropod shells has prompted several persistant lines of investigation into the biology of this group of crabs. The mechanisms of shell acquisition, particularly those involving conflicts between crabs termed "shell fighting", have been well studied (e.g. Reese, 1962; reviews in Dowds and Elwood, 1983, 1985). Despite complex experimentation and mathematical modelling, however, the characteristics which make shells attractive to individual crabs (i.e. that determine "shell adequacy") still remain largely unknown. Recent suggestions of "negotiation" in shell exchanges - involving shell swapping between two crabs to the benefit of both (e.g. Hazlett, 1978, 1983b, 1987) - have prompted fresh examinations of this aspect of shell aquisition, but the difficulty in deciding the extent of the "gain" experienced by each of the two participants has led to this idea finding little support (e.g. Elwood and Glass, 1981; Elwood and Neil, 1986).

The complex social behaviour of hermit crabs has been extensively reviewed (e.g. Hazlett, 1966, 1981a), and the displays aimed at maintaining personal spaces between individuals, and in establishing dominance orders for the distribution of resources, have been elucidated by detailed manipulations and modelling.

The associations between hermit crabs and their symbionts have also been carefully examined (e.g. summaries in Jensen and Bender, 1973; Cuadras and Pereira, 1977) and evidence of considerable subtleties in the relationships have emerged. These not only include instances of anemones protecting their crabs (e.g. Ross, 1971; McLean and Mariscal, 1973) but also show crabs feeding their anemones (Fox, 1965), crabs feeding from their anemones (Brightwell, 1951b), and even crabs manipulating the position of their anemones to act as counterweights when balancing a difficult shell (Balasch et al., 1977).

Thus, while there would appear to be an extensive literature on hermit crabs, the majority of these studies have concentrated upon isolated aspects of behaviour. Little attention has been paid to the long-term importance of the behaviour in the overall life history strategies of the species involved. Childress (1972), did comment upon crabs using larger than optimal shells in order to extend the time before a new shell needed to be found, and Scully (1983) has suggested that a reduced growth increment forced by a suboptimal shell is a physiological response which allows that same shell to still offer protection for a while until the crab encounters something larger. The link between these observations and an overall life history strategy for hermit crabs has not been made, however, and it is contended here that this is a serious limitation to the understanding of hermit crab biology.

The term "life history strategy" is generally taken (Cole, 1954) to refer to an organism's solution to the conflict between putting all of its effort into reproducing once and then dying (semelparity), or partitioning resources and reproducing repeatedly over several seasons (iteroparity). The concept of the "reproductive strategy" has become central to life history theory (e.g. Hirschfield and Tinkle, 1974; Stearns, 1976; Giesel, 1976), and estimates of the success, or "reproductive effort" (RE), of each strategy compare the efficiency of allocating resources (chiefly energy) to the production of gametes as opposed to non-reproductive (i.e. somatic) tissues or for repair. Interestingly, such work has not been extended to hermit crabs, even though this group has its life complicated in a way which is perhaps unique - since the eventual body size reached by an individual (and hence its total potential fecundity) is largely out of its control. For successful growth, and eventually reproduction, hermits require access to a supply of protective structures which they do not themselves manufacture; a deficiency in the gastropod shell resource will therefore lead to serious complications, not the least of which will be that a specific age or size required for reproduction may not be attainable. The largest individuals (and potentially those able to make the greatest contribution to the next generation) will be at the severest disadvantage under these circumstances since "shell-limitation" will inevitably affect these crabs before the smaller ones.

A life history strategy for hermit crabs cannot therefore ignore the shell resource, and must allow for the inevitable fluctuations in its quality. It is this theme which will be followed throughout this study - in an attempt to determine which strategies have been selected for in hermit crabs to enable them to make the best possible use of the available shell resource. Only when this is clear can it be seen how, in the long-term, each animal can maximise its own fitness.

Although commonly associated with the littoral zone, hermit crabs are fully marine animals. Little attention has been paid to considering why hermits forsake the relative stability of the deep sea in order to spend at least part of their life cycle in a hazardous and unpredictable environment such as the seashore. Indeed, marine organisms are seldom considered from this point of view of using the littoral zone as an integral part of a complete life history strategy. This aspect of hermit crab biology will be considered here.

In addition to investigating the life history strategy for P.bernhardus, this work also examined some of the specific aspects of the biology of this species which have been overlooked in the literature. For example, attempts to study a number of species collectively for information on breeding cycles (Pike and Williamson, 1959; Pike, 1961) have led to generalisations being made which have been uncritically accepted as fact and perpetuated through the literature - with the result that the picture of these animals' natural history has actually been clouded. This study, therefore, offers a contribution towards the biology and ecology of the commonest British species of hermit crab, Pagurus bernhardus, in an attempt to develop a clearer picture of its natural history. In particular, an attempt is made to determine the significance of that period in an individual's life which is spent in the littoral zone. The nature of the reproductive cycle and the period of gestation are determined for this species in order to fill gaps in the literature, and the environmental parameters most likely to influence reproductive success in intertidal populations are specifically identified. The extent to which the behaviour of these animals influences their distribution and residence time on the shore is investigated, and a number of aspects concerning the shell resource itself are examined. Emphasis is placed in this study upon the possible long-term consequences to a natural population of an inadequate shell resource (termed "shell-limitation"), and laboratory experiments are used to confirm the effects on growth and longevity that such a common phenomenon must have. Finally, the observed locomotory and reproductive behaviour patterns are discussed with reference to the overall life history strategy of this species.

An attempt has been made throughout this study to create an "animal-centered" view, and to consider all aspects of the biology which have been revealed as providing a clearer insight into the ways in which these animals are adapted to best exploit their environment.

1.3 THE ORGANISATION OF THE THESIS.

The aims of this research have been twofold. First has been the attempt to answer specific questions on the reproductive and migratory behaviour of Pagurus bernhardus, with particular reference to the time spent in the littoral zone. Second has been an attempt to integrate this knowledge with existing information on hermit crab biology in order to build up an overall picture of the life history strategies employed by this species - and thus to explain why individuals spend different parts of their lives in two such different environments.

Since the littoral zone habitat is therefore an integral part of the study, the thesis begins with a review of the area used for the collection of the crabs and the data relevant to them. The physical nature of the shore is described, and the fauna and flora typical of the area are listed.

Following this is an account of the shell resource available to the crabs in the area, which leads to a discussion of the concepts of "shell adequacy" and "shell preference". Both of these topics have been the subjects of extensive research and the literature contains many, frequently contradictory, attempts to explain these "phenomena" mathematically. An alternative, non-mathematical, index of shell quality is presented in this context to overcome the limitations that mathematical indices can be shown to have.

The questions requiring specific answers are addressed in the next three chapters. The effects on crab growth and longevity of what is referred to as shell-limitation are discussed in chapter 4, where the significance of shell size to the normal growth patterns of hermit crabs is determined for a population apparently isolated from a "large shell" resource. An examination of certain aspects of reproductive biology is presented in chapter 5 and then, in chapter 6, the ways in which shell contacts influence migratory behaviour are determined. The final chapter is a blend of summary and discussion, bringing together the material gathered during the research and providing a forum in which the life history strategy of this species can be discussed in a wider ecological context.

CHAPTER 2

THE NATURAL HISTORY OF THE STUDY AREA

- MOUNT'S BAY, SOUTH WEST CORNWALL

The habitat used during this study lies in the north-west corner of Mount's Bay, in the extreme south-west of Cornwall (Figure 2.1), and has the name "Battery Rocks". The rocks comprise an irregularly shaped mass of early Devonian slates and extend for some 200m due south of the monument on the seafront at Penzance (Grid reference SW 477 298) and for some 100m eastwards. The uppershore area is dominated by an intruded greenstone boss which, although strongly fissured, is little weathered. The bulk of the shore is of slate which slopes gently seawards and which, in the mid-shore region especially, is weathered into numerous broad, shallow rock pools. Typically these pools are quite small, and even the largest (measuring some 8-9m by 6m) is generally less than 0.5m in depth. A second, much larger, greenstone boss named "Carn Olva" dominates the lower part of the shore, though this is cut off except at low tide by a narrow gully. The shore is illustrated in Plates 1 and 2.

The rocky surface extends well into the bay, and at least 100m of the alga <u>Laminaria hyperborea</u> (Gunnerus) can be located beyond the low water mark. Diving conditions in the bay are generally good, but visibility is occasionally much reduced by sediment stirred up from the shallow coastal strip between the seaward edge of the rocks and the conspicuous "gear-pole" some 350m to the south-east. The shore would be categorised as "semi-exposed" in the sense of Ballantine (1961) and Lewis (1964), and is dominated by the barnacles <u>Chthamalus stellatus</u> (Poli) and <u>C.montagui</u> Southward in the low to middle shore regions, together with scattered limpets (<u>Patella</u> spp.), the dogwhelk <u>Nucella lapillus</u> (L.) and topshells - <u>Monodonta lineata</u> (da Costa) being particularly common in the upper-shore gullies and pools. Periwinkles, especially the edible <u>Littorina littorea</u> (L.), (once the basis of a flourishing industry) may occur in prodigious numbers in the upper shore pools, often exceeding 250 per m^2. Little or no alga

Figure 2.1

MOUNT'S BAY, CORNWALL, AND THE LOCATION OF THE STUDY AREA - THE BATTERY ROCKS, PENZANCE. (NATIONAL GRID REFERENCE SW 476298)

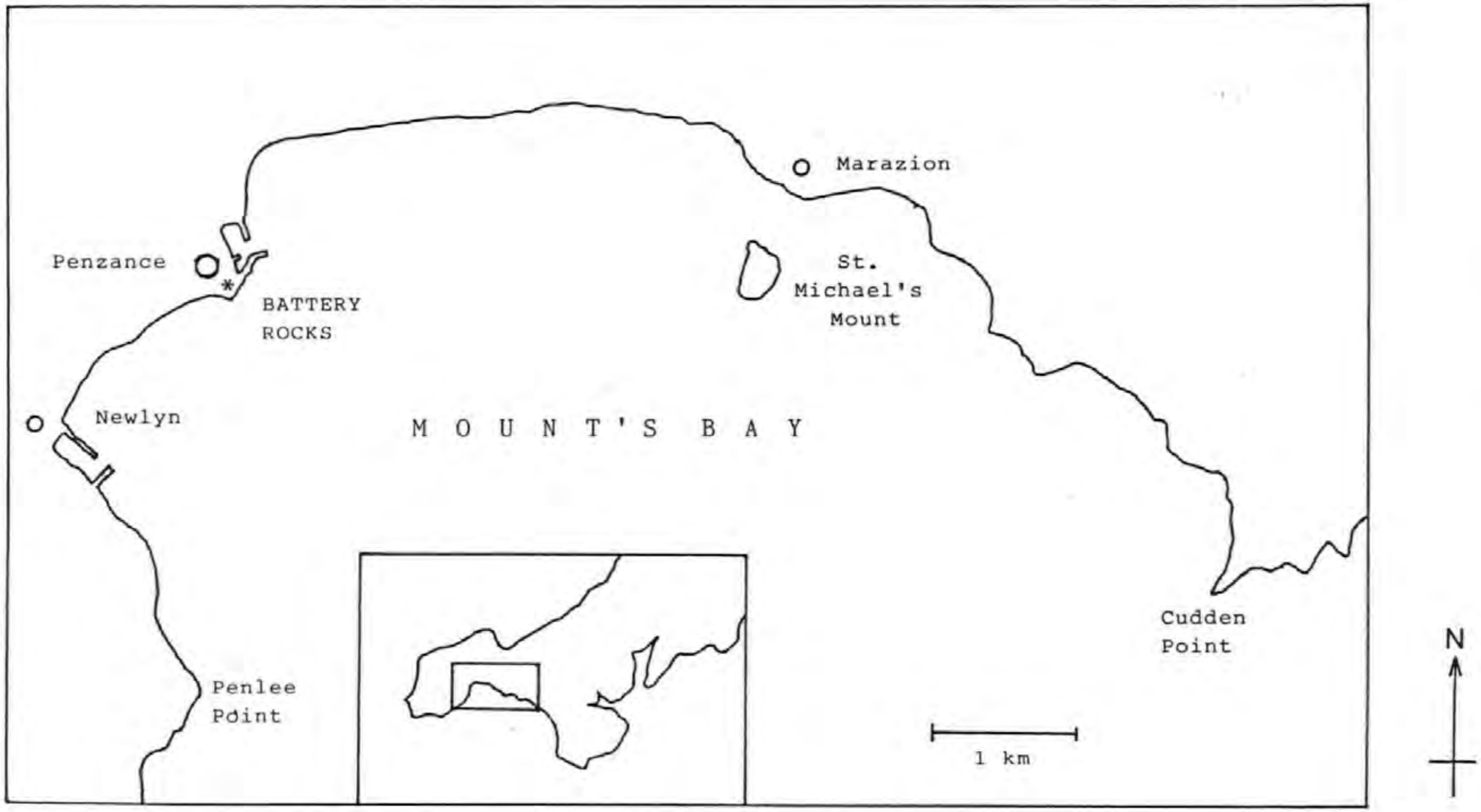


Plate 1

The Battery Rocks - view south-east to show the rock pools of the middle shore.

Plate 2

Aerial view of the Battery Rocks - view north-west.

[the rock pools of the middle shore and the offshore greenstone boss named "Carn Olva" are clearly visible in this view.]

exists on the middle to upper-shore, and only small isolated plants of *Pelvetia canaliculata* (L.) and *Fucus spiralis* L. are found. The lichens of the upper-shore are predominantly *Verrucaria* spp., *Lichina pygmaea* (Lightfoot) and occasional patches of *Xanthoria* spp. The area suffers from considerable tourist pressure in the summer months and much damage is done to all forms of plant and animal life at all levels on the shore. Bait collecting, school parties using the shore for educational purposes, and the general activities of souvenir hunters all add to the deprivation. Local naturalists have commented that the area has become noticeably poorer during the last 10-20 years.

Algal cover is much richer on the lower-shore and dense stands of *F.serratus* L. and *F.vesiculosus* L., together with *Laminaria digitata* Lamouroux, Laminaria hyperborea, *Saccorhiza polyschides* Batters and *Himanthalia elongata* S.F.Gray provide shelter for anemones, tunicates, echinoderms and crustaceans. Species of red algae are also common in this region and include dense clumps of *Chondrus crispus* Stackhouse, *Lomentaria articulata* Lyngbye, *Ceramium rubrum* C.A. Agardh and *Mastocarpus stellatus* (=*Gigartina stellata*) (Stackhouse). Encrusting lithophytes occasionally give an overall red colour to the bottom of the shore, and the rock pools are frequently carpeted with *Corallina officinalis* L.

The area has been well studied since at least the late 18th century, and many details of its fauna and flora have been recorded in the now defunct Transactions of the Penzance Natural History and Antiquarian Society. A recent summary of the flora and fauna is given in Powell *et al*. (1978), and regular updates to the fauna list are made by the Cornish Biological Records Unit at Exeter University. One such survey (7.9.86) confirmed that some 11 species of green algae, 21 species of brown algae, 30 species of red algae, 7 species of lichen, and at least 200 species of invertebrates were present on the shore (records with the C.B.R.U., c/o Institute of Cornish Studies, Trevenson House, Poole, Redruth, Cornwall). Some 30 species of gastropods were recorded in this survey, the majority of which are known to be utilised by hermit crabs and which cover between them almost every pattern of shell architecture likely to occur in these latitudes. The species include (in addition to those already mentioned) *Calliostoma zizyphinum* (L.), *Gibbula cineraria* (L.), *G.magus* (L.), *G.umbilicalis* (da Costa), *Littorina saxatilis* agg., *L.obtusata* (L.), *L.mariae* Sacchi and Rastelli, *Hinia reticulata* (=*Nassarius reticulatus*) (L.), *H.incrassata* (=*N.incrassatus*) (Strom), and *Ocenebra erinacea* (L.).

The tidal heights used to delineate the shore areas are as follows (Admiralty Tide Tables):

Tide level	height (m) above chart datum
EHWS	6.2
MHWS	5.6
MHWN	4.4
MTL	3.1
MLWN	2.0
MLWS	0.8

The rock pools used in this study are at a height of approximately 2.0m above chart datum - i.e. at the lower end of the middle shore.

During the period of this study a total of four species of hermit crab were recorded on the Battery Rocks: *Pagurus bernhardus*, *P.cuanensis* Bell, *Anapagurus hyndmanni* (Bell), and *Clibanarius erythropus* (Latreille). Of these only *P.bernhardus* was abundant, with the remaining three species being represented by a total of only five individuals out of some 2000 examined. Full details of these five individuals are included in Appendix II.

The circulation of the water in Mount's Bay was considered in the light of the apparent isolation of the Battery rocks fauna - especially the hermit crabs - which are dependant upon planktonic dispersal. A regular and strong current flow only appears about one mile offshore, and water movements inshore of a line from Penlee Point to Cudden Point (Figure 2.1) are wind-dominated and tend to be towards and parallel to the shore. This inevitably means that recruitment onto the Battery Rocks by forms with planktonic larvae will be limited. Any movement that could be predicted from float and dye tests would suggest that material could only be deposited on the rocks if it originated to the west, and would arrive as part of a leisurely west to east (i.e. clockwise) drift across the bay. These movements also effectively lock material into the bay, and the three outfalls that presently discharge untreated sewage into the sea off Penzance and the seven other pipes that discharge into other parts of the bay, must be considered as contributing to turbidity, occasional eutrophication, and lowered oxygen levels in the coastal waters - all to the detriment of planktonic and fixed marine life. Further problems facing the fauna and flora of Battery Rocks are that the open-air bathing pool situated immediately behind the shore (and dominating plate 2) flushes out its mildly chlorinated sea water at irregular intervals and at great pressure during the summer months, and the local council cleans the path around the outside of the pool (i.e.immediately above the rocks) with concentrated bleach approximately fortnightly during the same period - irrespective of the state of the tide.

Despite these problems, however, the Battery Rocks offer one of the richest and most accessible rocky shores in the area - which lent itself ideally to a long-term study such as this.

CHAPTER 3

THE HERMIT CRAB SHELL RESOURCE AND THE CONCEPT OF SHELL ADEQUACY

3.1 INTRODUCTION

The mechanisms by which hermit crabs assess the quality of the shell resource available to them is one of the most controversial areas of their biology. Almost every one of a shell's physical parameters has been considered as being primary in this assessment, including weight (Reese, 1962; Bach et al., 1976; Hazlett and Herrnkind, 1980), the weight: volume ratio (Markham, 1968), the angle of the columellar axis - and hence its ease of carriage (Dowds and Elwood, 1983), volume (Conover, 1978), rugosity, aperture size and shape, and even internal architecture (Reese, 1963; review in McClintock, 1985). Investigations into the phenomenon of shell selection (e.g. Hazlett and Herrnkind, 1980; Bertness, 1980, 1981b, 1981c; Dowds and Elwood, 1983; Blackstone, 1984; Elwood and Stewart, 1985) have tended to concentrate upon allowing animals access to an essentially unlimited choice of shells, where the underlying principle is that the animals should therebye come to occupy the shells which they feel are most optimally constructed. Analysis of the dimensions of both the crabs and their shells then allows correlations to be made, with the combination offering the highest correlation being assumed to be significant. The supposed "preferred" size or weight calculated in this way has been used to provide a base-line against which shell quality can be judged under natural conditions, and even in order to construct "indices" of shell quality such as the Weight Index of Reese (1962a) and the Shell Adequacy Index of Vance (1972a, 1972b).

This part of the study investigated the concept of shell "adequacy" by applying the Shell Adequacy Index (S.A.I.) above to individuals whose behaviour was subsequently observed for a prolonged period. It quickly became apparent during this experiment that the mathematical index had severe theoretical and practical limitations, and the need was felt to develop an alternative, more relevant, approach by which adequacy could be judged and compared in the field. Consequently, a "Subjective Index" of adequacy was devised and tested, and was compared against the Shell Adequacy Index. This subjective index was subsequently used in order to describe the adequacy of the shell resource on the Battery Rocks.

As a supplementary indicator of overall shell adequacy, members of the Battery Rocks population of <u>P.bernhardus</u> were also examined for the types of injuries typically sustained in shell swapping conflicts. Such injuries (e.g. lost or damaged limbs) are thought to be particularly common among individuals fighting over a poor quality shell resource (Scully, 1979).

In addition to choosing shells by the supposed adequacy of their physical parameters, a number of authors have suggested that crabs may deliberately choose particular species of shells (e.g. Bertness, 1980; Blackstone and Joslyn, 1984; Dowds and Elwood, 1985). These species would be selected irrespective of their abundance and would be sought out from a range of alternatives. To investigate whether particular species of shell were selected by the Battery Rocks crabs (irrespective of the adequacy or otherwise of their fit) it was decided to determine the relative abundances of the main gastropod species on the shore, and to make a comparison with the shell species found to be occupied by the majority of the crabs. The hypothesis that particular shell preferences would be indicated if a majority of animals were found in a shell species that was not the most abundant one on the shore, would then point the way for further trials where specific choices could be given under controlled conditions.

3.2 MATERIALS AND METHODS

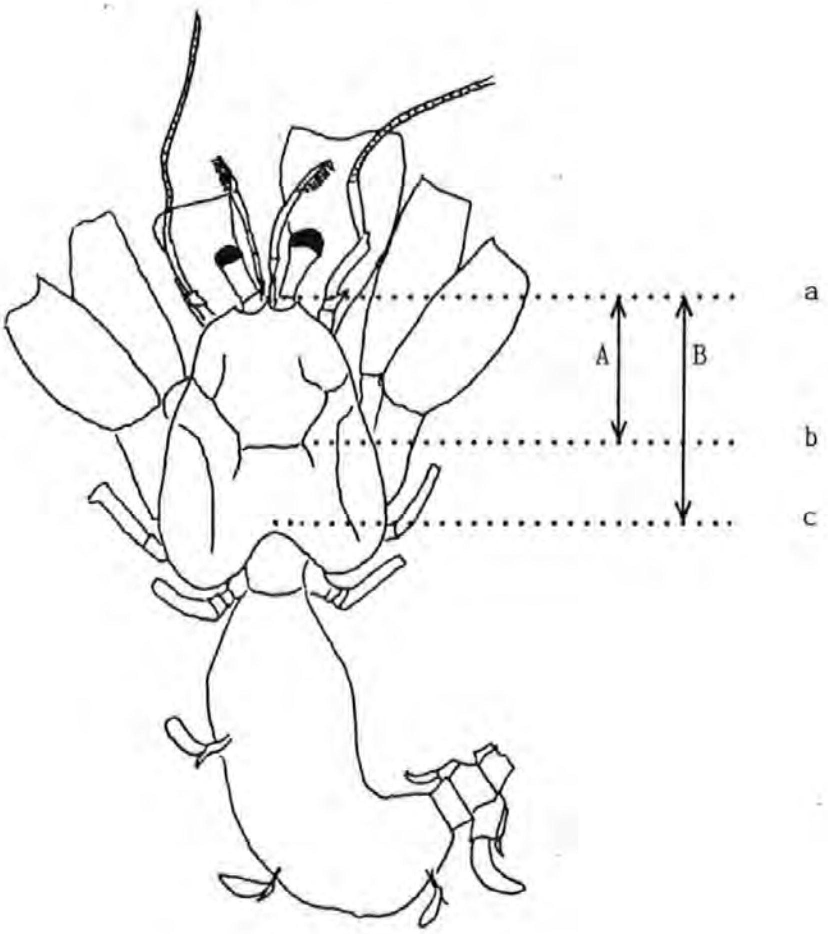
Visual searching of the shore was employed in order to collect crabs for this investigation since it provided the most efficient and rapid method of collecting large numbers of animals of a wide range of sizes. The resulting catch was not found to be dominated by either sex, and individuals were in shells of widely differing qualities. The crabs (n=72, collected after 30 minutes searching) were taken to the laboratory where they were isolated in broad, shallow, tanks of well-aerated sea water. These tanks were maintained at the temperature and photoperiod of the shore at the time. The crabs were used individually for shell choice tests and were given free access to empty shells covering a wide range of sizes and species. Each animal had access (in addition to its original shell) to at least 10 shells of each of the commonest 10 species recorded from the shore (in Table 3.6). These shells were chosen subjectively to cover a size range that extended from too large to too small to be practicable, but always with a majority that seemed close enough to the original shell to be thought quite suitable. All of the shells were numbered with enamel paint to allow individual recognition. Each crab was observed as regularly as possible over a period of 6 days - a time that Vance (1972b) considered more than adequate to enable a hermit to make its choice from a range of shells on offer. It was hoped to determine the quality of the shell finally selected by each individual using the Shell Adequacy Index of Vance (1972a), taking the most adequate shell as the one occupied by the crab for the largest number of observation periods. However, since it was found that most of the animals in this experiment had selected a different shell at each observation, it was decided to use the shell occupied at the final observation (i.e. after 6 days) to represent the "preferred" shell for all animals.

The crabs were removed from their shells by heating the shell apex with a soldering iron, and both the crab and the shell were measured for a number of parameters. The crabs were blotted dry and weighed on a Mettler P165 top-pan balance accurate to 0.1mg. The total body length was found to be particularly difficult to determine with accuracy since the abdomen of the hermit crab is coiled and flexible. Equally, measurements of limbs (although suggested as accurate estimates of crab size by some authors e.g. Neil, 1985; Perkins, 1985) were not considered suitable since some animals had limbs missing and a number of others were found to be in the process of regenerating them. Crab size was therefore measured using the dimension suggested by Markham (1968) of the anterior hard portion of the cephalothorax (the "shield"). This extends from the tip of the rostrum to the cervical suture (Figure 3.1) and has the advantage over the more traditional measure of the total cephalothorax length (the "carapace" length) favoured by earlier authors (e.g. Pike and Williamson, 1959) of not flexing and hence distorting during handling. Equally, since the shield is easily preserved this method has the added advantage in that the structure can be measured after moulting to prevent stress to the animal under study. The values of shield and carapace length were found to be highly correlated ($r=0.979$, $n=189$) and a conversion factor was calculated in order to determine the carapace value from that of a shield if necessary (carapace = 1.59 shield - 0.0273; Figure 3.2).

The shell measurements of total length and width, and aperture length and width (dimensions explained in Figure 3.3) were made with vernier callipers accurate to o.1mm. Weight was measured with the Mettler balance after the shells had been oven-dried at 110°C for 24 hours (to eliminate the problem of the different water holding

Figure 3.1

PARAMETERS USED IN THE MEASUREMENT OF PAGURUS BERNHARDUS



A = anterior hard portion of cephalothorax (SHIELD).
B = entire cephalothorax (CARAPACE).

a = rostrum .
b = cervical suture.
c = posterior notch (posterior margin of cephalothorax).

Figure 3.2

Regression of crab carapace length on crab shield length:

carapace = 1.59 shield - 0.0273 (n = 189)

Figure 3.2

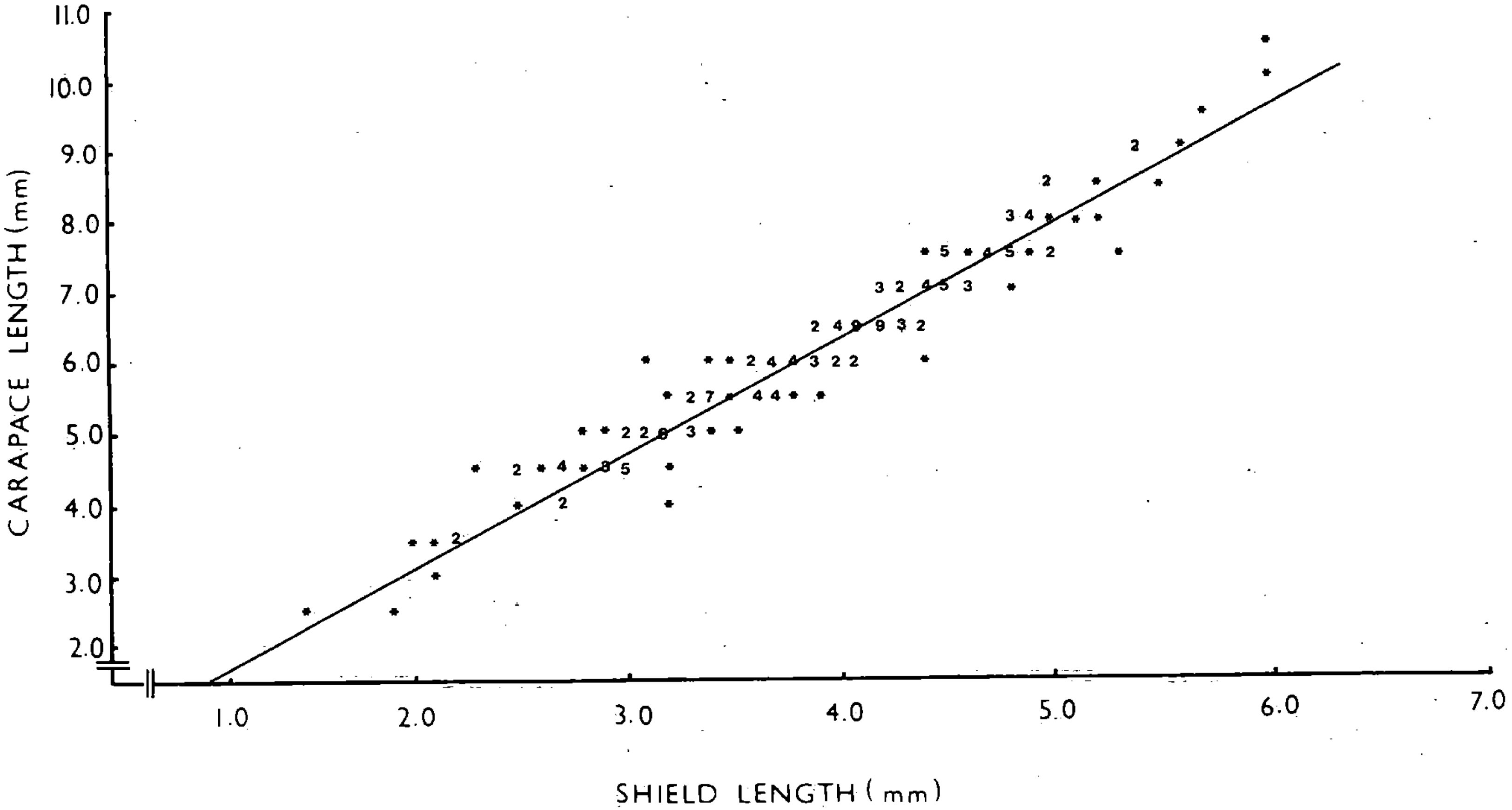
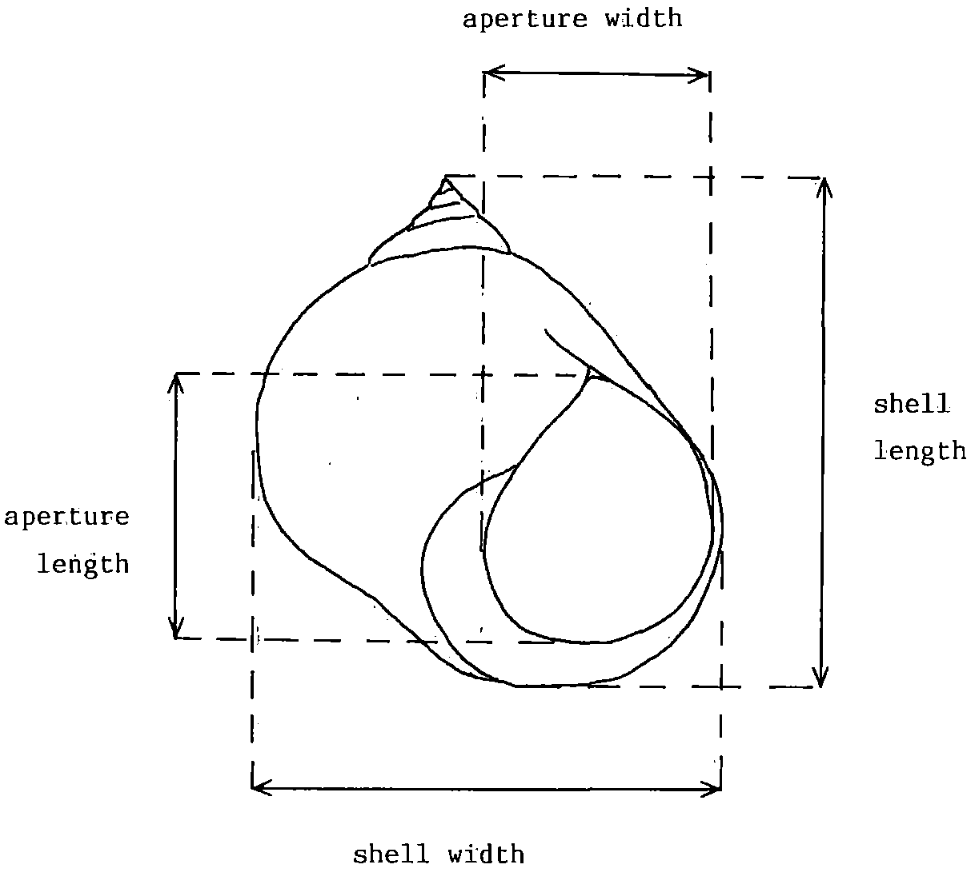

CARAPACE LENGTH (mm)
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
SHIELD LENGTH (mm)

Figure 3.3

PARAMETERS USED IN THE MEASUREMENT OF SHELLS



capacities of their various architectures). Volume was calculated by filling the dried shell (after weighing) with water from a microburette and recording the volume needed to just form a meniscus over the aperture. Gently "tapping" the shell as it was filled ensured that no air bubbles formed which may have distorted the readings.

