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PAGURUS BERNHARDUS (L.)—AN INTRODUCTION TO THE NATURAL HISTORY OF HERMIT CRABS

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ABSTRACT

The field biology of *Pagurus bernhardus*, the common hermit crab of the Eastern North Atlantic, is reviewed. The importance of the shell resource—the availability of appropriately-sized empty shells of gastropod molluscs—is highlighted as *the* controlling influence affecting all aspects of growth, behaviour and even reproduction. A comprehensive bibliography is provided.

INTRODUCTION

DESPITE their occurring on almost every shore in the British Isles, the role of hermit crabs in the ecology of rocky shores is little understood. This work aims to bring together much of the scattered literature on hermit crab biology in order to help anyone studying the shore to include the group with more confidence. Although there are many species world-wide, different hermit crabs do have a great deal in common. Consequently, although concentrating upon the common European species *Pagurus bernhardus*, the opportunity has been taken to broaden the literature base wherever possible to consider some of the wider aspects of the biology of these fascinating animals.

EXTERNAL MORPHOLOGY

Hermit crabs are Crustaceans, placed within the decapod infra-order Anomura[1]. The Anomura are characterised by having the last thoracic plate on the ventral side free of the carapace, having the fifth (and sometimes also the fourth) pair of pereiopods (walking legs) 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 Lomidea (represented by the single species *Lomis hirta*—McLaughlin, 1983*a*), the Galatheoidea (the squat lobsters and porcelain crabs), and the Hippoidea (the mole crabs). The possible origin of the hermit crabs from crevice-dwelling ancestors (which had progressively lost their abdominal calcification) attracted to the convenience offered by a more mobile shelter, is discussed by McLaughlin (1983*b*).

Hermit crabs are most readily distinguished from the other anomurans by the possession of a naked, unsegmented, and usually twisted abdomen, which is, typically, protected

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[1] The classification of the crustacea is in much confusion. Schram (1986) offers a compromise view and places the hermit crabs in the Infra-order ANOMALA. McLaughlin and Holthuis (1985), however, have argued for the retention of the name ANOMURA on the grounds of its familiarity. The term ANOMURA will be used throughout this paper.

by an empty gastropod shell. This abdomen is characteristically coiled to the right in a healthy individual. A further distinguishing feature of the hermit crabs which easily separates them from the more familiar brachyurans is that hermits can move forwards in a straight line, and do not move sideways "crab fashion".

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, 1981*a*). Although one tropical family (the Coenobitidae) with some 12 species is semi-terrestrial (termed "tree-crabs"), all other hermits 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). *P. bernhardus* is the most common hermit crab recorded in British waters, and is the only local species whose biology has been studied to any extent. The total number of species of hermit crab represented around Britain is, however, difficult to estimate since identifications of "hermit crabs" are often automatically ascribed to *P. bernhardus*. A figure of 10–15 species would, however, be suggested by the literature (Table 1). Although most commonly associated with the littoral zone and shallow coastal waters, *P. bernhardus* is known to have a bathymetric range down to at least 500 m (Selbie, 1921). Members of the genus *Pagurus* demonstrate some of the widest ranges of behaviour known among hermit crabs, with the consequence that their taxonomy has been the centre of considerable debate. This problem is reviewed by Ingle (1985) who traces the major subdivisions of the genus through the literature, details many of the nomenclatural changes, and cites the authorities for the original descriptions.

There are a number of well illustrated descriptions of hermit crab species with keys to their identification, including Selbie (1921), Allen (1967), Crothers and Crothers (1983), and Ingle (1985). An old but still useful key to the world-wide genera is given by Alcock (1905), while Provenzano (1959) and Williams (1984) key and describe many of the species of the N. American coast. Although numerous authors comment upon details of the anatomy of the species that they have investigated, the most comprehensive account of the anatomy of any hermit crab is given in the monograph on "Eupagurus" by Jackson (1913) (see page 228 on the use of the names *Pagurus* and *Eupagurus*). *P. bernhardus* itself is characterised by the following description: the 3rd maxillipeds (the largest pair of accessory feeding appendages) are broadly separated at their base, the right chela is larger than the left and has a bristly surface with the propodus (the fixed finger) being gently convex and covered by tubercles. The colour of the animal is generally green-brown when young but turns to a more red-yellow colour once a carapace length of some 20 mm has been reached. The right chela has a characteristic red line down the middle with a row of conspicuous tubercles along each side and converging towards the tip. There is a distinct, sharp, rostrum. A more detailed description is given in Selbie (1921).

Some of the most interesting reports on the behaviour of living animals (rather than straight anatomical accounts derived from preserved specimens) are given by Elmhirst (1947) and Brightwell (1951*a*, 1951*b*, 1953) who maintained animals in glass replicas of shells and were therefore able to observe how they held themselves in their shells, how they moved within their shells, and how they maintained currents of water through their shells (Fig. 1). It was the first of these authors who confirmed that the telson and uropods (see Fig. 2 for an explanation of the anatomical terms) served as hooks or clamps to hold onto the columella of the shell, and that the 4th and 5th pairs of pereiopods were used as struts against the shell wall in order to help the animal maintain its position. The 4th pair, in

Table 1. *Species of hermit crab recorded from British waters*

	Mount's Bay, S.W. Cornwall Lancaster (1988)	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 and South Pembrokeshire Crothers (1966)	Clyde Sea, Isle of Man and Channel Islands Pike and Williamson (1959)	English Channel Marine Biological Association (1957) (also Southward and Southward (1977))	Coast of Ireland Selbie (1921)	Coast of Cornwall Clark (1909)
Pagurus 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*)		*			*			*			
Paragurus pilosimanus Smith					*					*	
Nematopagurus longicornis Milne Edwards and Bouvier					*					*	
Diogenes pugilator (= *D. varians*) (Roux)		*	*		*			*	*	*	*
Clibanarius erythropus (= *C. misanthropus*) (Latreille)	*	*			*				*		

*recorded as present.

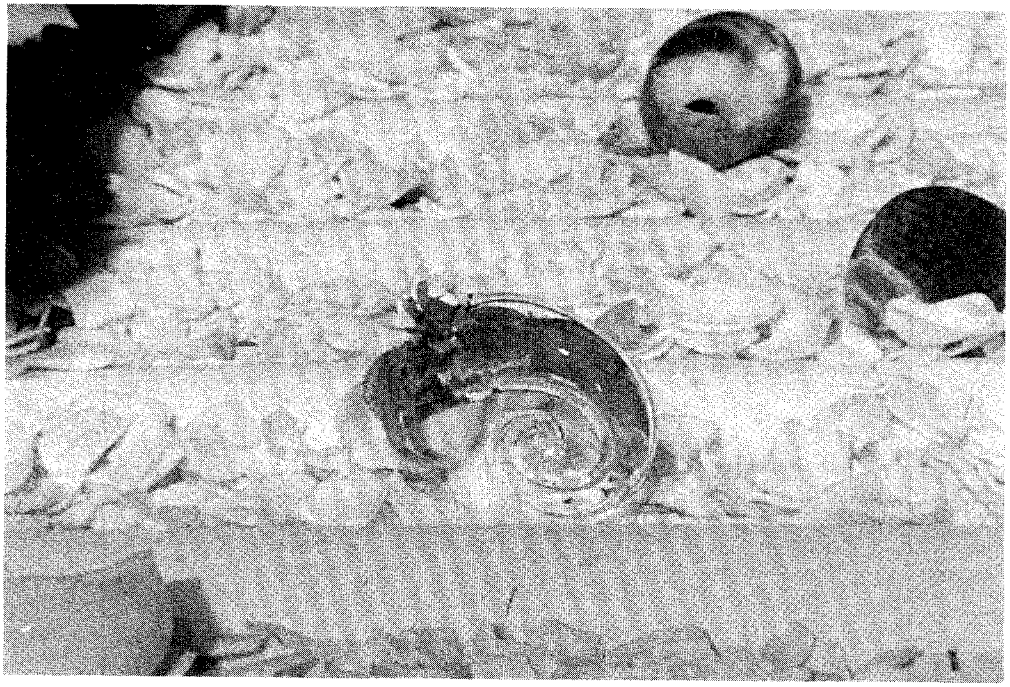

FIG. 1
Pagurus bernhardus occupying a replica glass shell.

particular, were seen to be responsible for cleaning the carapace, pleura, and limbs. General body movements together with movements of the pleopods produce water currents which sweep out faeces from as far as the shell's upper whorls, and also provide an adequate gill respiratory current. Contraction of the abdomen (while firmly attached to the shell's columella) allows an extremely rapid withdrawal motion in the event of any sudden danger in the vicinity.

The sexes of hermit crabs are only distinguishable with certainty after extracting the animals from their shells, but, once removed, the differences are plain. The female has 4 unpaired abdominal appendages (pleopods) on the left side only, and these are biramous with each branch more or less equal in size and bearing conspicuously long setae. In the male there are only 3 pleopods on the left side, and these are quite different from those of the female having a relatively inconspicuous inner branch and bearing reduced setae. It should, however, be noted here that in another common European species, *Pagurus prideaux,* the males are without pleopods. The surest way to identify the different sexes is to examine the bases of the walking legs for the reproductive openings—the gonopores are conspicuous on the coxal segments of the 3rd pereiopods in the female, and on the 5th in the male. These details are summarised in Fig. 3.

DISTRIBUTION

Hermit crabs are abundant and highly successful marine organisms, and the group is represented on sea shores and in shallow coastal waters world-wide. Many forms have a considerable bathymetric range—extending in the case of the N.E. Atlantic species *Parapagurus pilosimanus* to depths in excess of 4500 m (Selbie, 1921). Hermits occur so

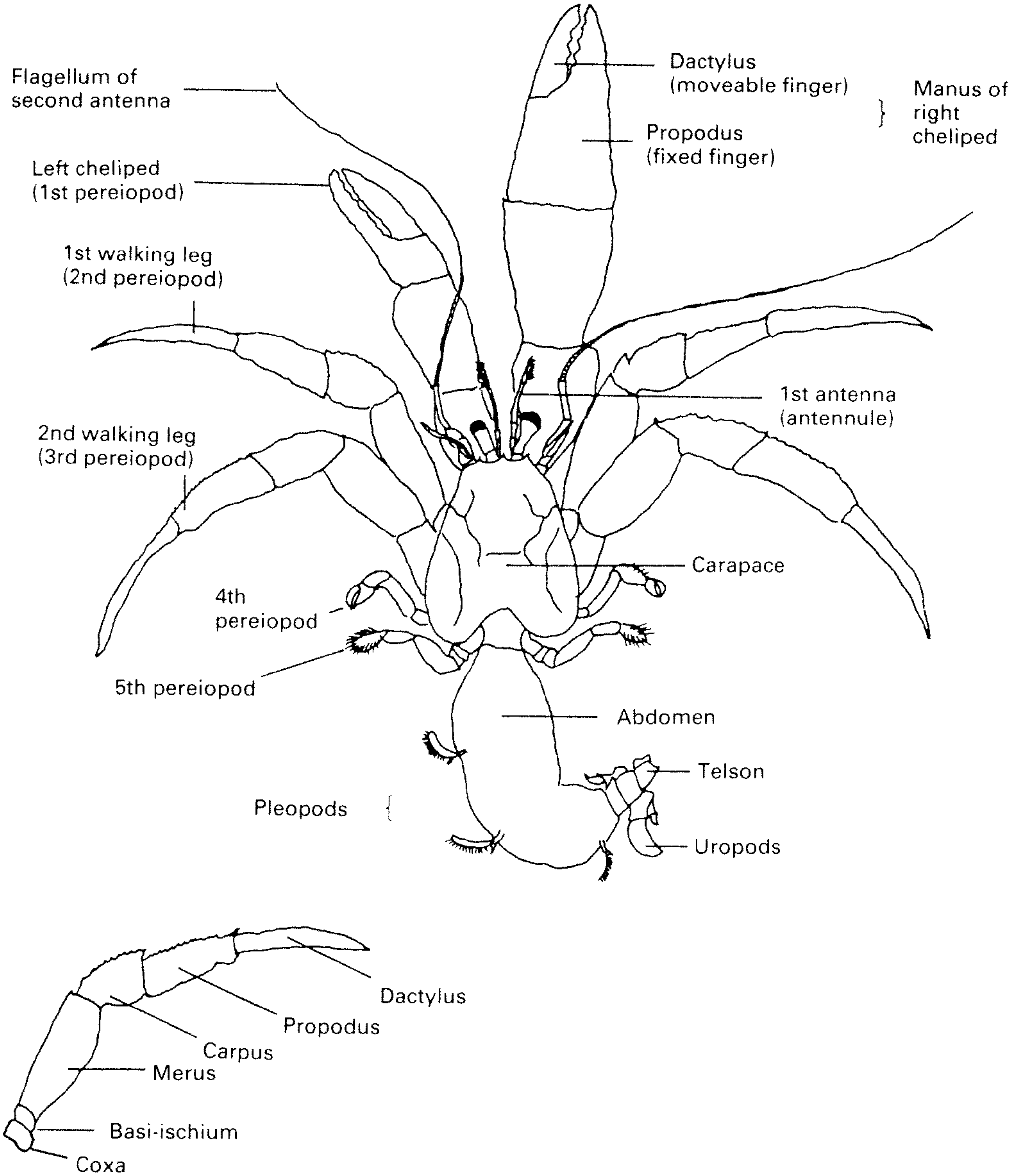

FIG. 2.

Some anatomical features of *Pagurus bernhardus* (after Jackson, 1913). The individual represented is a male. The segments of one of the walking legs are labelled from Warner (1977) and McLaughlin (1982).

commonly offshore in the N.E. Atlantic area 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 their distribution or abundance (perhaps because of their mobility) and, generally, their role in marine systems remains largely unexplored (Hazlett, 1981*a*).

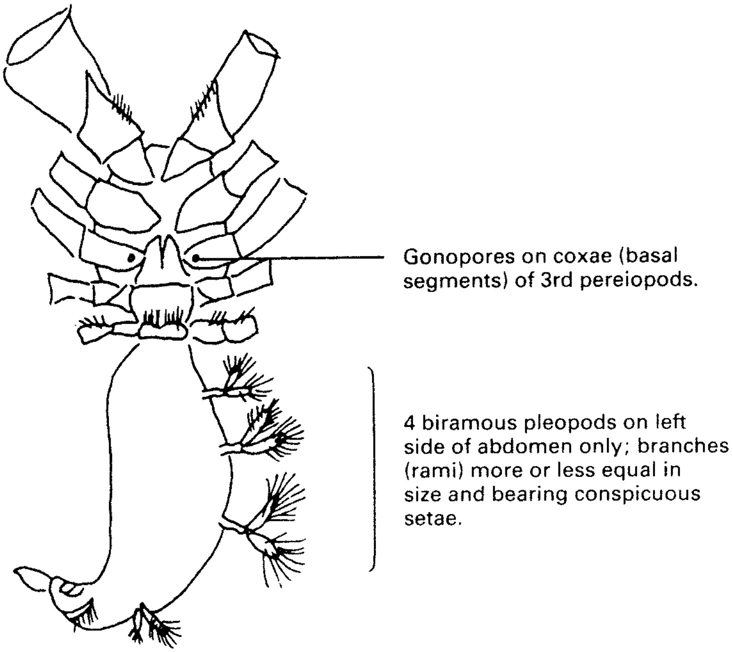

FIG. 3.
Some characteristics used to distinguish between the sexes of *Pagurus bernhardus* (after Jackson 1913). The individual represented is a female (ventral view). In males the gonopores open on the coxae of the 5th pereiopods, and there are only 3 biramous pleopods (the top ones are missing). The inner branches of these pleopods are much reduced in the male and bear less conspicuous setae.

