# Ecological studies on two species of hermit crabs *Pagurus bernhardus* (L.) and *Diogenes pugilator* (Roux) (Crustacea, Anomura, Paguridae) around the Gower Peninsula, South Wales

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by

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# SUMMARY

A field survey was conducted of an extensive intertidal population of Pagurus bernhardus at Mumbles Head, S. Wales. Mean densities of up of 80 $m^{-2}$ were observed in a rock pool and locally, higher densities of up to 500 $m^{-2}$ occurred. There was no evidence of tidal or seasonal migration, or emigration from the area although there was an influx of large males from the sublittoral during the breeding season. Sublittoral sampling of the species at a depth of 5 metres on a sandy substrate at Oxwich Bay, Gower, revealed a full range of small individuals in that habitat.

Comparison of the intertidal and sublittoral samples of hermits occupying Littorina littorea shells revealed differnces. Intertidal hermits of given carapace width occupied larger shells and the colour of the integument, the species of epizoites and the pattern of allometry of the major chela were also found to differ. To determine whether these were genetic or phenotypic differences, enzyme electrophoresis of tissue samples from both populations were compared. They proved identical.

Laboratory growth experiments confirmed the findings of earlier workers that moult increments are influenced by the size of available gastropod shells. Rearing studies indicated that small hermits observed as late as March must have been recruited the previous year. Growth rate of recruits was followed from field data. Postulated overall growth curves reconstructed from these data indicated a likely longevity of up to three years for intertidal Pagurus bernhardus and five for sublittoral populations. The high reproductive output of the numerous small hermits is facilitated by their precocious puberty.

Studies of Diogenes pugilator indicated that this species has stenotopic ecological requirements and can be regarded as a refugial species in its habitat of the lower tidal and shallow sublittoral surf-pounded sands. Unlike P.bernhardus it is tidally and seasonally migratory so does not have separated populations.

# CHAPTER 1

## General Introduction

This study is concerned with the ecology of two species of hermit crabs, *Pagurus bernhardus* (L.) and *Diogenes pugilator* (Roux), both of which are very common on the South Wales coast. Both have a distribution which is partly intertidal and partly sublittoral.

A major objective was to examine the relationship between the intertidal and sublittoral parts of the distribution but with particular attention to the intertidal.

Hermit crabs are crustaceans belonging to the class Malacostraca, order Decapoda. There is considerable disagreement about the classification of the Decapoda. For the present purpose, hermit crabs can be regarded as members of the suborder Reptantia. Within this suborder a recent author (Schram, 1986) classifies them under the Infraorder Anomala,Boas, 1880, which is divided into thirteen families. The species considered here belong respectively to the families:

1) Diogenidae Ortmann, 1892
2) Paguridae Latreille, 1803

There are sixteen British species of hermit crabs (Allen, 1967) which include only the one species, *Diogenes pugilator*, of the family Diogenidae. Of the other fifteen, most authorities assign 14 to the family Paguridae (the remaining species belongs to the Parapaguridae). The British Paguridae include seven species of the genus *Pagurus* (formerly *Eupagurus*, now correctly *Pagurus*, see Walton and Stevens, 1955). Most of these species are confined to the sublittoral. During the course of this study only the one species, *P. bernhardus*, was encountered. In many coastal areas of the British Isles another large hermit crab, *P. prideauxi*, is common but this did not occur in the study areas. It differs from *P.*

*bernhardus* in lacking the double row of tubercles on the major chela and the acutely pointed rostrum. Another species that occurs intertidally, *Clibanarius erythropus* (Latreille) a diogenid is confined to the south coasts of Devon and Cornwall (Southward and Southward, 1977).

Many aspects of the biology of hermit crabs have been studied in detail. Some of these will be referred to in later chapters. A few others will be noted here.

Feeding has been studied by several workers, a recent example being that of Schembri (1982) who studied 15 species in New Zealand, and Gerlach, Erkstrøm and Ekhardt (1976) who recorded filter feeding in *Pagurus bernhardus*. Generally hermit crabs are omnivores or scavengers, catching food with the chelipeds but also feed on detritus shovelled up with the 3rd maxillipeds for transfer to the mouth as a bolus.