Crab parameters of weight and shield length were then correlated for each individual with the parameters of length, width, aperture width, volume, and weight of the preferred shell. Aperture length was not found to be a useful parameter since the shells of Gibbula spp. have an almost circular aperture; the widest part of this was therefore taken as the aperture "width". The combination offering the highest correlation was then used to determine the S.A.I. - a measure of the theoretical adequacy of any shell to a given crab. A regression of the chosen crab and shell parameters was first employed in order to estimate the size of crab which would find any given shell to be an "adequate" fit: this value, when divided by the size of the animal actually in the shell, gave the adequacy of the shell to its occupant. The relationship:

$$\text{S.A.I.} = \frac{\text{size of crab for which shell is of preferred size}}{\text{actual size of crab in shell}}$$

gives three values for the interpretation of adequacy:

S.A.I. of 1 = crab is in shell that is adequate

S.A.I. of >1 = shell is larger than preferred

S.A.I. of <1 = shell is smaller than preferred.

The original shells occupied by the 72 crabs were then compared with their "preferred" shells in order to determine whether in each case a "better" shell had, in fact, been selected, and to estimate whether the animals had originally been in shells that could be considered "adequate".

As the experiment proceeded, however, it became clear that the assumptions behind the mathematical index made its validity more and more questionable. It was therefore decided to derive and test an alternative, more subjective, index based upon the apparent quality of fit of the shells involved. This aimed purely to identify whether or not a shell offered protection for the crab's body - a major justification for shell choice. Damage and the presence of epizoic "growths" were not considered to necessarily render a shell uninhabitable, but to perhaps only make it more difficult to manoeuvre. Four principle grades of quality were recognised:

1. The entire crab is able to withdraw into the shell such that no part of its body is visible from the outside. Such a shell offers excellent protection against "winkling out" and minimises the consequences of breakage to the lip, but it may be awkward to carry. A shell of this grade would generally be considered to be too large.

2. The animal's chelae may be visible when the rest of the body is withdrawn, but the remainder of the body is well protected. Such a shell would be easier to carry and would be, broadly speaking, "adequate".

3. The animal's chelae break the plane of the aperture when the body is withdrawn such that it appears cramped and may be in danger of being pulled out by another crab. Such a shell would still, however, be "adequate" for physical protection and for brood space.

4. The entire outer faces of the chelae are outside the aperture, together with part of the shield, the eyestalks, and the antennae. Although an apparently vulnerable position, no crab larger than the occupant is likely to find the shell suitable thus the risk of being pulled out would probably be small under normal circumstances. Such a shell is clearly too small, however, and offers the minimal protection to the vulnerable anterior part of the body.

In general, categories 2 and 3 may be regarded as "adequate" and are treated together in the results and discussion to follow.

Subjective Index values were given to both the original and the preferred shells so that the nature of the exchanges made by the crabs in the experiment could be compared using the two indices.

In order to examine whether particular shell species preferences existed among the members of the Battery Rocks population of P.bernhardus, 1000 living gastropods (excluding limpets) were first collected at random from the shore. The collection was from both rock pools and open rock surfaces and was made along a transect extending from the approximate high water mark to low water on a typical spring tide which exposed most of the shore. The shells were identified and recorded by species. An equal number of crabs were also collected from the shore at the same time, and their shells were identified for comparison.

3.3 RESULTS

The data referred to in these results are presented in full in Appendix III.

The highest correlation between crab and shell parameters was found to be between crab shield length and shell width (Table 3.1). Accordingly, these measurements were used to estimate shell adequacy employing the index of Vance (1972a). The size of crab which should find a shell of a given width to be optimal was found from the relationship:

shield = 0.262 shell width - 0.089

(Figure 3.4: ANOVA, F = 3.734, $p < 0.001$).

The S.A.I. values obtained for both the original and the preferred shells were then compared with the values obtained for the same shells with the subjective index. The nine possible types of exchanges are summarised in Table 3.2, which reveals considerable differences in emphasis between the two indices. The S.A.I., for example, suggests that only some 7% (n=5) of the shells originally occupied by the Battery Rocks crabs were "adequate" (categories 1,2, and 3) - a poor reflection on the state of the shell resource in this habitat. The Subjective Index, however, which relies upon the apparent quality of fit of each crab in its chosen shell, would put this figure closer to 80.5% (n=58).

In no categories do the two indices overlap and, perhaps most significantly, the fact that almost 60% (n=43, choice code 2) of the exchanges made were from originally adequate shells into equally adequate ones, is totally overlooked by the mathematical index. The unpredictable aspect of shell exchanging is emphasised by examining the shells occupied by one individual selected at random and observed over a period of 8 days (Table 3.3). This non-ovigerous female

Table 3.1

Crab and shell parameters: correlation coefficients for the calculation of shell adequacy

shell parameters: crab parameters:	width	volume	length	weight	aperture width
shield length	0.725	0.605	0.659	0.651	0.376
weight	0.706	0.717	0.571	0.548	0.333

Figure 3.4

Regression of crab shield length on shell width:

$\text{shield length} = 0.262\ \text{shell width} - 0.089\ (n = 72)$

Figure 3.4

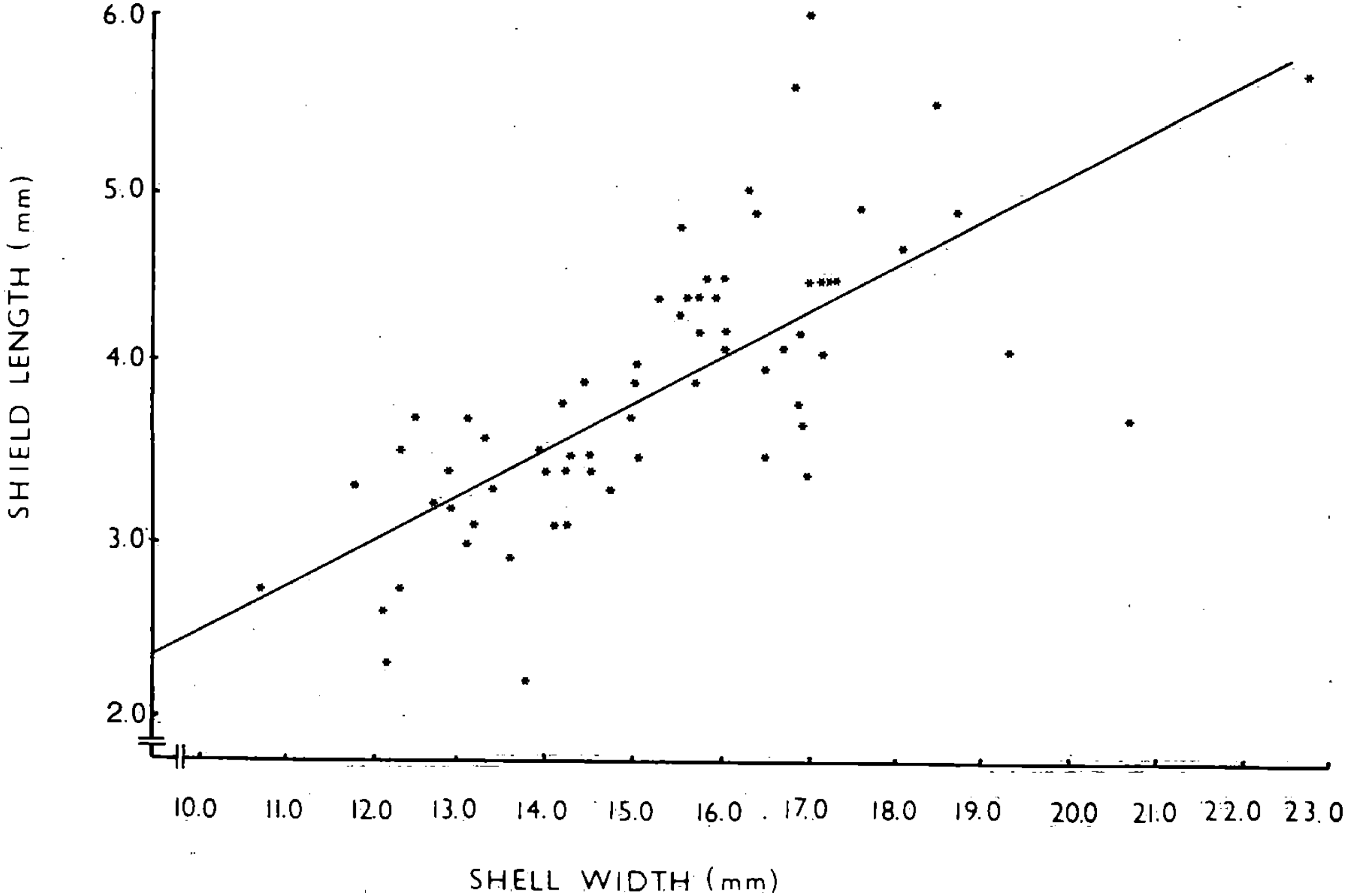

SHIELD LENGTH (mm)
6.0
5.0
4.0
3.0
2.0
10.0
11.0
12.0
13.0
14.0
15.0
16.0
17.0
18.0
19.0
20.0
21.0
22.0
23.0
SHELL WIDTH (mm)

Table 3.2

A comparison between the mathematically derived Shell Adequacy Index (Vance, 1972a) and a Subjective Index to examine the nature of shell exchanges made by *Pagurus bernhardus*.

Nature of exchange made		choice code number	number (%) making change	
original shell	new shell		according to S.A.I	according to S.I.
adequate	larger	1	2 (3)	6 (8)
	same size	2		43 (60)
	smaller	3	2 (3)	5 (7)
	(same shell)	2+	1 (1)	4 (5)
		total	5 (7)	58 (80.5)
too large	larger	4	12 (17)	
	same size	5	1 (1)	2 (3)
	smaller*	6	17 (24)	7 (10)
	(same shell)	5+	1 (1)	
		total	31 (43)	9 (13)
too small	larger*	7	22 (30)	5 (7)
	same size	8		
	smaller	9	12 (17)	
	(same shell)	8+	2 (3)	
		total	36 (50)	5 (7)

* denotes that the exchange made was an improvement.

Table 3.3

A demonstration of the inconsistency of shell selection behaviour: the shell exchanges made by one individual Pagurus bernhardus (a non-ovigerous female, shield length 3.8mm) over a period of 8 days (192 hours).

Time from start of observation (hours)	shell species occupied	width of occupied shell (mm)	S.A.I.
0	Littorina littorea	15.4	1.03
* 2	Nucella lapillus	15.6	1.05
3	L.littorea	13.6	0.92
10	N.lapillus	17.9	1.21
* 16	L.littorea	16.4	1.10
19	L.littorea	14.0	0.95
27	L.littorea	14.6	0.97
* 33	L.littorea	16.4	1.10
64	L.littorea	14.3	0.95
* 91	N.lapillus	15.6	1.05
108	Gibbula umbilicalis	13.6	0.92
126	N.lapillus	15.0	1.00
174	L.littorea	17.8	1.21
188	L.littorea	14.8	1.00
190	L.littorea	16.4	1.04
192	N.lapillus	16.9	1.13

* indicates that the same shell was re-occupied.

routinely exchanged shells throughout this period with no obvious pattern of improvement being made. This female was typical of all of the crabs observed in this study - a fact which forms the basis of the discussion to follow.

The main injuries observed in members of the Battery Rocks population are summarised in Table 3.4. The damage to chelae suffered by individual crabs clearly suggests that shell fighting is occurring between members of this population - but the relatively small number of injuries overall would seem to imply that the phenomenon is not widespread. The reason for this may be that the overall level of adequacy of the shells available to the population is quite high. This may be concluded from the value of 80.5% of shells as adequate obtained from the shell swapping experiments (Table 3.2), and the value of 62% obtained by applying the Subjective Index to crabs collected randomly from the shore (Table 3.5: combining the totals from categories 2 and 3).

The question of shell species preferences was examined by comparing the shell species most common on the shore (Table 3.6) with the species most commonly occupied by P.bernhardus from the same area (Table 3.7). No significant difference was found between the proportion of shell species represented on the Battery Rocks and the proportion of shell species occupied by P.bernhardus ($\chi^2 = 4.61$; d.f. = 8; $p > 0.05$). Thus, the relationship between the occupation of L.littorea and the abundance of this species on the shore does not suggest that shell "preferences" need to be invoked in this case.

Table 3.4

A summary of the typical injuries found to have been sustained by a random selection of *Pagurus bernhardus* from the Battery Rocks.

Total number of crabs examined for injuries	465	
Number with right chela missing or regenerating	32	
Number with left chela missing or regenerating	14	
Number with both chelae missing or regenerating	12	
Number with other combinations of limbs missing	15	
Total number (%) showing injuries	73	(16)

Table 3.5

The adequacy of the shell resource on the Battery Rocks - as described by the Subjective Index of shell quality.

shell species occupied by crabs	number collected	shell qualities			
		1 (too large)	2 (adequate)	3	4 (too small)
L.littorea	34	4	7	9	14
N.lapillus	23	11	7	2	3
Gibbula spp.	28	2	21	4	1
Hinia spp.	12			10	2
L.obtusata	2			2	
Calliostoma zizyphinum	1	1			
TOTAL	100	18	35	27	20

Table 3.6

The commonest species of gastropods (excluding limpets) represented on the Battery Rocks - determined from a random sample of 1000 individuals.

species	number recovered in a single random sample	percentage of total
Littorina littorea	706	70.6
Gibbula spp.	160	16.0
Nucella lapillus	74	7.4
L.saxatilis agg.	22	2.2
Monodonta lineata	18	1.8
Hinia incrassata	11	1.1
H.reticulata	4	0.4
L.obtusata/*L.mariae*	3	0.3
Calliostoma zizyphinum	2	0.2
TOTAL	1000	100

Table 3.7

The commonest species of gastropod shell found to be occupied by Pagurus bernhardus on the Battery Rocks - determined from a random sample of 1000 individuals.

species	number recovered in a single random sample	percentage of total
Littorina littorea	627	62.7
Gibbula spp.	201	20.1
Nucella lapillus	99	9.9
L.saxatilis agg.	24	2.4
Hinia incrassata	18	1.8
Monodonta lineata	14	1.4
L.obtusata/L.mariae	9	0.9
H. reticulata	5	0.5
Ocenebra erinacea	2	0.2
Calliostoma zizyphinum	1	0.1
TOTAL	1000	100

3.4 DISCUSSION

From the results of the experiments presented in this section it would seem that the traditional determination of shell adequacy is an exercise that suffers from having its basic philosophy severely flawed. All methods whether mathematical or purely subjective rely, as a criterion for adequacy, upon a crab that is given a choice between two shells coming to occupy the one that suits it best. Whilst inherently logical, this assumption none-the-less appears to be a serious oversimplification. Individuals in laboratory tanks can be observed to swap shells across a broad range of adequacy values on a random basis, and in the majority of these exchanges no predictable pattern of improvement seems to be obtained - as demonstrated by the individual in Table 3.3. Far from being satisfied with having found the best possible shell after 4-6 days as implied by Vance (1972b) in his original work on the Shell Adequacy Index, members of the Battery Rocks population continue to exchange quite freely throughout their captivity, however prolonged this may be. In one case, an individual studied in order to measure its growth increments was still routinely investigating both new and familiar shells after more than 300 days. In this time shells apparently quite suitable in size and quality were rejected in favour of broken ones, and shells dismissed on one occasion would be occupied only days later. This individual was quite typical of the animals studied during this investigation, and when returned to the shore it was observed over several hours to continue to explore new shells as available. This pattern of behaviour was consistently observed with animals in the field and cannot be viewed as a laboratory phenomenon.

Thus it may be concluded that while indices such as the S.A.I. offer apparently simple and easily determined estimates of shell quality, the "preferences" that they actually predict may be at best unreliable and at worst may even confuse an understanding of shell quality. The behaviour employed by a crab in selecting a shell is likely to be highly plastic, with a number of parameters being assessed and with no single one necessarily determining the overall suitability of any one shell (Mitchell, 1976; Kuris and Brody, 1976). Indeed, whatever parameters are chosen at any one time are likely to change as the animal grows and as its requirements alter (Hazlett, 1981a). Rigorous analysis of the mathematics behind many of these indices has even led to the suggestion (Gilchrist, 1984) that their relevance to the real situation has tended to become largely obscured, and that in consequence many of the relationships suggested for quantifying shell suitability may be nothing more than "analytical artifacts".

Reports of particular shell species preferences determined on the basis of similar trials must therefore also be regarded as questionable. The enormously wide range of shell species that are found to be occupied by hermits, and the fact that individuals will make use of any suitably sized shells in aquarium studies (however exotic they may be), all argue against there being specific requirements that must be met. Crabs have been kept in straight tubes and in replicas made of glass (Elmhirst, 1947; Brightwell, 1951a, 1951b, 1953; Coffin, 1960) and have been observed in some habitats in fragments of discarded and broken brachyuran exoskeletons (Fotheringham, 1976b) and even in bottle caps, fuses, and parts of beer bottles (Gilchrist and Abele, 1984). In the population under study the species of shell occupied by the majority of the crabs (Littorina littorea - 60% in Table 3.7) also happens to be the commonest species on the shore. However, when given free access to a wide range of shell species, the crabs do not choose this one exclusively (original and preferred shell choices are listed in Appendix III). This suggests that L.littorea is not necessarily the "preferred" species. The large numbers of L.littorea shells on this shore would appear to represent a healthy and renewable resource for the hermits, and a wide range of sizes (up to perhaps 3.5cm in length) is typical at all times of the year. While it has been suggested that L.littorea may live for perhaps 20 years in an aquarium (Woodward, 1913), it has been noted that on exposed coasts the longevity is markedly reduced (Daguzan, 1976), with the shells of some 2.0-2.5cm in length representing animals perhaps 3-4 years old at death (Moore, 1937). Since these shells are particularly tough (of 100 randomly selected broken shells picked up in a 30 minute period only 18 were of this species - the great majority were of the much thinner Gibbula spp.) their numbers and their rate of turnover will ensure that they will inevitably become the predominant source of potential new homes for the hermit crabs on this shore. This implies, therefore, that the range of shells occupied by hermit crabs is likely to reflect the recruitment of shells into the habitat (which will depend upon their abundance) and their subsequent survivability (a property of their physical toughness) much more than any specific preferences on the part of the crabs. Thus the hypothesis that shell preferences may exist within members of the Battery Rocks population was not upheld.

Thus it would seem that many of the results of shell choice experiments are flawed by being unnatural, and many shell species "preferences" merely reflect the occupation of those most abundant on the shore anyway. There must, therefore, be at least the suggestion that shell investigation in hermit crabs is little more than a genetically programmed drive to investigate any suitable object in the environment that just may lead to an improvement in an essential resource - which, by its borrowed nature, will almost always be capable of improvement. Certainly the less suitable a shell appears to be (i.e. if broken or partially occluded by detritus or by growths of other organisms) then the more effort a crab appears to put into the search for a replacement and the more ground it tends to cover in its searching (Reese, 1963; Neil and Elwood, 1986). The number of shell swaps that can be seen to occur when all of the shells available are of approximately the same apparently high quality clearly implies that shell swapping is a routine operation, and does not in itself indicate the occupation of a suboptimal shell. The animals are clearly aware of the suboptimal nature of damaged shells or those that are too large or too small, and can recognise both the necessity and opportunity to find another. The inevitability of such behaviour under the circumstances, and the enormous range of reasons that may determine the suitability of a particular shell for an individual's immediate requirements, argue most forcefully for a "gestalt" approach to shell selection, and stress the consequent difficulty that exists with trying to use any mathematical index of shell quality. In consequence, it may be that the more subjective approach described here (similar to that used by Abrams, 1978, for the semi-terrestrial hermit crab Coenobita compressus) may actually be more biologically meaningful for classifying the shell occupied by hermit crabs. Equally, since the mathematical index takes no note of the quality of the original shells occupied, the true nature of the shell resource available to the crabs is not revealed by this method. The subjective index, however, can allow a rapid estimate of quality to be obtained of both the original shell and of all subsequent swaps as they are made. "Judgements" of adequacy are still employed - but no alternative method successfully avoids this. The greatest weakness of the mathematical indices such as the S.A.I. is therefore seen as the implicit assumption that all of the exchanges made are improvements. That this is not necessarily so is clearly demonstrated here. The subjective index is therefore proposed as a means of overcoming these limitations.

The members of the population which were subsequently classified using the subjective index (Table 3.5) reveal that although the shells available to them seem on the whole to be adequate for their needs (some 62% occupying shells in categories 2 or 3 of the index), a proportion (approximately 20%) apparently occupy shells that are too small. It is also of note that the proportion of animals bearing the types of injuries typically sustained in "shell fighting" (16%: Table 3.4) exceed the figure of around 10% considered by Scully (1979) to indicate a population with a "suboptimal level of resource availability". These indicators taken together emphasise that a point must eventually be reached with this, as with any littoral population of hermits, where some members at least will become "shell-limited" - reaching the limits of adequacy that can be provided by the shells on offer. These animals will therefore need to seek a larger size range of shells than is typical of the littoral zone.

A study of the long-term consequences of shell-limitation upon growth and longevity in <u>Pagurus bernhardus</u> forms the basis of the next chapter.

CHAPTER 4

THE INFLUENCE OF SHELL SIZE ON HERMIT CRAB GROWTH AND LONGEVITY

4.1 INTRODUCTION

Although a number of studies relating shell size and crab size appear in the literature (e.g. Markham, 1968; Fotheringham, 1976a, 1976c), these works have tended to concentrate more upon the patterns of growth displayed by individuals than upon the long-term consequences of shell-limitation to entire populations. This chapter is concerned with the fate of the largest members of an intertidal population of hermit crabs which have outgrown the shells typical of this zone.

Pagurus bernhardus was found to be the commonest hermit crab on all of the accessible shores in Mount's Bay during the study period, and it was characteristic that the specimens located were all within a broadly comparable size range. The mean shield length of Pagurus bernhardus on the Battery Rocks was 3.9mm (S.D. ± 0.8mm, n=440) with males typically larger than females (males 4.1 ± 0.9mm, range 1.5 - 6.4mm, n=256; females 3.7 ± 0.7mm, range 1.7 - 5.4mm, n=184). The measurements for these littoral hermit crabs are therefore noteably less than are those reported for individuals of this species trawled from deep water, where shield lengths in excess of 20mm (i.e. with carapace lengths of 30-40mm) are apparently common (Selbie, 1921). No individuals approaching these latter dimensions were recorded anywhere in Mount's Bay in the period of this study. Detailed searches for the larger forms, involving examining the catches of commercial trawls from the bay, and using SCUBA techniques in the coastal strip (up to a horizontal distance from the shore of at least 500m), also revealed that no shells of a size which would be suitable for such individuals seemed to occur in the area. These would have included the shells of adult whelks such as Buccinum undatum L. and, perhaps, Neptunea antiqua (L.), both of which may exceed lengths of 8cm. Equally, no egg capsules, shells or shell fragments of these species were found cast up despite detailed searches of strand-lines and gullies throughout the study period.

Thus, the question of the future growth potentials of the largest crabs in this littoral population was considered since the largest shells to which they have access would not appear to exceed some 35mm in length (the size of the largest shell recovered during this study - a shell of L.littorea). Such crabs would, therefore , be shell-limited in the sense that they would seem to be denied the possibility of realising their full growth potential with the shell resource available to them.

A series of experiments were designed to establish the long-term consequences of shell-limitation upon the growth and longevity of individuals under such circumstances. It was also hoped to discover what strategies, if any, may have evolved to maximise the fitness of individuals facing this problem of natural shell-limitation.

The unpredictable nature of crustacean growth was considered as part of this work, and the equation proposed by Markham (1968) in order to describe hermit crab growth was examined for its applicability to a population such as this.

4.2 MATERIALS AND METHODS

Forty crabs were collected at random by visual search from the shore at Battery Rocks. The individuals represented a range of sizes and occupied many different types of shells. The size of the sample was dictated by the availability of aquarium tanks needed to house them. This experimental group was then randomly divided into two equal sub-groups. The animals were extracted from their shells by heating the apex with a soldering iron, and the shield length of each individual was measured using an ocular micrometer attached to a binocular microscope. Each crab was allowed to re-enter its shell after being measured. No significant differences existed between the mean lengths of the two groups of animals ($t = 0.269, p > 0.05$; Table 4.1). One group of crabs (designated group "A") was provided with access to shells larger than their own, including a number larger than any found in the area. The other group (group "B") was kept shell-limited and denied access to any shells larger in any dimension than those known for the area. The large shells were gathered from a number of sources and included Nucella lapillus with lengths of up to 51mm (collected by Dr J.H.Crothers from the shore at Porlock in Somerset), tropical species purchased from local curio shops, and even shells of the garden snail Helix aspersa (which proved particularly popular!).

The crabs were housed in shallow plastic aquaria, measuring some 45cm x 30cm, each of which was divided by fine mesh into 9 compartments of 15cm x 10cm. In each tank only the four corner compartments were used, each housing a single crab, such that no individual was close enough to make contact with any other. The central compartment in each tank was used to position an aerator, so as to provide all compartments with equal turbulence and oxygenation.

Thus, 10 tanks in all were used to house the crabs, and individuals were randomly allocated between them from each of the two groups. Each tank was filled with natural seawater maintained at 35‰, and the experiment was conducted in a constant environment with the water temperature maintained at the mean value for the area i.e. 12 °C, and the photoperiod maintained at a neutral 12L:12D. Shells were allocated such that each member of group A had access to its original shell plus 5-10 others larger than this in at least one dimension. Members of group B were given access to an equal number of shells, but only up to and not exceeding lengths of 35mm. In the case of the members of group A the shells were exchanged after a moult had occurred such that each crab always had shells in its compartment that were larger than the one it then occupied. No exchanges in excess of 35mm were made for members of group B. Exuviae were collected after ecdysis and the length of the shield was measured. Exuviae were returned to the crabs after measuring to enable the animals to extract from them the minerals that appear essential for successful hardening of the new exoskeleton (Elmhirst, 1947). The experiment was continued until the last individual had died and none were replaced after the investigation had begun. The shield lengths measured after each moult, the growth increments between each moult, and the intermoult durations, were recorded for each individual. In addition, the total longevity of each animal was noted - taking the start of the experiment as "day 1" - in order that the mean longevities under each regime could be compared.

To investigate the reliability of the growth equation suggested by Markham (1968), calculations were also made of the predicted number of moults that each crab should have undergone to reach its final size, for comparison with the actual number of moults observed. The growth equation is derived from Kurata (1962) and is given as:

$$L_s = -0.36 + 1.36\,(1.11)^s$$

where L_s = shield length, s = instar number, and the constants are derived from Kurata (1962) and Pike and Williamson (1959).

4.3 RESULTS

The measurements relating the effects of shell limitation to the growth and longevity of Pagurus bernhardus are presented in full in Appendix IV.

The main trends demonstrated by the data are summarised in Table 4.1, from which it can be seen that the sizes, the longevities, the intermoult durations, and the growth increments of the experimentally shell-limited crabs were all significantly reduced when compared with the non-limited crabs.

A comparison between the number of moults predicted on the basis of the growth equation, and the number of moults actually observed under each regime (Table 4.2) suggests that the equation does produce an acceptable estimate of instars for a population of crabs with access to the large shells essential for unrestricted growth. For a shell-limited population, however, represented by group B, the reliability of such an equation can be seen to be greatly reduced.

Table 4.1

The effects of shell size on the growth and longevity of two experimental groups of *Pagurus bernhardus*.

	Mean shield length at start (mm ± S.D.)	mean shield length at end (mm ± S.D.)	mean longevity under each regime (days ± S.D.)	mean intermoult duration (days ± S.D.)	mean growth increment (% ± S.D.)	number dying during ecdysis n (%)
Group A (not shell-limited)	4.49 ± 0.82	6.91 ± 1.63	182.35 ± 94.63	33.89 ± 16.92	11.09 ± 3.77	2 (10)
Group B (shell-limited)	4.55 ± 0.58	5.31 ± 0.49	72.90 ± 36.78	26.58 ± 11.64	7.74 ± 5.46	10 (50)
variance ratio (Bailey, 1959)	$F_{19,19} = 1.999$	$F_{19,19} = 11.066$	$F_{19,19} = 6.620$	$F_{79,42} = 2.113$	$F_{42,79} = 2.097$	
	$t = 0.269$	$d = 4.20$	$d = 4.82$	$d = 2.818$	$d = 3.59$	
	d.f. = 38	d.f. = 22	d.f. = 25	d.f. = 114	d.f. = 64	
	$p > 0.05$	$p < 0.01$	$p < 0.001$	$p < 0.01$	$p < 0.001$	

Table 4.2

A comparison between the mean number of moults predicted by the growth equation of Markham (1968) and the actual number observed for two experimental groups of crabs. (mean values ± S.D.)

Group	mean number of predicted moults	mean number of observed moults	t
A (not shell-limited)	3.95 ± 1.43	4.00 ± 1.45	0.110 d.f.= 38 $p > 0.05$
B (shell-limited)	1.50 ± 0.86	2.39 ± 1.14	2.641 d.f.= 34 $p < 0.05$

4.4 DISCUSSION

Since hermit crabs have evolved to protect their bodies within rigid structures which they do not themselves manufacture, it is inevitable that the quality of the available gastropod shell resource will influence hermit crab growth. Growth in crustaceans is generally considered to be an unpredictable phenomenon. Moult increments tend to vary not only between different individuals of the same age and initial size, but even between moults with the same animal (Hartnoll, 1982). Thus, predicting the growth potential of any crab is difficult - doing so for a hermit, with the added complication of shell-limitation, can be seen to be quite unrealistic. The clear implication of these experimental results is that the eventual size reached by a particular hermit may bear no relationship to the number of moults it has undergone or to its age at the time. Such a situation can only serve to reduce the relevance of growth equations when describing real populations - i.e. those where the individual histories of the members are unknown - or populations whose shell resources have not been rigorously scrutinised.

The results of these experiments show that significant limitations are imposed upon crab growth if the available shells are too small. Members of the shell-limited Group B attained smaller final lengths than did those in Group A, and underwent fewer moults in total. The growth increments of the shell-limited crabs were also significantly reduced, and one individual actually became smaller after a moult than it was before. However, the most serious threat which might be predicted from the experimental results is likely to be the significantly reduced longevity that a shell-limited individual or members of a shell-limited population may have when compared with otherwise similar but non-limited individuals elsewhere. Shell-limitation may be regarded as an inevitable problem for the largest members of any littoral hermit crab population, since there will generally be more small gastropod shells available on a shore than large ones (Scully, 1983). A critical point will, therefore, be reached when the animals approach the size limit for the largest shell species common on the shore - typically those of L.littorea and N.lapillus. These species may overlap in range with larger sublittoral forms, such as Buccinum undatum, as is suggested for example in the deep sheltered waters off Denmark (Jensen and Bender, 1973), but the smaller Buccinum (i.e. shell lengths of some 15-30mm) are not common in the littoral zone and would probably be too fragile to survive on any but the most sheltered shores. At some point, therefore, hermits in this situation will have to adopt a strategy that will bring them into contact with the larger shells of the sublittoral.

One obvious strategy would involve the animals migrating into deeper water, perhaps at certain times of the year such as winter, when a distinct stimulus would be available to allow for the co-ordinated migration of the entire population (e.g. Rebach, 1974). Studies on shell-limitation however (e.g. Fotheringham, 1975; McLean, 1983; Raimondi and Lively, 1986) have largely ignored the consequences that must exist for those populations that do not migrate to deeper waters or which inhabit areas devoid of large gastropod species. It is this latter situation which appears to exist for the Battery Rocks population, and which imposes upon them a form of "qualitative" shell-limitation - severely restricting their potential to exceed shield lengths of some 6-7mm (which they are clearly capable of doing if provided with larger shells).

Shell-limitation clearly places long-term restrictions on growth and longevity, but in addition a number of short-term problems will also influence the quality of life for affected individuals. Protection from predators will be reduced, the chances of being "winkled out" will increase (Conover, 1978), success in agonistic encounters will tend to be reduced (Childress, 1972), reproductive success will be affected (since only a small clutch can be carried - Fotheringham, 1976b, 1976c), and the problems of water loss will increase if the animal is exposed involuntarily on an open rock surface as the tide falls (Herreid, 1969). The increase in both individual crab dimensions (Drapkin, 1963) and population densities (Vance, 1972b; Spight, 1977) which may follow local increases in gastropod shell numbers or sizes only serve to reinforce the influence that shell-limitation must have on the potential development of entire populations.

The strategy which enables hermit crabs to make the maximum use of the shell resource available to them is investigated in the context of movement patterns and migration (Chapter 6). The implication of the reduced longevity affecting shell-limited populations will be taken further in the next chapter in the context of the attainment of sexual maturity.

CHAPTER 5

THE NATURE, INITIATION, AND CO-ORDINATION OF REPRODUCTION IN *PAGURUS BERNHARDUS*

5.1 INTRODUCTION

Although reproduction has been studied in a number of hermit crabs (e.g. Pike and Williamson, 1959; Hazlett, 1968b), sufficient variation can be noted both between and within species to suggest that further detailed study is needed of this aspect of their biology. This is particularly true if hermit crab life history strategies are to be understood more clearly. Between them hermit crabs display almost all of the known patterns of (sexual) reproductive behaviour - including seasonal breeding and continuous breeding (Hazlett, 1981a), breeding before moulting and breeding after moulting (Hazlett, 1968a), breeding while females are still ovigerous or after larval release (Coffin, 1960), and breeding where single or multiple copulations are the rule (Hazlett, 1972b).