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.* 1975*a*, 1975*b*) has indicated that, given a choice, *P. bernhardus* prefers a hard substratum to one of sand. It has been suggested (Barrett, 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 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 (Pike and Williamson, 1959; Perkins, 1985; Southward and Southward, 1977).

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). Other references to local, British, distributions of hermit crabs are given in Table 1.

FEEDING

Hermit crabs are perhaps best described as "omnivorous detritivores" (Hazlett, 1981*a*), and their highly flexible feeding behaviour is thought to be a key factor in their success as a group (Schembri, 1982*b*). Hermit crabs tend to be highly opportunistic feeders, and this habit adapts them particularly well to living in unpredictable environments (Scully, 1983*b*). Their gut contents may include anything from algal remains and fragments of microscopic shells, crustaceans and polychaetes, to sponge spicules, diatoms and foraminifera (Orton, 1927; Samuelson, 1970). Their diet may change seasonally to include much larger prey, e.g. ophiuroids, bivalves, amphipods, crangonids, and even smaller hermits, as available (Hunt, 1925). *P. bernhardus* has been observed to chip away at the fragile tests of the heart urchin *Echinocardium* to feed off the gonads within (Brightwell, 1951*b*), and may even attempt to break barnacles and tubiculous polychaetes (*Pomatoceros*) from stones and shells (Orton, 1927). Hermit crabs do not appear to make a habit of killing healthy gastropods, though this point is debated (see p 210). More bizarre feeding habits observed for hermits include plunging the claws into the gastric cavities of anemones to remove partially digested material (Brightwell, 1951*a*), filter feeding (Boltt, 1961; Gerlach *et al.*, 1976), scraping surface foam in rock pools (Scully, 1978), and even eating parts of themselves that have been crushed or damaged (Brightwell, 1951*b*)! Equally, cannibalism is common in many of the species studied (Hazlett, 1972*a*).

The crab's mechanism for locating food appears to depend more on taste than sight, and long unbranched hairs ("aesthetascs") located at the distal ends of the 1st antennae seem to be the principle organs of this sense. Other branched hairs on the mouthparts, on the dactyli of the walking legs, and along the biting edges of the chelae, also seem able to taste, and it is likely that a range of such receptors act together to analyse the nature of the food available (Hazlett, 1968*f*, 1971*a*, 1971*b*). The anatomy of the mouth parts and the feeding mechanisms of hermit crabs have been well studied (e.g. Caine, 1975, 1976; Greenwood, 1972; Kunze and Anderson, 1979; Patwardhan, 1935; Roberts, 1968; Schembri, 1982*a*). The relatively feeble mouth parts of hermit crabs (Orton, 1927) do not allow them to utilise exactly the same food as shore crabs such as *Carcinus*, and this fact may help to reduce the competition between them. The digestive enzymes produced by pagurids and aspects of the physiology of digestion in this group are discussed by Arnould and Jeuniaux (1982).

When feeding, the chelipeds (and occasionally the walking legs as well) scoop material up to the 3rd maxillipeds where hairs act like brushes to transfer particles to the mouth (Gerlach *et al.*, 1976; Orton, 1927). In addition to this "scooping" type of deposit feeding, at least three variations have been recorded (Schembri, 1982*b*) including "scrubbing" detritus from the surfaces of small granules, "scraping" it from larger surfaces, and "picking" it from crevices. If the sediment is fine enough, material may even be stirred up into a suspension and then filtered by the setae of the 3rd maxillipeds and other accessory mouthparts (Orton, 1927). The quantity of sediment sifted by a hermit crab feeding in these ways has been variously estimated as between 100 and 300 cm^3 per day (Thorson, 1966; Stachowitsch, 1979).

The loss of the larger claws does not appear to be a serious impediment to feeding, and crabs lacking both chelipeds can be observed to feed quite successfully in an aquarium using only their 3rd maxillipeds to manipulate food.

BREEDING BIOLOGY

The reproductive cycles of relatively few hermit crab species have been studied in detail, but the reproductive behaviour characteristic of the group is better known (e.g. Coffin, 1960; Kamalaveni, 1949; Helfmann, 1977; Hazlett, 1968*b*, 1972*b*). Studies on a number of species have indicated that, between them, hermit crabs display almost all the known patterns of (sexual) reproductive behaviour—including seasonal breeding and continuous breeding (Hazlett, 1981*a*), breeding before moulting and breeding after moulting (Hazlett, 1968*c*), breeding while females are still ovigerous or after larval release (Coffin, 1960), and breeding where single or multiple copulations are the rule (Hazlett, 1972*b*).

Mating behaviour has been observed in a number of species (including *Pagurus bernhardus*), and the general procedure is outlined by Hazlett (1968*b*). A male will typically carry a female about with him for some time prior to copulation (for several hours—or even several days, MacGinitie and MacGinitie, 1968), usually by grasping her shell by the rim with his small cheliped, and with the shell facing away from him. A male may be able to sense when a female is ready to mate, or may simply catch any female that he can at this time and retain contact with her—keeping other males at bay—until she is ready. The role of pheromones in mate searching is not known in this group.[1] The tendency for dominant males to deposit spermatophores indiscrimanately on any other individuals that they can overpower—including immature females and even other males—does, however, suggest that mate selection in these animals may be based more upon subordinate behaviour cues than upon individual recognition (Matthews, 1959; Salmon, 1983). When finally ready to mate the female is turned into a position facing the male and a period of mutual cheliped tapping begins, which may last 15–20 minutes. Copulation occurs with both individuals eased out of their shells and with their ventral surfaces apposed. They may remain like this for 4–6 minutes and may still hold together after copulation for up to 10 minutes more, but after that time the male will usually push the female away and subsequently has nothing further to do with her. Females are frequently observed to be still carrying mature eggs at the time of copulation, but quickly release them afterwards. The male may even help with this process (Hazlett, 1968*c*), and a second brood may be in place only hours after the first has hatched.

The actual site of fertilisation is unclear in *P. bernhardus*, though several strategies have been suggested for hermit crabs, including both internal fertilisation (with sperm being stored in a spermatheca until needed—Kamalaveni, 1949; Warner, 1977) and external fertilisation. In the last case the spermatophores may be placed on the coxopodites of the female's third and fourth pereiopods (where they have been observed after copulation in *P. bernhardus*—Hazlett, 1968*b*), and then may be ripped open by her fifth pereiopods as the eggs are extruded (Matthews, 1959). Since copulation has been observed in *P. bernhardus* shortly before moulting (Hazlett, 1968*b*—where the author notes that this is unusual since the routine in crustacea is generally to moult first and then mate), it is even possible that spermatophores may be taken by the female from her old exoskeleton and used as the new eggs are laid. A combination of mechanisms may, of course, be found to operate. Such uncertainty is not unusual in hermit crab reproduction, and similar confusions have been noted with other species (e.g. *Clibanarius chapini* and *C. senegalensis* from West Africa—Ameyaw-Akumfi, 1975). After copulation eggs are usually in place upon the pleopods within one hour (Coffin, 1960), although copulation itself does not inevitably result in egg laying (Matthews, 1959).

The stimuli which may initiate breeding in hermit crabs have been variously suggested (e.g. Emlen and Oring, 1977; 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 is, however, more

[1] A recent paper (Imafuku, 1986) does, however, suggest that males of at least one species may be able to discriminate between receptive and other females by detecting a water-borne chemical with their 1st antennae.

likely that a number of factors will be involved for any one population (Knudsen, 1964). Continuous and synchronous breeding is reported in a number of species, particularly tropical forms (reviewed in Hazlett, 1981*a*), but any precise synchrony in cool-water forms is generally thought to be less common (Warner, 1977). Factors such as fluctuating temperatures and photoperiods may influence gonadal maturation such that "breeding seasons" occur, but it is likely that within such seasons, especially if extended, individual females will tend to be asynchronous (with some being in the early stages of maturation, some getting ready to spawn, some spawning, and some already spent—Giese, 1959).

Collections of *P. bernhardus* made in various parts of Britain and Europe suggest that this species can be found breeding at almost any time of the year (Table 2), but direct comparisons between these observations can be confusing since some refer to littoral populations and some to sub-littoral ones. Detailed studies from the South West of England (Lancaster, 1988) and observations from South Wales (Crothers, 1966), Northern Ireland (Elwood and Stewart, 1987) and Brittany (Carayon, 1941), however, suggest that British littoral populations of *P. bernhardus* tend to breed predominantly during the months of November to May (i.e. breeding is periodic and not continuous). In particular, the stimuli of low water temperatures and winter photoperiods have been implicated in controlling this pattern, with temperatures below about 8–12°C regulating maturity and egg production in females, and with a reduced photoperiod influencing mating behaviour in males (Lancaster, *in preparation*).

The progress of reproductive maturity can be followed by observing the development of the ovaries in the females—as these paired structures can be clearly seen through the thin abdominal wall of individuals removed from their shells. A number of stages of development can be distinguished, and these are described in detail in Table 3. Sexually mature females (stage "4" females) are particularly conspicuous and have deep blue-black ovaries filling the abdomen and bulging with granular eggs waiting to be laid. Females in this state will be present in most littoral populations from about November onwards, and the first eggs will probably appear (attached to the abdominal appendages) shortly afterwards. Clutch sizes vary, depending upon such factors as the size of the female and the amount of available space inside her shell. Figures ranging from some 200–300 eggs for a female of shield length 3.0 mm to in excess of 1200 for a shield length of 5.0 mm are typical. Much larger clutches are possible for deep-water forms with shield lengths of around 20 mm; for example, a figure of 50 000 eggs quoted by Jackson (1913). Large numbers of eggs will, however, fail to reach full term since they are damaged by abrasion as the female moves around in her shell or may be lost as the clutch is waived in the water beyond the aperture for aeration. Estimates of up to 30% of a clutch being lost in these ways appear in the literature (Bach *et al.*, 1976; Fotheringham, 1980).

The period of gestation will be dependent to a certain extent upon water temperature but, at typical winter values of some 8–10°C, development may be expected to take approximately 43 days (range of 36–51 days, Lancaster, 1988). The progress of the eggs (followed in females kept without shells or in glass replicas) appears to follow a predictable pattern. At least seven stages can be recognised (Figure 4), which grade into each other at a predictable rate i.e.

stage 1–2	6–7 days
stage 2–3	12–14 days
stage 3–4	5–7 days

Table 2. *Months* Pagurus bernhardus *reported in the literature to be ovigerous*

Location	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 and Williamson (1959) p. 556	
Northern Norway						*	*	*					Dons (1915)	In Kamalaveni (1949)
Bohuslan (Sweden)			*	*	*	*	*						Nordgaard (1912)	
Øresund (Denmark)									*				Bookhout (1964) p. 277	
Firth of Clyde			*	*	*								Perkins (1985) p. 22	
Roscoff and 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 *et al.* (1963) p. 172	
Irish waters (Co. Down)	*	*	*	*	*							*	Elwood and Stewart (1997) p. 254	
Mount's Bay, S.W. Cornwall	*	*	*	*	*							*	Lancaster (1988)	

Table 3. *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 <3·0 mm) 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.

stage 4–5	5–7 days
stage 5–6	6–11 days
stage 6–7	2–5 days.

A female living in the littoral zone probably produces two clutches each season that she remains there. Females found with full clutches on their pleopods during the late winter (January/February) will probably produce their second clutch shortly afterwards. A third clutch is possible but, as sea temperatures rise in spring, the necessary stimulus appears to fade.

The embryological development of hermit crabs has been described for various species e.g. for *P. bernhardus* (briefly) by Jackson (1913), for *Clibanarius olivaceous* by Kamalaveni (1949), for *Pagurus samuelis* by Coffin (1960), and for *Pagurus prideaux* by Krainska (1934, 1936, 1938) and by Scheidegger (1976). General details on crustacean embryology are given by Anderson (1982).

Larval release may be a passive process (Matthews, 1959) or an active one—with larvae being forcibly released by the female snapping back into her shell after a partial emergence (Coffin, 1960) or by being blown out of the shell in the crab's exhalent current (Ameyaw-Akumfi, 1975).

LARVAL LIFE AND METAMORPHOSIS

Hermit crabs have planktonic larvae, allowing not only for dispersal but also enabling the young to grow without competition from adults for either food or habitat space. Two conspicuously different larval forms occur in hermit crabs: the first or *zoeal* form (defined as a crustacean larva that swims using its thoracic appendages) typically has four stages, while the second or *glaucothoëal* form (corresponding to the brachyuran megalopa as the stage swimming by using its abdominal appendages) has a single stage. The historical use of these terms and the reasoning—based upon the previous definition—behind regarding the anomuran glaucothoë as merely another form of megalopa (i.e. the earliest stage in the life cycle with functional pleopods), are discussed by Williamson (1982). The zoeae of hermit crabs can easily be distinguished from those of brachyuran crabs by being more shrimp-like in profile and by their having a long rostral spine in place of a tall dorsal spine. Equally, while the telson of brachyuran zoeae tends to be forked, that of the anomuran

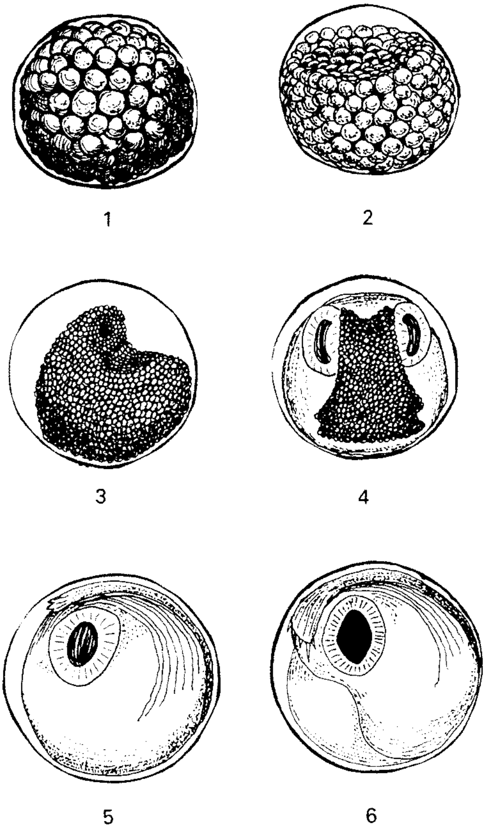

FIG. 4.