There is also a very extensive literature on social behaviour of hermit crabs particularly with regard to shell utilization (Hazlett, 1981).

The economic value of the hermit crabs, so far as their direct use to man is concerned, is almost negligible. Indirectly, they are of some value since they form the staple food of the larger fish - the remains of *P. bernhardus* are familiar objects among their stomach contents - and on some parts of the coast they are used by fishermen to bait their lines. Some of the fishermen declare that the hermits are "the very best bait you can get for cod; none better!" (Jackson, 1913).

Only one species seems to be used as food by the human race. The natives of the Islands of the Pacific, on which *Birgus latro* - the famous coconut crab - occurs, greatly prize the oily abdomen of the beast as a gastronomic delicacy. The British pagurids are not sufficiently common ever to be exploited commercially as a food for the table, but there seems no reason why such a clean and dry crustacean should not make as delectable a dish as its more favoured macrurid and brachyurid relations(Jackson, 1913).

The general distribution and life history features of the two species will now be outlined.

## *Pagurus bernhardus*

### Geographical Distribution

*Pagurus bernhardus* has a wide distribution on the coasts of the North Atlantic. Its northern limit is the North Cape. Its southern limit is North Africa. Westwards it occurs on the New England coast. Its detailed distribution follows.

### Scandinavia and Iceland

*P. bernhardus* extends along the whole coast of Norway round the North Cape into the Murman Sea (Birula), (Sars, 1882) and more generally in the Barents Sea (Bouvier, 1940). It is widespread around the Danish islands and partly into the Baltic Sea (Selbie, 1921; Markham, 1968).

Hansen (1908) found this species occurs off the south and south-west coasts of Iceland, where many other arctic-boreal species occur, but it has never been found on the north and east coasts noted for their restricted arctic fauna.

## North Sea

It occurs on all coasts of the North Sea. Its occurrence along the south and eastern coast of the North Sea was recorded by Tesh (1908). It occurs also on the coasts of Sweden (Goes) (Lagerberg, 1906). In view of the shallowness of the North Sea the species is probably widespread sublittorally there.

## British Isles

This species is found in great numbers on coasts of Great Britain, Ireland and the Channel Islands (Bell, 1853; Norman, 1861; Selbie, 1921; Moore, 1937; Bouvier, 1940; Marine Biological Association U.K., 1957).

## French and Iberian coasts

Its occurrence on the north coast of France, the Bay of Biscay and Portugal, was documented by Milne-Edwards and Bouvier (1897).

## Mediterranean

*P. bernhardus* is very rare on the coasts of the Mediterranean Sea being replaced there by other species of hermit crabs. Ten species of hermit crabs were reported from the coastal waters of Ras Beirut, Lebanon, but these excluded *P. bernhardus* (Bouvier, 1940).

## America

It has not been taken by any of the expeditions to Greenland, but is found along the east coast of North America from about New

York 40°N to 37°N (Milne-Edwards and Bouvier, 1893; Selbie, 1921).

## Bathymetric range

*P. bernhardus* occurs at various depths, from the littoral zone, where it often literally swarms in the rock-pools, downwards. The deepest record is 520 metres (Benedict, 1901). It occurs in greatest numbers between the shore and the 30 metres line, but it has also been collected at various localities from much greater depths, including several from 180 metres and one from 480 metres (Selbie, 1921).

## Gastropod shells occupied as carcinoecium

In intertidal and shallow water collections most of the specimens are found in the shells of *Littorina littorea* (L.), *Nucella lapillus* (L.), *Littorina obtusata* (L.) and *Nassarius reticulatus* (L.), in that order of preference.

The large sublittoral specimens of hermit crabs *P. bernhardus* have not such a large field of choice in the species of shell they can inhabit as have the intertidal hermit crabs. Larger *P. bernhardus* always seem to prefer the shells of *Buccinum undatum* (Jackson, 1913; Pike and Williamson, 1959). Selbie (1921) found that hermit crabs over 15 mm carapace length occupy the shells of *Buccinum* or *Neptunea*.