Particular areas requiring clarification for most species include the determination of the breeding period(s) for littoral populations at different latitudes, the identification of the stimuli that initiate and co-ordinate breeding in different populations, the establishment of the gestation periods for broods, and the clarification of the number of broods that can be produced while a female is reproductively active. These aspects of reproductive biology were investigated for a littoral population of Pagurus bernhardus.

The stimuli thought to initiate breeding in hermit crabs have been variously suggested (e.g. Orton, 1920; Reese, 1963; Ajmal Khan and Natarajan, 1977) as being photoperiod, sea temperature, the difference between sea temperature and air temperature, salinity, and food availability for both adults and larvae. It was, therefore, considered that each of these stimuli should be investigated both individually and, as far as possible, in combination, to determine their influence on the breeding of this littoral population of P.bernhardus. These stimuli were investigated using a range of artificial environmental regimes created under controlled laboratory conditions.

It was also hoped to discover whether any long-term or local ecological factors may have an influence on the population, perhaps thereby helping to explain some of the considerable differences in breeding periods noted for this species in the literature. The influence of such conditions has been suggested by several authors (e.g. Knudsen, 1964; Reese, 1968), emphasising the interaction that a number of separate factors may have in controlling reproductive behaviour.

Manipulation of the environmental conditions was employed in order to determine the number of broods that could be produced by a single female.

5.2 THE REPRODUCTIVE CYCLE OF PAGURUS BERNHARDUS ON THE BATTERY ROCKS.

5.2.1 MATERIALS AND METHODS.

Preliminary examination of the Battery Rocks habitat had revealed that hermit crabs were particularly abundant in the broad shallow pools towards the bottom of the shore. Individuals were collected on each spring tide over a three year period to determine whether breeding in this population was periodic or continuous, and to detect if it was synchronous (i.e. with all females at the same stage at the same time) or asynchronous. Ovigerous females were maintained in laboratory tanks in order to establish the gestation periods of their broods, and observations were made on the progress of egg development together with the cycle of maturity followed by the ovaries. Classifications of both patterns of development were derived in order to make comparisons between different females within the population.

To ensure that collections were as comparable as possible from one period to the next visual searching was employed, with a set time period of some 30 minutes being used on each occasion. In this way approximately the same amount of ground was covered in the same way each time, such that no bias seemed to be introduced into the way that the collections were made. Baiting (as recommended by Gilchrist and Abele, 1984) was not employed after it was found that hermit crabs on this shore did not in general respond to baits left in pools, and when it was seen that no additional animals appeared at baiting sites other than could have been easily collected by the former method. A collection of crabs was made during approximately every spring tide between October

1984 and May 1987.

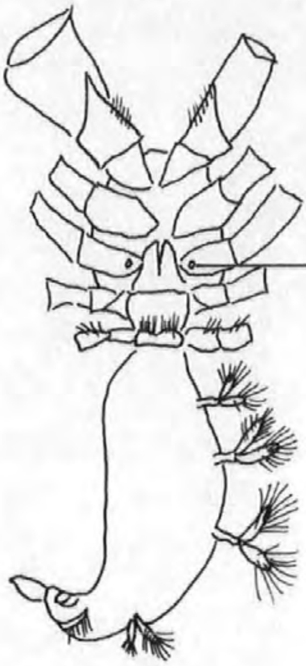
In the laboratory the crabs were extracted for study by cracking open their shells with a small bench vice. This was considered to be the least traumatic of a number of methods appearing in the literature (e.g. heating the shell apex - Reese, 1968, Fotheringham, 1976a; anaesthetising the animal in warm water - Scully, 1979; breaking open the shell with a hammer - Young, 1978; beating the apex with a piece of metal - Brightwell, 1951b) since the force could be applied both accurately and suddenly, and since the animals were never in a position where refusing to leave their shells could have resulted in death by suffocation or heat stress - an important consideration since it was found that ovigerous females were particularly reluctant to abandon their shells if these remained intact.

Once removed from their shells the animals were examined under a binocular microscope and were sexed by noting the positions of the gonopores and the arrangements of the pleopods (illustrated in Figure 5.1). The opportunity was also taken at this point to examine this cross-section of the population (almost 2000 individuals in total) for aberrations, and to check for the presence of parasites. Two "unusual" animals were found and a total of seven were seen to be carrying recognisable parasites. Details of these animals are included in Appendix II.

Records were made of the number of females and the number of males in each collection. The state of sexual maturity of each female was categorised on a scale of 0 - 4, based upon the colour and state of development of the ovaries. These structures are clearly visible through the thin abdominal wall. Descriptions of the grades used and their characteristics are given in Table 5.1. This classification allowed females in different states of

Figure 5.1

SOME CHARACTERISTICS USED TO DISTINGUISH BETWEEN THE SEXES OF PAGURUS BERNHARDUS
- after Jackson (1913).
(individual illustrated is a female - ventral view).



In males the following differences apply:

1. The gonopores open on the coxae of the 5th pereiopods.
2. There are only 3 biramous pleopods (those on segment 2 are missing), and the inner branches are much reduced and bear less conspicuous setae.

maturity to be compared, and hence allowed the synchrony of breeding within the population to be determined. Any occurrence of eggs on the pleopods of the females was recorded.

The definition of the "breeding season" for this study was extended beyond the months when ovigerous females were recovered to include those months when non-ovigerous females could, none-the-less, be seen to have mature (stage 4) ovaries. The percentage of ovigerous females was calculated on each occasion as a proportion of only those found to be larger than the smallest ovigerous female recorded during the study period (a female with a shield length of 1.7mm).

Table 5.1

THE CHARACTERISTICS USED TO CLASSIFY MATURITY IN FEMALE PAGURUS BERNHARDUS.

STAGE	CHARACTERISTIC
0	Ovaries "spent" - recently emptied; female with a full clutch of eggs on her pleopods.
1	Ovaries pale and with no obvious colouration; usually characteristic of very small (i.e. carapace < 3.0mm) and presumably immature individuals.
2	Half to whole of abdomen conspicuously purple (the typical "resting" condition).
3	Ovaries as two thin blue-black lines in the abdomen; not always granular. No purple colouration. Dark lines may appear to join proximally. Female becoming "mature".
4	Ovaries deep blue-black in colour and filling abdomen. Conspicuously granular and bulging with eggs about to be laid. The most mature stage.

5.2.2 RESULTS

A full list of the dates on which collections of crabs were made, together with a summary of the numbers of males and females examined on each occasion, is presented in Appendix V.

The months when female <u>Pagurus bernhardus</u> were found to be ovigerous on the Battery Rocks are listed in Table 5.2, which shows that reproduction in this population is seasonal rather than continuous, and is confined predominantly to the winter/spring period of December to April.

Mean values for the percentages of females found to be ovigerous in each of the months are presented graphically in Figure 5.2. This shows that almost 100% of females are ovigerous on this shore by the month of January, and that a second peak of 100% appears to occur in March. The disproportionately large deviations for the months of November and May are due to the small number of ovigerous females collected during these months, since breeding only begins in the last days of November and is completed by the beginning of May.

The different stages of ovarine development in the females examined are compared in Figure 5.3. Here the mean percentages of individuals at each of the five stages are given for each month. When viewed with the months of reproductive maturity in the centre, a pattern emerges which clearly complements that of Figure 5.2. The females begin to accumulate eggs (stage 3) during October, and are mature enough to breed (stage 4) by November. The number with eggs still to be released in January, together with the information that some 92% of these females are already ovigerous at this time (Figure 5.2), implies that a second brood is being prepared by these individuals. The number at stage 4

Table 5.2

The months when female *Pagurus* *bernhardus* were found to be ovigerous on the Battery Rocks.

months	1984	1985	1986	1987
J		*	*	*
F		*	*	*
M		*	*	*
A		*	*	*
M			*	study ended
J				
J				
A				
S				
O	study began			
N		*		
D		*	*	

Figure 5.2

Mean (+ S.D.) monthly values for the percentages of female *Pagurus bernhardus* found to be ovigerous on the Battery Rocks: 1984 - 1987.

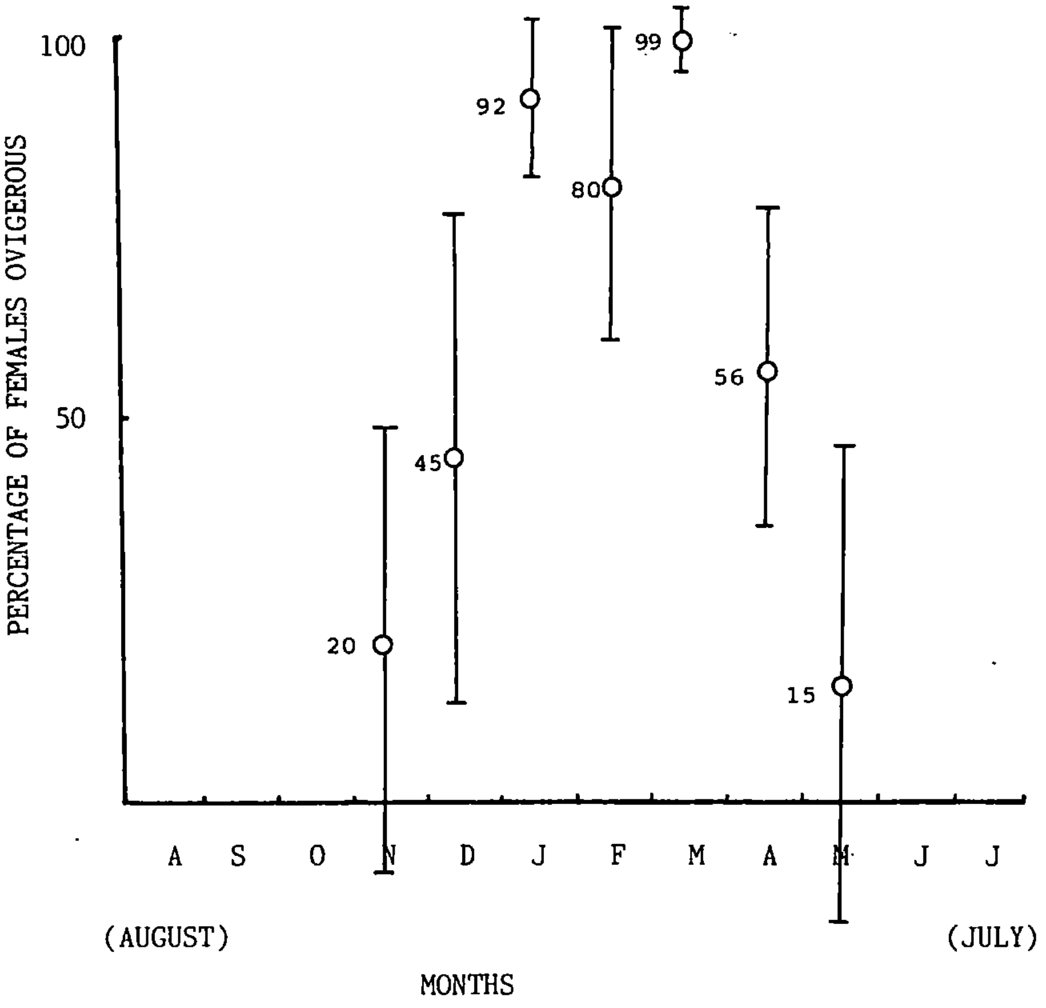
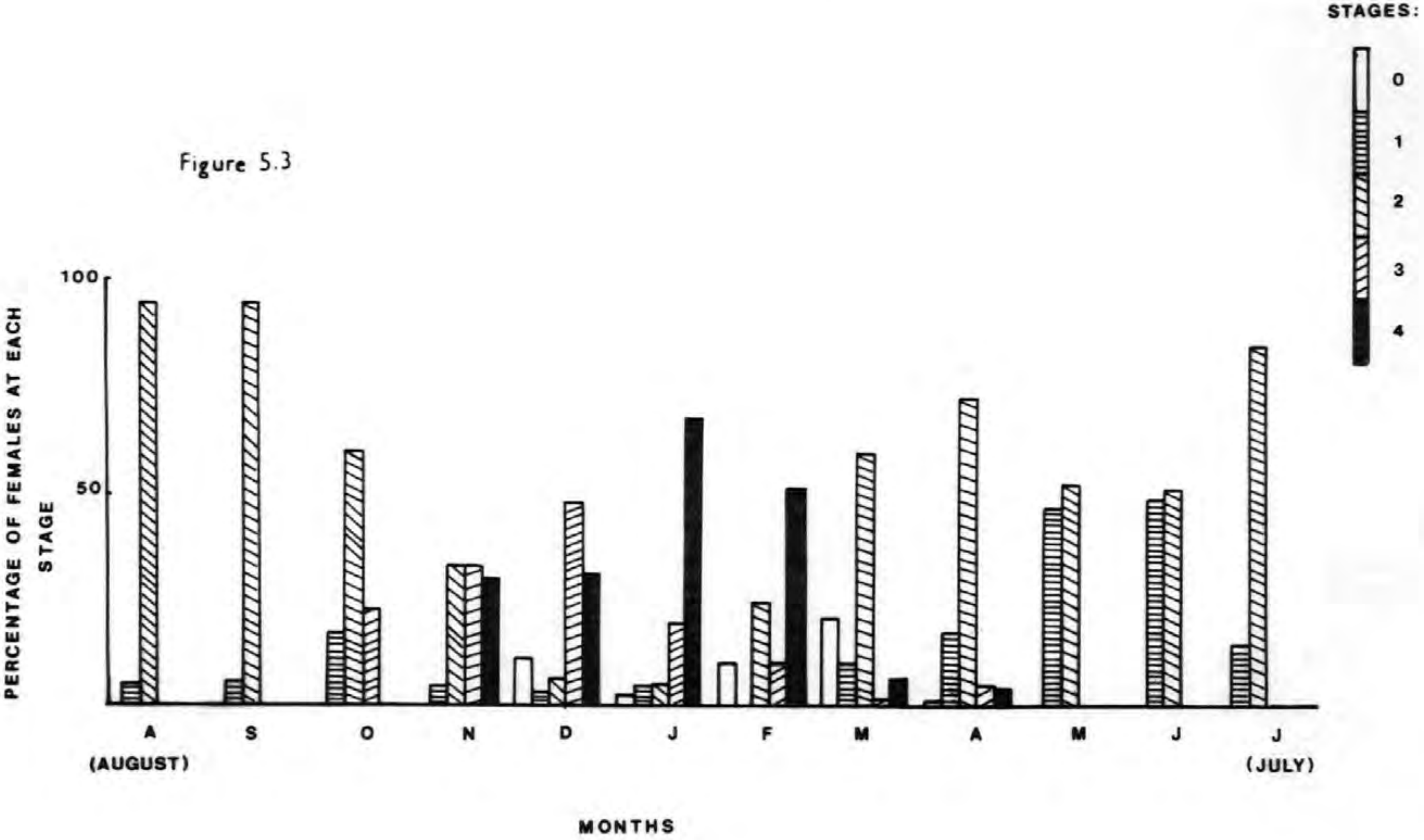


Figure 5.3

A comparison of the percentages of female Pagurus bernhardus demonstrating different stages of ovarine maturity during each of the months of the year (1984 - 1987).

Figure 5.3


STAGES:
0
1
2
3
4
100
50
PERCENTAGE OF FEMALES AT EACH STAGE
A
(AUGUST)
S
O
N
D
J
F
M
A
M
J
J
(JULY)
MONTHS

declines during February/March, with the dominant state of the non-breeding summer being stage 2. The "spent" females (stage 0) predictably follow this pattern by appearing after the first clutch is laid in December and disappearing with the last clutch in April. Immature females (stage 1) become conspicuous in the collections from March onwards as the young of the first broods settle from the plankton (a development time that requires some 60 days - Bookhout, 1964). The peak of these females in May and June will therefore be the juveniles of, what is for most adults, the second brood.

Thus it can be seen from these observations that breeding in this population of P.bernhardus is asynchronous - i.e. once breeding begins the females are not found to be in the same state of development at the same time.

The data collected for this part of the study are presented in full in Appendix VI.

5.3 THE GESTATION PERIOD OF PAGURUS BERNHARDUS.

5.3.1 MATERIALS AND METHODS.

In order to determine the gestation period for this species a number of ovigerous females were maintained in separate aquaria so that the progress of their egg development could be followed in detail. The females were kept isolated for this study in order to avoid any potentially aggressive and damaging encounters between them. Individuals were housed in either "drilled" shells or in glass replicas for these experiments. Stimulating a crab's abdomen with a fine nylon bristle via a hole drilled in the apex of its shell (Conover, 1978) was found to be a particularly efficient way of extracting an animal for routine study. The glass replicas (illustrated in Plate 3) were made from coiled tubes of blown glass by a local craftsman, but appeared difficult to manoeuvre and were only occupied by the crabs if no alternatives were available. The glass shells did, however, allow rapid examination of egg development with the minimum of disturbance to the female and were the preferred choice for this reason. The salinity, temperature, and photoperiod in each tank were maintained throughout at constant levels typical of the shore at the time - i.e. 35‰, 8-10°C, and 8L:16D.

Egg development was followed in a total of 27 females, taken from the population at different times during the three breeding seasons investigated. The eggs of these females demonstrated a consistent pattern of development, and seven separate stages were distinguished in order to follow their progress (Figure 5.4). Since most of the females were at slightly different stages of development when they were collected, a

Plate 3

Female Pagurus bernhardus shown occupying one of the replica glass shells used in the study of the gestation period of this species.

composite of the time intervals measured between these stages was subsequently used to estimate the total duration of gestation.

Figure 5.4

CONSPICUOUS STAGES IN THE DEVELOPMENT OF THE EGGS OF PAGURUS BERNHARDUS

1. Clutch deep black in colour. Individual eggs as solid balls of cells, each conspicuously dark and granular with yolk. Egg diameter 0.5mm.

2. Slight clear pole visible in eggs as they enter the gastrula stage. Yolk in cell-like granules ("yolk spheres"). Egg diameter 0.5mm.

3. Shape of embryo beginning to form, made dark and conspicuous by the enclosed yolk. First traces of eyes visible when viewed laterally. Egg diameter 0.5mm.

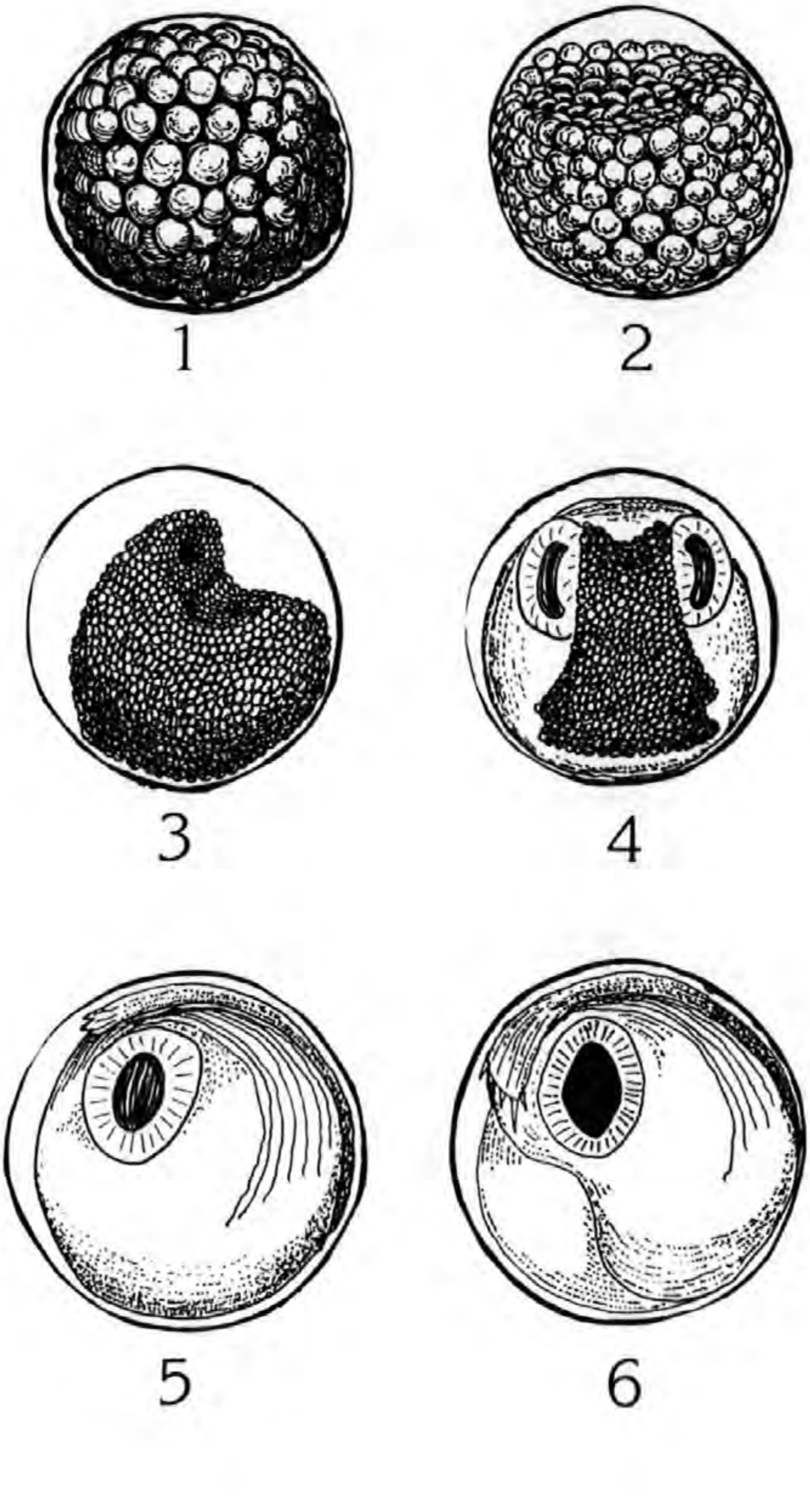
4. Limb buds visible on ventral surface. Differentiation occurring into cephalic and abdominal regions. Eyes rust-brown in colour and crescent shaped. Dark granular yolk disappearing. Egg diameter 0.5mm.

5. Zoeal shape better defined. Discernable eyes - ommatidia with rust-brown pigment. Spasmodic movements. Heart beating strongly, about 140 beats per minute. Yolk almost gone. Egg diameter 0.7mm.

6. Eyes clearly distinguishable and black. Translucent body. Zoeal form quite apparent. The "eye-dot" stage. Egg diameter 0.7mm.

7. (not illustrated): Hatched or hatch when touched. First zoeal stage (pre-zoeal stage very brief). Female with empty egg capsules on pleopods.

Figure 5.4 (cont.)



5.3.2 RESULTS

Under the conditions of this experiment the eggs followed the pattern of development described in Table 5.3.

Table 5.3
The durations of the stages of development of the eggs of <u>Pagurus bernhardus</u> when females were held under constant winter conditions in the laboratory.

stages	durations
1 - 2	6 - 7 days
2 - 3	12 - 14 days
3 - 4	5 - 7 days
4 - 5	5 - 7 days
5 - 6	6 - 11 days
6 - 7	2 - 5 days

This suggests that the full development of a single clutch could be expected to require some 43.5 days (range 36 to 51 days) at temperatures of 8-10°C.

5.4 THE STIMULI INITIATING AND CO-ORDINATING BREEDING IN PAGURUS BERNHARDUS.

5.4.1 MATERIALS AND METHODS.

Since breeding in this population had been shown to be seasonal, it was decided as a preliminary to this part of the study to eliminate from the list of possible influences any stimuli which did not show variation during the course of the year. Accordingly, the salinity of the water in Mount's Bay and the availability of food material on the Battery Rocks were tested during both the non-breeding period of May to October ("summer") and the breeding period of November to April ("winter").

The salinity was measured weekly over a twelve month period, using a hydrometer on a sample of water collected from a deep gully adjacent to the offshore greenstone boss named Carn Olva. The water close to the shore has numerous inputs both natural and man-made, but the dilution effect of rain water and fresh-water inflow is largely localised and as prone to change in summer as in winter. Since the mean value for the summer period (36.4 ± 1.8 ‰) was not found to differ significantly from the mean value for the winter period (35.8 ± 0.9 ‰; $t = 0.694$, d.f. = 47, $p > 0.05$), the influence of salinity was not investigated further.

Measurements of carapace length and body weight ($r = 0.889$, $n = 189$) were made on individuals collected at random during the period of one year, and regressions of weight on length were compared between the "summer" animals (weight = 0.1451 carapace - 0.5604; $n = 82$) and the "winter" animals (weight = 0.1903 carapace - 0.745; $n = 81$) for significant differences. It was hoped to detect any changes in weight for a given length between the two seasons that may have been due to differences in food availability. A significant difference was detected ($d = 2.97$, $p < 0.01$; Bailey, 1959) with the animals heavier per unit carapace length during the winter. Although no ovigerous females were included in the samples because of the inevitable weight increases produced by their eggs and the water trapped between them, it was thought to be unrealistic to exclude mature females (i.e. stage 4 females, with eggs about to be laid) since these made up such a substantial proportion of most winter samples. The slight differences in mean weights between the seasons may therefore be explained. Hermit crabs are broadly described as "omnivorous detritovores" (Hazlett, 1981a), and P.bernhardus generally scavenges on any organic material found on the shore (Hunt, 1925; Orton, 1927). Since the Battery Rocks are exposed to the outfalls of ten sewage pipes, all discharging untreated waste into the waters of Mount's Bay, there is never a deficiency of organic material in these waters. Food availability was not therefore regarded as a major influence on the reproductive status of these crabs.

The stimuli of temperature and photoperiod were investigated in a series of experiments constructed to test the responses of crabs collected in one season to the conditions typically prevailing in a different season. Thus crabs collected during the summer were exposed to winter regimes of temperature and photoperiod, while crabs collected during the winter were exposed to summer regimes of temperature and photoperiod. The underlying hypothesis behind such experiments was that, if summer or winter regimes do play a significant role in initiating breeding, artificial exposure to these regimes should suffice to stimulate or inhibit breeding behaviour irrespective of the natural regime beyond the laboratory. The interaction of the two parameters could also be established in this way. Should no positive association be found, further experiments could be conducted to identify perhaps longer-term or reinforcing stimuli not immediately apparent. Accordingly, experimental regimes were established as follows:

1. The winter regime for "summer" animals

Crabs were collected randomly from the shore early in July 1986. The animals were extracted from their shells with a bench vice, and were sexed and checked for parasites. Each crab was individually marked (the techniques used for marking are described in the next chapter in the context of studying migration) and was given a shell similar to its original but with a 1mm hole drilled near to the apex. Each shell was colour-coded to indicate the sex of its occupant. Three sub-groups were used for the experiment, each of which comprised 8 randomly selected females and 4 randomly selected males. Any individuals not selected for the experiments were returned to the shore, and were observed over a period of several days to ensure that the way in which they had been handled and marked had not affected their behaviour. None of the animals died during the following week, all were observed to feed normally, one moulted, and many dispersed to other pools where they could still be identified up to 3 weeks later. In addition, the experimental animals were observed in laboratory tanks for one week prior to the artificial regimes being imposed. None showed any evidence of any injuries or any behaviour that was considered in any way abnormal.

Three combinations of temperature and photoperiod were created under controlled conditions in the laboratory, and each sub-group was exposed to one such regime. The combinations were:

I. winter temperature (6-8°C) & summer photoperiod (16L:8D).
II. winter temperature (6-8°C) & winter photoperiod (8L:16D).
III. summer temperature (14-16°C) & winter photoperiod (8L:16D).

The normal rockpool population on the shore served as a fourth (control) group exposed to summer temperatures and summer photoperiods. The temperature values taken as typical of summer and winter in the area were determined from records of the inshore water temperatures of Millbay Docks, Plymouth (supplied by the Plymouth City Council), from intermittent readings from the shore at Battery Rocks, and from the open water temperatures of the English Channel (taken from the Channel Light Vessel at 49.9°N, 02.9°W - courtesy of the Marine Biological Laboratories at Plymouth). A summary of the readings from the Channel Light Vessel and from Millbay Docks is presented in Appendix VII. The daylengths typical of the two seasons were approximated from Whittaker's Almanack.

It was thus considered that all possible combinations could be covered with the equipment available. The winter temperatures were maintained by having each of the two appropriate sub-groups housed in separate small aquaria (with capacities of approximately 18 litres) which in turn were immersed in a larger (55 litre) tank filled with cooled tap water. The temperature of the larger tank was lowered by a HETOFRIG cooling unit with a capacity for cooling below 0°C. The photoperiods were controlled by covering each of the small tanks separately with individual lids, each mounting a single 18W "daylight" fluorescent tube, and with each lamp controlled by an individual time switch. The final arrangement of the experimental system is illustrated in Figure 5.5. The summer temperature / winter photoperiod regime used a similar system for controlling the daylength but had no temperature control - the tank was left to adopt the natural summer temperature and remained at a comparable value to that of the open pool without assistance. The experiment eventually ran for a total of 87 days (6 July 1986 to 30 September 1986).

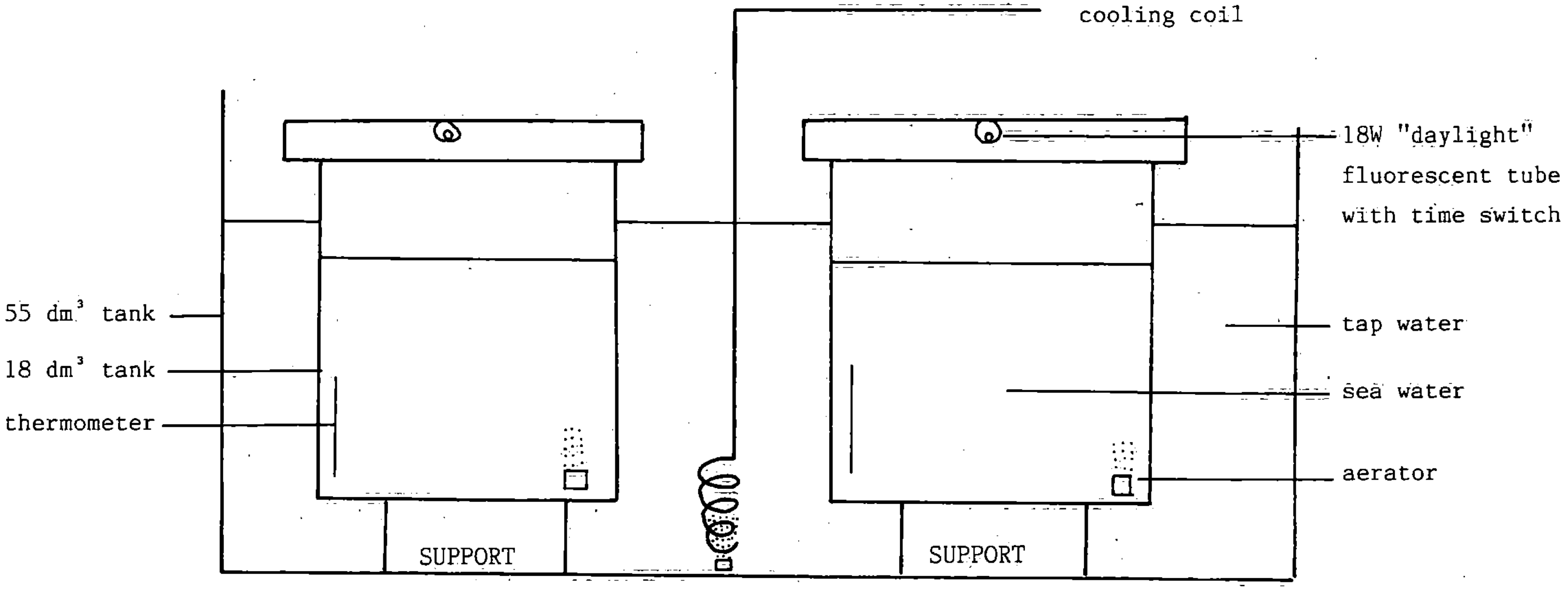
2. The summer regime for "winter" animals

In these experiments crabs were collected in late October 1986, and sub-groups were created and treated in exactly the same way as before. In addition, the females were checked for the presence of eggs on their pleopods and for the state of maturity of their ovaries. In no case was a female found to be ovigerous, and all had ovaries at stage 2. The rock pool population was again used as a control. The three experimental tanks were set up under laboratory conditions, with summer temperatures maintained by aquarium thermostatic heaters, and summer photoperiods created with fluorescent tubes and time switches as before. The regimes used were:

I. summer temperature (14-16°C) & summer photoperiod (16L:8D).
II. summer temperature (14-16°C) & winter photoperiod (8L:16D).
III. winter temperature (6-8°C) & summer photoperiod (16L:8D).
IV. winter temperature (6-8°C) & winter photoperiod (8L:16D) - the rock pool control.

Figure 5.5

The experimental design for exposing "summer" animals to an artificial winter regime of temperature and daylength.



Regime III was established in an unheated basement laboratory with the aquarium standing on a cooling plate. The experiment ran for a total of 82 days (21 October 1986 to 10 January 1987).

Each of the tanks used in the two sets of experiments held several large stones and a number of spare (drilled) shells. Thus refuges to avoid agonistic encounters were available, the crabs were not overcrowded, and shell-limitation would not inhibit breeding behaviour. Females in the experimental tanks were examined daily during the period of each trial, both for the presence of eggs and to monitor the state of maturity of their ovaries. The animals were fed on fresh or frozen mussel meat every other day. Intermittent observations were also made for breeding (i.e. copulatory) behaviour, and to detect any "abnormal" behaviour. The rock pool (control) animals were monitored each fortnight as part of the regular sampling of the littoral population.