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 0.5 mm.

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

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 0.5 mm.

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 0.5 mm.

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

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

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

zoea is more spade-shaped, forming a true tail fan (Williamson, 1965). These details are summarised in Figure 5. Anomuran larvae typically swim backwards (i.e. telson first) with the dorsal side uppermost and abdomen extended (Warner, 1977). The tail fan may be used to make escape movements or to reverse course after collision. The long rostral spine may aid flotation (by increasing surface area), enabling the animal to rest in the water column without sinking. Swimming seems to be a directed and not a purposeless movement, and sensitivity is shown to gravity and to both the intensity and direction of light. The larvae

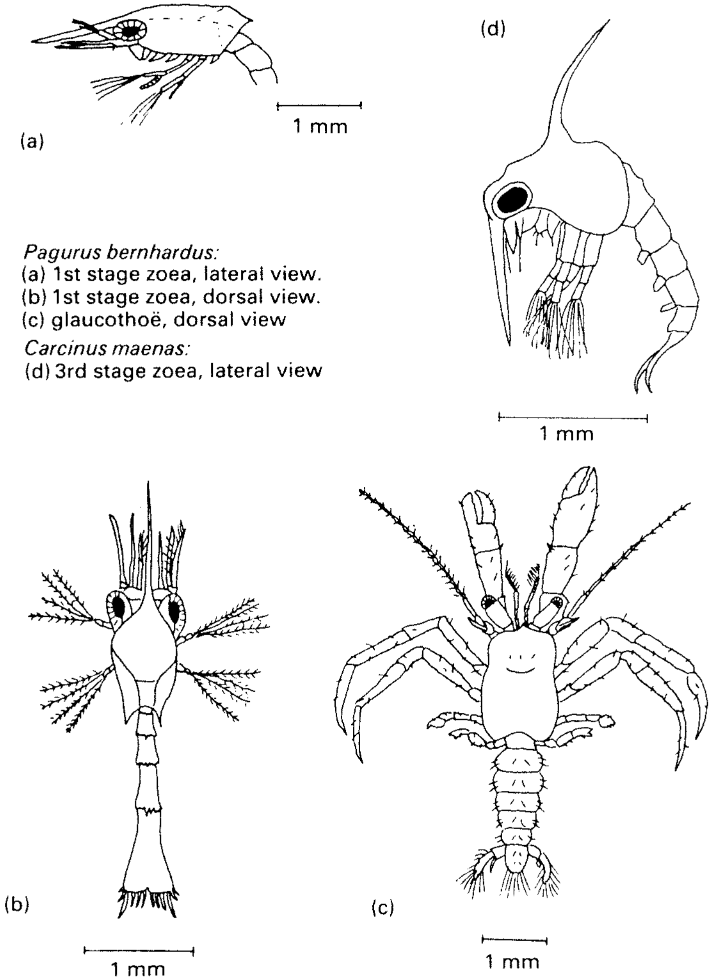

FIG. 5.
The larval forms of *Pagurus bernhardus*, with a zoea of the shore crab *Carcinus maenas* for comparison (after Williamson, 1911; MacDonald, Pike and Williamson, 1957; Crothers, 1967).

feed on a range of planktonic material but living and moving animal food seems to be preferred. The duration of each stage, and thus the length of larval life, appears to be dependent on temperature and, to a certain extent, upon adequate feeding—i.e. the attainment of a certain bulk seems to be necessary before it is possible to make the metamorphosis into the glaucothoë (Warner, 1977). Low temperature slows development, and salinities below about 15–20‰ seem to inhibit larval moulting altogether (Bookhout, 1964).

One of the most detailed studies of metamorphosis in hermit crabs is by Thompson (1904) for *Pagurus longicarpus*[1] (from New England waters, U.S.A.). Detailed descriptions and illustrations of the zoeal and glaucothoëal stages of *P. bernhardus* are given by Williamson (1911), Jackson (1913), and MacDonald, Pike and Williamson (1957). Keys to

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[1] There is some controversy over the identification of this species, and Roberts (1970) and Nyblade (1970) consider that Thompson confused the larvae of *Pagurus longicarpus* with those of a similar species *P. annulipes*.

the identification of the zoeae and glaucothoës of British hermit crabs are given by MacDonald *et al.* (1957), Gurney (1939), and by Pike and Williamson (1960*a*, 1960*b*).

Laboratory studies on larval development tend to be difficult since survival rates are generally low—MacDonald *et al.* (1957) found that larvae survived only some 10–14 days in laboratory tanks, and even Bookhout (1964) in his detailed work on larval rearing, only attained a survival rate of around 10–15%. Despite this, the latter author did manage to obtain an almost complete sequence of development times for *P. bernhardus* from Danish waters. When individuals were maintained at 10°C, and at a salinity of 30–35‰, the 1st zoeal stage was found to last around 11 days, the 2nd some 7–10 days, the 3rd 9–11 days and the 4th 12–15 days. Zoeal development may therefore be expected to be completed in some 39–47 days if conditions are favourable. The glaucothoëal stage was found to last a further 13–17 days. Complete larval development in *P. bernhardus* is, therefore, suggested to take about 60 days.

Larval life is usually considered to have ended by the 6th moult, i.e. the one immediately following the glaucothoë, when the change from the straight abdomen to the more typically coiled form occurs. At this point, the 1st "young hermit" stage (of Pike and Williamson, 1959) is attained. Thompson (1904) was of the opinion that crabs unable to find a suitable shell at this time would suffer considerable mortality, and figures of 60% are quoted as compared with less than 50% for those that do gain access to suitable shells. Bookhout (1964), however, observed that many glaucothoës without shells still made the critical moult to the young hermit stage at about the same time. A shell does, however, seem to be essential from this stage forwards.

GROWTH, MOULTING AND REGENERATION

Growth for a crustacean is a complex process, since the hard exoskeleton which surrounds it must first be shed before another, larger one, can be manufactured. What these animals gain, however, from such a rigid and inflexible structure is that, once hardened, their new exoskeleton provides them with almost total physical protection. The situation in hermit crabs is complicated by the fact that the calcified exoskeleton does not cover the abdomen, leaving this region soft and vulnerable. For successful growth therefore, hermit crabs have to depend upon protecting their bodies within structures which they do not themselves manufacture—suitably sized gastropod shells. Consequently, the sizes attained by hermit crabs are a reflection of the sizes of shells available to them. This can mean that crabs which only have access to small shells will not be able to grow as much or as quickly as those with access to larger shells. Thus, it is not surprising that the overall fitness of hermit crabs seems to be closely linked to the availability of this precious resource. Indeed, if the shells in which hermits are forced to live are too small, growth rates may be reversed (Lancaster, 1988; Lancaster, *in preparation*) and individuals may end up smaller after a moult than they were before! This may, however, be an advantage in the short-term since it provides a strategy whereby a suboptimal shell can be occupied for longer, allowing the crab to receive at least minimal protection until something better can be found (Scully, 1983*b*). Convincing evidence that entire populations of hermit crabs can be size-limited by the lack of any larger shells in their vicinity is given by Drapkin (1963), who observed that the mean size of *Clibanarius erythropus* (given as *C. misantropus*) in the Black Sea increased rapidly after the larger shells of the gastropod *Rapana bezoar* (accidentally introduced into the area some years before) became available to them.

Growth in hermit crabs is, therefore, an even more unpredictable phenomenon than in the case of other arthropods, and is a difficult property to analyse since size/frequency data, that often prove so useful elsewhere, are unreliable here (Kurata, 1962). Predicting the eventual size of a known individual is particularly difficult since growth increments are not constant from one moult to the next, even with the same animal (Hartnoll, 1982). Increments vary, not only between the sexes, but also between individual crabs of the same age and initial size. The only predictable patterns are: that smaller crabs increase more per moult than do larger ones (Butler, 1961), starved or captive animals grow less at each moult and moult less frequently than do wild ones (Hiatt, 1948; Wenner *et al.*, 1974; Kurata, 1962), moults are generally more frequent in warmer months than in colder ones (Travis, 1954), intermoult duration increases with age (MacKay and Weymouth, 1935) and as the salinity falls (Ajmal Khan and Natarajan, 1981), and individuals in the course of regenerating lost appendages have smaller increments than do undamaged specimens of the same size (Hartnoll, 1982). Since arthropods produce none of the useful structures such as scales, otoliths, vertebrae or fin rays that can be used either individually or statistically to give a measure of age, estimating this parameter in many crustaceans is virtually impossible. Nevertheless, Markham (1968) has suggested an equation to predict the number of moults that an individual *P. bernhardus* has undergone:

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

[where L_s = measured front carapace (= shield) length, and s = instar number. The constants are derived from Kurata (1962) and the figure (some 1.5–1.8 mm) quoted by Pike and Williamson (1959) for the total carapace length of the first young hermit stage of this species.]

Moulting has one considerable advantage in that it permits damaged limbs to be shed voluntarily in the event of capture. Loss of a limb may accelerate the process of moulting (Weis, 1982), and the new limb may be fully restored after 2 or 3 moults (Scully, 1986). In fact, this ability is often so well exploited by crustaceans that it has been estimated that, at any one time, at least 10% of individuals in any population are likely to be regenerating one or more lost appendages (Bush, 1930; Neil, 1985). Although undoubtedly an aid to short-term survival, the effects that autotomy may have on an individual's long-term prospects may be more serious, since the limb loss will influence its dominance (Mainardi and Rossi, 1972), its ability to mate, to communicate, to compete, to feed, and to manoeuvre into a new shell. However, even though the loss of one or more limbs may make locomotion difficult, it does not necessarily become impossible—Reese (1962*a*) mentions a glaucothoë lacking both chelipeds and its 1st and 2nd pereiopods that moved around its tank using its antennae, its 3rd maxillipeds, and its 3rd and 4th pereiopods, and was still able to enter a shell! All limbs will regrow after autotomy and in the same proportions as before. *P. bernhardus* is a "one-handed" species and the chelae will regenerate to their usual form (i.e. right larger than left) eventually (Bush, 1930). In this respect, hermit crabs differ from the brachyuran crabs such as *Carcinus maenas* where the left chela will develop into the master if the right one is lost (see Crothers, 1967). Moulting itself must not be regarded as without hazard since at least 4 days seem to be required for the next exoskeleton to harden (Hazlett, 1970*a*).

*In order to calculate the instar number directly from the length of the shield, this equation can be transformed to:

$$s = \frac{\mathrm{Log}_{10}\left[\dfrac{L_s + 0.36}{1.36}\right]}{0.0453}$$

During this time the animal is extremely vulnerable, and fighting, feeding, and locomotion are all very difficult.

The actual process of moulting (reviewed in crustacea generally by Passano, 1960, and for crabs in particular by Warner, 1977) is described by Elmhirst (1947), who maintained hermit crabs in glass shells and was thus able to observe this normally hidden process in detail: the soft exoskeleton of the abdomen is moulted first, and then the calcified carapace and limbs are moulted in one piece. The process most frequently occurs at night and the old exoskeleton will usually be eaten over a period of anything up to 3–15 days, presumably to recover valuable mineral salts. Even the large chela may be eaten after about 5 weeks.

SOCIAL BEHAVIOUR

An enormous variety of complex behaviour patterns are displayed by crustaceans (see reviews by Warner, 1977, and Schöne, 1961), and some of the most intensively studied are those exhibited by hermit crabs. Behaviour is known to be highly variable both within and between species (Hazlett, 1981*a*) and may even become so distinctive that individual populations are virtually isolated (e.g. Southward and Southward, 1977). Such differences may, however, allow several species to coexist in the same habitat even though their requirements for shells, food etc. may otherwise appear very similar (e.g. Vance, 1972*b*; Van der Laan and Kuris, 1979; Abrams, 1980, 1981; Bach *et al.*, 1976; Bertness, 1981*b*, 1981*e*; Grant and Ulmer, 1974; Hazlett, 1966*a*).

The most conspicuous types of social behaviour tend to be those that best distribute resources amongst the individuals fittest to exploit them. The most intense competition exists between animals of the same species, and it is common for potentially wasteful damage to the competitors (by direct conflict between them) to be avoided by having some form of ritualised behaviour. Thus the resources become evenly distributed throughout the population with the minimal physical injury to the individuals concerned. Much of the hermit crab literature deals with such interactions (particularly when the resource concerned is a gastropod shell), and emphasises the displays that are used to advertise dominance and subordination in conflict situations. Hermit crabs are particularly good at solving the problems of limited resources and are efficient at both exploiting what they have and contesting for what they have not. This quality perhaps more than any other may have led Eales (1967) to describe *P. bernhardus* as "pugnacious"!

The main types of behaviour studied in hermit crabs (excluding reproductive and feeding behaviour) can be categorised as follows (Scully, 1983*a*, Hazlett, 1972*a*, 1975*a*).:

1. Aggressive behaviour related to the aquisition or defence of a shell.
2. Behaviour aimed at investigating and examining an empty shell or object in the vicinity.
3. Displays aimed at maintaining personal distance between individuals (and unrelated to the shell resource).

Of these, numbers 1 and 2 are discussed in more detail under the topic of "Shell Selection".

In a detailed study of hermit crab social behaviour, Hazlett (1966*a*) concluded that when two individuals meet they tend to follow one of only three main courses of action—either they ignore each other completely, they mate, or they fight! The sexes of the individuals concerned to not appear to have any effect on interactions that do not involve mating (Winston and Jacobson, 1978). When two crabs come into contact, the distances over which they begin to react to each other vary enormously between individuals, but appear to depend little on their relative sizes. Individuals used to crowded conditions will generally tolerate a much closer approach before reacting than will those used to much free space (Hazlett, 1975*a*, 1979). Such increased tolerances presumably serve to prevent time and energy being wasted on constant disputes—though suddenly increasing the density of crabs in an area does markedly increase the frequency and intensity of aggressive interactions until individuals adjust to the overcrowding. Consequently, the most ritualised patterns of behaviour occur in naturally gregarious populations. It is amongst these individuals that the least damage might be expected during conflict situations (Mainardi and Rossi, 1972). Crabs with different histories can, therefore, become involved in disputes with unexpected outcomes—a large and dominant individual from a widely-spaced population (and hence one used to maintaining a large "personal space" around itself) can come "unstuck" when faced with a smaller individual from a densely-crowded population (and used to a much smaller personal space). As the larger crab approaches the smaller one it will rapidly cross the threshold distance at which it would normally expect a smaller opponent from a similar background to retreat. The smaller crab, however, does nothing as *its* personal space has not yet been breached. Thus, by doing absolutely nothing, this smaller crab will appear more dominant to the larger crab—which will tend, eventually, to retreat in confusion! Predicting the outcome of some interactions may therefore be difficult. Predicting that there will be an interaction can, however, be more certain, since aggressive acts are particularly common between two crabs when at least one of them occupies a shell that is sub-optimal in some respect. The eventual outcome of this type of contest is still unpredictable, however, since the information each crab receives about the other (essential in order to know whether the opponent is larger or more dominant) depends upon the role that each individual plays—whether as attacker or defender. The defender, by withdrawing into its shell, is unable to gather much information about its attacker. Hence, it will not know whether leaving its shell early on in the struggle may mean less damage or injury in the long run. The attacker, however, can judge from its opponent's size (the presence and size of its major cheliped is thought to be particularly significant here—Dunham, 1981; Neil, 1985) and the apparent size and state of its shell whether the attack is worth pursuing. Some of the factors that may help to predict the outcome of such conflicts are discussed by Hyatt (1983) and Dingle (1983), but, within a reasonable range, size is a good predictor of dominance in aggressive encounters between crabs (Hazlett, 1968*d*; Mainardi and Rossi, 1972). If the two animals are evenly matched, then the duration and intensity of a fight is likely to be determined by the behaviour of the non-initiator, i.e., by its willingness or otherwise to relinquish hold of its shell (Hazlett, 1978, 1980*b*).