## Commensals associated with *Pagurus bernhardus*

Shells inhabited by *P. bernhardus* are very often covered with colonies of the hydroid *Hydractinia echinata* (Fleming) (Selbie, 1921; Pike and Williamson, 1959; Hazlett, 1981). Jackson (1913) found that

50% of the shells which he examined (all sublittoral) have this growth upon them.

Hornell (1892) states that 90% of shells which have been taken possession of by hermit crabs contain the polychaete worm, *Nereis fucata*. Also in 1959, Pike and Williamson found this worm most commonly in specimens collected below tide marks. Jackson (1913) found that more than one of these polychaete worms may be found in a single shell of *Buccinum*.

The anemone, *Calliactis parasitica* (Couch), is a common associate on the south coast and in the Channel Islands, but is not found in the Irish Sea or in the Clyde Sea Area (Selbie, 1921; Pike and Williamson, 1959; Ross, 1960; Hazlett, 1981).

Wilson (1935) described the relationship between *P. bernhardus* and the position the anemone occupies on the shell. Occasionally, two or more of these anemones are found on one shell. It is thought the anemone shares the hermit's meals. The Plymouth Marine Fauna List (Marine Biological Association, 1957) also recorded that shells inhabited by *P. bernhardus* usually afford lodgement for one or more specimens of *C. parasitica* in the Plymouth area. Gotto (1969) states that sometimes several individuals of this anemone occur on a single shell; he discusses the relationship between the hermit crab and their anemone partners, *C. parasitica*.

## *Diogenes pugilator*

### Geographical Distribution

The geographical range of this species includes much of the eastern Atlantic sea-board, the Mediterranean, the Adriatic Sea, the

Black Sea, the Red Sea, the Gulf of Aden and the Persian Gulf (see map, Fig.1.1). In U.K. waters, they occur mainly in the south-west, the most northerly report being of those on the Island of Anglesey (Widdop, 1979).

Examination of Table 3.1 and Figure 3.1 shows that *D. pugilator* are common on both sides of, and even within the Suez Canal. The species has also been reported from the west African coast, but is, however, absent from South African waters (Stebbing, 1900). In the latter area, another species, *D. costatus*, "which appears to be very nearly related to *D. pugilator*"(Stebbing op. cit.) might possibly replace it. The earliest report of *D. pugilator* in the Red Sea (Alcock, 1905) was some 40 years after the opening of the Suez Canal. It seems possible, that the species has migrated from Mediterranean Sea into the Red Sea, and subsequently the Persian Gulf. The migration hypothesis is given further credibility by the report of Gurney (1927) who found *D. pugilator* to be abundant in the Bitter Lakes, which form part of the Suez Waterway System. Furthermore, the range of the species in the Indian Ocean is still restricted to the Persian Gulf and waters around the Red Sea, reports from further East being very dubious. (For example, the record by Alcock (1905) of the species on the Malaysian Peninsula was based on a single damaged specimen brought up in a trawl.) If the species is absent from Southern and Eastern African waters, as the current literature would seem to indicate, it is very unlikely that initial recruitment of the Red Sea populations came from larvae released in West Africa.

## Bathymetric range

The depth limit is rather uncertain, but Pike and Williamson (op. cit.) report that the greatest numbers occur just below low water level, this being confirmed at Aberffraw, Anglesey by O'Sullivan (1977).

## Gastropod shells occupied as carcinoecium

It has been recorded by Pike and Williamson (1959), that in Anglesey and Jersey *D. pugilator* was most frequently found in the shells of *Nassarius reticulatus* (L.) and less commonly in those of *Nucella lapillus* (L.) and species of *Littorina*, especially *L. littoralis* (L.) (=*obtusata*). Also Widdop (1979) found that *D. pugilator* were occupying shells of *Nassarius reticulatus* (L.), *Nucella lapillus* (L.) and species of *Littorina*, and were less common in *Gibbula* spp., *Natica alderi*, *Ocenebra erinacea*, *Buccinum undatum* and *Aporrhais pes-pelecani*.