5.4.2 RESULTS

The results of the experiment using an artificial "winter" regime are presented in Table 5.4. This shows that, while all of the females had ovaries at stage 2 at the start of the experiment, 13 of the 16 (81%) exposed to winter temperatures advanced to stage 3 within some 30-35 days. Seven of these females (44%) subsequently developed to stage 4 after an additional 10-15 days. None of the females in the control group on the shore, however, advanced beyond stage 2 during the duration of the experiment. Thus, a winter temperature regime clearly seems to advance the reproductive development of females exposed to it.

The influence of photoperiod is not so clear, however, since no significant differences were detected in the length of time required to reach stage 3 when the females in the winter daylength / winter temperature regime were compared with those in the summer daylength / winter temperature regime (ANOVA; $F_{1,11} = 0.598$).

The group exposed to winter photoperiods and summer temperatures produced results that reinforce the hypothesis that winter temperatures are needed for the development of the ovaries, since in the absence of the cold temperature stimulus no females matured beyond stage 2.

Copulatory behaviour was not observed directly on any occasion, but copulatory-type behaviour (i.e. with the males in close contact with the females and holding firmly on to their shells - Hazlett, 1968b) was witnessed on a number of occasions in the tank under the regimes of winter temperature combined with winter photoperiod. Only in this group did copulation itself apparently occur since only here was a clutch of eggs actually

Table 5.4

The reproductive development of individually marked female *Pagurus bernhardus*, collected during the summer and subsequently held under artificial regimes of temperature and photoperiod.

REGIME		FEMALE																							
Temperature	Photoperiod	1			2			3			4			5			6			7			8		
		a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
winter	summer	2	33	-	2	34	11	2	-	-	2	34	12	2	37	-	2	-	-	2	36	10	2	35	-
winter	winter	2	29	10	2	34	-	2	30	-	2	-	-	2	41	14	2	35	-	2	26	12	2	37	15
summer	winter	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-

a = the state of the ovaries at the start of the experiment

b = time (days) to reach stage 3

c = additional time (days) to reach stage 4 produced (female number 5, Table 5.4). No spermatophores were noted on the pereiopods of any of the females under the other regimes. The eggs were first noticed when at stage 1 and had progressed to stage 2 seven days later. At this point the female was found lying out of her shell, it was presumed attacked and killed by another member of the group. However, since two small males were also found in a similar state during the course of the experiment, it was not considered that the female's death was linked specifically to the fact that she was carrying eggs. Equally, had the eggs been unfertilised, they would not have followed such a conspicuous pattern of development.

It was also of note that in the regime of winter photoperiod and summer temperature males were frequently found to be clasping the shells of females in the manner described above. The rock pool population, however, differing from these only in the photoperiod regime, demonstrated no such behaviour. The role of photoperiod in influencing male copulatory behaviour is clearly suggested.

The results for the experiments using artificial summer regimes are presented in Table 5.5. The rock pool population at the time bred normally, but those individuals initially from the same population and exposed to artificially extended daylengths and warmer temperatures showed no development beyond the stage 2 that they started with. The crabs exposed to summer temperatures but winter photoperiods showed on the whole more aggressive copulatory-type behaviour but unconvincing ovarine development. Those in a regime of winter temperature and summer photoperiod produced advanced ovarine development with 6 (75%) reaching stage 4 within 40-45 days i.e. at approximately the same stage as the pool population at that time. This experimental group, however,

Table 5.5

The reproductive development of individually marked female <u>Pagurus</u> <u>bernhardus</u>, collected during the winter and subsequently held under artificial regimes of temperature and photoperiod.

REGIME		FEMALE																							
Temperature	Photoperiod	1			2			3			4			5			6			7			8		
		a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
summer	summer	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-
summer	winter	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-	2	-	-
winter	summer	2	29	11	2	30	10	2	31	14	2	60	-	2	33	12	2	32	14	2	71	-	2	39	13

a = the state of the ovaries at the start of the experiment

b = time (days) to reach stage 3

c = additional time (days) to reach stage 4 demonstrated no copulatory behaviour, no spermatophores were detected on the pereiopods of the females when they were examined, and no eggs - fertilised or unfertilised - were extruded by them.

Thus, winter temperatures are again implicated in the development of mature ovaries, while the copulatory behaviour of the male so essential for fertilisation appears to require a different stimulus - that of a winter photoperiod.

At the end of the experiment the crabs were released back onto the shore. One female at least subsequently bred - female number 8 (Table 5.5) was recaptured 19 days later with a full clutch of eggs on her pleopods (eggs at stage 2).

5.5 THE NUMBER OF BROODS THAT A FEMALE PAGURUS BERNHARDUS FROM THE LITTORAL ZONE CAN PRODUCE UNDER FAVOURABLE CONDITIONS.

5.5.1 MATERIALS AND METHODS.

An experiment was conducted with 24 ovigerous females collected from the shore at Battery Rocks in mid-January 1986. In each case the eggs carried were at stages 3/4 and the ovaries were at stage 2. The history of each individual was known from marking and recapture studies and the criterion for selection was that each had successfully carried one previous clutch that season. These animals were exposed to artificial temperature and photoperiod regimes in the laboratory in order to determine if they could produce a third clutch.

The following regimes were created with thermostatic heaters or cooling plates and fluorescent "daylight" tubes:

I. winter temperature (6-8°C) & winter photoperiod (8L:16D).
II. rising temperatures & winter photoperiod (8L:16D).
III. winter temperature (6-8°C) & increasing daylength.
IV. rising temperatures & increasing daylength.

Increases in temperature and photoperiod were timed to coincide as nearly as possible with the rates at which the natural temperatures and photoperiods were increasing on the shore.

Six females were exposed to each regime, and each female was individually marked and maintained in a separate compartment of the experimental tank together with three males of an equivalent or larger size. The females were extracted from their drilled shells and examined daily for evidence of copulatory behaviour -

particularly the presence of spermatophores on the pereiopods. The maturity of the ovaries and the progress of egg development were also monitored. The experiment had a duration of some 95 days (20 January 1986 to 25 April 1986) though all but the two females which subsequently produced broods were returned to the shore by day 44.

5.5.2 RESULTS.

The results of these experiments are summarised in Table 5.6. It can be seen that females matured again to at least stage 3 (by which time the eggs that they carried were almost ready to hatch) and even stage 4 when the temperature was maintained at the winter level. The ovaries failed to reach stage 4, however, or the eggs subsequently disappeared (were perhaps reabsorbed) if the temperature began to rise. When the winter photoperiod was maintained but the water temperature was allowed to rise, no further development occurred. Only when both photoperiod and temperature were maintained at winter levels did females produce another brood. Under the latter set of conditions elements of copulatory behaviour were observed - in all other regimes the individuals effectively ignored each other unless casual contacts were made. These contacts, however, provoked only displays of aggression typical of non-breeding encounters. Two females successfully produced new clutches (i.e. third clutches) in this experiment and these females were maintained under the winter regimes until the eggs hatched some 47/51 days later. After the eggs had hatched the temperatures and photoperiods were altered to the summer values over a period of days and the females were returned to the shore.

Table 5.6

The states of ovarine maturity in ovigerous female <u>Pagurus</u> <u>bernhardus</u> exposed to experimentally manipulated regimes of temperature and photoperiod.

REGIME		FEMALES					
Temperature	Photoperiod	1	2	3	4	5	6
		a b	a b	a b	a b	a b	a b
winter	winter	2 → 3	2 → 4*	2 → 2	2 → 4*	2 → 3	2 → 4
increasing	winter	2 → 2	2 → 2	2 → 2	2 → 2	2 → 2	2 → 2
winter	increasing	2 → 2	2 → 3	2 → 4	2 → 3	2 → 4	2 → 2
increasing	increasing	2 → 2	2 → 2	2 → 2	2 → 2	2 → 2	2 → 2

* = new clutch produced
a = state of ovaries at start of experiment
b = state of ovaries at end of experiment

5.6 SUMMARY AND DISCUSSION.

It can be seen from these experiments that reproduction in this littoral population of <u>P.bernhardus</u> is seasonal and asynchronous, and that two separable stimuli are needed to initiate and co-ordinate breeding. A cold water stimulus (i.e. 6-8°C) is needed by the female in order to promote egg production, while a winter photoperiod (i.e. 8L:16D) encourages copulatory behaviour in the male. The requirement for two separate stimuli would reflect the fact that a female would need a period for egg development before being mated. Gestation requires some 43 days and a female can produce at least three clutches if conditions remain favourable.

Copulation behaviour has been described in a number of species of hermit crab (e.g. Coffin, 1960; Hazlett, 1968b, 1972b; Helfman, 1977) and mating is thought to be initiated by the male. Indeed, the tendency for dominant males of many species studied to deposit spermatophores indiscriminately on any other individuals that they can overpower, including immature females and even other males (Matthews, 1959), does suggest that mate selection in this group may be based more upon subordinate behaviour cues than upon individual recognition (Salmon, 1983). The role of pheromones in mate selection has not been clearly shown in hermit crabs, though one species is thought to be able to discriminate between receptive females and other males by detecting a water-borne chemical with its first antennae (Imafuku, 1986). A response to an environmental stimulus in male <u>P.bernhardus</u> may therefore explain the unselective aspect of such behaviour in this species.

The breeding cycle of this population is therefore typical of cool-water crabs where seasonal and asynchronous breeding are the norm (Giese, 1959; Warner, 1977). This contrasts with many tropical species where continuous and synchronous breeding are thought to be common (Hazlett, 1981a). The literature is confusing over the exact duration of the breeding season in P.bernhardus since collections made in British and European waters appear to suggest that this species may breed at any time of the year (Table 5.7). A more critical review of the literature, however, indicates that the main reason for this variation must be that the majority of records do not distinguish between littoral and sublittoral populations. Of the references in Table 5.7 only two (Perkins, 1985; Elwood and Stewart, 1987) make clear that littoral populations are being sampled. Unfortunately the first author found only 13 ovigerous females in some 3000 animals examined and so can offer only a limited contribution towards an understanding of this aspect of the biology of P.bernhardus. The second work, however, shows sufficient agreement with the observations from Mount's Bay (recorded in Table 5.2) to confirm that littoral populations of this species breed only between the months of December to May inclusive - at least within the latitudinal ranges of these studies. In addition, the observations of ovarine development in the Battery Rocks population imply that females have no influence upon each others reproductive development, leading to the suggestion that physical stimuli and not the release of pheromones must initiate and co-ordinate breeding.

In this littoral population of P.bernhardus a predictable reproductive cycle therefore appears to occur. Females of all sizes typically have "resting" ovaries during the months of May to October when no conspicuous breeding activity can be seen. As the winter months approach (with their cold temperature stimulus) the

Table 5.7

MONTHS PAGURUS BERNHARDUS REPORTED IN THE LITERATURE TO BE OVIGEROUS

LOCATION	MONTHS J	F	M	A	M	J	J	A	S	O	N	D	REFERENCE
CORNISH WATERS			*	*			*	*					Clark (1909) P. 299
RAUNEFJORDEN (W.NORWAY)	*	*	*	*	*	*	*						Samuelson (1970) P.40
CLYDE SEA	*	*	*	*	*	*	*	*	*			*	Pike & Williamson (1959) P. 556
NORTHERN NORWAY						*	*	*					Dons (1915) } In Kamalaveni (1949)
BOHUSLAN (SWEDEN)			*	*	*	*	*						Nordgaard (1912) } In Kamalaveni (1949)
ØRESUND (DENMARK)									*				Bookhout (1964) P. 277
FIRTH OF CLYDE			*	*	*								Perkins (1985) P.22
ROSCOFF & ARCACHON (BRITTANY)	*	*	*								*	*	Carayon (1941) P. 115
DANISH WATERS			*	*	*	*	*	*	*	*			Thorson (1946) - In Reese (1968)
IRISH WATERS		*	*					*	*				Selbie (1921) P. 2
IRISH SEA	"very extended ... any time of the year"												Jackson (1913) P. 55
MILFORD HAVEN	*	*	*	*									Crothers (1966) P. 74
ISLE OF MAN	"larvae common march to june"												Bruce <u>et al</u>. (1963) P. 172
IRISH WATERS (CO. DOWN)	*	*	*	*	*							*	Elwood & Stewart (1987) P. 254
BATTERY ROCKS	*	*	*	*	*							*	

ovaries become mature by early November (stage 3 at first, becoming stage 4 within 1-2 weeks) and the first clutches appear soon afterwards. Females with full clutches on their pleopods may have empty ("spent") ovaries or they may still have eggs to release, but if so these eggs usually disappear within one week. Since clutch sizes will depend at least in part upon shell size and architecture (Fotheringham, 1976b; Bertness, 1981a) this latter point may reflect that the smaller females cannot release the full number of eggs that they manufacture since their shells will not accommodate them.

During the course of the breeding season a proportion of the ovigerous females appear to have ovaries at the resting stage (stage 2), suggesting a pause in their breeding activity, but a greater number seem to prepare a new clutch as soon as their existing one approaches maturity. Many females recovered in the months of January and February were seen to have ovaries bulging with new eggs while those on their pleopods approached hatching. Such females were also found to have males in close attendance. The trend then appears to be for ovaries to decline in maturity from about March or April onwards, and for the last clutch to be released by early May. This suggests that the majority of females in the littoral zone will probably produce at least two broods during each season, contradicting the opinions of Pike and Williamson (1959) whose study found no ovigerous females of this species to have mature ovaries in any of the (sub-tidal) collections which they made from the Clyde Sea area - a fact which led them to conclude that either broods must be well separated or that females would probably have only one brood each year. A later observation by Neil and Elwood (1985), however, to the effect that most of the ovigerous <u>P.bernhardus</u> that they collected on the coast of Northern Ireland contained developing eggs in their ovaries, is more in line with the situation from Mount's Bay, and may perhaps be closer to the norm for littoral populations.

A gestation period of some 43.5 days at temperatures of 8-10°C, as determined from these experiments, also differs from the assumption of Pike and Williamson (1959) that incubation in this species would probably take "more than three months". The figure does, however, agree closely with the value of 43.1 days for the gestation of Pagurus prideaux at 12.5°C reported by Wear (1974). Both values predictably contrast with data for two other species recorded in the literature from warmer waters e.g. Pagurus samuelis requiring 14 days at 26-28°C (Coffin, 1960), and Clibanarius olivaceous requiring 12 days at 25-34°C (Kamalaveni, 1949). The colder temperature appears to be necessary for P.bernhardus, however, since when, by accident, a female with eggs at stage 1 was returned to the wrong tank (one with a summer regime running at 18°C), development was completed in only 13 days. The larvae did not swim normally, however, and all died within hours of hatching (the female survived). A requirement of only a little over one month for gestation also suggests that it would be quite possible for a female to produce perhaps as many as three clutches in one season - as is clearly possible from the results in section 5.5. Rising temperatures and increasing daylengths with the advent of spring would, however, probably limit the number of broods to two on the shore.

When discussing the stimuli necessary to initiate breeding, it would not appear that previous, long-term, or reinforcing factors are implicated. Although these have been suggested for some brachyuran crabs (e.g. Knudsen, 1964), the presence in the

Battery Rocks population of ovigerous females with carapace lengths of less than 3.0mm would seem to argue against this requirement in hermit crabs. Such females are likely to be about 6 months old and hence would not have been exposed to any stimuli that may have acted upon the population during a previous breeding season.

[A chance observation by Thompson (1904) dating a hermit crab with a carapace length of 3.7mm to some 80 days past the glaucothoë stage would add to the 60 days determined by Bookhout (1964) as being the period needed for larval life, and the 40-50 days suggested here as being needed for egg development, to bring a total age for such an individual - species differences apart - of almost six months.]

Interactions, therefore, between the two triggers of photoperiod and temperature will provide a predictable stimulus which will ensure that larvae will be most abundant during the spring and early summer months to take advantage of the increased planktonic food typical of this period (Raymont, 1963). The significance of future food availability for the larvae in governing breeding is stressed by a number of authors (e.g. Boolootian, et al., 1959; Reese, 1968). Such a pattern would also ensure that sufficient time would be available for settling from the plankton during the summer, and for growth before the winter, to allow the animals to reach the size required for breeding to be possible during the same year. As previously described, the discovery of an ovigerous female from this population with a carapace length of 2.8mm lends support to the conclusion that females of this species are quite capable of breeding within their first year. The significance of this point to the life history strategy of the species will be discussed further in Chapter 7.

The hypothesis that low water temperatures profoundly influence breeding in hermit crabs receives support from one further source. When larval collections were recently compared around the British coast (Lindley, 1987) it was noted that the larvae of P.bernhardus could be found throughout most of the year in the cold waters of the North Sea suggesting a prolonged breeding season in these parts, but were typically found only from February to April in the warmer waters of the southwest and English Channel.

It may also be significant to note that in addition to the reproductive behaviour described in these experiments, the general behaviour of the crabs exposed to winter conditions was marked by a substantial increase in aggression. This same point was also noted during the course of routine field collecting during the colder winter months, and when extracting the animals from their shells at this time of the year. Shell exploratory behaviour, particularly on the part of the males, also increased under these conditions. The exact extent to which temperature and photperiods are taken into account during investigations into shell-swapping behaviour are seldom made clear in the literature, but may perhaps be of some relevance.

CHAPTER 6

THE NATURE AND CONTROL OF MOVEMENT PATTERNS IN A LITTORAL POPULATION OF *PAGURUS BERNHARDUS*

6.1 INTRODUCTION

The patterns of movements observed in different populations of hermit crabs are complex and variable. Some individuals may move several hundred metres in a day (e.g. Hazlett, 1981b) while others remain in essentially the same area for long periods of time (Hazlett, 1983a). Entire populations may migrate from the littoral zone at certain times of the year (e.g. Rebach, 1969, 1974; Fotheringham, 1975; Dugan, 1983), while other populations may show no evidence of migrations (e.g. Stachowitsch, 1979; Tomlinson, 1960). A littoral population of Pagurus bernhardus was studied in detail in order to determine the role of movement patterns in the life history strategy of this species.

Detailed searches were made of the sublittoral of Mount's Bay during a range of conditions and seasons, concentrating in particular on the stretch of seabed extending some 500m offshore from the Battery Rocks to depths of 15-20m. It was noticeable during these searches that the large forms of P.bernhardus (i.e. with shield lengths > 10-15mm) were conspicuously absent from the area, and that hermit crabs of all sizes were generally scarce offshore. No evidence was found of the types of sublittoral aggregations noted by Perkins (1985) from the Solway Firth, where synchronous migrations involving densities in excess of 8000 animals per hectare are quoted. Thus, while movement offshore is clearly possible for individuals from the littoral zone, it would not appear that conspicuous migrations involving the whole population or a substantial part of it occur in this area. It was, therefore, decided to concentrate upon the distribution of the individual members of the littoral population in an attempt to determine what patterns of movement, if any, were displayed. It was also hoped to identify the factors which may act to stimulate them to move - either as individuals or, although seemingly unlikely, as a population.

Since hermit crabs as a group are known to display complex patterns of social behaviour (e.g. Hazlett, 1966, 1972a, 1981a), many of which are aimed at maintaining a discrete personal distance between individuals, the question of whether or not these animals occupy and defend fixed territories was considered during this study. This required observing individually marked crabs over prolonged periods and comparing their positions from one day to the next. The problem of marking such small animals was addressed as a preliminary to this work. This part of the study also provided information on the dispersal patterns of littoral hermit crabs and led to experiments aimed at determining whether movement among these animals was essentially an individual or a population phenomenon.

The importance of a suitable shell resource has already been discussed in terms of individual growth, longevity, and reproduction. The influence of the shell resource on population size and individual patterns of movement was examined by experimentally manipulating both the quality and the quantity of the shells available on the shore. The movements of animals under these circumstances was monitored in an attempt to determine the importance of shell contacts to both crab migratory habits and residence times.

Experiments were also performed both on the shore and in the laboratory in order to determine what may enable these crabs to regulate their positions on the shore as tidal levels fluctuate around them. Hermit crabs were observed to wander freely around the shore at high water but were not found out of the pools at low water. The effects that different depths of water overhead might have on movement were investigated in this context, and the slope of the shore was examined to detect any influence that this may have upon behaviour.

As a result of these investigations it was hoped to have a clearer picture of how hermit crabs disperse themselves around the shore, and how this littoral phase in their life history enables them to maximise the potential of the resources available to them.

6.2 PATTERNS OF DISPERSAL IN A LITTORAL POPULATION OF PAGURUS BERNHARDUS.

6.2.1 MATERIALS AND METHODS.

To determine the pattern of distribution shown by individuals on the shore at Battery Rocks it was decided to examine the populations of several rock pools both during and between tidal cycles on a number of occasions spread over all seasons. A "nearest neighbour" measure was employed for this work. Since hermit crabs are characteristically both highly mobile and yet quite unpredictable, it was felt that a single measure could be used rather than a range of methods - the attempt for greater accuracy being considered unrealistic in a species whose members change their positions so frequently and react towards each other in so many different ways. Consequently the method of Clark and Evans (1954) was chosen (discussed in Southwood, 1966) as being both simple to use and easy to interpret. This method requires measurements to be taken between all of the individuals present in the area under study in order to determine the distance between any one and (irrespective of direction) its nearest neighbour at that moment. The value of the mean distance is then obtained for this set of observations, and the ratio of observed mean distance to expected mean distance is calculated and used to assess the departure from randomness. The equation used for mean observed distance ($\overline{r}_A$) is:

$$\overline{r}_A = \frac{\sum r}{N},$$

while the expected mean distance ($\bar{r}_E$) if the population is distributed randomly is given by:

$$\bar{r}_E = \frac{1}{2\sqrt{\rho}}\,.$$

In these equations N = the number of measurements of distance taken, r = the distance in specified units from a given individual to its nearest neighbour, and ρ = the density of the observed distribution as number of individuals per unit area. The units for the measurements of ρ and r are the same. The ratio:

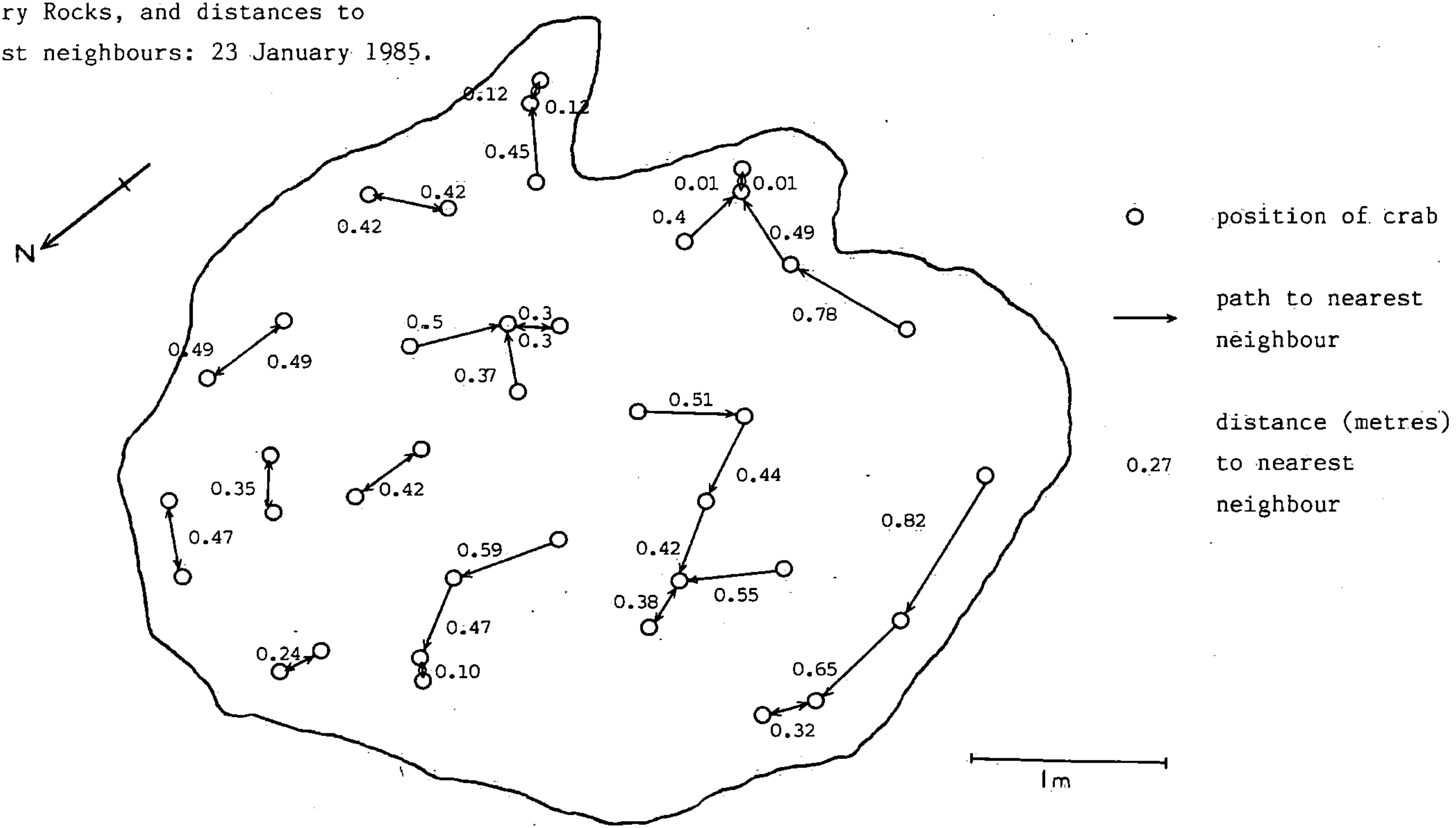
$$R = \frac{\bar{r}_A}{\bar{r}_E}$$

is thus a measure of the approach to or the departure from randomness, with R = 1 indicating a random distribution, R = 0 indicating maximum aggregation, and with R = 2.1491 indicating maximum (i.e. hexagonal) spacing. A representative "field diagram" of the measurements taken from one midshore pool during the study is reproduced as Figure 6.1.

Such measurements were repeated in the same pool on 13 occasions between November 1984 and February 1986. During this same period a further 4 sets of measurements were taken from a lower shore pool. Measurements were also made of the patterns of distribution shown by individuals during the course of 3 tidal cycles. It was hoped by these methods to reveal the typical distribution patterns of individuals in their rock pool habitats.

Figure 6.1

"Field diagram" showing the positions of hermit crabs (<u>Pagurus bernhardus</u>) in a mid-shore pool on the Battery Rocks, and distances to nearest neighbours: 23 January 1985.



6.2.2 RESULTS.

The calculated results for the values in the equations above are tabulated in full in Appendix VIII.

Summaries of the values for the nearest neighbour index "R" are presented in Tables 6.1 (for the measurements made between tidal cycles) and 6.2 (measurements made within tidal cycles). Of the three possible interpretations of the index described in the methods, the values of "R" calculated from these studies approximate most closely to the figure taken by Clark and Evans (1954) to represent a random distribution. A null hypothesis that there is no significant deviation from a random distribution in any case is upheld when χ^2 values are calculated from these results (Table 6.3). Thus it may be concluded that the hermits in the pools under study were randomly distributed both between and within tidal cycles at all times of the year, and showed no tendencies to form aggregations that might have suggested synchronous behaviour.

Attempts to study distributions during high tide periods by snorkelling over the area and by utilising SCUBA techniques were largely unsuccessful due to the exposed nature of the shore. A subjective view, however, would be that the pattern of distribution did not seem appreciably different at these times from that observed in the pools at low tide.

Since the positions occupied by the crabs were clearly not fixed, and since the spaces between them were not constant, it would also seem that territories were not held by the pool inhabitants. Territoriality, however, was investigated in more detail on another occasion with marked individuals, and will be discussed in a later section of this chapter.

Table 6.1

Nearest neighbour indices for the distribution of *Pagurus bernhardus* in two pools over a range of seasons and tidal cycles.

Date of measuring	Nearest Neighbour Index ("R")
1. Midshore pool	
10.11.84	0.967
23.1.85	1.016
6.3.85	0.860
24.4.85	0.977
3.6.85	1.143
5.7.85	0.982
31.7.85	1.006
2.9.85	1.034
2.10.85	0.828
13.11.85	0.998
13.12.85	0.863
25.1.86	0.855
25.2.86	0.796
2. Lower shore pool	
24.4.85	1.424
2.9.85	1.333
2.10.85	1.434
13.11.85	1.441

Table 6.2

Nearest neighbour indices for the distribution of Pagurus bernhardus in a single midshore pool during 3 separate tidal cycles.

Date of measuring	Time (hours)	Nearest Neighbour Index "R"
6.3.85	11.00	0.860
	12.00	0.903
	13.00	0.929
	14.00	0.874
31.7.85	12.00	1.006
	13.00	1.058
	14.00	1.121
	15.00	1.063
2.9.85	14.00	1.034
	15.00	1.145
	16.00	1.049

Table 6.3

Values of χ^2 and their probabilities for comparing the observed "R" values in Tables 6.1 and 6.2 with an expected value of 1.0 - examining a null hypothesis that the distributions of *Pagurus bernhardus* in littoral pools are random.

	Measurements made between tidal cycles in different pools		Measurements made within tidal cycles in the same pool		
	position of pool		dates of collection		
	midshore	lowershore	6.3.85	31.7.85	2.9.85
χ^2	0.154	0.673	0.050	0.022	0.025
d.f.	12	3	3	3	2
p	>0.90	>0.05	>0.90	>0.90	>0.90

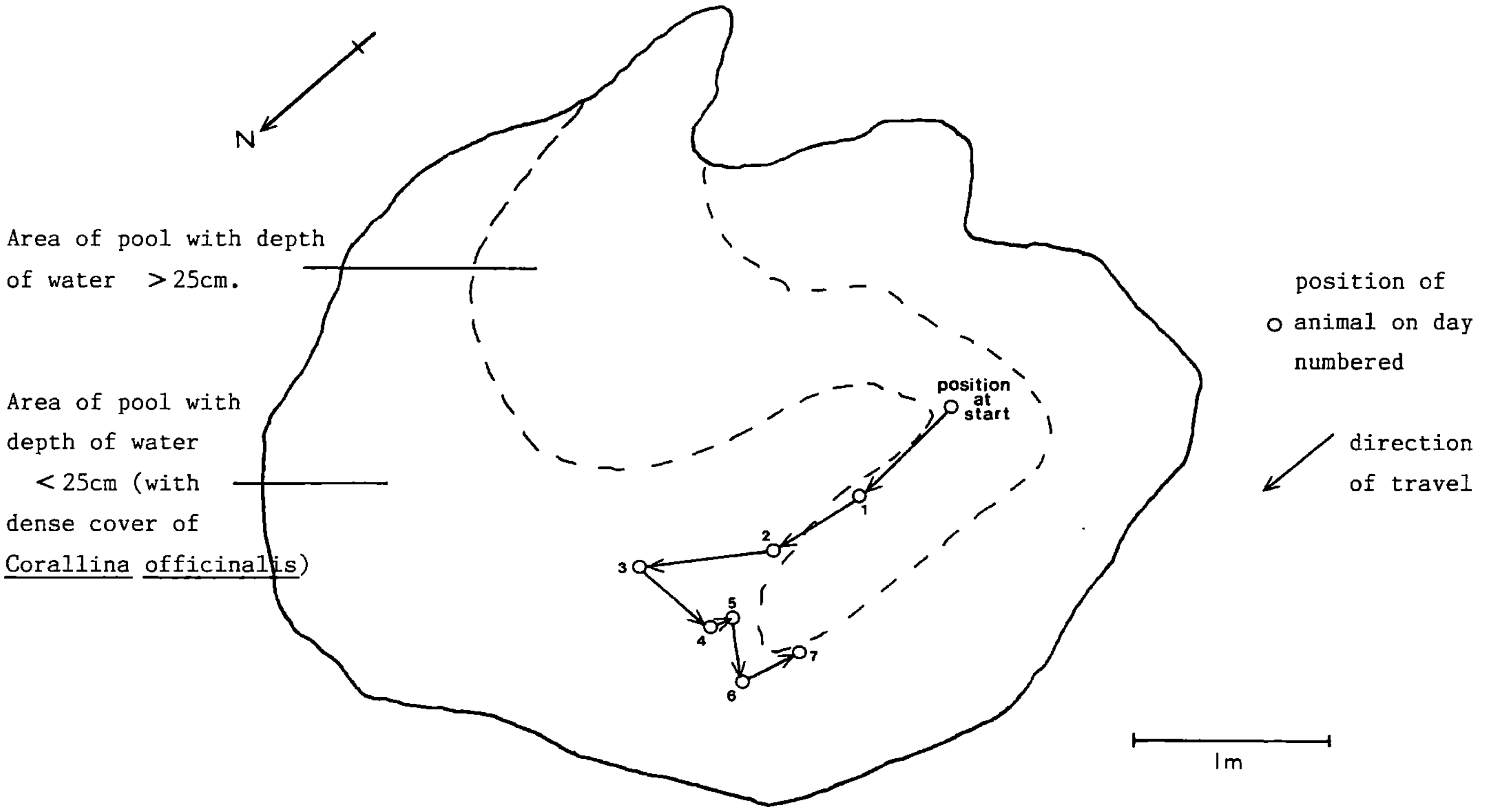
6.3 PATTERNS OF MOVEMENT IN A LITTORAL POPULATION OF PAGURUS BERNHARDUS.