Although hermit crabs interact for many reasons (and often aggressively), it is conspicuous that they tend to do relatively little damage to each other on these occasions. Much of the explanation must lie in the complex ritualised behaviour that the group displays, both interspecifically and intraspecifically (reviewed by Hazlett, 1981*a*). Displays of particularly effective visual and tactile signals—that efficiently express dominance and status—become ritualised and stereotyped as their value influences evolution. Efforts will not, therefore, be wasted by engaging in reproductive behaviour with members of other species, and losers of ritualised fights will have a much better chance of surviving (and reproducing) than if the conflicts were truly physical. Behaviour which occurs during territorial or dominance encounters is termed "agonistic" (to avoid any anthropomorphic suggestion that may be implied by the term "aggressive") and eventually tends to produce a dominance-order in which all individuals come to recognise their "place". Crab societies tend to be competitive rather than co-operative (Warner, 1977) and the advantages of maintaining a social order can be seen in any group exposed to wide fluctuations in the availability of resources: some individuals, at least, will survive during hard times by monopolising food/territories/mates etc. at the expense of the others, and thus the population will also survive. An analysis of agonistic behaviour in crustacea generally is given by Dingle (1983).

One way, in particular, by which hermit crabs avoid constant physical conflict is by maintaining a certain "personal space" around themselves into which other individuals are not welcomed (Hazlett, 1975*a*). The exact nature of this space varies but, as has been mentioned, the most aggression is displayed towards neighbours under conditions of the greatest crowding. It is under these conditions that there will be the greatest incentive for individuals to form a clear and distinct hierarchy—specifically to prevent excessive energy and time being spent upon display and conflict. In such situations (e.g. in aquaria) it is easy to distinguish the most dominant individual (the "alpha" individual of Hazlett, 1969*a*) and the least dominant, though others are less easy to rank. A more general term used to describe such an ordered arrangement within a group of animals is "dominance hierarchy" (Hazlett, 1979). The maintenance of such hierarchies depends, to a certain extent, upon each individual remembering its place with respect to the others—though the exact significance of memory and individual recognition are debateable (Hyatt, 1983). The eventual outcome of an interaction between any two individuals is much more likely to depend upon such factors as relative sizes and each individual's physiological or physical condition. A formerly dominant crab will tend to lose an encounter if it has recently moulted, or if it has lost or is regenerating appendages—particularly its chelipeds—since such a loss may make the animal appear more submissive or make it less able to hold on to its shell (Scully, 1983*a*; Hazlett, 1969*b*). Its previous social experiences are also important—winners will tend to win and losers will tend to lose! It therefore appears that it is a strong aggressor that is recognised and not an individual.

The displays themselves must be learned (or, if innate, then perfected) and here the role of experience is more clearly demonstrated. Hazlett and Provenzano (1965) reared young hermit crabs in isolation and then presented them with typical conflict situations involving others of their own species. Injuries were common in the fights that ensued, until the ritual displays were perfected. Equally, the youngest crabs often failed to recognise the displays made towards them by other individuals—but those that survived improved with time. The importance of experience is emphasised in the actions of another species of Caribbean hermit which, when presented with models in particular display postures, consistently gave the same display in response (Hazlett, 1966*b*). The types of display that an individual gives in a particular situation may well, therefore, depend upon those most frequently reinforced in its repertoire by experience. The most commonly executed displays observed in *P. bernhardus* have been categorised by Hazlett (1966*a*, 1968*a*, 1968*g*, 1972*a*) as:

1. Cheliped presentation—where one or both of the chelae are held forwards and point downwards, remaining perpendicular to the substratum (Figure 6a).
2. Cheliped extension—when a cheliped moves rapidly forwards and upwards until the limb is parallel to the substratum (a movement which may physically strike and move an opponent (Figure 6b).
3. Ambulatory raise—where the second and third pereiopods are moved rapidly away from the body until they lie at right angles to it. They may be held in this position for some time, and the display may be sub-categorised as single to quadruple raises depending upon the number of limbs involved. The limbs may even be extended into

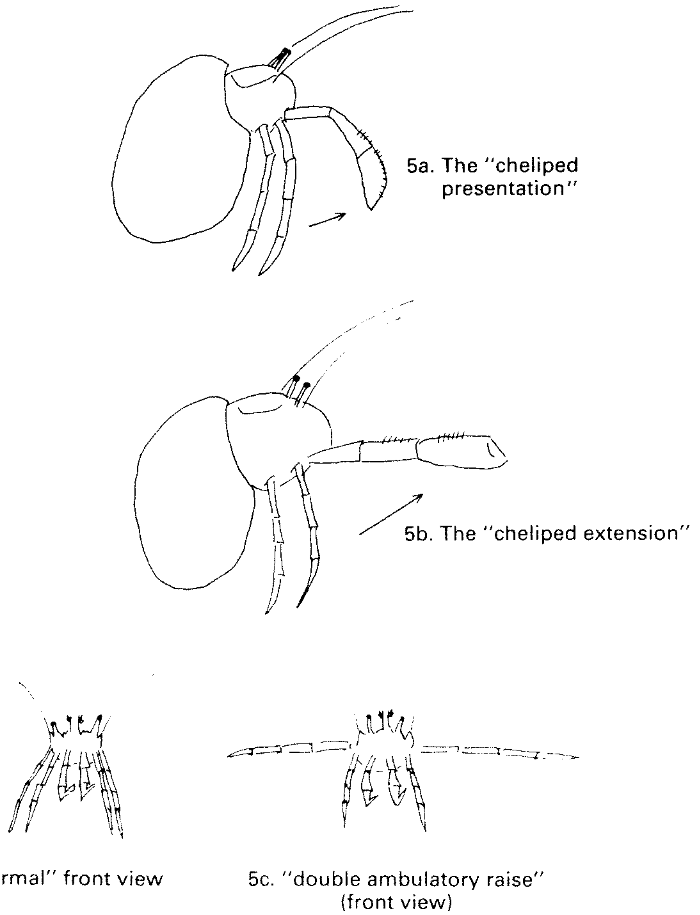


FIG. 6.
Diagrammatic representations of some common displays used by *Pagurus bernhardus* (after Hazlett, 1966a, 1968e, 1972a).

an "ambulatory poke", often striking the other crab in the region of the eyestalk (Figure 6c).

4. Dislodgement shaking—a predictable pattern of behaviour observed in the case of one crab grasping and climbing onto the shell of another, where the one climbed upon jumps up and down in an attempt to remove its attacker.

In addition, work with models has shown that the threatening nature of the displays can be further emphasised by the crab's own body position. A raised body position will increase a signal's aggressive value and a lowered body will decrease it (Hazlett, 1968*e*). In some cases up to six body-position characteristics must be present simultaneously in order to make a signal effective (Hazlett, 1972*c*). The submissive crab is usually obvious in any encounter since it retreats or ducks into its shell (Hazlett, 1975*a*), but in one species at least (Reese, 1962*b*) the loser of an agonistic bout was observed to simply lie on its side with its limbs limp and relaxed—perhaps a useful signal if escape is not possible.

Since hermit crabs seem to possess such a distinct set of displays with which to warn off neighbours, the question as to whether they occupy and defend fixed territories is worth asking. The whole field of animal spacing and territoriality is complex, and any interpretation of field data tends to be highly controversial (discussion in McBride, 1971). General observation shows no tendency for crabs to be found in the same parts of experimental tanks from day to day, and detailed studies of their migratory behaviour would generally argue against the occupancy of fixed positions for any prolonged periods of time. Some crustaceans (e.g. fiddler crabs) do occupy fixed territories (Dingle, 1983) and the advantage of possessing such a "personal space" are well documented in terms of resource partitioning and breeding success (e.g. Hyatt, 1983). Hermit crabs only appear to maintain the space immediately around themselves wherever they happen to be, and they are not inclined to defend a fixed piece of ground from one period to the next. Equally, these personal fields are highly flexible, depending upon conditions of overcrowding, and may not necessarily be the same in all directions—usually being greatest towards the front, the direction from which an "attacker" is most likely to be first seen.

THE SHELL RESOURCE

The shell-carrying habit is so fundamental to the biology of hermit crabs that very few aspects of their behaviour appear unaffected by it (Hazlett, 1966*a*). The adaptations associated with shell use enable hermits to exploit the intertidal environment very successfully, avoiding extreme conditions by creating micro-habitats within their shells—which thereby provide "all the advantages of a burrow without any of its restrictions" (Reese, 1969). This closeness of association is very easily demonstrated, since, on any shore inhabited by these animals, empty gastropod shells are rare—and the intense competition that is often witnessed, even for damaged shells, illustrates how the aggression, ritualised display, and fighting behaviour so typical of this group has evolved.

Hermit crabs are highly vulnerable if deprived of their shells. Naked crabs will generally accept a wide range of objects as substitutes, but the statement by Brightwell (1951*b*) that "the hermit crab . . . will die if not provided with a home" seems exaggerated. Mortality is certainly higher for animals evicted from their shells (cannibalism may be a particularly important factor—Samuelson, 1970), but if *P. bernardhus* is protected from attack and is able to cling to some form of shell material (this seems necessary for withstanding the stress of being without a shell) it can certainly survive for many months in the laboratory. This observation is contrary to those of Allee and Douglis (1945) that shell-less *Pagurus longicarpus* do not feed unless housed in a more or less suitable shell.

The advantages of possessing a shell have been particularly well studied, and can be briefly summarised as follows:

1. Protection from predators.
2. Protection for the soft and vulnerable abdomen from mechanical abrasion by a rough substrate (Bollay, 1964).
3. Protection from temperature fluctuations—either by allowing withdrawal into the shell if conditions become severe, or by permitting movement away from an area if conditions become intolerable (Reese, 1969).
4. Protection from water loss—particularly important for those species that are semi-terrestrial or those that find themselves exposed at low tide (Herreid, 1969).
5. Protection for salinity stress (Davenport *et al.*, 1980; Shumway, 1978).
6. Protection for the brood (Taylor, 1981).

The shell resource can prove a limiting factor in hermit crab population dynamics, affecting both population size and the rates of individual growth, development, and longevity

(Hazlett, 1981*a*; McLean, 1983; Scully, 1983*b*; Raimondi and Lively, 1986; Lancaster, 1988). Empty undamaged gastropod shells tend to be scarce in natural habitats occupied by hermits, and sub-optimally sized and damaged shells are frequently used and even fought over. Animals denied access to the larger shells required for growth tend not to live as long as others which find them. Increases in hermit crab population densities can quickly follow local increases in gastropod shell numbers, and the value for the mean body size of an entire population can increase if the crabs are given access to shells larger than those usually available to them (Drapkin, 1963). In addition, certain strategies seem to have developed to maximise the shell resource available to a population e.g. slightly larger than optimal shells may be preferred by the crabs, since these extend the time before another shell need be found. Individuals may display complex ritualised shell-fighting or even swapping behaviour (see p 212/214), and competition for shells can become so intense that appendages (particularly the chelipeds) may be lost in violent conflict. A large proportion of the numbers present may have one or more limbs missing—a means by which a shell-limited population can be recognised in the field!

A shortage of adequate shells (a reasonable definition of "shell-limitation") may be a common problem for the majority of hermit crab populations. Since there are generally even fewer of the largest shells available, the largest crabs probably feel the effects of this limitation most severely. Such limitation may be quantitative (insufficient shells to go around) or qualitative (plenty of shells, but of the wrong size, damaged or buried), or a mixture of both, but individuals forced to occupy sub-optimal shells will inevitably be at a disadvantage. Damaged shells (and those with holes) will facilitate the entry of commensals, parasites, and egg predators (*in* Taylor, 1981), and may well make it easier for other crabs to crush the shells or to force an eviction. Such a shell will also be a less safe refuge in the event of salinity stress, since water will leak out of the holes if the crab is exposed on an open surface or water of a different chemistry may infiltrate. An individual forced to occupy too large a shell may be at a disadvantage since additional energy demands will be imposed by the extra weight (Elwood and Glass, 1981), and it may find movement and manoeuvering difficult (Hazlett, 1970*b*). On the other hand, if the shell is too small, the problems of water loss, reduced reproductive success (by reducing the animal's size at maturity and hence its potential clutch size—e.g. Bertness, 1981*c*), reduced growth (e.g. Fotheringham, 1976*a*, 1976*c*; Lancaster, 1988), reduced protection from predators (Vance, 1972*a*), reduced success in agonistic encounters (Childress, 1972) and the increased chances of being "winkled out" by predators (Conover, 1978) will all serve to decrease the animal's chances of survival. There is even a suggestion that the dimensions of the shell occupied has an effect on the crab's eventual size and shape—particularly with regard to the growth of its appendages (Blackstone, 1985, 1986). Animals in smaller shells have a restriction placed upon their body growth but develop larger claws to enhance their chances in sexual combat. The results of such work are, however, open to wide interpretations (see Huxley, 1932).

SHELL SELECTION BEHAVIOUR

The first signs of this vital area of behaviour appear during the glaucothoë stage (Thompson, 1904; Hazlett and Provenzano, 1965). Here, exploratory movements made during random wanderings (when no visual orientation seems to occur, see Reese, 1962*a*), first bring the animal into contact with gastropod shells, and providing one is of an appropriate size and shape, enable it to effect an entry. It is at this time that the shell resource comes under one of its greatest strains, particularly if larvae of more than one hermit species are settling at the same time with essentially the same requirements. In such cases, evolution has favoured mechanisms that partition the resource—by differing the times of larval release (Bertness, 1981*d*) or the period of larval development, by timing the release to coincide with the period of maximum abundance of suitable shells, or by varying larval size (Wang and Jillson, 1979).