In the following chapters, different aspects of the ecology of the two species are examined.

Chapter 2 reports field studies of an intertidal population of *Pagurus bernhardus* at Mumbles Head, Swansea, South Wales, and of a sublittoral population at the nearby Oxwich Bay.

Chapter 3 describes an experiment designed to resolve the status of the intertidal population of *Pagurus bernhardus* by using enzyme electrophoresis.

Chapter 4 reports field studies of a population of *Diogenes pugilator* at Rhossili Bay, Gower, South Wales.

Chapter 5 deals with the growth of two species using results obtained from laboratory experiments and from the field studies.

Studies on the reproduction of the two species of hermit crab are reported in Chapter 6. These are based on field studies of the breeding season together with laboratory histological studies of the ovaries and embryonic development.

Studies of larval development of the hermit crab, *Pagurus bernhardus*, in the laboratory based on rearing larvae in different combinations of temperature and salinities are reported in Chapter 7.

Finally, Chapter 8 reviews these findings and draws some conclusions.

Figure 1.1

Map showing the geographical distribution of the hermit crab, *Diogenes pugilator* (Roux). Arrows indicate records of this species (largely based on Widdop, 1979).

Table 1.1

A summary of the geographical distribution and the abundance of the hermit crab *Diogenes pugilator* (Roux) (from Widdop, 1979).

| REFERENCE | LOCALITY | REMARKS |
|---|---|---|
| | ATLANTIC: | |
| | Wales | |
| Pike & Williamson 1959 | Anglesey | Well established |
| O'Sullivan 1977 | " | On clean sand |
| Widdop 1979 | " | " |
| Sabar 1980 | " | " |
| Bell 1853 | Cardigan Bay | |
| | England | |
| Allen & Todd 1900 | A number of areas in | On sand |
| Norman & Scott 1906 | the south-west | |
| Marine Biol. Ass. 1957 | | |
| | Channel Islands | |
| Pere'z 1929 | Various sites | Common on clean sand |
| Pike & Williamson 1959 | | |
| | France | |
| Bouvier 1891 | Normandy coast | On sand and mud |
| Selbie 1921 | " | |
| Pere'z 1929 | Brittany coast | |
| Selbie 1921 | Bay of Biscay | |

Table 1.1 (cont.)

| REFERENCE | LOCALITY | REMARKS |
|---|---|---|
| Selbie 1929 | Spain and Portugal | |
| | Africa | |
| Selbie 1921 | Cape Verde, Senegal | On sandy shores |
| Selbie 1921 | Gaboon River | |
| Bouvier 1940 | Kotonu, Dahomey | |
| Forest 1955 | Angola | |
| | MEDITERRANEAN | |
| Balss 1955 | Generally | Common |
| Selbie 1921 | France | |
| Bouvier 1940 | Marseilles | Abundant |
| | Italy | |
| Selbie 1921 | Genoa | |
| Selbie 1921 | Naples | |
| Selbie 1921 | Sicily | |
| Bouvier 1940 | Beirut | |
| | North Africa | |
| Selbie 1921 | Algeria, Morocco, Sudan | |
| | Adriatic Sea | |
| Selbie 1921 | Various sites | |

Table 1.1 (cont.)

| REFERENCE | LOCALITY | REMARKS |
|---|---|---|
| | Black Sea | |
| | Various sites | On sandy shores |
| Alcock 1905 | RED SEA | |
| Selbie 1921 | Generally | Common |
| Nobili 1906<br>Gurney 1927 | Suez Canal | Very common on sandy shores |
| Nobili 1906 | Gulf of Aden | Widely distributed |
| Nobili 1906 | Persian Gulf | |
| | INDIAN OCEAN | |
| Selbie 1921 | Bay of Bengal | Questionable |
| Alcock 1905 | Malaysian Peninsula | " |

# CHAPTER 2

## Field Studies of *Pagurus bernhardus* (L.)

## 2.1 INTRODUCTION

It is a striking feature of *Pagurus bernhardus* (L.) that in many localities, it occurs both intertidally and sublittorally. Offshore it grows to a large size usually occupying the whelk shell, *Buccinum undatum* (L.). The individuals occurring on rocky shores occupy only the shells available on the shore, namely those of winkles and top shells which are obviously very much smaller than *B. undatum* shells and this is sufficient to explain superficially why only small *P. bernhardus* are found intertidally. Larger specimens are too big to fit inside a *Littorina littorea* shell so they would be unprotected.