6.3.1 MATERIALS AND METHODS.

The midshore pool used for the majority of the nearest neighbour measurements was also used for this part of the study. This pool is situated some 2.0m above chart datum, has an average depth of 0.2m (range 0-0.5m), and has a surface area of some 22m^2. It demonstrates a number of different habitat types (e.g. bare rock, beds of the alga Corallina, fine gravel, small boulders, ledges, clefts etc.), has a typical (poor) distribution of available shells, and has a close proximity to deeper water a matter of 1-2m horizontally to the south-east. Animals were collected from this pool on three occasions - during July 1985, November 1985, and April 1986 - and were marked at the pool side on at least two of their non-chelate pereiopods with a sequence of dots of enamel paint applied via a strand of cotton stretched across a spring wire. Three dots of one or more colours represented the code. No specific numbers were allocated to the sequences in the field (the colours were recorded by their initial letters in the order used - top to bottom), and numbers were only allocated for convenience when tabulating the results. After marking, each animal was returned to its original position in the pool - a position which had been marked on a scale diagram with reference to a grid constructed over the pool on a series of fixed points. Each experiment ran for a period of 6-7 days during a spring tide, and each animal was located (if possible) and its position noted, on each consecutive day. A diagram constructed for each individual (an example is reproduced as Figure 6.2) then

Figure 6.2

The pattern of movement displayed over a 7 day period by one marked crab (individual no. "7", July 1985).



allowed its pattern of movement to be determined. The details that could be obtained from such diagrams included the distance covered since the last observation (necessarily a minimum estimate), the direction taken since the last observation (expressed in compass degrees from the previous location), and the final point reached by the conclusion of the trial - or the animal's last known location.

From this information it was possible to detect whether movements were purposeful or random, and whether movement appeared to be an individual or a population phenomenon. It also gave some indication of the distances that could be covered within a single tidal cycle. The "meander ratio" suggested by Hazlett (1983a) was employed to quantify the pattern of movement. This expresses the distance moved by an animal between the first and final observations as a ratio of the sum of all of the distances it has covered during the study period:

$$\text{Meander Ratio} = \frac{\text{distance moved between first and last location}}{\text{sum of all of the distances moved}}$$

A small ratio is taken to indicate back and forth (i.e. random) movement, while a figure approaching unity indicates a consistent (i.e. purposeful) movement in one direction.

The significance of these measurements was examined by means of a computer simulation, comparing the actual meander ratios with predicted mean ratios <u>assuming</u> random movement. A hypothetical individual was allowed to take an unlimited number of steps in a randomly selected direction, and the distance it would have travelled at the end of the day (r) was derived from the exponential distribution:

$$F(r^2) = 1 - e^{-r^2} .$$

One thousand such "trials" were used to generate the mean ratio for each day, and the simulation ran to provide data covering a period of 30 days.

6.3.2 RESULTS

The data collected during this part of the study are presented in full in Appendices IXa (July 1985), IXb (November 1985), and IXc (April 1986).

The values calculated for the meander ratios in each of the study periods are listed in Table 6.4. No significant differences occur between the mean values for these ratios when the different study periods are compared (ANOVA; $F_{2,35} = 4.106$).

Since a value of 1.0 indicates a purposeful movement (i.e. all movements in the same straight line) it can be seen from the data that no individual moved in a continuous straight line throughout the period during which it was observed.

When the measured values of the meander ratios are plotted alongside the computer-simulated mean ratios for random movements (Figure 6.3) it can be seen that on no occasion do the observed values differ more significantly from the predicted mean ratios than two standard deviations. Thus it may be concluded that the animals moved randomly across the shore throughout the period during which they were observed.

When the final positions reached by each individual at the end of the investigation are compared with the start positions (summarised in Figures 6.4, 6.5, and 6.6) it can also be seen that no consistent direction was taken by the animals and no set distance was covered in the time period studied. It may therefore be concluded that movement is essentially an individual and not a population phenomenon among these crabs.

Table 6.4

The "Meander Ratios" calculated for a number of individually marked <u>Pagurus bernhardus</u> during three study periods on the shore at Battery Rocks.

July 1985		November 1985		April 1986	
days observed	meander ratio	days observed	meander ratio	days observed	meander ratio
3	0.379	4	0.662	6	0.414
2	0.179	6	0.312	5	0.678
6	0.194	6	0.422	6	0.329
2	0.552	5	0.785	3	0.230
7	0.663	6	0.584	6	0.215
4	0.864	6	0.593	6	0.120
7	0.463	6	0.285	6	0.389
3	0.719	3	0.398	5	0.280
6	0.329	4	0.363	6	0.151
6	0.277	6	0.550	2	0.268
4	0.068	6	0.566	4	0.274
7	0.199	6	0.567	5	0.193
4	0.417				
mean ± S.D.		mean ± S.D.		mean ± S.D.	
0.408 ± 0.050		0.507 ± 0.052		0.295 ± 0.052	

Figure 6.3

The Meander Ratios calculated for marked Pagurus bernhardus on the Battery Rocks during the study periods of July 1985 (●), November 1985 (■), and April 1986 (▲) plotted against the equivalent predicted mean values for random movement.

Figure 6.3

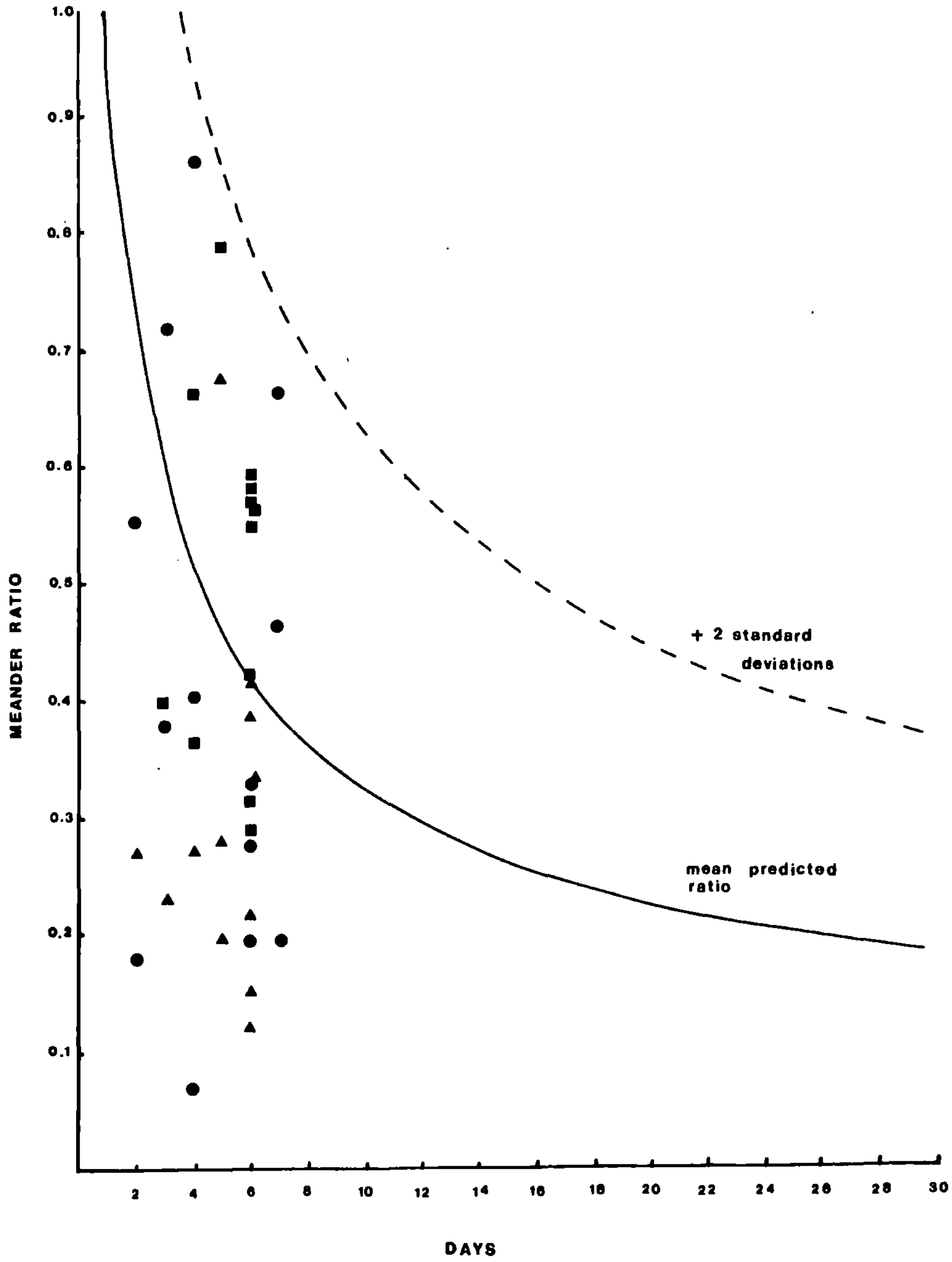

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
MEANDER RATIO
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
DAYS
+ 2 standard deviations
mean predicted ratio

Figure 6.4

Summary of the directions (degrees magnetic) and distances of movement of individually marked crabs on the Battery Rocks: July 1985.

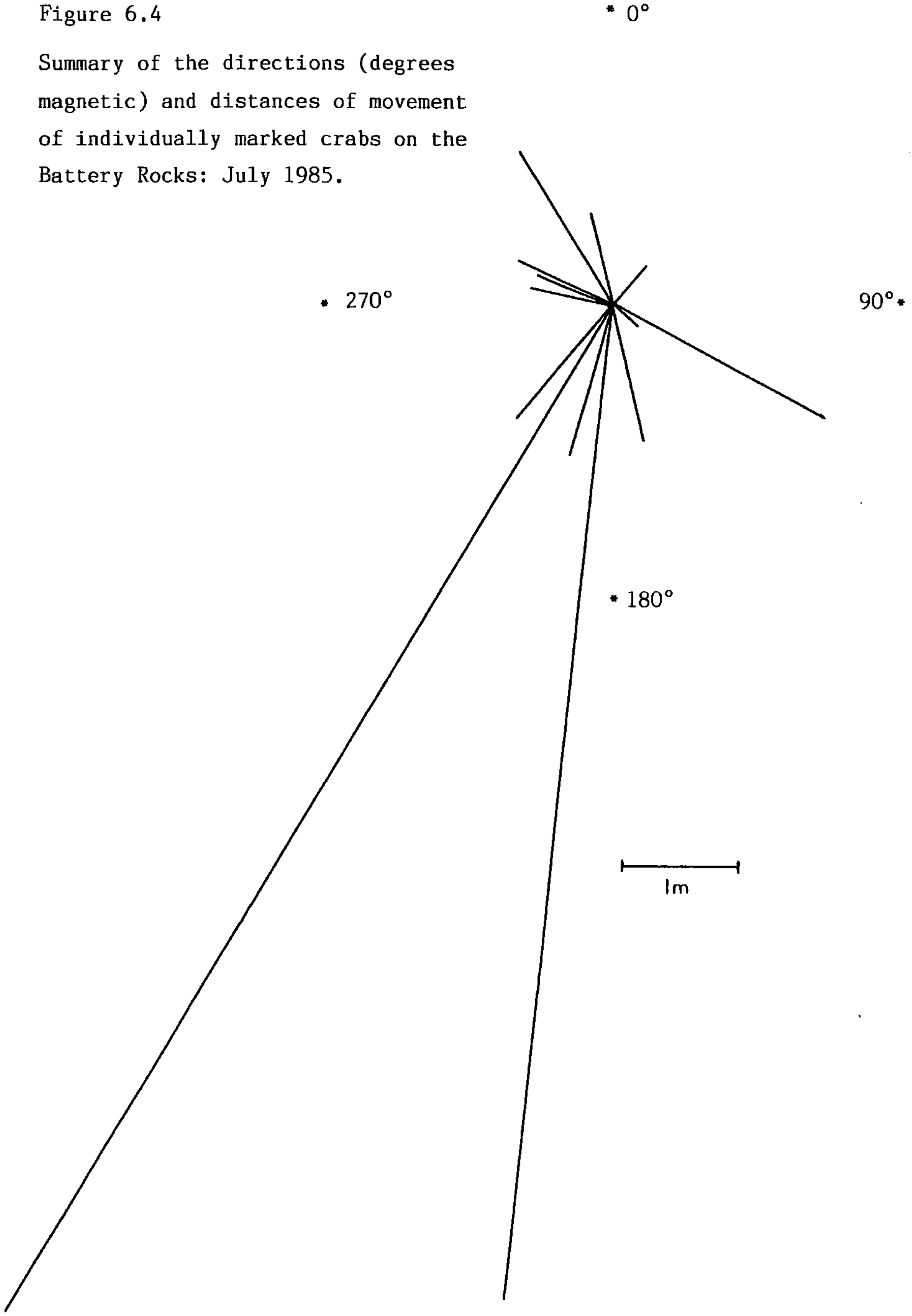


Figure 6.5

Summary of the directions (degrees magnetic) and distances of movement of individually marked crabs on the Battery Rocks: November 1985.

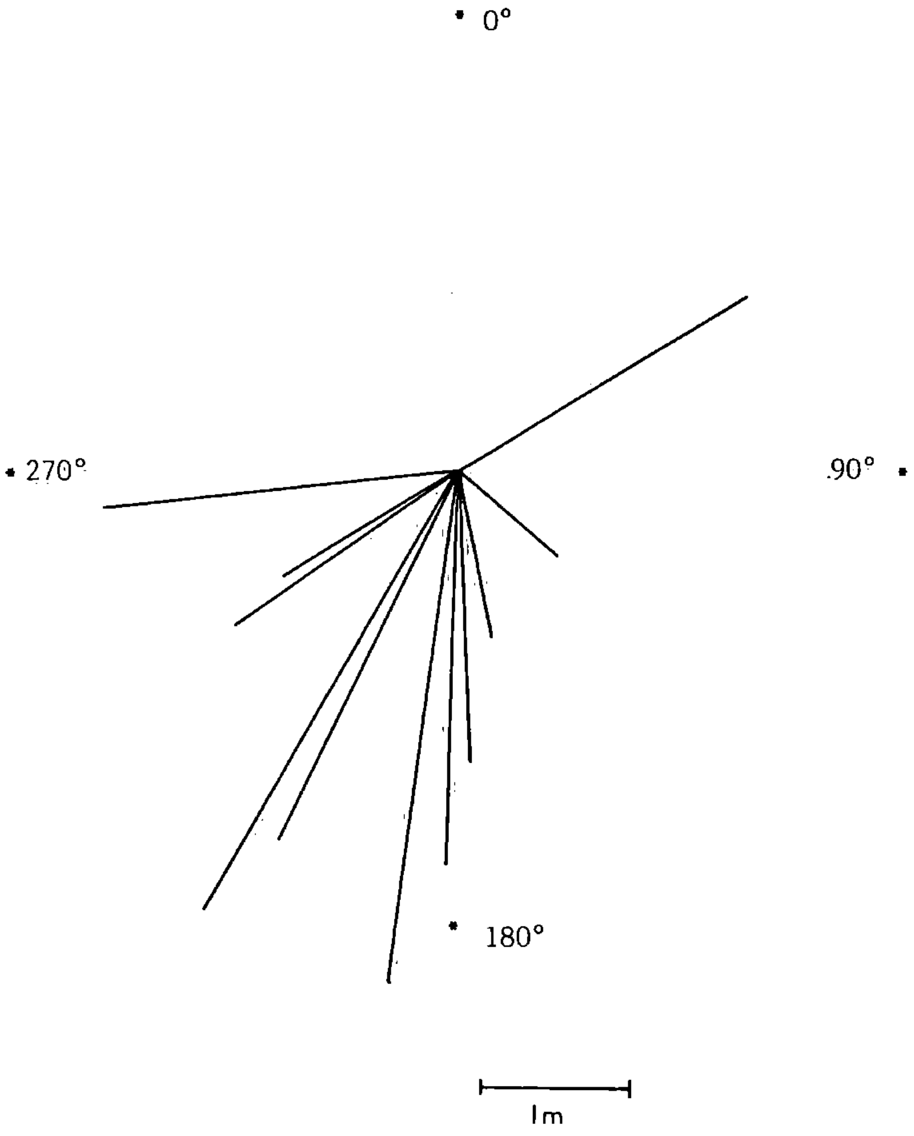
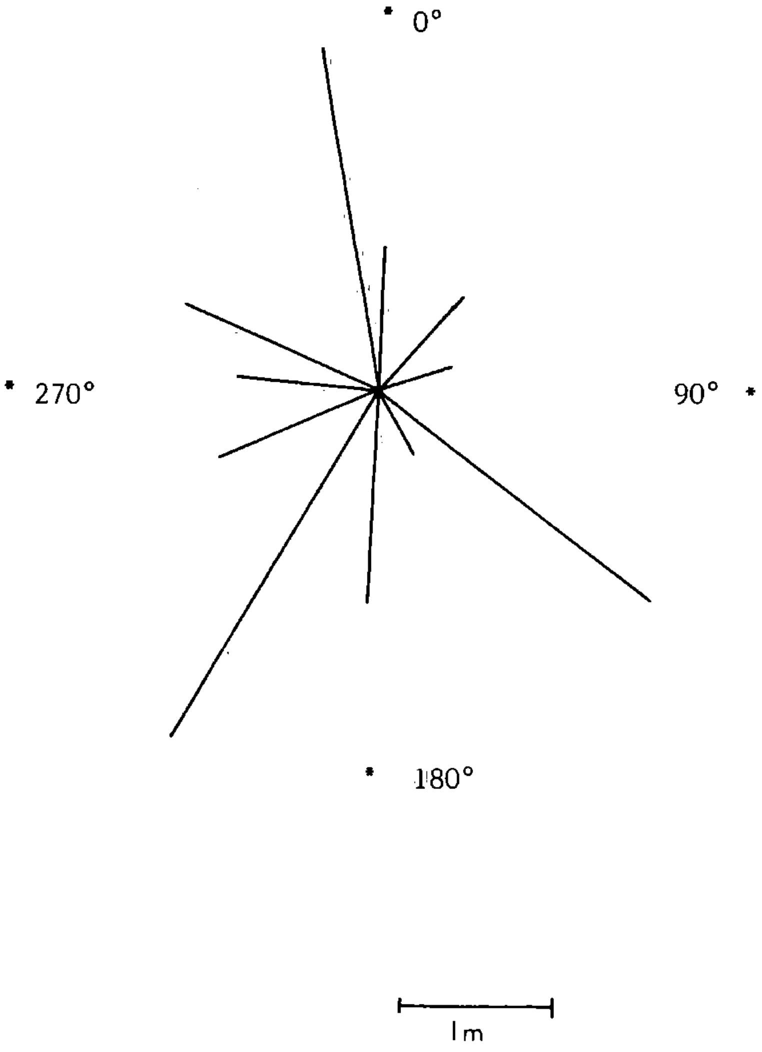


Figure 6.6

Summary of the directions (degrees magnetic) and distances of movement of individually marked crabs on the Battery Rocks: April 1986.



6.4 THE INFLUENCE OF SHELL CONTACTS ON RESIDENCE TIMES AND POOL POPULATION SIZES.

6.4.1 MATERIALS AND METHODS

As a preliminary to the study of how shell contacts may influence the sizes of littoral hermit crab populations and the residence times of individuals on the shore, it was first considered necessary to determine the mean population densities within the pools themselves. Accordingly, three shallow and accessible pools were thoroughly searched on 13 occasions over a period of some 16 months, and the numbers of P.bernhardus collected were recorded on each occasion. The general characteristics of the pools chosen for this study are summarised in Table 6.5.

Table 6.5
Characteristics of the three pools used for estimating the mean population density of Pagurus bernhardus on the Battery Rocks.
(* indicates substrate present)

pool	height (m) above chart datum	position on the shore	surface area (m^2)	substrates/habitats		
				Corallina	fine gravel	boulders
A	2.1	midshore	22	*	*	*
B	1.2	lowershore	7	*	*	*
C	2.5	midshore	50	*	*	*

Having established a "base-line" population density for the shore, a programme of artificial shell enrichment was then begun in one of the midshore pools, while a programme of shell impoverishment was carried out in the other. The shell enriched pool (pool "A" above) had as many empty shells of all sizes added to it as could be located in the area (a total of some 400-500 shells being added prior to the start of the investigation). The impoverished pool (pool "C" above) had all unbroken or potentially habitable empty shells removed. In addition, any dead or sluggish gastropods (i.e. any failing to withdraw into their shells upon being disturbed) were also removed from pool C to prevent their becoming a potential part of the hermit crab shell resource. The gastropods in pool C were checked daily during the study period, and any other shells carried into this pool between the tides were removed. By this means it was assumed that the crabs in residence in pool C would have access to no other shells but their own for the duration of the experiment. No such precautions were taken with pool A, however, and indeed every opportunity was taken in this case to enrich the shell resource available to its occupants. Any dead or injured gastropods were actually transferred from pool C to pool A to help to increase the shell resource still further.

The two pools were selected because of their similarity in height above chart datum and because of their broadly comparable distribution of habitats. The fact that pool A had a smaller surface area than pool C was not thought to make them unsuitable for this study since part of the larger pool consisted of deeper (0.5-1.0m) water with a substrate of large boulders, which consistently failed to reveal any hermits when examined by snorkelling. The overall "habitable" surface area of pool C, at some $30m^2$, was not considered to be appreciably larger than that for pool A.

At the start of the investigation both pools were thoroughly searched and all of the hermit crabs were collected and taken to the laboratory for marking. None of the animals showed any physical abnormalities, none were parasitised, no females were ovigerous (all females had ovaries at stage 2), and a spread was noted between the sizes, species of shell occupied, and the distribution of the sexes.

The technique devised for marking the animals and their shells had to be both efficient (in that a large number could be quickly and individually marked) and reliable (in that the marks would be easy to distinguish and would last for the duration of each phase of the experiment). Due consideration for the criteria that must be observed in marking (as reviewed generally by Southwood, 1966, and for Crustacea in particular by Cronin, 1949, and by Rebach, 1983) imposed specific constraints in that the marks were not to have been toxic and must not have influenced the animals' behaviour in any way or have increased their risks due to predation. With large animals the attaching of numbered tags is seldom difficult, but with animals whose shields (the only hard parts to which tags could have been securely fixed) are typically only some 3-4mm in length, this was found to be impractical. Equally, the chelipeds could not be marked since these are vulnerable in conflicts. Marks for the shells alone were not considered satisfactory due to the possibility of shell swapping. The method eventually chosen was to mark the carapace of an individual with a pattern of dots of quick-drying enamel modelling paint in such a way that only a small number of paint colours allowed a large number of animals to be marked. Small dots were placed on the animal (previously removed from its shell and blotted dry) with the finest brushes available (0000 series) so as not to interfere with the animal's movements or sensory perception. The dots were allowed 1½-2 minutes to dry before the crab was placed in a beaker of seawater in order to recover. The crab was also allowed to re-enter its shell at this time. The coding on the crabs was such that each number could be distinguished by the sequence of dots read in order moving clockwise around the carapace (Figure 6.7). Any position not required for a particular number was marked with white. Thus individual number 1 was marked as WRWWW, and number 99 would have been WWOOW etc. By this method 599 animals could have been individually marked with only 6 colours of paint. Each additional colour would have added a further 100 animals to the total. The paint marks were not found to be toxic (no animals held in laboratory tanks during a 5 week trial period died as a result of this treatment) and, if given sufficient time to dry, were found to last and still be visible for up to 4 weeks. After this time abrasion against the lip of the shell usually removed the mark, or the animal may have moulted. Even if most of the mark was removed, however, it was found that a lens usually gave a clue to the colour of what remained. It was decided that if any of the dots could not be distinguished then the animal would be ignored in subsequent work. In observations made after this treatment no marked individuals were seen to be victimised by unmarked animals of the same or larger size, and no marked animal appeared to show any "abnormal" traits of behaviour. Thus, it was concluded that the method was adequate for the task required of it.

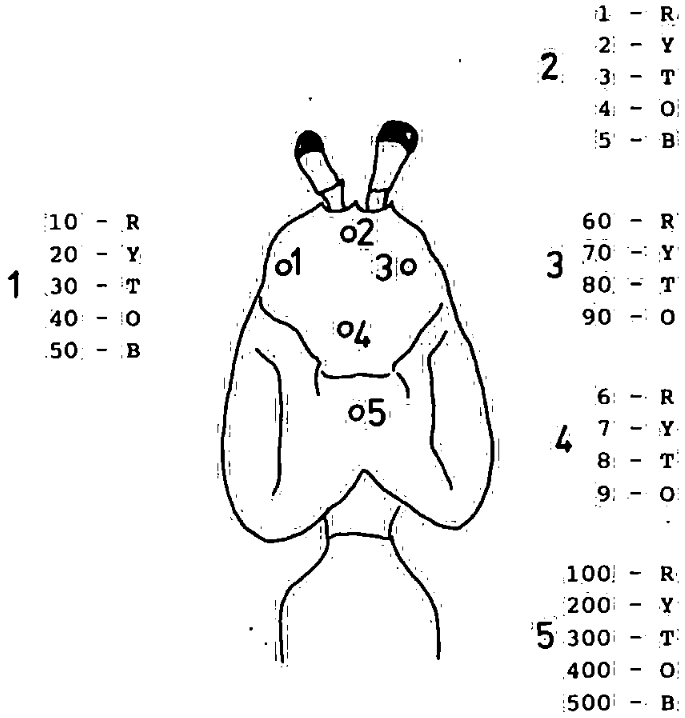
The numbering of the shells was uncomplicated, and each was marked with the corresponding numeral written in spirit ink on a small drop of "liquid paper".

The animals were kept in separate tanks during marking and subsequent recovery to prevent any stress due to overcrowding. Thus on day 1 of the experiment it was known that the only crabs in each of the two pools (n = 32 in the enriched pool A, and n = 27 in the impoverished pool C) were the individually marked ones just introduced. In addition to the mark carried by each animal, its shell was also given a colour code. A paint dot was placed near to

Figure 6.7

A METHOD FOR INDIVIDUALLY COLOUR-MARKING THE CARAPACE OF <u>PAGURUS BERNHARDUS</u>

- modified from Southwood (1966).



Colours (enamel modelling paint):

R - RED
Y - YELLOW
T - TAN
O - ORANGE
B - BLUE
W - WHITE

the shell aperture so as to be inconspicuous from above (hence attracting no attention to the animal) but ensuring that should any individual have managed to travel from one of the pools to the other then its origin would have been immediately apparent. A paint mark of the appropriate colour was also placed on each of the additional shells introduced into pool A.

On each day from the start of the experiment, for a period of 21 days, the two pools were thoroughly searched. Every crab found was examined for marks and had its position noted on a scale diagram of the pool. Details were recorded of the numbered animals located to allow a measure to be made of their respective residence times under the two regimes, and to detect whether any individuals were consistently found in the same positions. Records were also made of any new arrivals which had appeared since the last count. Once located, each new arrival had its shell marked according to the day of the experiment on which it was first noticed and by its order of location. Thus, the first new crab found on day 2 of the experiment was numbered "2_1" etc. The pereiopods of these new arrivals were also marked with colour dot sequences in order to allow identification even if shell swapping occurred. By these means the progress of the new arrivals could be monitored in the days to follow. It was thus found possible to determine the residence times for the new arrivals to each of the two pools as well as for the original inhabitants. Comparisons of pool population sizes and residence times could therefore be made upon the basis of the only difference considered to exist between the two habitats - that of the shell resource.

At the end of the 21 day period it was hoped to determine whether the manipulation of the shell resource would have any long-term effects upon the population densities of the two pools, and to determine how long the effects of impoverishment might last in the large pool. Both pools were therefore monitored for a further period of one month, and their population densities were re-measured at the end of this time. To determine which animals in particular had chosen to stay in each of the pools and which had left, both the original inhabitants and the new arrivals were "scored" by the subjective index of shell adequacy at the time that they were first marked. This was to allow any relationship between crab residence times and shell quality to be established.

Opportunity was also taken as part of this study to observe the recolonisation of another midshore pool which was regularly emptied of all of its resident crabs. In a study of a population of <u>Clibanarius</u> <u>vittatus</u> in the Gulf of Mexico, Fotheringham (1975) observed that a shore from which all hermits had been collected quickly became re-populated, returning to its pre-sampling density within only a few days. From this he concluded that the local population must be both "very large and very active". It was hoped to analyse the characteristics of the Battery Rocks population using the same criteria. The pool selected for this study had a surface area of some $25m^2$, and was thoroughly searched on 21 occasions between 10 November 1984 and 13 December 1985. All hermit crabs found were identified and removed to the laboratory where they were kept in large, shallow tanks of well aerated and cooled seawater for 3-4 days. During this period the empty pool was monitored for new arrivals. The new arrivals were collected and counted before the original inhabitants were returned. The newly increased pool population size was then monitored to see if it remained at the higher level until the next sampling date.

6.4.2 RESULTS

The number of Pagurus bernhardus collected from the three rock pools during the preliminary part of this work are recorded in Table 6.6, and suggest that a mean population density of some 1.81 ± 1.80 (i.e. between 0 and 4) individuals commonly occur per m^2 of pool area on this shore.

The residence times of the original marked inhabitants of the two pools are presented in Appendices Xa (impoverished pool) and Xb (enriched pool). The residence times of the new arrivals into each of the pools are listed in full in Appendices XIa (impoverished pool) and XIb (enriched pool). Analysis of these data (Table 6.7) shows that, irrespective of their status as original inhabitants or new arrivals, the crabs remained longer in the artificially enriched pool than in the impoverished pool.

Population data from the midshore pool which did not have its shell resource manipulated in any way (Figure 6.8) indicate that, under these circumstances, crab numbers tended to remain essentially within the range of the mean and standard deviation values throughout the 13 months of the study (mean pool population size of 28.90 ± 5.47 i.e. 1.16 m^{-2}). Even in the short time that this pool was left empty it can be seen from Figure 6.8 that new arrivals promptly appeared on each sampling date (mean number of new arrivals 12.6 ± 4.9). By the criteria mentioned above this would therefore suggest that the population of P.bernhardus on the Battery Rocks may be considered to be "large and active". That the increased numbers (resulting when the original inhabitants were replaced) were not maintained until the next sampling date, however, will form a critical part of the discussion to follow.

At the end of the experiment in which the shell resources had

Table 6.6

The numbers of Pagurus bernhardus collected from three intertidal pools on the Battery Rocks in order to determine the mean population density of this species on the shore. [pool characteristics in Table 6.5].

Date of collection	pool A	pool B	pool C
10.11.84	28	24	20
23.1.85	35	26	17
6.3.85	30	27	19
24.4.85	22	28	24
3.6.85	28	30	22
5.7.85	23	29	18
31.7.85	20	29	16
2.9.85	18	24	12
2.10.85	23	25	18
13.11.85	34	27	20
13.12.85	24	28	21
25.1.86	36	25	23
25.2.86	30	27	19

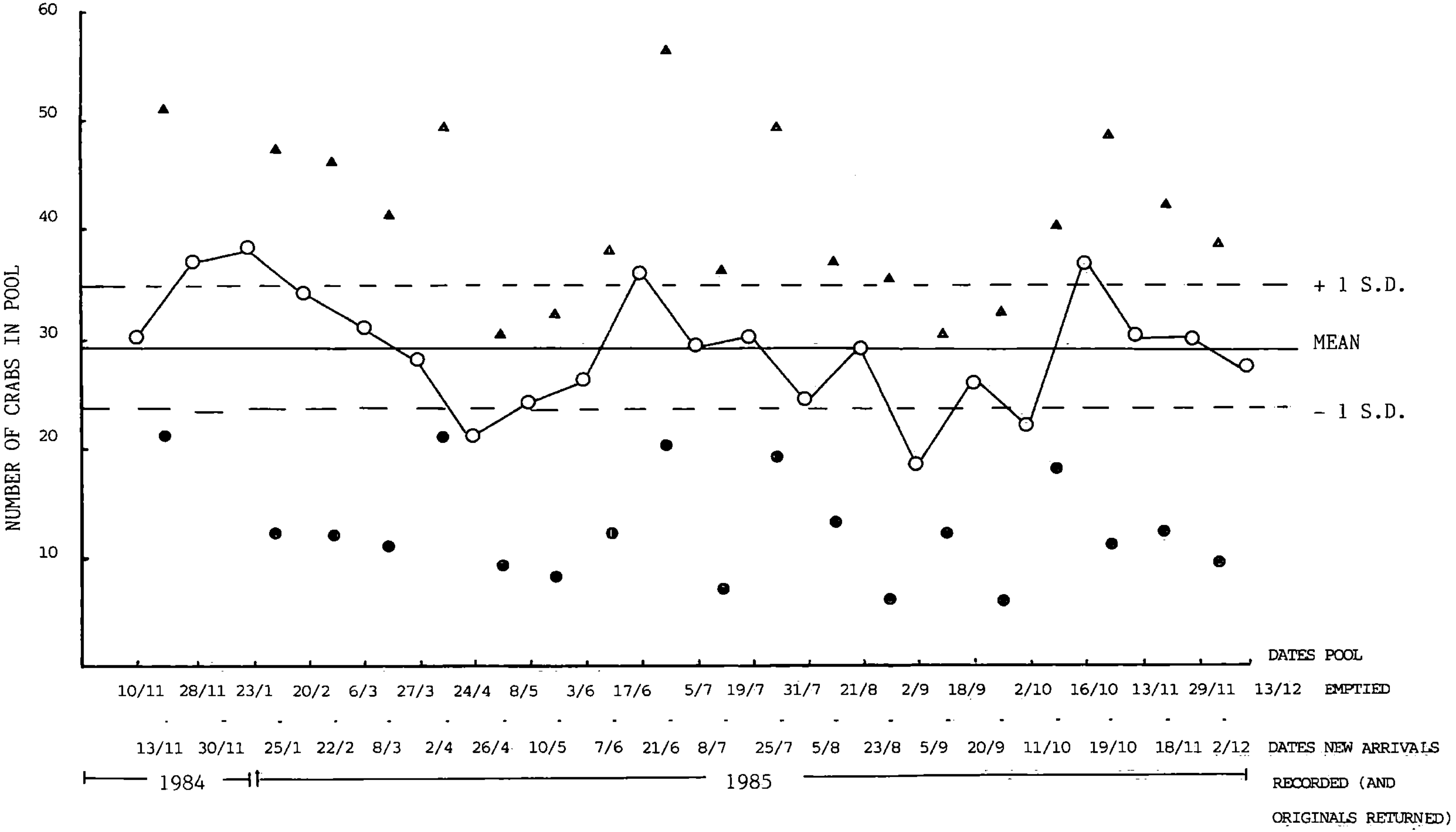
Table 6.7
The mean residence times (days ± S.D.) of the original inhabitants and of the new arrivals compared between the shell-enriched and the shell-impoverished pools.