The parameters by which a particular shell is chosen by an individual hermit crab (or by which it assesses whether its existing shell is worth defending) are far from clear and represent one of the most controversial areas of their biology. Almost every physical parameter has been considered as being primary: the shell's weight (Hazlett and Herrnkind, 1980; Reese, 1962*a*; Bach *et al.*, 1976), its weight:volume ratio (Markham, 1968); the angle of its columellar axis—and hence its ease of carriage (Dowds and Elwood, 1983); the relationship between the crab's weight and the shell's width (Vance, 1972*b*); a shell's volume; its rugosity; its aperture size or shape; even its internal architecture. It is much more likely, however, that the behaviour employed by a crab is highly plastic, and that a number of parameters are assessed with no single factor determining the overall suitability of any one shell (Mitchell, 1976; Kuris and Brody, 1976). Indeed, whatever parameters are used at one time are likely to change as the animal grows and as its requirements alter (Hazlett, 1981*a*).

The controversy over which parameters take precedence has arisen since many of the investigations have been conducted under highly artificial conditions—with the animals under test often being given access to totally unrealistic choices of shells. The underlying principle behind such tests is that an animal given an unrestricted choice of shells should eventually come to occupy one which is optimally constructed. The shell's dimensions can then be measured and those crab and shell parameters with the highest correlation can be assumed to be significant. The supposed "preferred" size/weight etc. has been used to provide a base-line against which shell quality can be judged under natural conditions, and even in order to construct certain "indices" of shell quality such as the *Weight Index* of Reese (1962*a*) and the *Shell Adequacy Index* of Vance (1972*a*, 1972*b*). Unfortunately, all of these estimates rely upon a crab "recognising" the ideal qualities of the shell it occupies and remaining in it for some time afterwards. It can, however, easily be demonstrated that some crabs can continue to exchange shells throughout their time in captivity if given the opportunity to do so, and that the swaps may be quite spontaneous and unpredictable. This can mean that the shell occupied after 24–48 hours (the usual criterion) may have little relevance to preferences in the long-term. In fact, after a rigorous analysis of the mathematics behind many of these indices, Gilchrist (1984) has suggested that their relevance to the real situation is obscure, and that many of the relationships suggested may be nothing more than "analytical artefacts".

The animals themselves are, however, clearly aware of the sub-optimal nature of their shells if these are damaged, are too large, or are too small. They can recognise both the necessity and opportunity to find another. The inevitability of such behaviour, and the enormous range of reasons that may determine why a particular shell will not be suitable for an individual's needs, argue most forcefully for a "gestalt" approach to shell selection. It also stresses the difficulty in trying to assign mathematical "rules" to shell quality. In consequence, it may be that a more subjective approach is more appropriate in "classifying" the adequacy of shells occupied by a population. Such a scheme would involve identifying whether or not a shell offers protection for the crab's body (damage and the presence of epizoic "growths" may not necessarily render a shell uninhabitable, perhaps only making it more difficult to carry). Four grades of quality could form the basis for such a classification:

1. The entire crab may be withdrawn into the shell such that no part of its body is visible from the outside—such shells offer excellent protection against being "winkled-out" and minimise the consequences of breakage to the lip, but they may be awkward to carry.
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.
3. The animal's chelae break the plane of the aperture when the animal is withdrawn such that it appears cramped and may be in danger of being pulled out by another crab.
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, so the risk of being pulled out would probably be small under normal circumstances. Such a shell is clearly too small and offers the minimal protection to the vulnerable anterior of the body, but is very easy to carry.

Of these four grades, numbers 2 and 3 may be regarded as broadly optimal, while grade 1 would be sub-optimal being too large, and grade 4 would be sub-optimal being too small. Intermediate grades could obviously be created but most cases could probably be accommodated within these four.

Not only does no single parameter of shell quality appear unvaryingly essential to a crab, but no single type of shell is consistently chosen. This is clearly demonstrated by the sheer number of shell types that can be found occupied by hermits, and the fact that individuals will make use of any suitably sized shells in an aquarium study, however exotic they may be. Crabs will also utilise straight tubes and replicas made of glass (Fig. 1), and have even been observed to use fragments of discarded and broken brachyuran exoskeletons, bottle caps, Cola cans, fuses, and parts of beer bottles if no shells are available (Fotheringham, 1976*b*; Gilchrist and Abele, 1984)! Particular preferences for the shells of certain gastropod species have been suggested by some authors, though the exact nature of the "choice" is usually confused by their relative abundance in the habitat. It would, however, make perfect sense to assume that an individual can detect a shell's suitability and can reject one that is unsuitable. Presumably, the more unsuitable a shell is then the greater will be the tendency to abandon it and search elsewhere—a point demonstrated by Neil and Elwood (1986) who showed that crabs occupying poor quality shells approach and contact new shells more quickly, and spend longer investigating them, than do animals in "better" shells. Some of the reasons why a shell may be rejected as unsuitable are listed by Kellog (1976) as: fewer than 1.5 whorls intact (shell provides negligible protection from predators), material wedged tightly in the aperture or fouling organisms sealing off the aperture (crab unable to enter the shell), broken whorl hindering emergence from the aperture (crab unable to walk efficiently), anterior end broken and columella damaged (negligible protection and difficulty with gripping shell), and shell badly corroded (provides negligible protection).

In British waters, *P. bernhardus* does tend to be associated with particular species of shells—but these will most likely represent compromises between availability and opportunity, as well as reflecting the sheer survivability of empty shells in an environment subject to considerable physical forces. The most common shells are (in order of size): *Hinia reticulata* (=*Nassarius reticulatus*), *H. incrassata* (=*N. incrassatus*), *Bittium reticulatum* and juvenile *Littorina "saxatilis"* for the smallest crabs i.e. immediate postglaucothoë and "young hermits"; small *Gibbula* spp./*L. obtusata* for animals to 0.5 g; *L. littorea*/*Nucella lapillus* for animals 0.5–1.5 g (and carapace lengths of up to 14 mm); and *Buccinum undatum* for animals 1.4–7.6 g (and above 15 mm carapace lengths) (data Jackson, 1913; Elwood *et al.*, 1979; Pike and Williamson, 1959).

In at least one area of deep, sheltered water off Denmark (Jensen and Bender, 1973), *L. littorea* and *B. undatum* have been recorded as overlapping in size, i.e. with *L. littorea* at 10–35 mm and *B. undatum* at 15–90 mm but, although the larger *L. littorea* can be found quite commonly on British shores, the smaller *Buccinum* are probably too fragile to survive in the littoral zone on any but the most sheltered coasts. The area of overlap may represent a critical stage in the life cycle for many populations, particularly if no offshore population of *Buccinum* is available (as appears to be the case in, for example, parts of south-west Cornwall—Lancaster, 1988).

The manner in which a crab orientates towards a potential new shell is also of importance. Since blinded animals do not seem to take significantly longer than normal ones to find and enter shells (Reese, 1963), chemotaxis has been suggested. Attractive molecules may be liberated from damaged snail tissues (McLean, 1973; Rittschoff, 1980*a*; 1980*b*), or from symbionts such as *Hydractinia* (Jensen, 1970). It has even been suggested that calcium leached from shells may have a powerful attractive effect on hermit crabs (Mesce, 1982). Since the attractive effect can be abolished when the shells are coated with a sealant (to prevent the release of calcium), it is even possible that the reason why hermits do not tend to orientate towards living gastropods may be because many of these shells possess a periostracum, and thus when no calcium is being released from a shell it is simply not recognised as such by a crab. Once contact has been made, certain sequences of investigative behaviour tend to occur in almost all of the hermit crab species studied—aimed, presumably, at extracting as much information as possible about the new shell before becoming committed to the highly risky manoeuvre of leaving the safety of the old one. The new shell is first rolled around until the aperture is available for probing, then the chelipeds are inserted to check the inside for obstructions before the first tentative insertion of the abdomen is made (Reese, 1963, 1962*a*; Scully, 1986). This process may be repeated several times, and the animal may alternate between the new shell and the old until it is satisfied with the new one or rejects it as unsuitable. The loss of appendages does not necessarily prevent a crab from selecting and entering a shell, though the process may take longer due to the reduction in the amount of sensory input and loss of dexterity (Reese, 1963). A crab may use its chelipeds as calipers to obtain a measure of the aperture width (Kinosita and Okajima, 1968). The duration of such investigations is, inevitably, variable, depending upon the risks associated with the manoeuvre and its potential benefits (Elwood and Stewart, 1985), but it is not uncommon for five minutes or more to elapse before a decision is finally made (Neil and Elwood, 1985).

The ultimate source of the shells used by a population of hermit crabs lies with the gastropods themselves. 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 (Rutherford, 1977; Brightwell, 1951*b*, 1953; Purtyman, 1971). Scully (1983*b*), 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 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. Shells are rendered

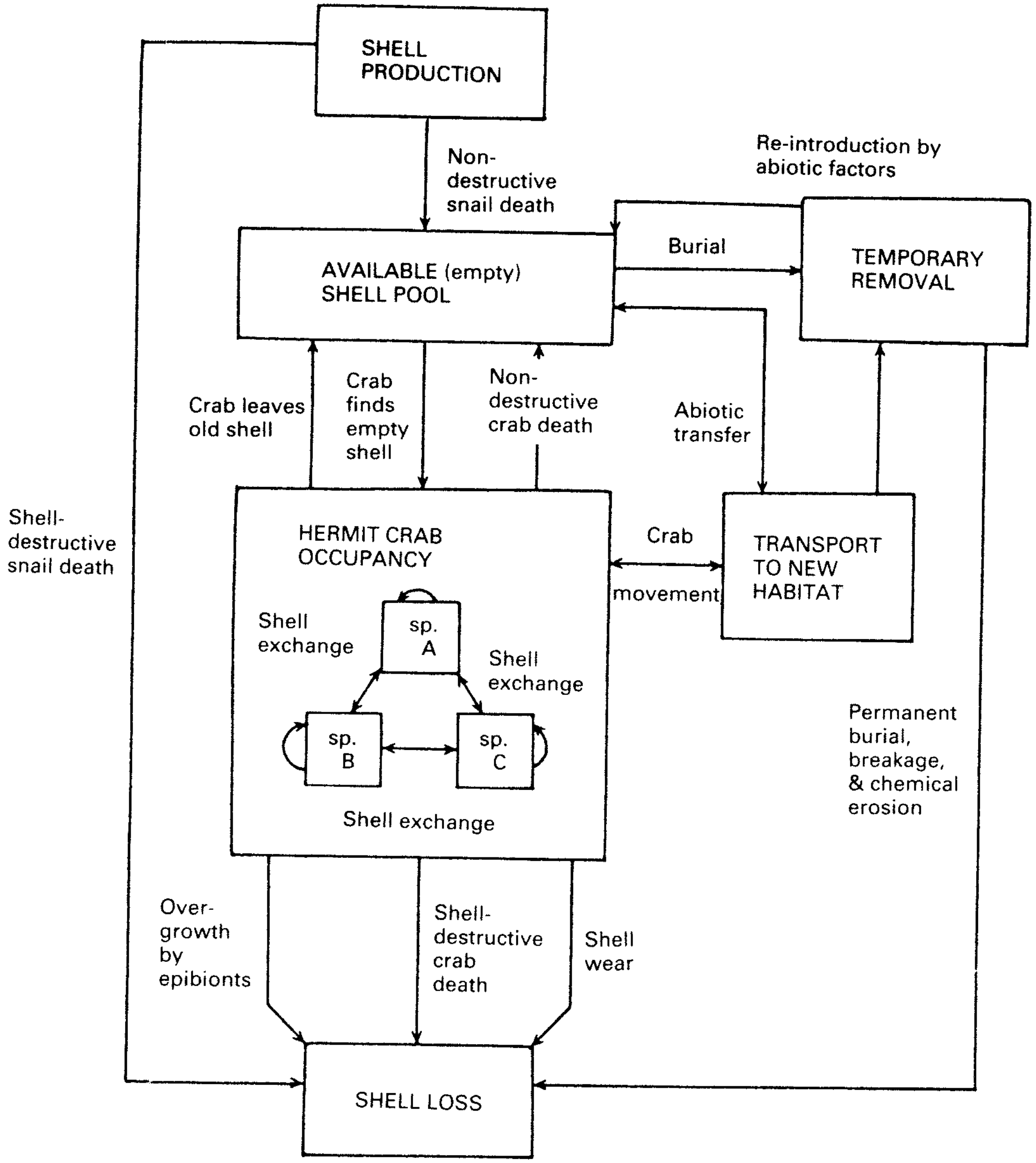


FIG. 7.
Flowchart of shell movement in a guild of hermit crabs (after Hazlett, 1981a).

unavailable to a population by various means: they may be removed from the area by currents (Vance, 1972*b*), by the emigration of other crabs (taking the shells with them), by burial (Kellog, 1976), or they may be broken or eroded until they are uninhabitable (in Scully, 1983*b*). Spight (1977) suggests that a shortage of empty shells is only to be expected in the intertidal environment, since the only thing keeping them there is the activity of the hermits themselves.

Notwithstanding the occasional chance encounter with a suitable empty shell, most of the shells that a crab comes into contact with will either be damaged, occupied by a living snail, or occupied by another crab. Of these, it is probably the latter situation that offers the most potential, and it is thought that direct aggression employed against another crab either to force an eviction or an exchange, is the most usual way that a hermit crab obtains a new shell. Equally, the useful shells will have a tendency to be recycled in a predictable way until accidentally lost or damaged (Figure 7—from Hazlett, 1981*a*).

The mechanisms of shell fighting have consequently received a great deal of study (e.g. Hazlett, 1966*a*, 1967, 1970*c*, 1972*b*, 1981*a*; Vance, 1972*a*; Elwood and Glass, 1981; Dowds and Elwood, 1983, 1985). Considerable subtleties and complexities have been indicated for this method of aquisition, and contests occur not only between members of the same species but even between members of different species. A shell-less crab can even manage to evict a housed crab by direct aggression if it is strong enough (Allee and Douglis, 1945). Shell fights follow a generally predictable pattern, and involve the attacker in manipulating the other crab's shell and usually "rapping" its own shell against it a number of times before attempting to pull the occupant out and flinging it away. A particularly good account of a shell fight is given by Dowds and Elwood (1983). Since the evicted crab is so often seen to make use of the attacker's discarded shell, it has been suggested that perhaps a process of "negotiation" is actually occurring to the potential benefit of both parties (i.e. Hazlett, 1978, 1980*a*, 1983*b*, 1984, 1987). This is disputed by a number of other authors, however, who consider this to be an unrealistic interpretation since the chief beneficiary in any shell dispute is likely to be the largest crab (Neil, 1985; Elwood and Neil, 1986; Elwood and Glass, 1981; Dowds and Elwood, 1983). Indeed the whole question of shell fighting as a "real" phenomenon has been questioned (*in* Bertness, 1981*e*), with the suggestion that it may be merely a laboratory phenomenon, but the number of observations that have been made and the range of situations investigated imply that it is no mere accident or laboratory artefact. A crab will not necessarily fight every other individual that it meets. Occasions when a fight is likely can be predicted on the basis of the quality of shells available to a population—the poorer the shell that each crab occupies the more likely will a fight become. This can reach an extreme when an individual in a grossly sub-optimal shell meets another of the same size or smaller in a shell even slightly better (Scully, 1983*b*). Under these circumstances, severe injuries can be caused to a crab that chooses to resist an attack. It has been noticed that whole populations of crabs may become so shell-limited that individuals will fight whenever they meet—and the victor may only decide after the conflict whether the newly won shell is even worth examining (Vance, 1972*a*).