The occurrence of only small specimens of *P. bernhardus* on the shore has been interpreted as evidence of an offshore movement of the hermit crabs as they get larger. It has been suggested that larger specimens move offshore in order to find larger shells that are not available on the shore (Wilson, 1935; Yonge, 1954; Pike and Williamson, 1959).

Such an offshore movement of growing crabs might also be a normal stage in the life cycle associated with the movement out to breeding grounds. The size range on the shore would thus represent immature individuals.

The objective of this study was to look for evidence in support of these interpretations but also to consider alternative explanations especially the hypothesis that the animals comprising the intertidal population are permanent residents breeding there and that they do not normally progress to a subsequent sublittoral existence. To this end it was necessary to study both intertidal and sublittoral populations.

## 2.2 MATERIALS AND METHODS

### 2.2.1 Shore surveys

A preliminary study showed that *P. bernhardus* were particularly abundant locally in a large shallow pool at Mumbles Head, Swansea, South Wales, so this was selected for detailed study.

A transect line was established through this pool from the nearby low water to the north and extended beyond the pool to the south.

The vertical heights on the transect were measured using a simple levelling instrument and a metre pole. The actual level of the low tide (on a calm day) was assumed to correspond to the predicted height given in Admiralty Tide Tables and this was used as a datum point. Horizontal distances were measured using a specially made surveying line, accurately marked at 5 metre intervals. Sampling was conducted at suitable intervals along this transect line.

A careful survey of the dimensions of the pool was made. The extremities were permanently marked by metal posts driven into the substrate. These posts were placed at the eastern and western extremities of the pool, and two more posts at the north and south limits.

It was then measured using a line knotted at 1.0 m intervals from the datum point (metal post) at the eastern end (Fig. 2.5).

Depths were recorded at metre intervals along the transverse axis.

Monthly samples of the hermit crabs in the pool were made between

October 1982 and December 1983. On each sampling day seven 1 $m^2$ quadrats at fixed points on a 1.0 m wide transect line were sampled (Fig. 2.5). The exact position of each of these was determined by re-establishing both datum cords. All the hermit crabs within each 1.0 m square quadrat were collected. The quadrat was then moved to the next fixed point across the width of the pool. In this way all the hermit crabs within each of the seven 1.0 $m^2$ quadrats were collected for analysis.

Care was taken to ensure that all the shells in the quadrat were inspected, looking under rocks and other obstacles in order to get a correct measure of density.

In a separate study, random 0.25 $m^2$ quadrats were studied in another area at Mumbles Head, where *Pagurus bernhardus* was found to be plentiful (see ●, Fig. 2.1) and a similar quadrat near the survey pool.

A short-term mark-recapture experiment was conducted on the *P. bernhardus*, to determine their movement in the main pool. In this experiment, 125 hermit crabs were collected from one square metre of the pool. Their shells were individually marked (after drying outer surface) by a spot of quick-drying spray paint on the aperture margin. A bright white paint was used so as to be easily distinguished to facilitate recovery. The marked shells still occupied by their hermit crabs were returned to the same square metre. 24 hours later all the hermit crabs in the main square were collected and the whole area of the pool was extensively searched for other marked shells.

### 2.2.2 Sublittoral surveys

Collections of sublittoral *P. bernhardus* were made for comparison with littoral population. The offshore samples were collected using a beam trawl (3 m width with a 20 mm mesh net and a 9.0 mm cod-end) from the College ship, a 30 m stern trawler, the "Venturous". Sampling was at approximate monthly intervals at a depth of 5-20 m below Chart Datum in Oxwich Bay. On one occasion, a finer mesh net was used. Each trawl was of 20 to 35 minutes duration. Poor weather conditions often interrupted this otherwise regular sampling. All the hermit crabs caught were transported alive, in seawater, to the laboratory, where they were preserved in 4% seawater formalin or 75% ethanol.