Pool environment	Mean residence times (days ± S.D.)	
	original inhabitants	new arrivals
shell enriched	16.48 ± 6.25 (range 3-21+ days; n=27)	5.90 ± 4.87 (range 1-15+ days; n=21)
shell impoverished	6.78 ± 4.98 (range 1-21+ days; n=32)	3.40 ± 1.94 (range 1-8 days; n=30)
Variance Ratio (Bailey, 1959)	$F_{26,31} = 1.575$	$F_{20,29} = 6.308$
	$t = 6.644$	$d = 2.232$
	d.f. = 57	d.f. = 24
	$p < 0.001$	$p < 0.05$

Figure 6.8

The fluctuation in the population size (○———○) of *Pagurus bernhardus* in a midshore pool regularly emptied of crabs, with details of the number of new arrivals into the empty pool (●) and the consequently increased population size (▲) as the original inhabitants are returned.

Figure 6.8


60
50
40
30
20
10
NUMBER OF CRABS IN POOL
+ 1 S.D.
MEAN
- 1 S.D.
DATES POOL EMPTIED
10/11 28/11 23/1 20/2 6/3 27/3 24/4 8/5 3/6 17/6 5/7 19/7 31/7 21/8 2/9 18/9 2/10 16/10 13/11 29/11 13/12
13/11 30/11 25/1 22/2 8/3 2/4 26/4 10/5 7/6 21/6 8/7 25/7 5/8 23/8 5/9 20/9 11/10 19/10 18/11 2/12
DATES NEW ARRIVALS RECORDED (AND ORIGINALS RETURNED)
1984
1985

been manipulated, the impoverished pool was left with a population size of 4 (from an original size of 32 - Table 6.8). The enriched pool had a population size of 24 (original size 27 - Table 6.9). When both pools were re-examined one month later, the population of the impoverished pool had risen to 16 while that of the enriched pool had risen to 34. Thus the addition of a substantial number of shells to one pool did increase its long-term population size. Equally, the impoverished pool appeared to be recovering a renewed shell resource over the same period. Indeed, 22 empty shells were found in this pool when it was re-examined, 8 of which were intact and habitable by the criteria of Kellog (1976) i.e. entry would not be impeded by detritus or by the growths of tubiculous polychaetes, and none of the whorls were so damaged as to reduce the protection afforded by the shell as a whole.

The subjective indices of adequacy for the animals marked and examined for this study are listed in full in Appendices XIIa (impoverished pool) and XIIb (enriched pool). The residence times for the crabs in shells of different qualities are analysed in Table 6.10. This demonstrates that the animals remaining for the longest periods in the impoverished pool were the smaller animals (i.e. those in shells of adequacy values 1-2). Although there are no significant differences between the residence times of the smallest crabs (adequacy value 1) when the different pools are compared, it can be seen that the residence times in the impoverished pool became significantly shorter when compared with the enriched pool as the animals began to outgrow the shells available. For those crabs in the enriched pool the possibility of shell swapping would mean that the nature of the original shell would be less important. Indeed, of the 48 marked crabs observed in the enriched pool (Table 6.9), 24 (50%) swapped shells during the course of the experiment (in

Table 6.8

The composition of the population of Pagurus bernhardus in the shell-impoverished pool during the course of the experiment to determine the influence of shell contacts on crab residence times.

Days into experiment	number of original marked animals in pool	new arrivals that day	previous new arrivals still resident	total number of crabs in pool
1	32	0	-	32
2	28	2	-	30
3	28	1	1	30
4	23	3	2	28
5	17	1	3	21
6	14	3	4	21
7	12	2	4	18
8	12	2	4	18
9	11	0	6	17
10	8	1	6	15
11	8	0	4	12
12	7	2	3	12
13	4	3	4	11
14	4	0	4	8
15	2	1	3	6
16	2	2	3	7
17	1	1	5	7
18	1	3	5	9
19	1	0	4	5
20	1	3	4	8
21	1	0	3	4

Total observed = 32 + 30 = 62

Table 6.9

The composition of the population of <u>Pagurus bernhardus</u> in the shell-enriched pool during the course of the experiment to determine the influence of shell contacts on crab residence times.

Days into experiment	number of original marked animals in pool	new arrivals that day	previous new arrivals still resident	total number of crabs in pool
1	27	0	-	27
2	27	2	-	29
3	27	0	2	29
4	25	3	1	29
5	25	0	4	29
6	25	2	3	30
7	24	2	5	31
8	24	0	6	30
9	23	3	5	31
10	23	0	7	30
11	20	1	6	27
12	20	0	7	27
13	20	2	6	28
14	19	0	8	27
15	19	2	6	27
16	17	0	7	24
17	16	0	7	23
18	16	0	6	22
19	16	1	6	23
20	16	0	6	22
21	16	3	5	24

Total observed = 27 + 21 = 48

Table 6.10

A comparison of the mean residence times (days ± S.D.) of crabs in shells of different qualities between the shell-enriched and shell-impoverished pools.

Pool environment	shell qualities (subjective index of adequacy)			
	1 (too large)	2	3	4 (too small)
shell-enriched	9.00± 8.76 (n=4)	12.04± 8.17 (n=23)	12.21± 7.91 (n=14)	12.14± 6.59 (n=7)
shell-impoverished	10.80± 7.60 (n=5)	6.58± 3.83 (n=24)	3.74± 2.26 (n=23)	2.10± 1.73 (n=10)
Variance Ratio (Bailey, 1959)	$F_{3,4}$ = 1.329	$F_{22,23}$ = 4.54	$F_{13,22}$ = 12.26	$F_{6,9}$ = 14.54
	t=0.331	d=3.585	d=3.908	d=3.935
	d.f.=7	d.f.=31	d.f.=14	d.f.=7
	$p>0.05$	$p<0.01$	$p<0.01$	$p<0.01$

Appendix XIIb). In the impoverished pool 62 crabs were marked in total (Table 6.8), but only 1 swapped its shell (in Appendix XIIa). Thus the stress of shell limitation was removed under the regime of shell enrichment.

By noting the positions of marked animals from day to day on scale diagrams (similar in construction to Figure 6.2) it was also possible to observe from this study that individuals did not tend to occupy fixed positions in the pools, and did not habitually occur in the same part of any one pool from one day to the next. Thus it may be concluded that hermit crabs on this shore show no evidence of territorial behaviour.

6.5 THE EFFECT OF DEPTH AND SLOPE ON THE MOVEMENT OF *PAGURUS BERNHARDUS*.

6.5.1 MATERIALS AND METHODS

A number of crabs were collected at random from the Battery Rocks during the summer of 1986. They were transferred to the laboratory and held in 50 litre glass aquaria filled with well-aerated, cooled seawater previously collected from the same shore. Animals were taken on a falling tide and were transported to the laboratory with the same depth of water overhead as occurred at the moment of their collection. By this means it was hoped to keep the pressure to which they were exposed as constant as possible before the start of the experiment. The crabs were tested individually by being placed in the centre of a circle of radius 10cm (a distance over which observation predicted that they would be likely to move in a straight line) and they were timed to cover this distance with different depths of water overhead. The water was drained from the tank to the required depth with a siphon, and the depth was read from a scale fixed to the outside of the glass.

A second series of experiments were then conducted with the tank tilted at a shallow angle (some 30° from the horizontal - a typical slope for the middle part of the shore at Battery Rocks). Individuals collected and treated as before were placed onto the slope with a fixed depth of water overhead and were scored according to whether their subsequent movement was upslope, alongslope, or downslope. By this means it was hoped to determine whether the slope upon which an animal found itself would influence its pattern of movement in any way as the depth of water overhead decreased with a falling tide.

Each of the animals used in the experiment was given the minimum of handling, each animal was used only once, no baits or incentives were used, and all animals were of approximately the same size (judged by the sizes of the large chelipeds and at least one of the other pereiopods). None of the animals had lost or were rejenerating pereiopods. The experiment was conducted during the summer months to ensure that the patterns of movements would not be influenced by any aspects of reproductive behaviour. The base of the tank was clear of any obstruction that may have influenced "exploratory" behaviour, and no substrate was present which may have influenced locomotory speed. The laboratory was evenly illuminated to prevent any shadow effects, and the animals were not disturbed by any movements in the vicinity.

6.5.2 RESULTS

The mean times taken for the crabs to move a distance of 10cm are recorded in Table 6.11. The depth values are recorded in increments of 5cm.

The differences between the means are significant (ANOVA; $F_{5,63} = 12.33$) with the time taken to cover the set distance being the least when the depth overhead is less than 5cm (d = 5.00; $p < 0.001$).

The proportions of individuals which chose to move upslope, alongslope, or downslope when exposed to different depths of water overhead are represented in Figure 6.9. This histogram is pivoted around the mid-point of the alongslope "segment" and demonstrates that the movement is predominantly downslope when the depth overhead is below some 5cm, but becomes less predictable with depths greater than this.

Thus it may be concluded that the depth of water overhead influences both the speed and the direction of movement of hermit crabs on the shore, with the effect being particularly significant when the depth falls to 5cm or less.

Table 6.11

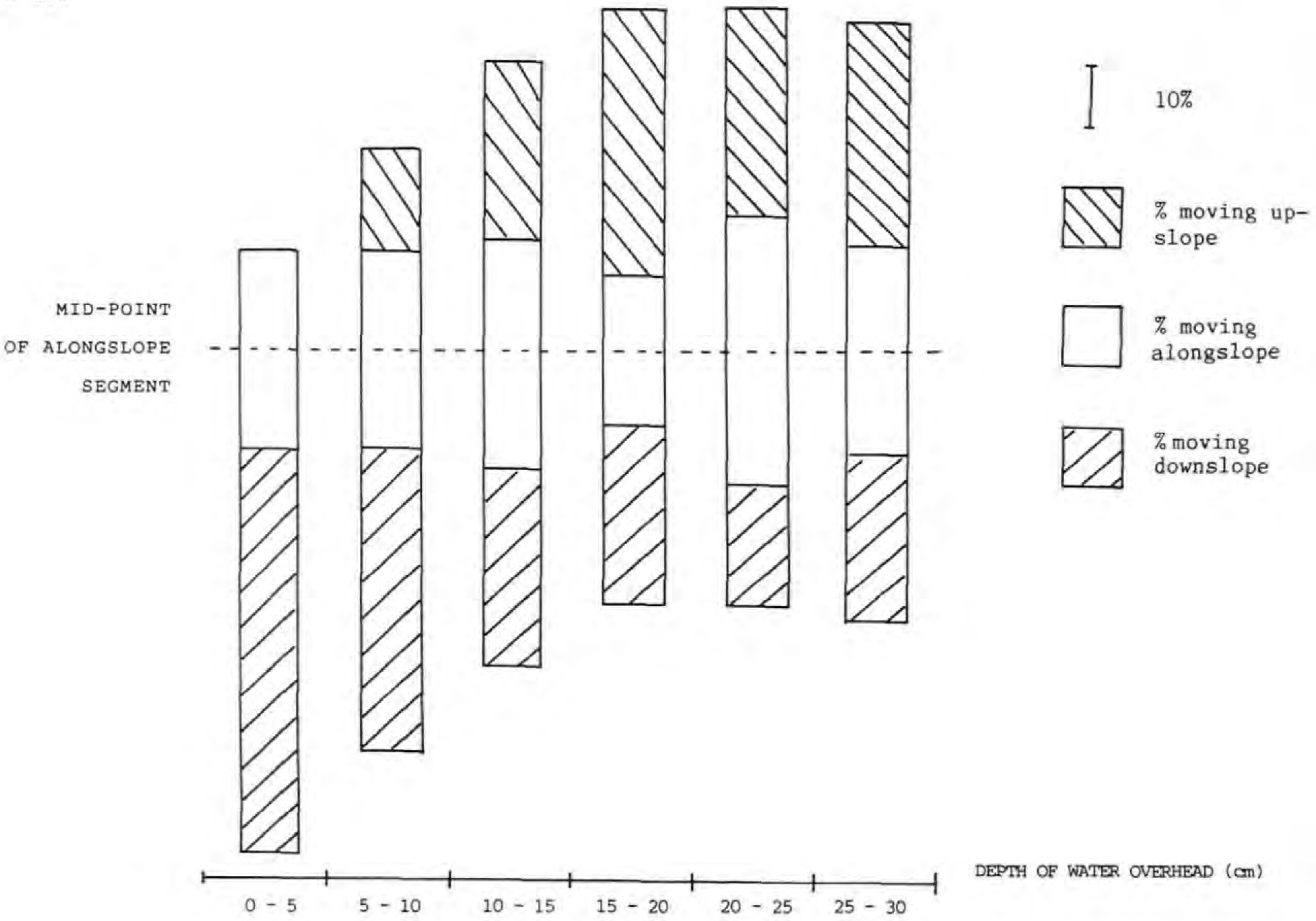
Mean times (seconds ± S.E.) taken by individuals to cover a set distance of 10cm in a laboratory tank when exposed to different depths of water overhead.

Depth overhead (cm)	number	mean time (s) ± S.E.
25 - 30	12	7.01 ± 0.34
20 - 25	11	5.75 ± 0.39
15 - 20	11	7.41 ± 0.53
10 - 15	10	7.79 ± 0.67
5 - 10	11	6.62 ± 0.53
0 - 5	13	3.68 ± 0.13

Figure 6.9

The proportions of Pagurus bernhardus moving upslope, alongslope, or downslope in response to different depths of water overhead.

Figure 6.9


MID-POINT
OF ALONGSLOPE
SEGMENT
10%
% moving up-slope
% moving alongslope
% moving downslope
DEPTH OF WATER OVERHEAD (cm)
0 - 5
5 - 10
10 - 15
15 - 20
20 - 25
25 - 30

6.6 DISCUSSION

The patterns of movements and migrations observed in different populations of hermit crabs offer yet another demonstration of the enormously diverse and unpredictable behaviour typical of this group. Some individuals have been shown to wander great distances during a 24 hour period - individuals termed "errant" by Mitchell (1973) and "nomadic" by Hazlett (1983a) - while others may remain in essentially the same area for long periods of time. Some may be sessile since they occupy fixed (i.e. attached) tubes, some may move 0.5m in a day but then return to the same spot, and others may meander 20m or more in a day but effectively change their net positions by only some 1-2m (Hazlett, 1981a). Nomadic movements may occur both along the shore (with the crabs remaining in essentially the same zone) or perpendicular to it (exposing the animals to a range of zones), though any measurements made of the distances covered can only ever be regarded as minimum estimates, since these animals rarely cover any appreciable amount of ground in a straight line. Hermit crabs will stop and change direction in order to investigate objects in their vicinity, to avoid or interact with other crabs, to feed, to attend sites of gastropod predation (and hence sites of potential new shell availability - McLean, 1973; Rittschof, 1980a, 1980b), and in order to avoid their own predators (Hazlett, 1981b; Stachowitsch, 1979). These movements may be made even more unpredictable by such complications as the habit of at least one species to routinely turn to its left if no specific stimulus attracts it (Mackay, 1945), and the tendency of most hermits to continually change direction when moving towards two separated stimuli such that they perform a zig-zag route between them (alternately making for one or the other and not for a point midway between the two - Fraenkel and Gunn, 1961). Such random movements may result in some animals entering quite novel environments - perhaps even being the first vagile animals to re-enter "graveyard" areas, and reintroducing other forms to these areas carried in with them as epizoites (Fedra *et al.*, 1976).

Migrations by large groups of crabs may be more conspicuous than the random movements made by individuals, and entire populations have been noted to effectively disappear from their habitats at certain, usually unfavourable, times of the year only to re-appear again later. The population of *Pagurus longicarpus* migrates from the littoral zone of Rhode Island, U.S.A. where it has bred during the summer into deeper water during the winter (Rebach, 1969, 1974), as does that of *Clibanarius vittatus* in Texas (Fotheringham, 1975) and *Pagurus bonairensis* in Florida (Dugan, 1983). Avoidance of debilitatingly cold temperatures (which would leave the animals sluggish and more vulnerable to predation) may be the reason for these movements. An alternative explanation, however, may be that migrations could provide a means of allowing the animals to routinely enter deeper water where encounters with large gastropod shells would be more likely. It may even be that the situation is in fact reversed, in that the population may as a rule live offshore and may only migrate into the littoral zone temporarily in order to congregate and hence facilitate the finding of a mate. Such patterns of population migration are not, however, universal strategies, and many populations mentioned in the literature show no evidence of routine migrations, either for individuals or groups (e.g. Tomlinson, 1960; Stachowitsch, 1979; Hazlett, 1983a). Equally, homing behaviour is not thought to occur in hermit crabs (Rebach, 1978).

Irrespective of the cause of a movement, however, and whether it is short-term or long-term, each animal must seek a balance between its benefits (in terms of the potential acquisition of resources) and its costs (the expenditure of energy, the risks of increased predation or exposure to environmental stresses, and the use of time that could perhaps be more profitably spent elsewhere - Hazlett, 1981b). The situation observed in any population, therefore, can only ever represent the most advantageous compromise available to its members.

The issue of the control and co-ordination of migrations has largely been addressed to populations, and less to individuals. Stimuli such as the tidal cycle itself (with its associated temperature and pressure changes) perhaps combined with lunar and solar influences, have been suggested as control mechanisms to co-ordinate the movements of populations (Rebach, 1983). The random movements observed by many authors, however, and conspicuous in the Battery Rocks population studied here, argue most forcefully for stimuli which act at the individual level. The responses to pressure noted in a wide range of littoral animals (in Naylor and Atkinson, 1972) may indicate just such a stimulus - particularly since threshold responses have been shown at small fractions of one atmosphere (Knight-Jones and Qasim, 1955). Cuticular pressure receptors of the gas-plastron type (Digby, 1972) may, therefore, explain the sensitivity observed in members of this Battery Rocks population to heads of water of as little as 5cm - a pressure equivalent of only some 4-5 x 10^{-3} Bars. It is the significance of individual response in littoral hermit crabs which has been addressed here as part of this study into the life history strategies of Pagurus bernhardus.

The nearest neighbour measurements taken on this shore indicate that P.bernhardus is distributed randomly in rock pools on the Battery Rocks, both within and between tidal cycles at all times of the year. Members of this population show no tendencies to form the sort of aggregations that might suggest synchronous migratory behaviour. Thus, although associations will occasionally be enforced by irregularities in the terrain or for the purposes of mating, the members of this littoral population appear, on the whole, to live isolated and independant lives. The question of territoriality in littoral hermit crab populations was therefore considered as a possible strategy to maintain separation. The whole field of animal spacing and territoriality is generally regarded as complex, and the interpretation of field data tends to be highly controversial (McBride, 1971). Hazlett (1969) noted no tendency for crabs to be found in the same parts of experimental tanks from day to day, and reports of their migratory behaviour would appear to generally argue against the occupation of fixed positions for any predictable amounts of time. Some crustaceans (e.g. fiddler crabs) do occupy fixed territories (Dingle, 1983), and the advantages of possessing such areas - forms of "personal space" - are well documented in terms of resource partitioning and breeding success (Warner, 1977; Hyatt, 1983). Hermit crabs generally, however, only appear to maintain the space immediately around themselves wherever they happen to be, and do not seem to be inclined to defend a fixed piece of ground from one period to the next. Equally, these personal spaces tend to be flexible, depending upon conditions of overcrowding: they may become smaller when individuals are more densely packed together, and they may not necessarily even be the same in all directions - usually being greatest towards the front, the direction in which an attacker is most likely to be first seen (Meadows and Mitchell, 1973). On the Battery Rocks, marked crabs were not habitually found to occupy fixed positions in pools, and the nearest neighbour studies reflect the essentially random arrangement of each individual relative to the others. Scraps of food material placed near to particular animals provoked no recogniseable displays which might have related to ownership - the first animal to detect the material made for it and if more than one individual arrived at the site at the same moment then it was typically the larger individual that won the prize. This was noted irrespective of which animal had travelled the least distance and hence which may have been within its own "territory". Thus, territoriality was not considered to be a factor in the life history strategy of this population. Insufficient studies have been reported in the literature to determine whether a lack of territorial behaviour is typical for this species. However, in view of the other aspects of behaviour investigated during this study, it is suggested that the occupation and defence of a fixed piece of ground or of the resources therein, is not a necessary strategy for this species.

When studying the movement patterns of P.bernhardus on the Battery Rocks, it was conspicuous that individuals did not move synchronously in any set direction, and none were motivated towards particular geographical goals. Movements could not be described as migrations and were typically erratic. The crabs were predictably influenced by such aspects of behaviour as shell examination and attraction to food or to other objects conspicuous enough to warrant investigation. Few interactions with other crabs were noted during these experiments, but population densities were not great and the small numbers rarely brought animals into contact. Thus it may be concluded that whatever stimulus motivates these animals to move around the shore operates at an individual level.

The results of the experiments on shell enrichment and shell impoverishment clearly demonstrate the importance of shell contacts in influencing both movements and residence times. In a pool where the shell resource was not manipulated, the mean population size of the crabs remained within narrow limits over a prolonged period. New arrivals remained only a short time and, irrespective of the repopulation which occurred when the pool was empty, the "carrying capacity" of the pool was essentially unaffected when the shell resource remained constant. The population size and the residence times of the inhabitants were, however, both significantly increased when a pool was enriched by an increased number of empty gastropod shells. Equally, a pool from which all spare, unbroken, shells had been removed showed a population decline, with the residence times of the inhabitants being significantly reduced under these circumstances. Thus, although the shell resource may not always be the primary factor controlling crab population size (Gilchrist, 1986), it must be concluded that the number and quality of shell contacts should be one of the most significant factors to be considered when attempting to predict or understand hermit crab population dynamics.

The quality of the shell resource also influences the residence times for individuals in pools, and may influence the migration of hermit crabs around the shore and from one pool to another. This would suggest that an animal's increasing size could act as a key stimulus to migration, having its effect once the adequacy of any individual's shell contacts becomes reduced. This would be particularly significant when a crab fails to encounter any shells larger than the one it presently occupies, or when no shells of improved quality are available.

The relationship between shell quality and pool residence time re-emphasises the influence of shell-limitation upon behaviour. The animals residing for the longest periods in the pools were conspicuously those in the (relatively) larger shells i.e. shells of subjective adequacy values 1-2, and hence crabs not subject to shell limitation. A crab arriving in a smaller shell (i.e. value 3-4) however would be unlikely to remain for any prolonged period unless it subsequently encountered shells larger than its own. Thus a pattern of dispersal becomes evident in hermit crabs that does not conform to the traditional strategies of dispersal suggested for other groups (e.g. Gaines and McClenaghan, 1980): to account for the dispersal by "social subordination", for example, would be inappropriate since among hermits it is the largest (and hence the most dominant) animals which must move on; "genetic-behavioural polymorphism" is again inappropriate since the most aggressive individuals will also be the largest and hence the most shell-limited. Equally, if there are no larger shells available then aggression towards less dominant individuals will bear no rewards since these subordinates will already be in smaller shells. "Saturation-presaturation dispersal" is not a relevant explanation since it is not population density <u>per se</u> which is the problem, but more an absolute defficiency of resources. Finally, the strategy cannot be explained by "social cohesion" since, as discussed, hermits are not social animals. Thus, a different mechanism must be sought to explain hermit crab dispersal strategies, an explanation which must take account of the absolute requirement of these animals for protective structures which they do not themselves manufacture - a situation with few parallels in other groups studied. Since the motivation for migration clearly seems to be shell-limitation, the patterns of dispersal may therefore be suggested to be due more to "resource depletion" than to any social or aggressive interactions, and thus movement may be more a "resource dependant" phenomenon than a density dependent one in this situation. This will be discussed further in Chapter 7 in the context of the overall life history strategy of this species.

In addition to the effects of shell enrichment on hermit crab movement patterns and residence times, it was also noted during these experiments that adding spare shells to a system greatly reduced the aggression which frequently accompanied sudden (artificial) increases in population densities. It was also noticeable that fewer "aggressive" interactions occurred between individuals in the shell-enriched pool than in the impoverished pool. This further emphasises the powerful effect that a surplus of this resource can have on the behaviour of hermit crabs.

Hermit crab movement is not only influenced by shell contacts. Although Hazlett (1981b) considers that the nature of the substrate is the primary influence on movement patterns in hermit crabs, it can be seen from these experiments that the depth of water overhead and the slope of the shore both significantly affect an animal's speed and the direction it follows. The role of this sensitivity to depth and slope, and the way in which it complements shell-contact as a mechanism for controlling dispersal, is discussed in the broader context of life history strategies in the next chapter.

CHAPTER 7

OPTIMAL LIFE HISTORY STRATEGIES IN *PAGURUS BERNHARDUS*

It will be the strategies which hermit crabs employ in order to best exploit the shell resource available to them which will ultimately determine the fitness of each individual. Thus, natural selection acting upon the most successful individuals (i.e. those making the greatest proportionate genetic contribution to subsequent generations) will dictate which strategies will become established in the repertoirs of particular populations. Since hermit crabs are predominantly deep-water forms that sacrifice the security of the sublittoral for a period of their lives, this littoral "phase" must have definite and reinforcing advantages to make the hazards acceptable. These advantages must be identified before the overall life history strategies employed by this group can be understood.

Any successful strategy must first reflect the fact that hermit crabs face a unique set of difficulties - imposed as a direct result of their habit of protecting their bodies within structures which they do not themselves manufacture: the shells of gastropod molluscs. A shortage of this vital protective resource will be an inevitable feature of any intertidal habitat, however, since empty gastropod shells will quickly be rendered useless by breakage, erosion, burial, or removal by currents (Vance, 1972b; Kellog, 1976). It has even been suggested (Spight, 1977) that it would be unrealistic to expect a surplus of shells to be available since it is only the activities of hermit crabs which will keep shells circulating in this region (a situation which has implications for the relationship between shell numbers and population size, since it implies that it may not be the number of shells that limits the number of crabs but perhaps the other way around). Thus, there can never be enough shells to satisfy all potential "customers" and, as a result, all populations of hermit crabs will inevitably be "shell-limited" to some extent. This must lead to many individuals compromising over shell quality and occupying what must be, to them at least, sub-optimal shells i.e. too large to be comfortably carried, too small to permit growth after ecdysis, too badly damaged to protect the body when withdrawn etc. Most crabs will, therefore, benefit at some time from obtaining an alternative shell in order to improve their chances of survival.

For most animals - including other arthropods - growth and development proceed according to a genetic programme influenced only by environmental factors such as food supply or environmental temperature. With hermit crabs, however, the eventual size reached is highly dependent upon the availability of a resource over which the animals have little direct control. The ultimate source of the shells used by a population of hermit crabs lies with the gastropods themselves and various authors have attempted to determine the mechanisms by which shells are obtained. Natural snail mortality is an obvious source, but active predation upon snails has not been ruled out (Brightwell, 1951b, 1953; Purtyman, 1971; Rutherford, 1977). Scully (1983), however, considers that most of these latter observations involved attacks on sick or injured snails, or were staged under artificial circumstances which did not permit the snails any escape, and that such predation is probably rare under normal circumstances. However, when predators do attack and kill snails, it is inevitable that hermits move in and attempt to take over any undamaged and newly vacated shells - even though they themselves played no part in the predation. Notwithstanding the occasional chance encounter with a suitable empty shell, therefore, most of the undamaged shells that a crab comes into contact with will either be occupied by a living snail, or by another crab. Hermits rarely seem to investigate or exploit the former source where the presence of an intact periostracum on a living gastropod may mask the release of calcium from the shell which is thought (Mesce, 1982) to act as the stimulus for shell investigation. Thus the most realistic potential for any hermit to improve its shell would seem to be offered by one that is already occupied by another crab. Direct aggression employed against another crab (of the same or even another species) either to force an exchange or an eviction will, therefore, be the most usual way that a hermit crab obtains a new shell under natural circumstances.

If there are no larger shells available, however, it has been demonstrated that growth will not occur and that after perhaps a small number of static or even reduced moults the animal will die (Chapter 4). Thus, shell-limitation can reduce longevity and can influence the eventual dimensions that individuals (and even entire populations - Drapkin, 1963) may attain. Since the problem will become more severe for the largest individuals, it can be seen that the shell resource is ultimately the most powerful single factor determining hermit crab population dynamics. Survival for most hermit crab populations will therefore depend upon their overcoming the size-detrimental restrictions imposed by a frequently inadequate shell resource - restrictions which may, for example, lead to individuals being unable to attain a prescribed age or size established as the criterion for reproductive maturity. The importance of selecting the most optimal shell is, therefore, paramount. Unfortunately, gastropod shells by their very borrowed nature are unlikely to be perfect in every required parameter - implying that the nature of shell choice and selection must either be enormously complex or very simple. The animals must either select only certain species of shell by subjecting them to a most rigorous analysis of their various combinations of dimensions, or they must simply test every potential new home with a view to compromising over "best-fit". Since the mathematical indices of shell preference have been shown to be flawed, and since no predictable formulations governing shell choice have been convincingly demonstrated, it is considered here that random investigation is likely to play the most significant role - a situation which may go further towards explaining why individuals will continue to examine and move into new shells even after they have been allowed a choice of innumerable apparently optimal residences. Thus the subjective index of shell suitability proposed in Chapter 3 may contribute to a more realistic understanding of the shell resource available to a population.

In order to maximise the chances of each individual coming into contact with the best possible shell resource, and to enable it to grow as efficiently as possible, to attain the full potential of its programmed longevity, and to reproduce, an individually centered programme of movement is suggested (Chapter 6). This implies that it is the quantity and the quality of its shell contacts which determines whether an individual remains in a specific area or moves on. If shell contacts are frequent (both of empty shells and of those occupied by other crabs - since even these will be likely to become available eventually) the stimulus to move on will be reduced, and the animal may remain in one pool or on a particular stretch of shore or seabed for a prolonged period. However, if such contacts are infrequent, or if the only available shells are too small or are too badly damaged or eroded to offer satisfactory protection, then the stimulus to move on will be greater. By this means the smaller individuals - those likely to be satisfied by the largest range of shells - will remain in the littoral zone until they attain a size that can no longer be satisfactorily protected by the largest shells available. It may even be that settlement will be encouraged in this region in order to specifically exploit the gastropod resource so typically rich here. When stimulated to migrate an offshore movement will occur, since the sensitivity to water pressure that also keeps the crabs safely in the pools as the tide falls will ensure that movements will be into the sublittoral - the area where the larger gastropods (and their shells) are more likely to be encountered. This may also explain why hermits of a wide range of sizes may be noted sublittoraly, since they are not encouraged to move by some specific age or seasonal stimulus, but by a response to shell adequacy as each individual has perceived it.

Although no particular regard was taken of sex ratios of crabs collected during this investigation, the data summarising the proportions of males and females in each collection (Chapter 5) do not suggest that the 1:1 ratio predicted as common for natural populations (Fisher, 1930) occurs. Different size classes are not evenly represented in this population (Figure 7.1), and analysis of this size-frequency data, plotting the percentages of males in specified size classes against the size classes themselves, does not reveal a straight line at the 50% level that would confirm a 1:1 relationship (Figure 7.2). The pattern which does emerge, however, is of the type that has been termed "anomalous" (Wenner, 1972), and confirms both that the average size of the males in this population is larger than that of the females, and that the largest size classes are essentially male dominated. Several explanations are possible for this pattern, including differential migrations of particular size-classes into or out of the study area, differential

Figure 7.1

The distribution into size-classes of 440 *Pagurus bernhardus* collected randomly from the Battery Rocks.