MOVEMENTS, MIGRATIONS AND ACTIVITY RHYTHMS

The patterns of movement displayed by hermit crabs are diverse and unpredictable. Some individuals in a population may wander over great distances while others remain in much the same area for long periods of time. Hazlett (1981*a*) noted that some individuals are effectively sessile since they occupy fixed (i.e. attached) tubes or shells, while some move half a metre or so in a day but always return to the same spot. Others meander 20 m or more in a day but only change their net position by some 1–2 m. Equally, "nomadic" movements of several hundred metres in a day may occur, which may be lateral (with the crabs remaining in the same zone on the shore) or perpendicular to the shoreline (exposing them to a wide range of conditions). Stachowitsch (1979) followed the movements of tagged crabs for periods of up to 2 years, and was able to conclude from recaptures (around 50% after 1 year and 24% after 2 years) that the average range of movement of most of the individuals observed did not exceed 15 m during this time. The suggestion that a type of "home range" may operate cannot, therefore, be ruled out for this population, since random wandering should have taken them further. Similar patterns of behaviour are recorded by Hazlett (1983*a*) for two Caribbean species—though here the term "site attachment" is used to describe their limited overall range of movement—and by Tomlinson (1960) for a population of unnamed hermits off the Californian coast. Occasionally, long-term population migrations occur e.g. *Pagurus longicarpus* migrates from the littoral zone off Rhode Island U.S.A., where it breeds during the summer months, into deeper water during the winter (Rebach, 1969, 1974), as does *Clibanarius vittatus* in Texas (Fotheringham, 1975).

Possible reasons for long-term migrations have been suggested to include:

1. Avoidance of debilitatingly cold winter temperatures in the shallow littoral zone, which would leave the crabs sluggish and more prone to predation (Rebach, 1974).
2. To provide a mechanism for concentrating breeding crabs in the narrow littoral zone area after they have spent the winter period in the deeper water offshore—thereby facilitating their finding a mate (Fotheringham, 1975).
3. Encouraging the crabs to move offshore for at least part of their life cycle in order to have access to larger types of shell—since the larger gastropods tend to be deeper water forms (Fotheringham, 1975).

Short-term migrations of the "alongshore" or "on-off shore" patterns typically involve individuals which occupy substandard or damaged shells (Hazlett, 1983*a*). Such movements may bring the crabs into potential shell-yielding situations. Indeed, it does appear that the poorer the shells are that the crabs occupy or come into contact with, then the greater is the tendency for them to migrate (Hazlett, 1981*b*; Lancaster, 1988). The erratic and seemingly random nature of such movements are amplified by each crab's tendency to stop and change direction in order to investigate objects that it passes. Furthermore, they will divert to interact with other crabs (either by deliberately approaching or avoiding them), and they will make frequent stops to feed. Equally, the animals will often respond to "windfall" deposits of food which may result in a complete change of direction (Stachowitsch, 1979), and to sites of gastropod predation (where "new" shells are becoming available—McLean, 1973). This latter response is thought to be due to chemical attraction—possibly to amino acids or small peptides released into the water from the breakdown of gastropod flesh (Rittschoff, 1980*a*, 1980*b*). These patterns may be further complicated by the tendency of most hermit crabs to continually change their minds when presented with two separated stimuli such that they perform a zig-zag path between them (alternately making for one or the other) with no predictable outcome until they make their final turn (Fraenkel and Gunn, 1961). One positive advantage that results from such "wandering" behaviour is that hermit crabs may become the first organisms to repopulate "graveyard" areas after conditions return to normal (Fedra *et al.*, 1976), and may, incidentally, help to introduce other forms, carried as epizoites.

Variations in speeds of movements may be due to food availability (where a hungry animal will tend to move more quickly towards a potential food source) and danger from predators. These two factors may be further influenced by the type of substrate that the animal is crossing. A rough surface (as well as impeding progress directly) may trap more food, will contain more "nooks and crannies" to investigate, will tend to offer more protection from predators, and hence will encourage slower overall movement than will an open, bare, surface which will make the animal more conspicuous to a predator and which will probably contain little of interest to explore. On this basis Hazlett (1981*b*) considered substrate-type to be the greatest single factor accounting for the enormous variations observed in the movement patterns of hermit crabs. Variations have also been observed on a diurnal basis—Stachowitsch (1979) noted that *Paguristes oculatus* was predominantly active by day in the N. Adriatic, while Mitchell (1973) noted the same for *P. bernhardus* originating from the Millport area of the U.K. Mitchell maintained a number of *P. bernhardus* under conditions of 24 hours continuous illumination and observed that the animals' most active periods coincided with the equivalent hours of natural daylight—concluding that some form of inbuilt diurnal rhythm of activity exists in this species. This pattern is the opposite of the observations of Ball (1968) on two Pacific species of *Pagurus*, which were more active in the dark. The possible inability of *P. bernhardus* to dark adapt its eyes (Bröcker, 1935) may account for this difference. Eriksson *et al.* (1975*b*) also failed to find any evidence of appreciable nocturnal activity in *P. bernhardus*. This tendency of at least certain hermit crabs to be more active by day (whilst most brachyuran crabs are nocturnal) may well be as a result of the protection they feel afforded by their shells (Warner, 1977).

Periods of activity separated by periods of inactivity also seem typical of hermit crabs (McLean, 1973). Cues for the phasing of activity rhythms may include the tidal cycle for intertidal populations (especially periods of immersion followed by periods of exposure to the air, the temperature changes occurring as the tide returns to flush out a rock pool, and the pressure changes associated with the rising and falling tide), and perhaps diurnal, semi-lunar, lunar, and annual cycles of temperature/day-length etc. for sub-littoral populations (Naylor and Atkinson, 1972). It is unlikely, however, that any one factor will operate singly at all times, and many complex interactions are likely.

Environmental cues for longer-term migrations (those returning the crabs to a particular environment after a prolonged absence in a substantially different area) are also thought to be both complex and interactive. Cues known or thought to be used by migrating crustaceans include the slope of the beach, surface wetness, surface particle size, visual landmarks (such as pebbles and light/dark boundaries), short-term memories of movements (termed a "kinesthetic" memory), the chemical qualities of the water (i.e. due to surface/land run-off, zoo/phytoplankton composition, levels of ammonia, nitrates, etc), water currents, wave action, wind direction etc. (reviewed by Rebach, 1983). Additionally, some littoral crustaceans are known to use the position of the sun and the polarisation of blue sky as navigation cues to direct them towards or away from the sea (Krasne, 1973)—though cloud cover may restrict this ability somewhat. The use of multiple cues for orientation is possible, and Rebach (1981) suggests that when more than one cue is significant these will tend to be arranged hierarchically. The monitoring of slope is thought to be one of the most important of these cues—especially when downslope corresponds with offshore. The angle of the slope is perceived by the statocyst organ at the base of the 1st antenna—lobsters being able to perceive slopes of only 1–3° by this mechanism (Cohen, 1955). Water chemistry cues are probably monitored by the aesthetascs (long, thin, cylindrical sensory hairs) at the tip of the 1st antenna (Rebach, 1981).

Despite all of the evidence of complex control of migration it is not thought that specific "homing" behaviour occurs in hermit crabs (Rebach, 1978).

PREDATORS

Despite the protection of their shells, hermit crabs fall victim to a wide range of predators. Remains of the anterior hard portions of hermit crab carapaces are commonly found in the stomachs of commercially caught fish, especially cod, wolf-fish, and dogfish (Brightwell, 1953; Vance, 1972*a*; Pike, 1961; Eales, 1949). Ballan wrasse, common in the shallow waters off the Norwegian coast during the summer months, have yielded many hermit crab remains—including shell fragments—in their stomach contents (Samuelson, 1970). Other predators include sea birds, brachyuran crabs (especially *Cancer* species), octopus, and starfish (Perkins, 1985; Samuelson, 1970; Vance, 1972*a*; Ross, 1971). Many gulls attack hermit crabs left stranded in small pockets of water as the tide recedes, flying up and then dropping them onto rocks below to crack open the shells and so gain access to the animals within (Rebach, 1983). In addition, hermit crabs themselves may attack and devour their own kind (Hazlett, 1970*b*; Perkins, 1985). Cannibalism is one of the main problems of keeping these animals in captivity.

Human predation is not usually a problem for this group of crabs, although it is reported that hermit crab abdomens are boiled and sold in markets in France (Brightwell, 1951*a*)—where they are said to taste very like prawns (!)—and fishermen may occasionally use naked hermits as bait for bass and cod. The terrestrial hermit *Coenobita* was formerly a delicacy (baked in its shell) in Jamaica, and the coconut crab *Birgus latro* was once prized for its oily abdomen among the Pacific Islanders (Jackson, 1913).

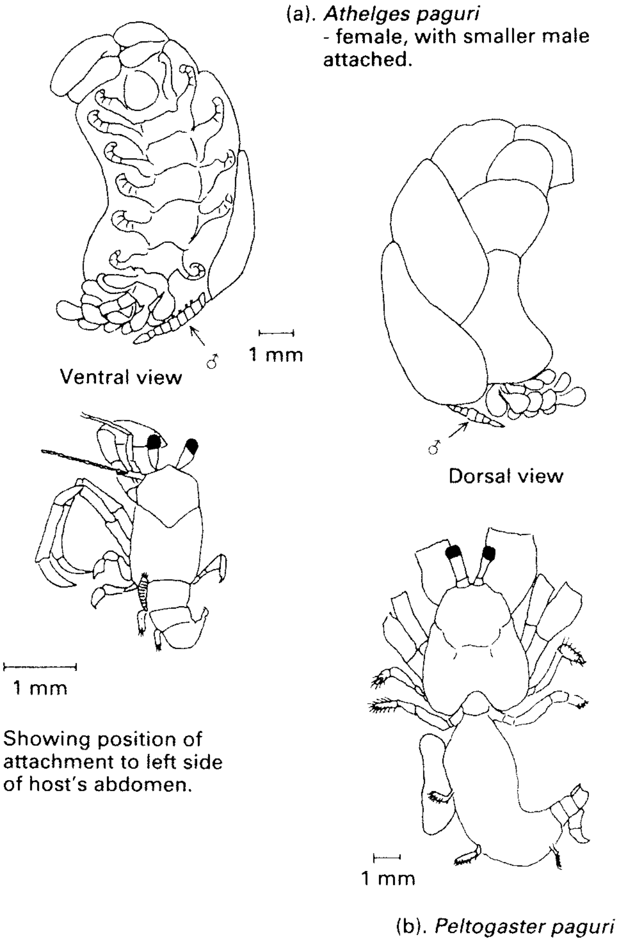
Apart from a withdrawal reflex into the shell at any sign of danger, hermit crabs have another "reflex" that may help their survival. At the approach of a shadow or any sudden movement, they will often let go and simply drop off any rock or surface that they may be on. This may take them out of sight and hence danger—but it may also land them in a new and potentially even more hazardous situation than before!

PARASITES

Two types of isopod *Athelges paguri* and *Pseudione hyndmanni*, and one barnacle *Peltogaster paguri*, are commonly referred to in the literature as being parasitic on *Pagurus bernhardus*.

Both isopods are oval in shape, assymetrical, and conspicuously segmented. *Pseudione* is thought to occur chiefly in the branchial cavity of the crab (where the female may attain a length of 10 mm and the male around 2 mm), while *Athelges* is more usually found attached to the upper part of the abdomen—though it has been reported from both the branchial chamber (Cattley, 1938) and from the thorax (Pike, 1961). *Athelges* can be distinguished from *Pseudione* by the former possessing 4 pairs of conspicuous stalked pleopods towards the posterior end of the body to each of which are attached a pair of greatly expanded plate-like lamellae (Figure 7a). Full descriptions are given by Pike (1953, 1961). Sars (1899: *Pseudione* P.202, *Athelges* P.210) and Naylor (1972). Levels of infestation in natural populations are not thought to be high—Pike (1953) reported a 1.5% infection rate for the animals he collected from the Irish Sea, while I noted only 2 *Athelges* from 2000 individuals of *P. bernhardus* examined over a 4 year period in S.W. Cornwall.

The parasitic barnacle *Peltogaster paguri* is usually conspicuous as either a glowing red spot showing through the crab's abdominal tissues if it has not yet erupted, or if it has, then as a vivid red sac fixed to the dorsolateral surface of the left side of the crab's abdomen (Figure 7b). Another species of parasitic barnacle, however, occurs almost as commonly on *P. bernhardus*, but is less commonly mentioned in the literature. This is the superficially similar *Clistosaccus paguri*. This barnacle most frequently occurs on the left side of its host's abdomen dorsal to its pleopods, and can be distinguished from *Peltogaster* by its white body. Detailed histological examination also reveals its internal anatomy to be quite different from that of *Peltogaster*. Descriptions are given in Smith (1906: p. 117) and Hoeg and Lutzen (1985) whilst a recent account of biology may be found in Hoeg (1982). Smith (1906), comments that the parasite is attached via its host's gonads such that parasitised males are effectively castrated and may come to develop the sexual characters of females (e.g. ova development). If parasitised at a very early age such males may even retain the



(a). *Athelges paguri*
- female, with smaller male attached.

(b). *Peltogaster paguri*

FIG. 8.
Two common parasites of *Pagurus bernhardus* (after Sars, 1899; Pike, 1961; Hoeg and Lutzen, 1985).

pleopod on their second abdominal segment. The pleopods of a parasitised female may come to resemble those of a normal male (Thompson, 1904), though, generally, such a female only appears to suffer an arrested development. In a study of anomurans off the west coast of Norway, Samuelson (1970) observed that female *P. bernhardus* parasitised with *Peltogaster paguri* were not breeding, although it was well into the breeding season at the time. The effects of parasitic castration are not so clear cut in the case of *Athelges paguri*, however, but Giard (1886) did note that males parasitised by this isopod had pleopods of the female number and form. These parasites usually occur singly on their hosts (with the conspicuous forms of both *Athelges* and *Peltogaster* being females, each carrying a much smaller hyperparasitic male—see Reinhard, 1942, for a discussion of this with *Peltogaster*), and, although MacGinitie and MacGinitie (1968) have recorded 23 unspecified *Peltogaster* on a single *Pagurus*, Rainbow *et al.* (1979) comment upon a general lack of gregarious behaviour in the larvae of this species—an unusual situation among barnacle cyprids.

Peltogaster may itself fall prey to the hyperparasitic isopod *Liriopsis pygmaea* (described by Sars, 1899: p. 242), an organism which first lies within the body cavity of the barnacle before eventually erupting out onto its body surface.

ASSOCIATIONS

Hermit crabs and their "commensals" have long been a source of curiosity, and the total number of species with which an individual crab may be associated could well exceed several dozen (Table 4). Records exist for many species of hermit crabs e.g. Fotheringham (1976*c*), Cuadras and Pereira (1977) and Taylor (1979), while Hazlett (1981*a*) reviews the field of associations generally.

The principal relationships discussed in the literature are those between hermit crabs and anemones. Indeed, such relationships are even thought to be so reliable that they are used in some taxonomic works as clues to identification (e.g. Campbell, 1976; Barrett and Yonge, 1958). These include, in particular, the association between *Pagurus bernhardus* and *Calliactis parasitica*, and *P. prideaux* with *Adamsia carciniopados*. These relationships are, however, neither simple nor inevitable since *A. carciniopados* has also been recorded in association with both *P. bernhardus* (Jackson, 1913) and with *P. alatus* (as *P. excavatus*—Mainardi and Rossi, 1969*a*), while *C. parasitica* has been observed with at least two other hermits (*Dardanus arrosor* and *Clibanarius erythropus*) and may occur on the shells of living gastropods (Ross, 1967; Rees, 1967). Equally, both *P. bernhardus* and *C. parasitica* seem able to live quite happily apart—though relationships between *A. carciniopados* and *P. prideaux* are not so clear, since each is thought to decline without the other (Manuel, 1981). The actual benefit that each partner receives in the relationship is not clear. In some cases it appears that the stinging cells of the anemone protect the crab from attack by such predators as the octopus and other crabs (Ross, 1971; McLean and Mariscal, 1973). Pike (1961) even suggests that one of the principal reasons why he so seldom found the remains of *P. prideaux* in the stomachs of predatory dogfish and cod may have been because of the protection offered by the anemones. Such protection is not always impregnable, however, since Brightwell (1953) commented that a crab protected by 3 large anemones was dismembered by Wrasse that seemed quite indifferent to the discharging nematocysts. A more inglorious role has been noted for at least one anemone by Balasch *et al.* (1977) who observed a crab prodding and moving its passenger around until, presumably, it occupied a more convenient position—being used, it would seem, as little more than a counter balance to make an awkward shell easier to carry! The chief benefit to the anemone is probably the opportunity given it to occupy a hard substratum in an otherwise barren landscape of mud or shell gravel (thus enabling it to inhabit apparently unsuitable regions), together with being able to supplement its diet by intercepting food particles when the crab eats (Ross, 1967). However, the observations initially made by Wortley (1863) and later confirmed by Fox (1965) that specimens of *P. prideaux* may actually feed their symbiotic anemones do suggest an even further subtlety to this relationship. The anemones are not totally dependent upon scraps from their hosts, however, but are efficient predators in their own right. Brightwell (1951*a*) observed *Calliactis parasitica* seizing and holding large prawns that could easily have escaped smaller anemones. Equally, the anemone may not have everything its on way since the same author (Brightwell, 1953) also observed *P. bernhardus* to consume enormous numbers of eggs being shed from its anemone and even, on another occasion, to plunge its chela into the anemone's gastric cavity and remove quantities of partially digested food!

The anemones may be transferred by the crabs from shell to shell (Cowles, 1920; Ross, 1979*b*; Fox, 1965), or the anemone itself may initiate the move (Ross, 1960; Ross and Sutton, 1961). Dominant crabs are often seen to encourage the presence of anemones and have even been observed to remove anemones from the shells of subordinates and place them on their own shells (Ross, 1979*a*; Mainardi and Rossi, 1969*b*)!

Table 4. *Species recorded in association with* Pagurus bernhardus *(after Tait, 1972, and Jensen and Bender, 1973)*

Protozoa	
Zoothamnium spp.	
Folliculina spirorbis Dons	
Cibicides lobulatus (Walker and Jacob)	
Porifera	
Cliona celata Grant	Boring into shell
Ficulina ficus (Olivi)	
Suberites domuncula (Olivi)	Sponge may eventually dissolve away shell to enclose crab directly
Coelenterata	
Hydractinia echinata (Fleming)	
H. carnea (M. Sars)	
Dicoryne conferta (Alder)	
Perigonimus repens (Wright)	
Campanularia johnstoni (Alder)	
Gonactinia prolifera (M. Sars)	
Epizoanthus incrustatus (Düben and Koren)	
Calliactis parasitica (Couch)	Sea anemones
Adamsia carciniopados (Otto)	
Turbellaria	
Macrostomum sp.	
Nemertini	
Tubulanus linearis (McIntosh)	
Polychaeta	
Eulalia bilineata (Johnston)	
Nereis fucata (Savigny)	
Polydora ciliata (Johnston)	Boring into shell
Arenicola marina (L.)	
Fabricia sabella (Ehrenberg)	
Exogone naidina (Örsted)	
Dodecaceria concharum (Örsted)	Boring into shell
Hydroides norvegica (Gunnerus)	
Pomatoceros triqueter L.	
Serpula vermicularis L.	
Spirorbis spirillum (L.)	
S. pagenstecheri Quatrefages	
S. spirorbis (L.)	
Bryozoa	
Lichenopora verrucaria (Fabricius)	
Electra pilosa (L.)	
Callopora lineata (L.)	
Tubulipora sp.	
Alcyonidium polyoum (Hassall)	
Hippothoa hyalina (L.)	
Copepoda	
Sunaristes paguri Hesse	In topmost whorl of shell
Cirripedia	
Alcippe lampas Hancock	Boring into last whorl of shell close to columella (easily overlooked); edge of mantle protrudes through a small slit.
Verruca stroemia (O. Fr. Müller)	
Balanus balanus (L.)	
B. improvisus Darwin	
B. crenatus Bruguière	
Semibalanus balanoides (L)	

Table 4. *Continued.*

Amphipoda	
Podoceropsis nitida (Stimpson)	In tubes, often on outside of shell, particularly in sutures
Metopa rubrovitata G. O. Sars	
Aora typica Kröyer	
Eurystheus maculatus Johnstone	
Melita obtusata (Montagu)	
Orchomenella nana Kröyer	
Decapoda	
Porcellana longicornis L.	
Polyplacophora	
Lepidopleurus asellus Spengler	
Gastropoda	
Acmaea tessulata (Müller)	
A. virginea (Müller)	
Precuthona peachii (Alder and Hancock)	a nudibranch thought to feed exclusively on *Hydractinia*
Acanthodoris pilosa (Müller)	
Lamellibranchia	
Monia patelliformis (L.)	
Heteromonia squamula (L.)	
Hiatella arctica (L.)	usually found boring into rock!
Mytilus edulis L.	
Anomia ephippium L.	in last whorl, just inside entrance
Tunicata	
Styela coriacea (Alder and Hancock)	

(This is not meant to be an exclusive list—many of these species were recorded in Scandinavian waters and their British counterparts, where different, would be additional to the list. Also, no account is taken here of parasites).

[Some of the more interesting associates are described in annotation.]

A second common associate of *P. bernhardus* is the hydroid *Hydractinia echinata,* which probably also finds the firm substrate provided by the gastropod shell a valuable point of attachment. As a bonus, food is made available to the colony as the crab disturbs the sediment over which it moves. Equally, *Hydractinia* may directly consume the crab's eggs as they are aerated or its larvae as they are released (Fotheringham, 1976*c*; Rees, 1967; Christensen, 1967). The benefit to the crab is therefore uncertain, since the hydroid generally appears to provide neither camouflage nor protection (Jensen, 1970), and may even sting the crab that carries it with its nematocysts (Brooks and Mariscal, 1985*b*).

Perhaps the third most commonly mentioned associate of *P. bernhardus* is the polychaete *Nereis fucata*, which constructs a mucus tube for itself within the upper whorls of the gastropod shell. This worm has been reported as occurring in between 3–20% of shells collected from the Clyde Sea—depending upon depth (Pike and Williamson, 1959), in 10% of the shells occupied by *P. bernhardus* off Millport (Cram and Evans, 1980), and in around 30% of the shells in Liverpool Bay (Jackson, 1913). Although Brightwell (1951*a*, 1951*b*) was originally of the opinion that the presence of the worm is no inconvenience and causes the crab no discomfort, Fotheringham (1976*c*) mentions that a related polychaete, *Neanthes succinea,* readily consumes the eggs of its commensal crab *Clibanarius vittatus,* and thus must be considered potentially destructive to its brood. Equally, considering that one of the simplest ways to evict a hermit crab is to tickle its abdomen via a hole drilled in one of the upper whorls of the shell (see p. 225) it would seem that stimulation of this sensitive area by a worm might cause the crab some discomfort. The shell entry behaviour of the worm is described by Gilpin-Brown (1969) and by Cram and Evans (1980), who comment upon its non-specific nature. The worm appears to respond to a wide range of stimuli and has been observed to effect entry into the shells of at least 5 different crab species. The behaviour of the polychaete inside the shell of its host is described by Elmhirst (1947) who observed his animals in glass replica shells.

Thus the overall relationships between hermit crabs and their associates are complex and unpredictable. Many commensals will occupy potential brood space or space that may may be used for increased growth after moulting, and they may represent a threat to both the crab's eggs and larvae. Under the circumstances, the term "commensal" may be inappropriate, suggesting as it does an association from which the crab loses nothing. It may be that the older definition (de Bary, 1879) of "symbiosis" as a situation where two dissimilar organisms live together in close association, may be more realistic. Perhaps the finest description, though, of these interactions is provided by Scully (1983*b*) who refers to a hermit crab and it associated symbionts as a "community in motion"!

PHYSIOLOGY

The shells enclosing the bodies of hermit crabs impose no respiratory constraints upon them. These animals are capable of generating water currents within their shells powerful enough to sweep faecal material out from the apex (Brightwell, 1951*a*), and presumably, therefore, also capable of keeping aerated water circulating to the gills. *P. bernhardus* has been shown to be capable of surviving for up to 7 hours in anoxic sea water (Davenport *et al.*, 1980) and so must be able to remain totally withdrawn inside its shell (and hence effectively cut off from any new suppy of oxygen) for at least that time. Hermit crabs are probably oxygen conformers and allow their consumption to fall as the amount of gas in the surrounding water declines. They may survive total anoxia by respiring anaerobically in a manner similar to that used by fiddler crabs trapped in waterlogged burrows (Teal and Carey, 1967).

A fall in oxygen consumption (and hence a reduction in activity) occurs as salinity levels decline, particularly below about 50‰ salinity. This suggests a reason for the inability of some species (including *P. bernhardus*) to penetrate estuaries to any great extent. *P. bernhardus* has been studied to determine its salinity tolerances (Davenport *et al.*, 1980; Davenport, 1972*a*, 1972*b*; Shumway, 1978) and does appear to be reasonably euryhaline, particularly when of the size range typical of the littoral zone. The animals do, however, tend to withdraw into their shells as values approach 20–22‰, and generally remain withdrawn until levels return to around 32–33‰. The animals probably trap small amounts of water inside their shells as they withdraw and only emerge again as this is gradually "recharged" by "fresh" sea-water diffusing in, indicating that conditions are once again favourble. The secret of osmotic tolerance for these animals appears to be primarily one of conforming i.e. tolerating osmotic swelling in the soft abdomen, enhanced by the production of copious urine. Since the salinities to which they are usually exposed will seldom fall below 25‰, there would be little need to develop a more sophisticated mechanism, nor acquire a greater tolerance (any fresh-water inflow into a rock pool tends to remain on the surface and mixes only slowly, if at all, during a tidal cycle—Pyefinch, 1943). The crabs may, however, consciously avoid osmotic stress by moving away (if at all possible) from waters which are becoming diluted. Shumway (1978) observed that activity increased among hermit crabs as salinities started to fall, and that withdrawal only tended to occur if escape was not possible. The ability of a hermit to detect changes in salinity was demonstrated by Roberts (1971), who found that larval *P. longicarpus* could detect differences as small as 2·5‰.

The temperature extremes which can be tolerated by hermit crabs depend upon both their degree of acclimation and upon the usual temperatures experienced in their natural habitats. Using resumption of normal behaviour as a measure of survival (i.e., the reoccupation of gastropod shells after exposure to experimentally induced temperature regimes) Fraenkel (1960) estimated that the upper lethal limit for *P. longicarpus* was 30°C. While this value is lower than for some other animals tested (i.e. 40–41°C for *Littorina littorea* taken from open rock surfaces) the finding does none-the-less reflect that some hermit crabs are quite capable of surviving conditions more extreme than they are likely to encounter in nature. Maynard (1960) suggests that the optimal temperature for most temperate decapods will be in the range of 20–30°C, at which the heart rate will be maximal, but that above this value the beat tends to become irregular before finally stopping between 36–52°C (see also p. 225).

Hermits respond very rapidly to sudden movements, and Elmhirst (1947) noted that movements "some feet away" were detected. Colour vision has not been convincingly demonstrated, but spectral curves of the optical system of *P. bernhardus* (Stieve, 1960) have indicated a fall in photic response beyond 600 nm (i.e. the orange-red part of the spectrum), suggesting a reason for the inability of some individuals to respond to red-coloured colonies of *Hydractinia*. Early claims that hermit crabs can detect polarised light (e.g. Kerz, 1950) have been disputed (Waterman, 1961*b*) on the grounds that inadequate controls were performed in the original experiments.

Most hermit crabs do not voluntarily spend a great deal of time out of water, and appear sensitive to water loss. In a study of 3 species of hermits from southern California, U.S.A., Young (1978) found that each one had characteristic desiccation tolerances varying from an average of 44 minutes to 158 minutes, and that survivable weight losses in these species (as percentages of total body water content—around 60% in hermit crabs) appears to greatly exceed values reported elsewhere for brachyuran crabs—i.e. around 40–50% as against 20%. How this relates to the actual differences in the amounts of "spare" body water in the two groups is less clear, however, and it may be that hermit crabs, with their soft abdomens, simply have more water to lose (see also Herreid, 1969).

Pressure responses in crustaceans have been studied in both larvae and adults (e.g. Knight-Jones and Qasim, 1967; Rice, 1964; Qasim and Knight-Jones, 1957). They have frequently shown such a positive correlation that a sensitivity to pressure has been suggested as providing a mechanism for controlling activity in adult crabs. This would allow maximal activity to be co-ordinated with the period of high tide—and hence with the availability of the largest suitable habitat range (Naylor and Atkinson, 1972). However, the exact nature of the response to pressure is difficult to gauge, since activity patterns in the species studied often have an endogenous periodicity (i.e. they are maintained even under constant conditions) and the animals themselves demonstrate different sensitivities at different times of the year. The thresholds for pressure responses in crustaceans have been shown to be small fractions of one atmosphere (Knight-Jones and Qasim, 1955)—values probably insufficient to have any effect on a solid or a liquid, but possibly sufficient to bring about a compression change in a gas. Since crustaceans do not have a swimbladder but do have semiconducting substances (lipids and polyphenols) in their cuticles, it has been proposed that the cuticle itself may act as an electrode, exploiting the potential normally existing between the animal and the surrounding water to cause a discharge of hydrogen ions at the outer surface and thereby create a fine film of gas (a "gas plastron") around certain parts of the animal. These would occur especially in areas where the cuticle is thinner, i.e. around the bases of bristles or on tubercles, and would be sensitive to deformation under the smallest of pressure changes (reviewed by Digby, 1972). These compressions could in turn be detected by sensitive hairs in the cuticle, and may help to explain why handling specimens, even gently, frequently seems to lower their ability to detect pressure, and hence tends to lead to abnormal behaviour, for a few day after capture. This cathodic effect would also provide a mechanism for the deposition of calcium salts in the cuticle, since the hydrogen ions discharged produce an alkaline environment around the outside of the cuticle, precipitating salts in the vicinity (Digby, 1984, 1985). This mechanism also explains how the enormous range of other ions found in the cuticle could come to be deposited (a mixture which appears too complex to be due to the selectivity of enzymes).