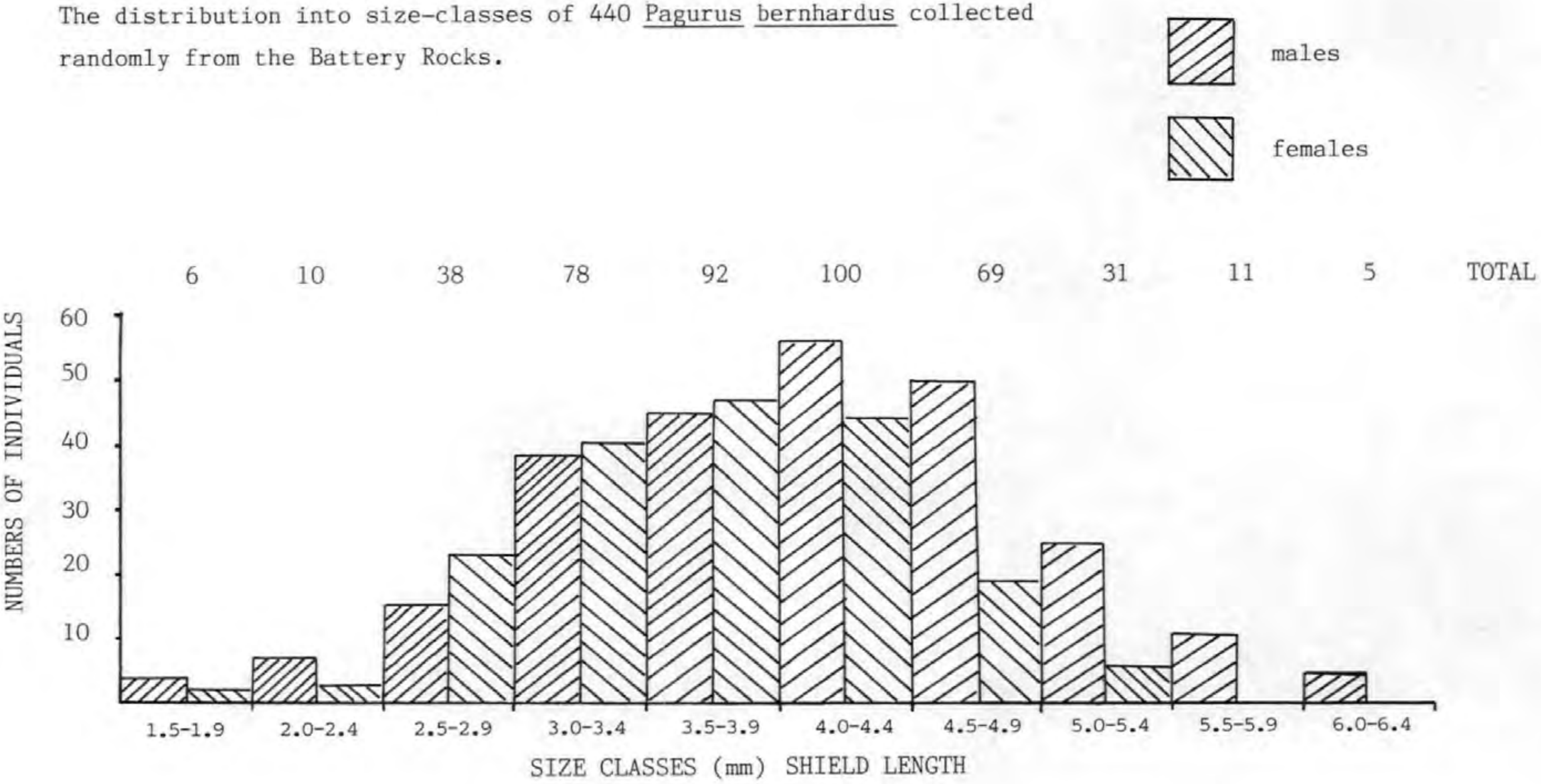
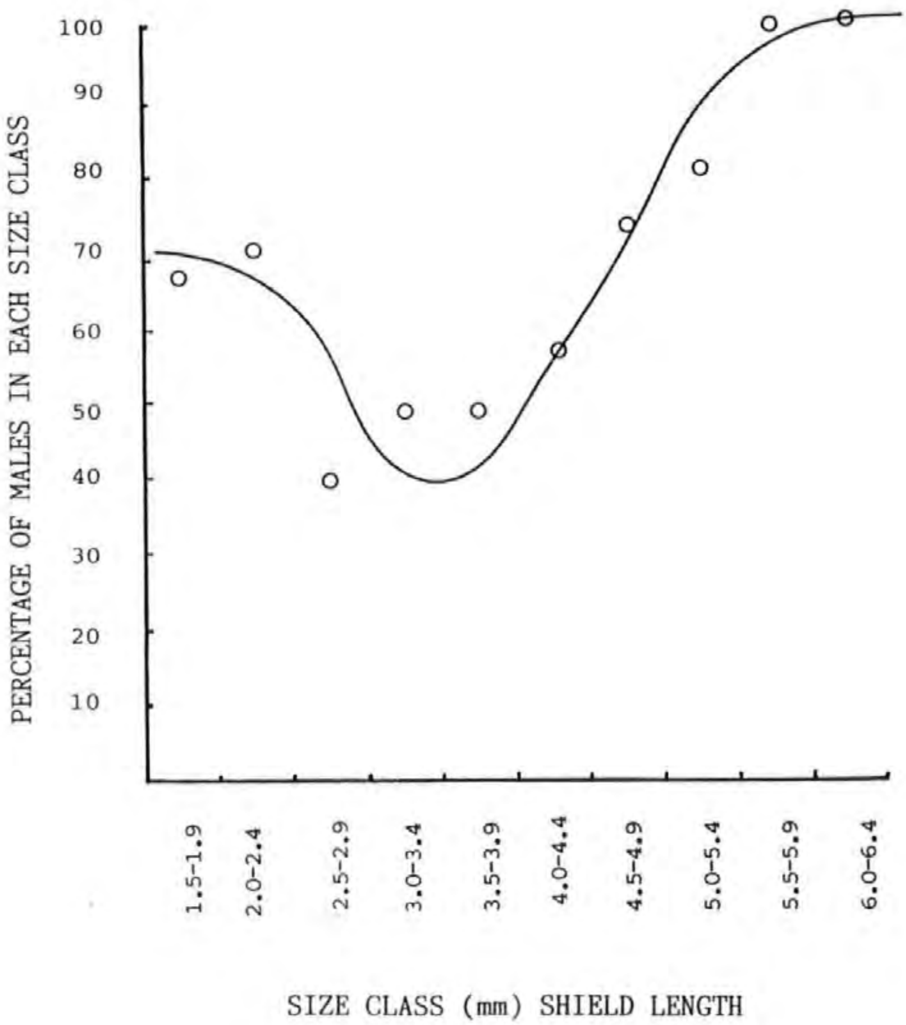


Figure 7.2

The anomalous probability curve for the sex ratios of Pagurus bernhardus collected from the Battery Rocks (after Wenner, 1972).



patterns of mortality, or sex reversal. It has, however, been suggested (Hartnoll, 1982) that such a trend is to be expected in crustaceans, since female growth will inevitably be reduced in comparison to that of males of the same age as a result of the small growth increments, suppression of ecdysis by egg carrying, and long intermoult periods, which characteristically accompany sexual maturity in the females of this group (also Passano, 1960). If this latter explanation is sufficient to explain the pattern of sex ratios observed in the Battery Rocks population, then what may be of particular significance is that females on this shore consistently appear to attain reproductive maturity (and hence begin to fall behind the males in terms of growth) at sizes well below those at which they would find themselves physically shell limited, and that breeding when at such a small size is an established way of life among these animals.

Breeding at a small size is far from unique to this population, of course, and the phenomenon may indeed be taken to be common. Ovigerous females of this species are frequently recorded in the littoral zone when at sizes typical of this study (e.g. Marine Biological Association, 1957; Crothers, 1966). Further afield, Bertness (1981c) has commented upon a situation in which three species of hermit crab occurring sympatrically on a Panamanian shore compete for the available shells, with the inevitable result that the most competitively-subordinate species becomes confined to the most inferior shells. This situation therefore resembles the case under study in that severe shell limitation occurs, but differs in that while the Panamanian limitation is quantitative (with insufficient shells to go around - although large shells do occur), that of the Battery Rocks population is qualitative (with all of the shells being too small).

Significantly, the subordinate Panamanian species is also noted to breed at a small size when its range overlaps with that of its dominant neighbour - with individuals channeling energy into reproduction under such circumstances at the expense of growth. This would appear to be an effective response to a selection pressure that would otherwise severely reduce their evolutionary fitness. Despite all of the advantages of waiting until a large body size is attained before commencing breeding - i.e. increased resistance to predation and physical stresses, coupled with the inevitable opportunity of producing a larger clutch in due course - this "plasticity" in behaviour which allows such a pattern to be sacrificed can perhaps be seen to be one of the most important adaptations shown by this group of animals. The observation that the Panamanian species, like the Battery Rocks population of P.bernhardus, actually begins to breed before its members become physically shell limited may indicate how advantageous it could be for "precocious" breeding to become established as a life history strategy. (The term precocious breeding is introduced here to describe the allocation of resources to reproduction at the expense of growth before shell limitation has an effect.)

That energy allocated to growth could turn out to be ultimately inefficient could never be known beforehand, but if some members of a population had a tendency to breed at a small size anyway (i.e. smaller than the maximum that they could attain in the shells available to them), while others would ordinarily only breed at a larger size (having put effort into rapid incremental growth as shells allowed), then it may be that the smaller females could produce more offspring in due course from a number of small clutches than the larger individuals would find possible from a smaller number of large clutches. With longevity being reduced for a shell limited individual it may also be that such larger females may not live long enough to breed more than once or perhaps twice upon finding themselves shell-limited. Thus, precocious breeders would be at a selective advantage when the shell resource is inadequate, and the trait of allocating energy to egg production at such an early stage in the life cycle would increase in subsequent generations (also Gadgil and Bossert, 1970; Schaffer, 1974). The provision of both iteroparity and precocity (usually a semelparous feature) within this group can be seen as a type of stochastic or "bet-hedging" behaviour (review in Todd, 1985), but with the selective force here being an unpredictable resource rather than an unpredictable physical environment. This strategy of precocious breeding is not seen as an example of, or trend towards, progenesis - a phenomenon common among crustaceans, but resulting in a truncation of development with the premature appearance of reproductive organs. These precociously-breeding females are "small adults" and not neotenous larvae. Since it is thought to be more efficient to devote energy to the production of gametes rather than somatic tissue (Calow, 1983) the strategy of precocious breeding in shell limited hermit crabs will have selective reinforcement. The long-term consequences of precocious breeding for the individuals concerned cannot be stated, although it has been shown (Calow, 1977) that development and future fecundity may suffer as a result of the premature diversion of resources into breeding (taking contributions to growth as contributions to future fecundity). Although fecundity is size-related in hermit crabs as in all malacostraca (Jensen, 1958), the total output of eggs in the lifetime of a single female would be difficult to estimate since there is no satisfactory way of ageing any of these animals (Kurata, 1962). Thus the data needed to determine the effects of precocious egg production on the total fecundity are not available. It is, however, contended that the disadvantages associated with shell-limitation as discussed here will have more serious long-term consequences than any disadvantages associated with precocious breeding.

That precocious breeding is an established phenomenon in the Battery Rocks population, and not merely a response to a short-term shell limitation, is indicated during work outlined in Chapter 6. Females were breeding at sizes below those where the effects of shell-limitation would be felt even when the pools in which they were found had been artificially enriched by extra shells several months before (including a number of shells far larger in size than would occur there normally). Precocious breeding is therefore suggested as a vital strategy to assist these animals to maximise their reproductive output in the face of shell-limitation (and also, incidently, to give them a measure of independance in the face of declining gastropod numbers).

Since females of this species do not manufacture eggs continually (Carayon, 1941), a stimulus will be necessary to initiate breeding. The non-breeding period will be available for growth (as discussed, egg carrying suppresses ecdysis - Passano, 1960), and breeding "seasons" will become established. Equally, a period during which females are becoming mature, yet when no mating is observed, suggests that two separable stimuli are involved - one affecting egg production and the other influencing mating behaviour. It is shown in this work that two separable stimuli do operate in this way, with low sea temperatures influencing egg production, and short day lengths influencing breeding behaviour in the males. By these means no reinforcing stimuli are needed (i.e. stimuli held over from one season to the next) and females are able to breed upon their first exposure to the appropriate stimuli - i.e. within their first year of life. The tendency for both of these stimuli to be more intense in the littoral zone than in the sublittoral may perhaps reinforce the advantages of spending at least part of the life cycle in this region. Under such a regime of temperature and photoperiod breeding will occur continuously as long as the stimuli persist, though precise synchrony between females is not needed and is not seen to occur. Gestation is shown to require some 30-50 days under winter conditions which, coupled with a period for larval development of some 60 days (Bookhout, 1964), suggests that the first young hermit stages will be on the shore about 3-3½ months after breeding has begun.

For the animals that eventually come to occupy deeper waters, the temperatures and photoperiods will be more constant. This will result in sublittoral populations being able to breed throughout the year, and may account for the many observations (Chapter 5) that sublittoral populations always seem to contain at least some ovigerous females. Under these conditions, however, each female will probably produce only one brood during each year, with periods of breeding alternating with periods of growth.

The reproductive strategy of this hermit crab species therefore appears to be one of overlapping iteroparity, in that individuals breed repeatedly but have specific breeding seasons (i.e. breeding requires specific motivating stimuli), and individuals of different ages breed side by side with overlapping generations. Breeding precociously i.e. at the first exposure to these stimuli, enhances the efficiency of this strategy by removing the need for first attaining a specific age or size - a requirement which may not be possible for reasons quite beyond the experience of other groups of animals. This early onset of breeding by females will also result in their having slower growth rates than males - a factor which may help to reduce the competition for shells between the sexes (particularly if more than one brood is produced during each season). The strategy of producing a number of small clutches over a prolonged period of time may therefore increase the overall fitness of each female when compared with the risks of delaying breeding until a specific size has been reached - even though at such a size larger clutches could be carried.

In conclusion therefore it can be seen that the members of this species found on the Battery Rocks interact with one another only when breeding and when competing for the shells that are essential for their protection and for their growth. At other times they demonstrate a solitary, errant existance, exhibiting no evidence of territoriality or site attachment. The crabs have access to a shell resource which does not appear to be limiting in terms of the quantity of material available, but which does impose a size limitation upon the larger individuals. This situation is exacerbated by the apparent absence in the offshore waters of any of the larger species of gastropod whose shells must eventually be exploited in order to permit growth to the typical "adult" size. The shells most frequently found to be occupied by the crabs on this shore belong to the gastropod species most commonly represented, and no shell-choice preference was demonstrated or is implied. Equally, the ability of individuals from this shore to grow to a size greater than the largest naturally occuring in the habitat when provided with larger shells clearly argues against their being an abnormal or "dwarf" population. By the very unpredictability of the shell resource, it is therefore considered that littoral populations of hermit crabs will inevitably suffer from at least some form of shell-limitation, and will have been subject to selection pressures in terms of growth, longevity, and reproductive success which will have encouraged strategies to compensate for their dependance on this resource. Consequently, the niche for this group has come to contain two fundamentally different components - a littoral component providing both the small shells needed by the juveniles and the extremes of temperature and photoperiod needed to encourage breeding, and a sublittoral component providing the larger shells needed to enable the crabs to achieve their asymptotic maximum size. Encouraging larval settlement in the littoral zone (where gastropod shells tend to be at their most abundant) exposes the young hermits to the widest possible range of potentially useful gastropod shells. Small shells are rarely limiting in this habitat, and they will tend to have a high turnover rate. Young hermits will find that this stage in their lives offers relatively few problems in terms of growth. A random series of movements around the shore, stimulated by the number and quality of shell contacts then ensures that the animals will either be able to locate and remain in pools with adequate resources for their immediate needs or will be able to move into deeper waters if these needs are not satisfied. Individuals that do not make contact with a source of new and "improved" shells move further and further in search of alternatives, particularly as they become increasingly stressed by the limitations of their existing shells. Since movements occur when the animals are submerged (an apparent response to the pressure of water overhead) such movements will tend to take them into progressively deeper waters where, if anywhere, the largest shells are likely to be found. Those crabs that encounter such a resource enter the sublittoral population of the larger "adult" forms typical of benthic grab and trawl samples. Those that do not find larger shells will presumably become so stressed by delayed or suppressed ecdysis that they die.

In order to overcome the problem of reduced growth and longevity shown to result from shell-limitation, precocious breeding has become established as a normal part of a life history strategy. Females breed within their first year of life, responding to the stimuli of low water temperatures (and reduced daylengths), such that they produce several small but significant broods while the dangers of shell-limitation are at their least. The dependence upon quantifiable stimuli results in breeding "seasons" for the littoral forms, and allows for non-breeding periods to be used for growth. Thus, even if an individual eventually becomes so seriously shell-limited that its growth and longevity are compromised, it will already have reproduced - even if the broods are smaller than would have been the case had it waited until attaining a specific age-related body size. Such a strategy will also help to relieve the strain on the shell resource at this time by slowing the growth of the females in comparison to males of the same age, thus allowing males access to the slightly rarer larger shells with less competition. Hence the adequacy of the smaller shells to this group may be increased for longer periods. Under the more stable conditions of temperature and photoperiod typical of the sublittoral, the seasonal influences on reproduction are removed and a new pattern of annual breeding becomes established i.e. allowing breeding and growth to alternate, with the result that at least some members of sublittoral populations can be found breeding at almost any time of the year.

Thus the patterns of locomotory and reproductive behaviour observed in hermit crabs are part of a complex life history strategy which supremely adapts them to a life in which they face unique problems. The use of the littoral zone for a part of their life cycle can be seen to be an integral component of this strategy.

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APPENDICES

APPENDIX I.

THE NOMENCLATURE OF *PAGURUS BERNHARDUS*.

The International Commission on Zoological Nomenclature intervened in the debate over the generic name of the common European hermit crab in 1954 since this animal had come to be known by two different generic names during the previous 100 years.

The common hermit crab of European waters was named as *Cancer bernhardus* by Linnaeus in the 10th edition of the *Systema Naturae* (1758) based, it would seem, upon descriptions and illustrations provided by a number of other authors. The species was originally described as having the left chela larger than the right, with this structure being smooth in texture:

"*chelis cordatis laevibus*: *sinistra majore*".

However, since this description does not apply to the crab now known as *Pagurus bernhardus*, it is believed that Linnaeus confused at least two other species (perhaps *Diogenes pugilator*, *Paguristes oculatus*, and *Pagurus bernhardus*) thus rendering the original description invalid. In the 12th edition of the *Systema Naturae* (1767) the description was amended to:

"*chelis cordatis muricatis*: *dextra majore*"

emphasising the characteristic tubercles roughening the chelae and the fact that the right chela is always larger than the left. This second definition is now accepted as definitive.

In 1775 hermit crabs were separated from the genus *Cancer* by Fabricius, who included all the conspicuously non-brachyuran crabs in a new genus, Pagurus. Pagurus bernhardus was later taken as the type for the genus Pagurus by Latreille in 1810.

The second generic name, Eupagurus, dates from 1851, when Brandt re-examined the original classification of Linnaeus and, because of a disagreement over the identity of the type specimen, decided to assign the common hermit crab to a different genus.. Eupagurus bernhardus was the name in general use for the first half of this century.

The controversy was examined by the Commission who voted that the name Pagurus should be retained on the grounds that:

1. Pagurus was the oldest and best known name in use for any genus of hermit crab.
2. Pagurus is the type genus of the sub-family PAGURINAE, the family PAGURIDAE, and the section PAGURIDEA (now the super-family PAGUROIDEA - the group containing all the known hermit crabs).
3. Pagurus is the derivative genus of Anapagurus, Catapagurus, Holopagurus, Mixtopagurus etc.

The generic name Eupagurus was, therefore, declared invalid in 1957 (Opinion 472; Hemming, 1957).

APPENDIX II

SUMMARY OF THE ANIMALS COLLECTED FROM THE BATTERY ROCKS.

Number of crabs extracted from their shells for examination:	1968
Total number of males examined:	1082
Total number of females examined:	886
Number of ovigerous females examined	332

Largest male examined (24.4.85)	shield:	6.4mm
	carapace:	11.2mm
	weight:	1.063g
Largest female examined (19.7.85)	shield:	5.4mm
	carapace:	9.0mm
	weight:	0.966g
Smallest ovigerous female (29.11.85)	shield:	1.7mm
	carapace:	2.8mm
	weight:	0.132g
Smallest individual examined	carapace:	0.9mm
Largest shell found (<u>Littorina littorea</u>)	length:	35mm

Mean crab size (shield length ± S.D.)	3.9 ± 0.85mm (n=440)
Mean size of males:	4.1 ± 0.9mm (n=256)
Mean size of females:	3.7 ± 0.7mm (n=184)

Species of hermit crab recorded (Identifications from Allen, 1967; Crothers and Crothers, 1983; Ingle, 1985):

<u>Pagurus bernhardus</u> abundant

<u>Pagurus cuanensis</u> 1 found 19.7.85 (male, carapace 5.0m).

<u>Clibanarius erythropus</u> 1 found 8.5.85 (female, carapace 10.2mm).

<u>Anapagurus hyndmanni</u> 3 found (9.1.86/21.7.86/17.9.86) - not removed from their shells.

APPENDIX II (contd.)

SUMMARY OF THE ANIMALS COLLECTED FROM THE BATTERY ROCKS.

Aberrations found:

1 female *Pagurus bernhardus* with pleopods on right side of body (collected 21.8.85) shield 4.7mm.

1 *Pagurus bernhardus* with male pleopods and gonopore on 5th right pereiopod, but with gonopore on coxa of 3rd left pereiopod (collected 14.12.86).

Parasites:

1 mature *Peltogaster paguri* (identified from Smith, 1906) on female *Pagurus bernhardus* collected 11.3.86. Female not ovigerous.

Immature *Peltogaster paguri* (visible as "glowing red spot" through tissues of crab's abdomen - Smith, 1906: p.55):

on male (not measured)	11.2.86
on male (shield 4.8mm)	24.4.85
on male (shield 3.8mm)	19.7.85
on male (shield 3.9mm)	25.2.86

1 female *Athelges paguri* on female *Pagurus bernhardus* (shield 3.2mm) collected 13.11.85 (Identification from Sars, 1899; Pike, 1953, 1961; Naylor, 1972: confirmed British Museum (Natural History) 10.12.85).

1 female *Athelges paguri* with smaller male attached, on female *Pagurus bernhardus* collected 8.4.86.

APPENDIX III.

CRAB AND SHELL PARAMETERS FOR THE DETERMINATION AND COMPARISON OF SHELL ADEQUACY.

In the following tables the superscripts apply to the information below:

[1] Shell species:
L = Littorina littorea (L.)
N = Nucella lapillus (L.)
G = Gibbula umbilicalis (da Costa) / G. cineraria (L.)
M = Monodonta lineata (da Costa)
C = Calliostoma zizyphinum (L.)

[2] Shell Adequacy Index (after Vance 1972a, 1972b), where:
an S.A.I. value of 1 = shell is of an adequate size
an S.A.I. value of >1 = shell is too large
an S.A.I. value of <1 = shell is too small.

[3] Subjective Index of Adequacy, where:
an S.I.A. value of 1 = shell visibly too large
an S.I.A. value of 2/3 = shell broadly optimal
an S.I.A. value of 4 = shell visibly too small.

[4] The nature of the shell choice made, compared by the two indices above. Details of all of the choices are listed in Table 3.2:

1	original shell adequate,	new shell larger
2	"	, new shell same size
3	"	, new shell smaller
2+	"	, remained in same shell
4	original shell too large,	new shell even larger
5	"	, new shell same size
* 6	"	, new shell smaller
5+	"	, remained in same shell
* 7	original shell too small,	new shell larger
8	"	, new shell same size
9	"	, new shell smaller
8+	"	, remained in same shell.

(* denotes that the exchange made was an improvement)

APPENDIX III (contd.)

CRAB AND SHELL PARAMETERS FOR THE DETERMINATION AND COMPARISON OF SHELL ADEQUACY

CRAB PARAMETERS			ORIGINAL SHELL		"PREFERRED" SHELL PARAMETERS						SHELL ADEQUACY INDEX[2]		SUBJECTIVE INDEX[3]		NATURE OF CHOICE MADE[4]	
SEX	SHIELD LENGTH mm.	WEIGHT g.	SPECIES[1]	WIDTH mm.	SPECIES[1]	WIDTH mm.	LENGTH mm.	APERTURE WIDTH mm.	VOLUME cm^3	WEIGHT g.	ORIGINAL SHELL	"PREFERRED" SHELL	ORIGINAL SHELL	"PREFERRED" SHELL	ACCORDING TO S.A.I.	ACCORDING TO SUBJ. INDEX
♀	4.4	0.499	N	16.1	N	15.7	25.2	5.5	-	2.669	0.94	0.91	2	3	9	2
♂	3.7	0.208	L	13.4	G	12.5	8.5	5.0	0.25	0.877	0.92	0.86	2	3	9	2
♀	4.1	0.329	L	15.6	L	17.1	21.6	6.9	0.30	3.170	0.97	1.07	3	2	7	2
♂	5.7	1.086	L	18.4	L	22.7	28.7	9.8	1.42	6.055	0.83	1.03	3	2	7	2
♂	3.4	0.200	N	13.4	L	14.2	16.4	6.1	0.31	1.589	1.00	1.07	3	3	1	2
♀	3.5	0.179	G	14.3	G	14.3	8.8	6.1	0.30	1.378	1.04	1.04	2	2	5+	2+
♂	3.7	0.416	L	13.8	L	20.7	26.3	7.8	1.05	5.207	0.95	1.44	3	1	7	1
♂	4.4	0.488	L	15.8	L	15.7	21.0	6.7	0.62	3.015	0.92	0.91	3	3	9	2
♂	2.9	0.155	N	12.6	G	13.6	10.6	5.0	0.31	1.406	1.11	1.20	2	2	4	2
♂	3.5	0.209	N	13.9	N	12.3	20.6	4.4	0.37	1.528	1.01	0.89	3	4	6	3
♂	3.4	0.300	N	14.2	L	14.5	17.3	6.3	0.24	1.750	1.07	1.09	3	2	4	2
♀	3.5	0.171	G	14.7	L	14.5	19.2	6.5	0.35	2.025	1.07	1.06	2	2	6	2
♀	2.2	0.061	L	10.9	G	13.8	8.8	5.7	0.17	0.932	1.26	1.60	1	1	4	5
♂	6.0	0.947	L	16.8	G	17.0	9.3	6.7	0.42	1.584	0.72	0.73	3	3	7	2
♀	3.1	0.146	L	13.1	G	14.1	9.2	5.2	0.54	1.014	1.08	1.16	2	2	4	2
♂	4.5	0.401	G	12.8	N	15.8	26.7	6.4	0.48	2.692	0.72	0.90	2	3	7	2
♀	3.4	0.212	L	14.0	L	12.9	16.4	5.5	0.26	1.447	1.05	0.97	2	2	6	2

APPENDIX III (contd.)

CRAB AND SHELL PARAMETERS FOR THE DETERMINATION AND COMPARISON OF SHELL ADEQUACY

CRAB PARAMETERS			ORIGINAL SHELL		"PREFERRED" SHELL PARAMETERS						SHELL ADEQUACY INDEX[2]		SUBJECTIVE INDEX[3]		NATURE OF CHOICE MADE[4]	
SEX	SHIELD LENGTH mm.	WEIGHT g.	SPECIES[1]	WIDTH mm.	SPECIES[1]	WIDTH mm.	LENGTH mm.	APERTURE WIDTH mm.	VOLUME cm^3	WEIGHT g.	ORIGINAL SHELL	"PREFERRED" SHELL	ORIGINAL SHELL	"PREFERRED" SHELL	ACCORDING TO S.A.I.	ACCORDING TO SUBJ. INDEX
♀	4.0	0.246	N	15.7	L	15.0	18.1	6.9	-	1.819	1.00	0.96	3	3	3	2
♂	3.4	0.253	N	14.5	G	14.0	8.7	6.4	0.37	1.143	1.09	1.05	2	2	6	2
♀	3.2	0.185	N	14.3	G	12.7	9.8	6.1	0.22	1.148	1.14	1.01	1	2	6	6
♂	2.7	0.167	L	12.7	G	12.3	8.7	4.8	0.49	1.236	1.20	1.16	2	2	6	2
♀	3.1	0.154	N	13.1	G	14.2	10.9	5.6	0.18	1.399	1.08	1.17	3	2	4	2
♂	3.9	0.331	G	13.0	N	15.7	17.1	5.3	0.52	3.285	0.85	1.03	4	2	7	7
♂	4.8	0.702	L	18.4	N	15.5	28.9	6.7	0.74	2.917	0.98	0.83	3	4	9	3
♂	3.1	0.151	M	12.4	N	13.2	20.5	4.0	0.24	2.226	1.02	1.09	3	2	4	2
♂	2.7	0.102	L	13.0	G	10.7	7.8	5.0	0.12	0.703	1.23	1.00	1	2	6	6
♀	3.5	0.224	G	14.7	G	13.9	9.1	6.5	0.36	1.225	1.07	1.01	2	3	6	2
♂	3.2	0.168	L	13.8	G	12.7	8.9	5.4	0.31	1.270	1.10	1.01	2	2	6	2
♂	4.1	0.280	N	13.9	L	19.3	24.6	17.2	0.48	4.725	0.87	1.21	4	1	7	7
♂	4.4	0.310	G	13.3	N	15.9	27.3	6.2	-	2.702	0.77	0.93	4	3	7	7
♂	4.9	0.507	N	17.8	L	17.6	22.2	7.9	0.71	3.751	0.93	0.92	3	3	6	2
♀	3.8	0.230	G	12.5	L	14.2	16.4	6.4	0.39	1.576	0.84	0.95	4	3	7	7
♀	3.3	0.128	L	12.8	G	13.4	10.3	5.7	0.24	1.244	0.99	0.96	2	2	9	2
♂	3.2	0.188	1	13.1	L	12.9	15.8	5.7	0.26	1.433	1.04	1.03	1	2	6	6

APPENDIX III (contd.)

CRAB AND SHELL PARAMETERS FOR THE DETERMINATION AND COMPARISON OF SHELL ADEQUACY

CRAB PARAMETERS			ORIGINAL SHELL		"PREFERRED" SHELL PARAMETERS						SHELL ADEQUACY INDEX[2]		SUBJECTIVE INDEX[3]		NATURE OF CHOICE MADE[4]	
SEX	SHIELD LENGTH mm.	WEIGHT g.	SPECIES[1]	WIDTH mm.	SPECIES[1]	WIDTH mm.	LENGTH mm.	APERTURE WIDTH mm.	VOLUME cm^3	WEIGHT g.	ORIGINAL SHELL	"PREFERRED" SHELL	ORIGINAL SHELL	"PREFERRED" SHELL	ACCORDING TO S.A.I.	ACCORDING TO SUBJ. INDEX
♂	4.5	0.570	L	17.8	L	17.2	22.6	7.1	0.41	3.186	1.02	0.98	2	3	6	2
♀	4.2	0.325	L	13.7	L	16.0	19.1	6.6	0.34	2.266	0.83	0.98	3	2	7	2
♂	4.1	0.383	L	16.0	L	16.0	19.7	7.1	0.36	2.083	1.00	1.00	3	3	2+	2+
♂	4.1	0.329	L	16.2	L	16.7	19.8	7.4	0.24	2.377	1.01	1.04	2	1	4	1
♂	4.4	0.359	N	15.9	L	15.6	20.1	6.8	0.54	2.096	0.93	0.91	3	4	9	3
♂	4.5	0.456	M	17.2	L	16.0	19.9	7.2	0.62	2.423	0.98	0.91	2	2	9	2
♀	4.2	0.270	L	15.3	G	15.7	9.4	6.1	-	1.239	0.93	0.96	3	2	7	2
♀	3.4	0.220	G	13.0	L	17.0	20.7	7.1	-	2.809	0.97	1.28	3	2	7	2
♀	3.5	0.260	L	19.7	L	15.0	18.0	6.7	-	1.982	1.45	1.10	1	2	6	6
♂	5.6	0.912	L	19.4	L	16.8	21.4	7.1	-	2.641	0.89	0.77	2	3	9	2
♀	3.7	0.304	G	14.9	L	16.9	19.9	-	-	2.384	1.03	1.17	2	1	4	1
♂	5.0	0.623	N	18.6	L	16.3	18.9	-	-	1.953	0.96	0.84	2	3	9	2
♀	4.0	0.325	L	16.2	L	16.5	20.6	6.8	-	3.024	1.04	1.06	2	1	4	1
♂	3.9	0.313	M	15.1	L	15.0	16.9	6.8	-	1.740	0.99	0.98	3	3	9	2
♂	4.9	0.659	L	17.0	N	16.3	27.1	6.7	-	2.689	0.89	0.85	3	4	9	3
♂	4.9	1.014	L	16.7	N	18.7	31.2	6.7	-	4.203	0.87	0.91	3	2	7	2
♂	4.5	0.292	M	15.2	L	17.1	20.4	7.1	-	2.788	0.86	0.97	3	2	7	2

APPENDIX III (contd.)

CRAB AND SHELL PARAMETERS FOR THE DETERMINATION AND COMPARISON OF SHELL ADEQUACY

CRAB PARAMETERS			ORIGINAL SHELL		"PREFERRED" SHELL PARAMETERS						SHELL ADEQUACY INDEX[2]		SUBJECTIVE INDEX[3]		NATURE OF CHOICE MADE[4]	
SEX	SHIELD LENGTH mm.	WEIGHT g.	SPECIES[1]	WIDTH mm.	SPECIES[1]	WIDTH mm.	LENGTH mm.	APERTURE WIDTH mm.	VOLUME cm^3	WEIGHT g.	ORIGINAL SHELL	"PREFERRED" SHELL	ORIGINAL SHELL	"PREFERRED" SHELL	ACCORDING TO S.A.I.	ACCORDING TO SUBJ. INDEX
♂	4.5	0.480	G	13.1	L	17.3	20.8	7.3	0.47	2.511	0.74	0.99	2	1	7	1
♀	2.6	0.059	L	12.1	G	12.1	8.4	5.0	0.20	0.848	1.18	1.18	1	1	5	5
♀	4.2	0.304	L	17.1	N	16.0	27.1	5.2	0.48	3.497	1.04	0.98	1	2	6	6
♀	3.5	0.196	N	14.1	N	16.5	24.4	5.0	0.31	3.487	1.03	1.21	2	1	4	1
♀	4.7	0.401	L	17.2	N	18.1	26.5	6.0	0.62	4.247	0.94	0.99	2	2	7	2
♂	5.5	0.624	L	17.0	N	18.5	30.2	6.4	0.52	4.528	0.79	0.86	3	2	7	2
♀	4.4	0.331	L	15.3	L	15.3	20.1	7.6	0.38	2.168	0.89	0.89	3	3	8+	2+
♂	3.3	0.160	L	11.8	L	11.8	15.1	5.0	0.41	1.200	0.91	0.91	3	3	8+	2+
♂	3.3	0.187	G	11.4	G	14.7	9.2	6.2	0.38	1.231	0.88	1.14	3	2	7	2
♂	4.5	0.525	L	16.9	N	17.0	29.1	6.3	0.38	4.504	0.96	0.97	2	2	7	2
♀	3.6	0.165	N	12.7	N	13.3	21.5	5.1	-	1.759	0.90	0.94	4	3	7	7
♂	4.2	0.381	L	14.7	N	16.9	24.8	5.3	-	3.264	0.89	1.03	3	2	7	2
♂	2.3	0.078	L	10.7	G	12.2	7.5	4.8	-	0.639	1.18	1.35	3	2	4	2
♀	3.9	0.261	L	16.1	L	14.4	17.3	6.7	-	1.872	1.06	0.94	2	3	6	2
♀	3.7	0.173	G	12.9	N	13.1	21.8	5.1	-	1.758	0.89	0.90	2	2	7	2
♂	3.7	0.226	L	16.9	L	14.9	17.9	6.6	-	1.798	1.17	1.03	1	2	6	6
♀	3.0	0.120	M	11.8	G	13.1	8.9	5.1	-	0.797	1.00	1.11	3	2	1	2

APPENDIX III (contd.)