Further aspects of crustacean physiology are discussed in greater detail in Waterman (1960, 1961*a*) and Warner (1977).

THE COLLECTION, CARE AND STUDY OF HERMIT CRABS

Being, on the whole, quite conspicuous animals, hermit crabs are usually not difficult to find. Gastropod shells in uncharacteristic places or positions, or which move suddenly or rapidly, are likely to contain hermits. Once a few have been picked up (and the correct "search image" attained) others almost seem to leap out! Thus, visual searching is one of the simplest methods for collection and can be used effectively both in the littoral zone (where pools towards the bottom of the shore will be most productive) and by divers in the shallow sublittoral. Other techniques have also been used, and Gilchrist and Abele (1984) mention that no less than 52 descriptions of methods exist in the literature for the collection of hermit crabs. These include sampling along transects, the use of trawls (for deeper waters that cannot be searched by SCUBA diving), baiting, pitfall traps etc. Quantified sampling can be most easily accomplished by either thoroughly searching fixed areas or by searching large areas for fixed times. Ideally, a range of methods should be used to sample a population and baiting in particular should not be overlooked. This seems to attract those more reclusive individuals that occupy broken shells and which do not wander in the open unless attracted to a specific stimulus. These animals are undersampled in a random visual search.

Once collected, it quickly becomes clear why the routine study of hermit crabs is so difficult—they must be removed from their shells before correct identification can be confirmed or the animals can be sexed or accurately measured. Many methods have been suggested for accomplishing this but all involve some hazard for the animals and all need patience and care. Hermits frequently leave their shells when temperatures rise above the "normal" levels to which they are accustomed (perhaps as a "last resort" way of avoiding becoming overheated), and recommendations to artificially heat the apex of the shell or to anaesthetise the animals in warm water commonly occur. Unfortunately, although these methods may work for some animals on some occasions, they must be executed very carefully. Any slight movement in the vicinity while a crab is emerging from its shell will bring about a reflex withdrawal and it will retreat to the very back of the shell where it may rapidly succumb to the heat and die before the shell can be cooled. Females with eggs are particularly reluctant to abandon their shells and considerable mortality may result in a sample of reproductivity active individuals treated in this way.

The animals also tend to shed their limbs very easily under such circumstances, and it can be almost impossible to remove an individual forcibly if the telson does not relax or if it is prevented from releasing its hold on the columella. The most effective methods for removing a crab from its shell are either to "tickle" its abdomen with a length of fine nylon line via a small (1 mm) hole drilled in the apex of the shell, or to crack the shell open with a small vice. This latter method sounds brutal but, since the force can be applied suddenly and very precisely, the crab appears to suffer no ill-effects whatever. In the long-run this may well prove to be the least traumatic method of all. The animal can quickly be separated from the fragments of its home if placed in a shallow dish filled with cool sea-water (it will, in fact, extract itself if left for a moment) and will then vent its indignation on anything in its vicinity! Use of a hammer for this purpose is not to be recommended since the pressure cannot be applied anything like so accurately. Generally, the idea is to make the animal's home uninhabitable without stressing it to death; with practice and care large numbers of animals can be removed for routine study with no casualties. A replacement supply of empty shells will, of course, be needed when this method is used—drilled shells being especially useful if the animals are part of a long-term study.

Crabs can be successfully maintained in laboratory tanks for several months, perhaps even years, either in shells, in glass replicas (see Fig. 1), or even "naked" in separate beakers. The glass replicas will be used if the animals have nothing else to cling to, but these appear difficult to carry and are seldom chosen if there is anything else to hand—even another crab! If left naked in a beaker it seems particularly important, in order to prevent stress, that the animals have something to grip or hide beneath such as a broken mussel shell. The beakers themselves can be placed in a large tank filled with sea-water (30–35‰) at a temperature of 10–15°C, providing that this is aerated sufficiently violently to bring about water movement and turbulence. Cool water (i.e. 6–10°C) seems preferable for promoting survival, but if the water temperature rises only slowly the animals will probably survive higher values providing that there is adequate oxygenation. Naked crabs should not, however, be placed in beakers with any form of substrate since the sensitive abdomen will be damaged and, in the case of ovigerous females, eggs will be abraded and lost. Feeding is straightforward—small pieces of raw fish, mussel, shrimp etc. every 2–3 days seems quite adequate, but uneaten food should be removed after the first day to prevent it clouding the water. Moulted exoskeletons should be left in the tanks since these are usually eaten to replace minerals needed in the hardening of the new skeleton. Beakers should be cleaned at least once a week. If natural photoperiods are not possible (i.e. if the tanks are in a constant environment chamber) then an artificial photoperiod of approximately 15L:9D seems to be particularly satisfactory, but continuous dim light is preferable to continuous bright light if no control is possible. If all of the animals are introduced into the same tank to begin with, they appear to quickly adapt to the crowded conditions—but many fights will occur in the first few days. Darkness and cool temperatures, coupled with the minimal of disturbance, appear to help reduce problems at this stage. Subsequent additions, however, will frequently suffer "bullying" from established residents. If a large tank is used and the animals are free to roam around, it may also prove useful to add a number of large stones or pieces of algae to provide refuges—hermit crabs are not sociable animals! Equally, they are accomplished mountaineers and will climb out of beakers or mesh cages if they can reach the rim!

Parameters for measuring hermit crabs have tended to concentrate upon the anterior hard portion of the body—the cephalothorax—and upon the lengths of the large claws. Of these, the length of the cephalothorax is perhaps the most useful since appendages can be lost or may be regrowing (and not yet attained full size). The total body length is particularly difficult to measure accurately since the abdomen is coiled and rather flexible. A refinement on the total cephalothorax length (usually called the "carapace" length) is to measure the anterior, hard, portion (i.e. from the rostrum tip to the cervical suture—

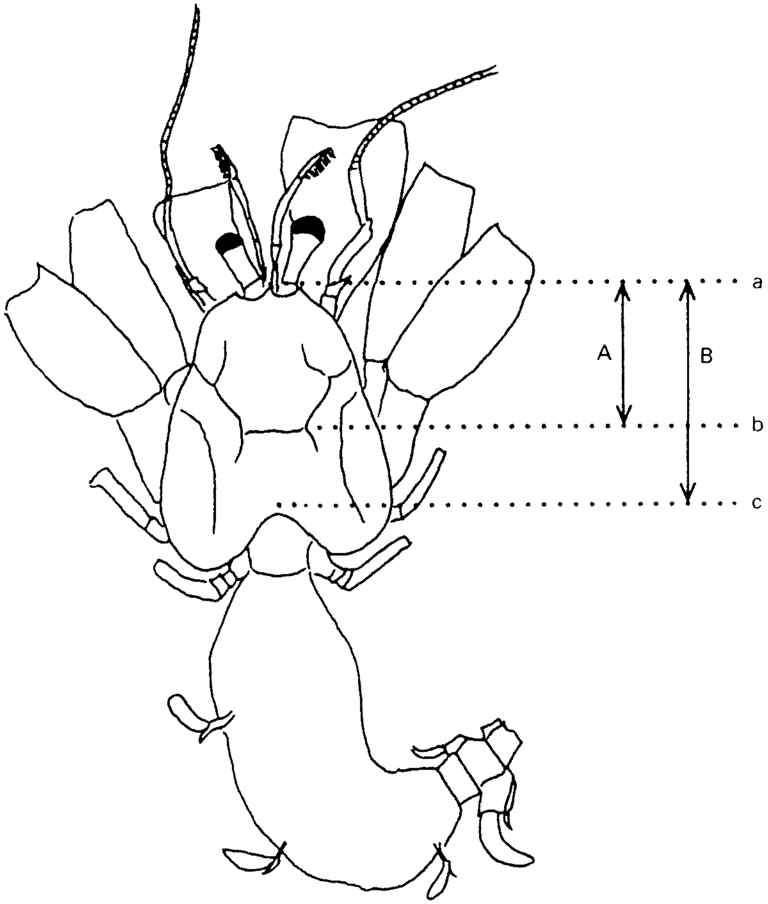


FIG. 9.
Parameters used in the measurement of *Pagurus bernhardus* (after Markham, 1968). A = anterior hard portion of the cephalothorax (the "SHIELD"), B = the entire cephalothorax (the "CARAPACE"), a = rostrum, b = cervical suture, c = posterior notch (the posterior margin of the cephalothorax).

Figure 9). This is a more realistic measure since it does not flex (and hence distort) and because it can be easily preserved and measured after moulting. This front portion—usually termed the "shield"—can be easily measured either by Vernier callipers, or using an eye-piece graticule attached to a dissecting microscope. The measure is highly correlated with the carapace length and a conversion factor can easily be calculated for obtaining one from the other.

The volume of a crab's shell is most conveniently measured by filling it with water from a microburette and recording the volume added. All shell weights need to be of dried specimens to overcome the different water holding properties of the various shell architectures. Crab weights should be of individuals gently blotted—slight errors due to water held in the branchial chambers, or between the eggs of a clutch, are inevitable.

If the animals are to be used in behavioural studies it may be necessary to mark them individually. With larger forms this is seldom difficult as long as the standard criteria for the marking of animals are followed (i.e. the marks must be non-toxic, and must not influence the animal's behaviour or increase its risks due to predation, etc.). These criteria

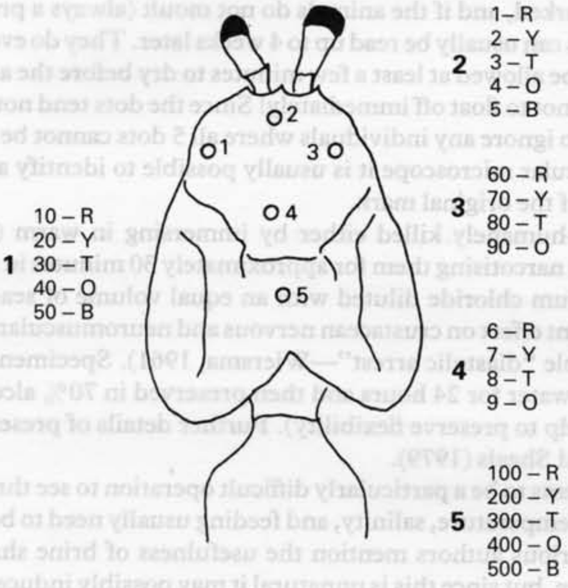


Fig. 10.

A method for individually colour marking the carapace of *Pagurus bernhardus* (modified from Southwood, 1966). Colours of enamel modelling paint found particularly useful are Red, Yellow, Tan, Orange, Blue and White. The dots are placed with the finest brushes (e.g. 0000 series) and are read clockwise around the carapace; any position not required is replaced by white. Thus, individual number 1 would be WRWWW, number 99 would be WWOOW etc. More colours can be added as required to take the total number of individual marks beyond the 599 possible with these six colours.

If the paint is allowed to dry before the crab is returned to the water, the paint dots should remain visible for up to four weeks.

are reviewed generally by Southwood (1966), and for crustacea in particular by Rebach (1983) and by Cronin (1949). While shells can be easily marked with quick drying paint (i.e. modelling paint) or with plastic tags, or even with numbers drawn with a spirit pen (perhaps on a drop of "liquid paper"), the marking of the crabs themselves is more difficult—particularly when the entire animal is only a few millimetres in length. Marked shells are particularly convenient for study and do not appear to attract predators any more than unmarked shells (Bertness, 1981*a*) providing that the marks are not too conspicuous. However, in areas popular with tourists, it may be found that small children are very much more proficient at picking out marked shells than any natural predators! Equally, marked shells do not appear to affect the behaviour of the crabs themselves (Reese, 1963) and so often represent the simplest method of following individuals for some time. Floating plastic tags—perhaps buoyed up by a small piece of polystyrene foam—can be used to help identify crabs submerged in deeper waters. If the animal does need to be marked, however, one method that is possible is to use a system in which coloured dots (of quick drying enamel modelling paint) are placed on the carapace with a very fine brush in a pattern such as is illustrated in Figure 10. The dots must be small (i.e. smaller than a number could be drawn) so as not to interfere with the animal's movements or sensory perception, but the code must be comprehensive enough to allow a large number of animals to be recognised as individuals. Using only six different colours the method illustrated allows up to 599 individuals to be marked, and if the animals do not moult (always a problem with tagging crustacea) the marks can usually be read up to 4 weeks later. They do eventually wear away, however, and must be allowed at least a few minutes to dry before the animal is returned to the water if they are not to float off immediately! Since the dots tend not to wear at the same rate it may be wise to ignore any individuals where all 5 dots cannot be clearly identified—though with a binocular microscope it is usually possible to identify a colour from only a very small portion of the original mark.

Animals may be humanely killed either by immersing in warm (not hot) water, by freezing them, or by narcotising them for approximately 30 minutes in a saturated aqueous solution of magnesium chloride diluted with an equal volume of sea-water (magnesium ions have a depressant effect on crustacean nervous and neuromuscular activity, eventually leading to irreversible "diastolic arrest"—Wiersma, 1961). Specimens should be fixed in 5% formalin in sea water for 24 hours and then preserved in 70% alcohol (a few drops of 5% glycerol may help to preserve flexibility). Further details of preserving and fixing are given in Lincoln and Sheals (1979).

Larval rearing seems to be a particularly difficult operation to see through to completion since conditions of temperature, salinity, and feeding usually need to be maintained within very fine limits. Various authors mention the usefulness of brine shrimp eggs (*Artemia* spp.) as a food source, but since this is unnatural it may possibly induce abnormal development (Roberts, 1974). Nauplii of copepods and barnacles may well be the best answer (moving food seems to be preferred—Gurney, 1939) but would need to be cultured. Larvae seem to have been best raised in individual dishes floated in large tanks (to maintain a stable temperature and to facilitate changing of the water and cleaning) subject to light regimes of 12L:12D in an otherwise constant environment chamber (Hazlett, 1971*c*).

NOMENCLATURE

The International Commission on Zoological Nomenclature intervened in the debate over the generic name of the common 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).

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