CRAB AND SHELL PARAMETERS FOR THE DETERMINATION AND COMPARISON OF SHELL ADEQUACY

CRAB PARAMETERS			ORIGINAL SHELL		"PREFERRED" SHELL PARAMETERS						SHELL ADEQUACY INDEX[2]		SUBJECTIVE INDEX[3]		NATURE OF CHOICE MADE[4]	
SEX	SHIELD LENGTH mm.	WEIGHT g.	SPECIES[1]	WIDTH mm.	SPECIES[1]	WIDTH mm.	LENGTH mm.	APERTURE WIDTH mm.	VOLUME cm^3	WEIGHT g.	ORIGINAL SHELL	"PREFERRED" SHELL	ORIGINAL SHELL	"PREFERRED" SHELL	ACCORDING TO S.A.I.	ACCORDING TO SUBJ. INDEX
♂	4.9	0.380	N	18.1	N	14.8	25.0	4.8	0.64	3.383	0.95	0.77	3	4	9	3
♂	4.1	0.314	C	16.3	N	16.0	26.7	6.5	–	2.670	1.02	1.00	1	2	6	6
♂	4.3	0.314	N	16.7	L	15.5	19.8	6.9	–	2.095	1.00	0.92	2	3	3	2
♂	3.8	0.236	L	15.8	L	16.9	20.3	6.9	–	2.553	1.06	1.14	3	2	4	2

APPENDIX IV

THE EFFECTS OF SHELL-LIMITATION ON HERMIT CRAB GROWTH AND LONGEVITY FOR TWO GROUPS OF INDIVIDUALS - ONE PERMITTED ACCESS TO LARGE SHELLS (GROUP 'A'), AND ONE DENIED ACCESS TO LARGE SHELLS (GROUP 'B').

The data are arranged under the following headings:

a	The individual number of the animal.
b	The sex of the individual.
c	The shield length (mm) measured after each moult. A maximum of eight moults were recorded during the experiment - these are distinguished by the subscripts c_1 to c_8.
d	The intermoult duration (days) / The growth increment (%).
e	The number of days survived after the last moult.
f	The total longevity (days) for each individual - taking the start of the experiment as day 1.
g	The number of moults predicted by the growth equation of Markham (1968).
h	The actual number of moults observed.

APPENDIX IV (contd.)

THE EFFECTS OF SHELL-LIMITATION ON HERMIT CRAB GROWTH AND LONGEVITY: CRABS PERMITTED ACCESS TO LARGE SHELLS (GROUP 'A').

a	b	c_1	d	c_2	d	c_3	d	c_4	d	c_5	d	c_6	d	c_7	d	c_8	e	f	g	h
1	♂	5.9	27/17	6.9	33/16	8.0	42/19	9.5	64/7	10.2							80	246	5	4
2	♂	4.9	31/14	5.6	33/11	6.2	47/8	6.7	40/10	7.4							62	213	4	4
3	♂	3.7	1/8	4.0	12/12	4.5	21/13	5.1	29/8	5.5	40/16	6.4	32/12	7.2			10	145	6	6
4	♂	4.3	1/14	4.9	24/10	5.4											6	31	2	2
5	♂	6.1	8/18	7.2	32/15	8.3	37/16	9.6	51/10	10.6	58/7	11.4					74	260	6	5
6	♀	3.9	18/8	4.2	27/12	4.7	30/13	5.3	41/15	6.1	38/11	6.8	58/6	7.2	72/5	7.6	60	344	6	7
7	♀	5.2	11/10	5.7	20/10	6.3	37/8	6.8	43/7	7.3							58	169	3	4
8	♀	4.6	14/11	5.1	29/16	5.9				DIED DURING ECDYSIS							-	43	3	2
9	♂	4.1	18/12	4.6	21/13	5.2	39/17	6.1	52/6	6.5							63	193	4	4
10	♀	3.5	12/8	3.8	29/10	4.2	40/12	4.7	42/15	5.4	50/7	5.8					78	251	4	5
11	♂	4.2	14/9	4.6	30/11	5.1	46/16	5.9	60/7	6.3							64	214	4	4
12	♀	5.1	19/12	5.7	34/17	6.7	43/7	7.2	64/4	7.5							72	232	4	4
13	♀	4.3	27/12	4.8	31/14	5.5	18/7	5.9	52/8	6.4	64/5	6.7					80	272	4	5
14	♂	4.7	2/4	4.9	23/4	5.1	31/12	5.7		DIED DURING ECDYSIS							-	56	2	3
15	♀	3.1	4/10	3.4	28/15	3.9	37/18	4.6	47/11	5.1	70/8	5.5	64/9	6.0			71	321	6	6
16	♀	3.9	11/18	4.6	31/11	5.1	39/8	5.5									27	108	3	3
17	♂	4.3	18/9	4.7	21/13	5.3	41/11	5.9									21	101	3	3
18	♂	4.7	14/8	5.1													22	36	1	1
19	♀	3.6	19/11	4.0	31/12	4.5	42/18	5.3	47/11	5.9							29	168	5	4
20	♂	5.8	29/12	6.5	41/14	7.4	54/11	8.2	61/7	8.8							59	244	4	4

APPENDIX IV (contd.)

THE EFFECTS OF SHELL-LIMITATION ON HERMIT CRAB GROWTH AND LONGEVITY: CRABS DENIED ACCESS TO LARGE SHELLS (GROUP 'B').

a	b	c_1	d	c_2	d	c_3	d	c_4	d	c_5	d	c_6	d	c_7	d	c_8	e	f	g	h
1	♂	3.8	5/10	4.2	21/12	4.7	32/15	5.4	31/5	5.7	29/2	5.8					42	160	3	5
2	♂	4.2	21/14	4.8	37/10	5.3	42/4	5.5	51/5	5.8	DIED DURING ECDYSIS							151	2	4
3	♀	4.7	19/13	5.3													12	31	1	1
4	♂	4.4	32/16	5.1	38/2	5.2					DIED DURING ECDYSIS							70	1	2
5	♀	3.6	2/8	3.9	29/10	4.3	34/2	4.4	27/0	4.4	DIED DURING ECDYSIS							92	2	4
6	♀	4.3	1/12	4.8	42/2	4.9											21	64	1	2
7	♀	5.2	29/-2	5.1	31/2	5.2	24/0	5.2			DIED DURING ECDYSIS							84	0	3
8	♂	4.9	11/6	5.2	28/6	5.5	19/2	5.6			DIED DURING ECDYSIS							58	1	3
9	♂	4.8	14/17	5.6													37	51	1	1
10	♀	4.6	31/9	5.0	42/4	5.2					DIED DURING ECDYSIS							73	1	2
11	♂	5.1	30/16	5.9	42/3	6.1	21/2	6.2			DIED DURING ECDYSIS							93	2	3
12	♂	4.1	16/12	4.6	28/15	5.3											39	83	3	2
13	♂	4.4	18/7	4.7	27/11	5.2	41/2	5.3									4	90	2	3
14	♀	4.0	31/15	4.6													11	42	1	1
15	♀	5.1									DIED WITHOUT MOULTING							22	-	-
16	♀	3.9	8/8	4.2	29/14	4.8											32	69	2	2
17	♀	5.3	17/0	5.3							DIED DURING ECDYSIS							17	0	1
18	♂	5.0	31/16	5.8	42/7	6.2											22	95	2	2
19	♂	5.7									DIED WITHOUT MOULTING							41	-	-
20	♂	3.9	11/10	4.3	29/9	4.7											32	72	2	2

APPENDIX V

THE DATES ON WHICH COLLECTIONS OF P.BERNHARDUS WERE MADE FROM THE BATTERY ROCKS IN ORDER TO DETERMINE THE REPRODUCTIVE CYCLE OF THIS POPULATION

DATE OF COLLECTION	NUMBER OF CRABS EXAMINED	NUMBER OF MALES	NUMBER OF FEMALES	FEMALES OVIGEROUS	% (n) FEMALES OVIGEROUS
29.10.84	46	30	16		
10.11.84	48	26	22		
28.11.84	50	40	10		
23. 1.85	34	16	18	*	89 (16)
20. 2.85	48	24	24	*	100 (24)
6. 3.85	32	20	12	*	100 (12)
27. 3.85	35	25	10	*	100 (10)
24. 4.85	52	26	26	*	61 (16)
8. 5.85	24	6	18		
3. 6.85	44	34	10		
17. 6.85	38	24	14		
5. 7.85	45	28	17		
19. 7.85	45	24	21		
31. 7.85	57	35	22		
21. 8.85	46	19	27		
2. 9.85	36	24	12		
18. 9.85	30	16	14		
2.10.85	27	15	12		
16.10.85	42	22	20		
13.11.85	52	26	26		
29.11.85	32	22	10	*	40 (4)
13.12.85	36	20	16	*	69 (11)
9. 1.86	41	22	19	*	79 (15)
25. 1.86	37	13	24	*	100 (24)
11. 2.86	32	14	18	*	55 (10)
25. 2.86	42	18	24	*	92 (22)
11. 3.86	44	16	28	*	93 (26)
25. 3.86	36	20	16	*	100 (16)
8. 4.86	29	15	14	*	64 (9)
23. 4.86	26	10	16	*	75 (12)
7. 5.86	30	15	15	*	60 (9)
22. 5.86	36	26	10		

APPENDIX V (contd.)

THE DATES ON WHICH COLLECTIONS OF P.BERNHARDUS WERE MADE FROM THE BATTERY ROCKS IN ORDER TO DETERMINE THE REPRODUCTIVE CYCLE OF THIS POPULATION

DATE OF COLLECTION	NUMBER OF CRABS EXAMINED	NUMBER OF MALES	NUMBER OF FEMALES	FEMALES OVIGEROUS	% (n) FEMALES OVIGEROUS
4. 6.86	28	14	14		
18. 6.86	32	13	19		
6. 7.86	48	27	21		
21. 7.86	30	18	12		
3. 8.86	27	9	18		
18. 8.86	30	12	18		
1. 9.86	26	15	11		
17. 9.86	30	20	10		
6.10.86	23	13	10		
21.10.86	32	20	12		
3.11.86	34	26	8		
17.11.86	24	18	6		
2.12.86	26	22	4		
14.12.86	28	20	8	*	50 (4)
30.12.86	34	18	16	*	62 (10)
29. 1.87	29	18	11	*	100 (11)
16. 2.87	27	16	11	*	73 (8)
2. 3.87	28	11	17	*	100 (17)
17. 3.87	37	18	19	*	100 (19)
1. 4.87	35	15	20	*	70 (14)
14. 4.87	34	13	21	*	48 (10)
29. 4.87	36	19	17	*	18 (3)
11. 5.87	38	16	22		

APPENDIX VI

THE STATES OF OVARINE MATURITY OF THE FEMALE PAGURUS BERNHARDUS FROM THE BATTERY ROCKS DURING THE PERIOD 29.10.84 - 11.5.87

DATE OF COLLECTION	FEMALES:		STATES OF OVARINE MATURITY									
			0		1		2		3		4	
	number	whether ovigerous	n	%	n	%	n	%	n	%	n	%
29.10.84	16				4	25	12	75				
10.11.84	22				6	27	12	55			4	18
28.11.84	10						8	80			2	20
23.1.85	18	*	2	11			2	11			14	78
20.2.85	24	*	8	33			8	33			8	33
6.3.85	12	*	7	58			5	42				
27.3.85	10	*			4	40	6	60				
24.4.85	26	*	1	4	9	35	14	54			2	8
8.5.85	18				3	17	15	83				
3.6.85	10				6	60	4	40				
17.6.85	14				10	71	4	29				
5.7.85	17				5	29	12	71				
19.7.85	21				6	28	15	72				
31.7.85	22				3	14	19	86				
21.8.85	27				4	15	23	85				
2.9.85	12						12	100				
18.9.85	14						14	100				
2.10.85	12						12	100				
16.10.85	20						18	90	2	10		
13.11.85	26						4	15	7	27	15	58
29.11.85	10	*							2	20	8	80
13.12.85	16	*					4	25	4	25	8	50
9.1.86	19	*							7	37	12	63
25.1.86	24	*					2	8	8	33	14	59
11.2.86	18	*					2	11	2	11	14	78
25.2.86	24	*					4	17	8	33	12	50
11.3.86	28	*	3	11	1	4	18	64			6	21
25.3.86	16	*			3	19	11	69			2	12
8.4.86	14	*			7	50	6	43	1	7		
23.4.86	16	*			2	12	12	75	1	6	1	6
7.5.86	15	*			15	100						

APPENDIX VI (cont.)

THE STATES OF OVARINE MATURITY OF THE FEMALE PAGURUS BERNHARDUS FROM THE BATTERY ROCKS DURING THE PERIOD 29.10.84 - 11.5.87

DATE OF COLLECTION	FEMALES:		STATES OF OVARINE MATURITY									
			0		1		2		3		4	
	number	whether ovigerous	n	%	n	%	n	%	n	%	n	%
22.5.86												
4.6.86	14				4	28	10	72				
18.6.86	19				7	37	12	63				
6.7.86	21				1	5	20	95				
21.7.86	12						12	100				
3.8.86	18						18	100				
18.8.86	18						18	100				
1.9.86	11				1	9	10	91				
17.9.86	10				1	10	9	90				
6.10.86	10				6	60	2	20	2	20		
21.10.86	12						2	17	18	83		
3.11.86	8						4	50	4	50		
17.11.86	6								6	100		
2.12.86	4								4	100		
14.12.86	8	*	2	25					3	37	3	37
30.12.86	16	*	3	19	2	12			5	31	6	38
29.1.87	11	*			2	18			1	9	8	73
16.2.87	11	*	1	9			4	36	1	9	5	45
2.3.87	17	*	7	41			8	47	1	6	1	6
17.3.87	19	*	3	16			15	79	1	5		
1.4.87	20	*			2	10	14	70	2	10	2	10
14.4.87	21	*					20	95	1	5		
29.4.87	17	*					17	100				
11.5.87	22						22	100				

APPENDIX VII

MONTHLY MEAN SEA TEMPERATURES (°C) FOR INSHORE WATERS (MILLBAY DOCKS, PLYMOUTH) AND OFFSHORE WATERS (CHANNEL LIGHT VESSEL): 1984 - 1985. (figures in parenthesis represent the highest and lowest temperatures recorded).

	1984		1985	
Month	Inshore waters	Offshore waters	Inshore waters	Offshore waters
JANUARY	-	-	8.2 (9.4/7.2)	10.1 (12.0/9.0)
FEBRUARY	-	-	6.7 (7.5/5.6)	9.2 (10.0/8.0)
MARCH	-	-	7.7 (8.1/7.5)	9.0 (9.0/9.0)
APRIL	-	-	9.7 (11.1/7.8)	9.4 (10.0/8.0)
MAY	-	-	11.2 (12.8/10.0)	10.4 (11.6/11.0)
JUNE	-	11.8 (12.0/11.0)	13.7 (14.4/12.8)	11.6 (12.2/11.0)
JULY	-	14.5 (16.0/12.6)	15.7 (16.4/13.9)	13.9 (15.0/13.0)
AUGUST	-	15.7 (17.0/15.0)	14.9 (15.6/14.4)	14.7 (15.0/14.0)
SEPTEMBER	-	15.7 (17.0/15.0)	14.8 (15.6/14.2)	15.0 (15.0/15.0)
OCTOBER	13.7 (14.4/13.1)	14.2 (15.0/14.0)	14.5 (15.6/12.8)	14.6 (15.0/14.0)
NOVEMBER	12.0 (12.8/11.4)	13.4 (14.1/12.6)	-	13.4 (14.0/12.0)
DECEMBER	10.3 (10.8/9.4)	12.0 (13.0/12.0)	-	11.9 (12.0/11.0)

APPENDIX VII (contd.)

MONTHLY MEAN SEA TEMPERATURES (°C) FOR INSHORE WATERS (MILLBAY DOCKS, PLYMOUTH) AND OFFSHORE WATERS (CHANNEL LIGHT VESSEL): 1986 - 1987. (figures in parenthesis represent the highest and lowest temperatures recorded).

	1986		1987	
Month	Inshore waters	Offshore waters	Inshore waters	Offshore waters
JANUARY	-	10.3 (11.3/10.0)	6.5 (7.0/5.0)	9.6 (12.0/9.0)
FEBRUARY	-	8.0 (9.0/6.7)	5.0 (5.0/5.0)	8.2 (9.0/8.0)
MARCH	5.4 (6.0/5.0)	7.0 (8.0/6.9)	6.2 (7.0/5.0)	8.0 (8.0/8.0)
APRIL	6.6 (8.8/6.0)	8.0 (8.0/8.0)	9.0 (10.0/7.0)	9.4 (10.0/8.0)
MAY	10.0 (11.0/8.8)	9.0 (10.0/8.0)	10.25 (11.5/10.0)	10.1 (11.0/10.0)
JUNE	13.2 (16.8/11.0)	11.5 (12.0/10.0)	-	-
JULY	14.5 (15.0/14.0)	12.8 (13.0/12.0)	-	-
AUGUST	14.3 (15.0/13.5)	14.2 (15.0/13.0)	-	-
SEPTEMBER	13.1 (13.5/13.0)	14.4 (15.0/13.0)	-	-
OCTOBER	12.5 (13.0/12.0)	12.9 (14.0/12.0)	-	-
NOVEMBER	11.4 (12.0/10.5)	12.1 (13.0/12.0)	-	-
DECEMBER	9.3 (10.5/7.5)	12.0 (12.0/12.0)	-	-

APPENDIX VIII

THE DISTRIBUTION OF CRABS IN LITTORAL POOLS DURING THE STUDY PERIOD - DATA FOR THE CALCULATION OF THE NEAREST NEIGHBOUR INDEX.

Small mid-shore pool (surface area $22m^2$)

Date of collection	N	$\sum r$	$\bar{r}_A$	ρ (m^2)	$\bar{r}_E$	R
10.11.84	30	12.44	0.415	1.36	0.429	0.967
23.1.85	38	14.66	0.386	1.73	0.380	1.016
6.3.85	31	11.23	0.362	1.41	0.421	0.860
24.4.85	21	10.53	0.501	0.95	0.513	0.977
3.6.85	26	13.67	0.526	1.18	0.460	1.143
5.7.85	29	12.40	0.427	1.32	0.435	0.982
31.7.85	24	11.58	0.482	1.09	0.479	1.006
2.9.85	18	10.28	0.571	0.82	0.552	1.034
2.10.85	22	9.10	0.414	1.00	0.500	0.828
13.11.85	30	12.84	0.428	1.36	0.429	0.998
13.12.85	37	12.32	0.333	1.68	0.386	0.863
25.1.86	32	11.37	0.355	1.45	0.415	0.855
25.2.86	34	10.92	0.321	1.54	0.403	0.796

Lower shore pool (surface area $7m^2$)

24.4.85	28	9.98	0.356	4.00	0.250	1.424
2.9.85	24	8.65	0.360	3.43	0.270	1.333
2.10.85	25	9.50	0.380	3.57	0.265	1.434
13.11.85	27	9.88	0.366	3.86	0.254	1.441

APPENDIX VIII (contd.)

THE DISTRIBUTION OF CRABS IN THE SAME MID-SHORE POOL DURING THREE INDIVIDUAL TIDAL CYCLES - DATA FOR THE CALCULATION OF THE NEAREST NEIGHBOUR INDEX.

Date of collection	Time	N	$\sum r$	$\bar{r}_A$	ρ (m^2)	$\bar{r}_E$	R
6.3.85	11.00	31	11.23	0.362	1.41	0.421	0.860
	12.00	31	11.79	0.380	1.41	0.421	0.903
	13.00	31	12.12	0.391	1.41	0.421	0.929
	14.00	31	11.41	0.368	1.41	0.421	0.874
31.7.85	12.00	24	11.58	0.482	1.09	0.479	1.006
	13.00	24	12.18	0.507	1.09	0.479	1.058
	14.00	24	12.88	0.537	1.09	0.479	1.121
	15.00	24	12.23	0.509	1.09	0.479	1.063
2.9.85	14.00	18	10.28	0.571	0.82	0.552	1.034
	15.00	18	11.37	0.632	0.82	0.552	1.145
	16.00	18	10.43	0.579	0.82	0.552	1.049

APPENDIX IX

THE DIRECTIONS OF TRAVEL AND DISTANCES OF MOVEMENT OF INDIVIDUALLY MARKED CRABS ON THE BATTERY ROCKS:

APPENDIX IXa	JULY 1985
APPENDIX IXb	NOVEMBER 1985
APPENDIX IXc	APRIL 1986

Measurements for each of the 7 days comprise the direction of travel (degrees magnetic) and the distance moved (metres), taken as a straight line from the previous days position.

All directions in degrees magnetic.
All distances in metres.
Meander Ratio after Hazlett (1983a).

APPENDIX IXa

THE DIRECTIONS OF TRAVEL AND DISTANCES OF MOVEMENT OF INDIVIDUALLY MARKED CRABS ON THE BATTERY ROCKS - JULY 1985.

	DAYS CRABS OBSERVED														MEAN DISTANCE (m) BETWEEN OBSERVATIONS	TOTAL DISTANCE MOVED (m)	DISTANCE FROM START (m)	POSITION FROM START (°)	MEANDER RATIO
CRAB NO.	1		2		3		4		5		6		7						
	°	m	°	m	°	m	°	m	°	m	°	m	°	m					
1	193	1.3	156	0.87	11	0.92									1.03	3.09	1.17	168	0.379
2	2	1.35	168	1.0											1.17	2.35	0.42	40	0.179
3	301	0.6	119	0.3	232	0.3	353	1.6	190	3.3	57	0.97			1.18	7.07	1.37	197	0.194
4	237	0.45	7	1.0											0.72	1.45	0.8	344	0.552
5	166	0.56	190	1.07	112	1.14	95	0.65	354	1.1	211	8.0	246	0.3	1.83	12.82	8.5	187	0.663
6	220	1.9	15	0.8	185	1.37	210	7.5							2.89	11.57	10.0	212	0.864
7	342	0.67	354	0.52	20	0.67	248	0.45	180	0.17	293	0.36	175	0.4	0.46	3.24	1.5	328	0.463
8	335	0.3	109	2.1	183	0.52									0.97	2.92	2.1	118	0.719
9	227	0.9	207	0.3	250	1.0	192	0.5	52	0.95	58	0.3			0.66	3.95	1.3	220	0.329
10	46	0.27	260	0.32	226	0.47	55	0.5	116	0.22	290	0.75			0.42	2.53	0.7	290	0.277
11	18	1.35	265	0.42	138	2.14	280	1.2							1.28	5.11	0.35	128	0.068
12	199	1.18	342	0.45	254	0.28	3	0.82	204	0.32	261	0.62	43	0.85	0.64	4.52	0.9	294	0.199
13	287	0.5	189	0.5	320	0.4	25	0.28							0.42	1.68	0.7	282	0.417

APPENDIX IXb

THE DIRECTIONS OF TRAVEL AND DISTANCES OF MOVEMENT OF INDIVIDUALLY MARKED CRABS ON THE BATTERY ROCKS - NOVEMBER 1985.

CRAB NO.	DAYS CRABS OBSERVED														MEAN DISTANCE (m) BETWEEN OBSERVATIONS	TOTAL DISTANCE MOVED (m).	DISTANCE FROM START (m).	POSITION FROM START (°)	MEANDER RATIO
	1		2		3		4		5		6		7						
	°	m	°	m	°	m	°	m	°	m	°	m	°	m					
1	194	0.57	92	0.79	205	0.7	203	0.81							0.72	2.87	1.9	177	0.662
2	298	1.47	156	1.0	136	0.89	68	0.78	197	0.85	219	0.4			0.90	5.39	1.68	182	0.312
3	149	1.1	196	0.64	320	0.9	252	0.57	7	0.24	250	0.82			0.71	4.27	1.8	236	0.422
4	225	1.52	219	0.5	106	0.42	178	1.1	257	0.73					0.85	4.27	3.35	210	0.785
5	256	0.9	212	0.82	118	0.9	139	0.5	102	0.48	203	0.8			0.73	4.4	2.57	182	0.584
6	332	0.7	103	0.57	139	0.42	110	0.52	67	0.35	32	1.3			0.64	3.86	2.29	59	0.593
7	250	0.63	353	0.58	85	0.88	125	0.7	204	1.01	218	0.26			0.67	4.03	1.15	168	0.285
8	253	1.3	12	0.89	183	1.2									1.13	3.39	1.35	239	0.398
9	254	0.52	150	0.67	110	0.85	11	0.44							0.62	2.48	0.9	129	0.363
10	115	1.44	244	0.92	176	1.0	236	0.5	178	1.42	303	0.86			1.02	6.14	3.38	188	0.550
11	187	1.0	319	1.06	255	0.39	158	0.57	185	1.43	230	0.32			0.79	4.77	2.7	206	0.566
12	247	0.78	25	0.62	55	0.22	300	0.82	240	1.0	222	0.74			0.70	4.18	2.37	264	0.567

APPENDIX IXc

THE DIRECTIONS OF TRAVEL AND DISTANCES OF MOVEMENT OF INDIVIDUALLY MARKED CRABS ON THE BATTERY ROCKS - APRIL 1986.

	DAYS CRABS OBSERVED																		
CRAB NO.	1		2		3		4		5		6		7		MEAN DISTANCE BETWEEN OBSERVATIONS	TOTAL DISTANCE MOVED (m).	DISTANCE FROM START (m)	POSITION FROM START (°)	MEANDER RATIO
	°	m	°	m	°	m	°	m	°	m	°	m	°	m					
1	2	0.62	131	0.91	62	1.37	124	0.35	226	1.0	166	1.3			0.92	5.55	2.3	127	0.414
2	161	0.85	228	0.95	179	0.34	304	0.88	195	0.92					0.79	3.94	2.67	211	0.678
3	142	0.74	236	0.4	155	1.3	294	0.6	47	0.92	334	0.3			0.71	4.26	1.4	183	0.329
4	241	0.68	21	0.51	133	0.85									0.68	2.04	0.47	152	0.230
5	22	0.7	140	0.51	129	0.57	4	0.85	295	0.8	152	0.52			0.66	3.95	0.85	41	0.215
6	16	1.7	158	1.43	193	1.3	290	1.85	19	0.71	165	1.1			1.35	8.09	0.97	212	0.120
7	54	0.9	291	1.43	65	1.27	107	0.32	352	0.84	262	1.1			0.98	5.86	2.28	350	0.389
8	102	0.77	186	1.17	316	0.6	267	0.34	294	1.15					0.81	4.03	1.2	248	0.280
9	352	1.19	282	0.9	71	1.04	144	1.26	271	1.1	225	0.8			1.05	6.29	0.95	276	0.151
10	47	1.6	148	0.55											1.07	2.15	0.55	68	0.268
11	180	1.0	310	0.97	200	1.2	354	2.01							1.29	5.18	1.42	293	0.274
12	100	1.58	262	0.69	11	1.32	351	0.54	250	1.06					1.04	5.19	1.0	3	0.193

APPENDIX Xa

RESIDENCE TIMES (DAYS) FOR THE INDIVIDUALLY MARKED INHABITANTS OF A MID-SHORE POOL WITH AN ARTIFICIALLY IMPOVERISHED SHELL RESOURCE.

	Days into experiment																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
crab no. 1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
2	*	*	*	*																	
3	*	*	*																		
4	*																				
5	*																				
6	*	*	*	*	*																
7	*	*	*	*	*	*															
8	*	*	*	*																	
9	*	*	*	*																	
10	*	*	*	*	*	*	*	*													
11	*	*	*																		
12	*	*	*	*	*	*	*	*	*	*	*										
13	*	*	*																		
14	*	*	*	*	*	*	*	*	*												
15	*																				
16	*	*	*	*	*	*	*	*	*	*	*	*									
17	*	*	*	*	*																
18	*	*	*																		
19	*	*	*																		
20	*	*	*	*	*	*	*	*	*												
21	*																				
22	*	*	*	*	*	*	*	*	*												
23	*	*	*	*	*	*															
24	*	*	*	*																	
25	*	*	*	*	*	*	*	*	*	*	*	*									
26	*	*	*	*	*	*	*	*	*	*	*	*									
27	*	*	*	*																	
28	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					
29	*	*	*	*	*																
30	*	*	*	*	*	*	*	*	*	*	*	*	*	*							
31	*	*	*	*																	
32	*	*	*	*	*	*	*	*	*	*	*	*	*	*							

APPENDIX Xb

RESIDENCE TIMES (DAYS) FOR THE INDIVIDUALLY MARKED INHABITANTS OF A MID-SHORE POOL WITH AN ARTIFICIALLY ENRICHED SHELL RESOURCE.

	Days into experiment																				
crab no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
2	*	*	*	*	*	*	*	*	*	*											
3	*	*	*	*	*	*	*	*	*	*	*	*	*								
4	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
5	*	*	*	*	*	*	*	*													
6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
7	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
8	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
9	*	*	*																		
10	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
11	*	*	*	*	*	*															
12	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*						
13	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
14	*	*	*	*	*	*	*	*	*	*											
15	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
16	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
17	*	*	*	*	*	*	*	*	*	*											
18	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
19	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
20	*	*	*																		
21	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
22	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
23	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
24	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*						
25	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
26	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
27	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					

APPENDIX XIa

THE RESIDENCE TIMES OF NEWLY ARRIVED PAGURUS BERNHARDUS IN A MID-SHORE POOL WITH AN ARTIFICIALLY IMPOVERISHED SHELL RESOURCE.

crab number	residence time (days)
2_1	1
2_2	3
3_1	4
4_1	3
4_2	1
4_3	7
5_1	3
6_1	5
6_2	2
6_3	1
7_1	4
7_2	7
8_1	6
8_2	6
10_1	2
12_1	4
12_2	1
13_1	2
13_2	5
13_3	8
15_1	4
16_1	3
16_2	3
17_1	4
18_1	3
18_2	3
18_3	1
20_1	2+
20_2	2+
20_3	2+

[+ indicates crab still resident on last day of experiment]

[2_1 is individual number given to first new crab found on day 2]

APPENDIX XIb

THE RESIDENCE TIMES OF NEWLY ARRIVED PAGURUS BERNHARDUS IN A MID-SHORE POOL WITH AN ARTIFICIALLY ENRICHED SHELL RESOURCE.

crab number	residence time (days)
2_1	2
2_2	13
4_1	2
4_2	14
4_3	4
6_1	7
6_2	5
7_1	2
7_2	15+
9_1	13+
9_2	6
9_3	1
11_1	11+
13_1	9+
13_2	7
15_1	7+
15_2	1
19_1	2
21_1	1+
21_2	1+
21_3	1+

[+ indicates crab still resident on last day of experiment]

[2_1 is individual number given to first new crab found on day 2]

APPENDIX XIIa

INDIVIDUALLY NUMBERED "ORIGINAL" AND "NEWCOMER" CRABS PLACED IN CATEGORIES ACCORDING TO THE ADEQUACY (SUBJECTIVE INDEX) OF THEIR SHELLS: THE POOL WITH THE ARTIFICIALLY IMPOVERISHED SHELL RESOURCE.

1		2			3			4	
(shell too large)								(shell too small)	
Number of Original	Number of Newcomer	Number of Original		Number of Newcomer	Number of Original	Number of Newcomer		Number of Original	Number of Newcomer
1	4_3	3	8	3_1	2	2_2	4_1	4	2_1
28	6_2	10	12	5_1	5	4_2	6_1	7	6_3
	13_3^*	14	18	7_1	6	8_1	12_1	11	10_1
		20	22	7_2	9	13_1	13_2	15	12_2
		23	24	8_2	13	16_1	16_2		17_1
		25	26	15_1	16	18_1	20_2		18_3
		29	30	18_2	17				
		32		20_1	19				
				20_3	21				
					27				
					31				

APPENDIX XIIb

INDIVIDUALLY NUMBERED "ORIGINAL" AND "NEWCOMER" CRABS PLACED IN CATEGORIES ACCORDING TO THE ADEQUACY (SUBJECTIVE INDEX) OF THEIR SHELLS: THE POOL WITH THE ARTIFICIALLY ENRICHED SHELL RESOURCE.

1 (shell too large)		2			3		4 (shell too small)	
Number of Original	Number of Newcomer	Number of Original		Number of Newcomer	Number of Original	Number of Newcomer	Number of Original	Number of Newcomer
2*	7_1	1	17	2_1	3	4_2*	11*	2_2*
7		5*	19*	4_1	4*	4_3	18*	9_2
9		6	20	6_1*	10	7_2*	21*	11_1*
		8	22*	6_2*	12	9_3		13_2*
		13*	23*	9_1*	16*	15_1*		
		14	24	13_1*	25*	21_2		
		15*	26*	15_2	27	21_3		
				19_1				
				21_1				

[* denotes that the individual subsequently swapped into at least one other shell].