In the laboratory, the hermit crabs from the various habitats were examined. They were removed from their shells by various methods sometimes using bone forceps on the largest shells. The shell species and sex of the crab were noted and the length and breadth of the carapace, and chela length were measured, using a vernier caliper for the larger specimens, and a calibrated eyepiece graticule for the small ones. This method of measurement was adapted from Markham (1968).

Information on breeding condition was collected and some specimens were dissected for further work on the gonads. A few females were preserved for histological study of ovarian development, in both 4% seawater formalin and seawater-Bouin's solution. These results are reported in Chapter 6. The incidence of epizoites was noted, and the presence of internal and external parasites was recorded (see Appendix A for parasites).

Where necessary, statistical tests were applied to the data.

## 2.3 RESULTS

Initial analysis of the data consisted of graphical plots making visual comparisons easier. The size characteristic chosen to represent the hermit crab size was the width of the hard carapace, these being grouped into size classes, the frequency being converted to a percentage of the sample and thus a histogram drawn.

The principal results are shown in Figures 2.1-2.23, Tables 2.1-2.13 and Plates 2.1-2.2 on pages 38 to 75 at the end of the chapter.

### 2.3.1 Distribution, abundance and size

Because of the problems of sampling the sublittoral populations, much more attention was paid to the intertidal hermits. Inevitably the methods used were different so the results will be set down separately, dealing with the intertidal results first.

### 2.3.1.1 Intertidal population

The map (Figure 2.1) shows the area used for studying intertidal *Pagurus bernhardus*. To the north side of Mumbles Head, conditions are comparatively sheltered: grade 6 on the exposure scale (Ballantine, 1961) but more exposed (grade 3-4) on the south side. The hermit crabs are confined to the area between the islands and the headland where shallow pools of water remain at low tide on a beach composed of boulders, cobbles and smaller stones (Plate 2.1). The map (Figure 2.1) indicates the position of the transect through the principal study pool and also the position of the random quadrat sites (mentioned in the methods section).

### 2.3.1.1i Transect study

The results of this study are set out in Figure 2.2 and clearly show that abundance of hermit crabs is associated with pools but that lower densities are to be found in other wet areas provided they are not well drained. Further away from the transect site specimens were to be found at higher levels - to mid-way between MLWN and MTL where suitable substrate occurred. The distribution was not particularly associated with the sheltered side of the area. Hermits were to be found at low tide mark on the exposed south side, where suitable substrate occurred.

### 2.3.1.1ii Quadrat study

Special counts were made to demonstrate the local high abundance of hermits and at the same time to sample the *Littorina littorea* shells still occupied by the original mollusc. The first set of such quadrats was made near the mainland at the point marked by a dark circle on the map (Fig. 2.1).

A total of 196 gastropod shells were collected from the first 0.25 m² and they were found to consist of:-

a) Ninety-nine shells of *Littorina littorea* occupied by hermit crabs, *P. bernhardus* (mean shell width was 13.2 mm).

b) Eighty-one shells had live winkles in them (mean shell width was 11.5 mm).

c) The remaining shells were empty and measured 11.3 mm in mean shell width.

The second 0.25 m$^2$ had 161 shells and they were found to consist of:-

a) Ninety-two gastropod shells of *Littorina littorea* inhabited by *Pagurus bernhardus* (mean shell width 11.7 mm).

b) Fifty-nine shells were occupied by live winkles (mean shell width 13.7 mm)

c) The remaining 10 were empty with mean shell width 13.6 mm (Fig. 2.3).

Shells occupied by hermits exceeded the others in both replicates. The size range of the shells retaining the original mollusc was similar to that of those occupied by hermits. The percentage of empty shells was very low (8.16%) and of these, some were unsuitable for occupation by hermits because they were held down by byssus threads of *Mytilus edulis*.

Also a collection was made from a square (0.25 m$^2$) at the edge of the large pool between the two islands, and all results were plotted in a histogram (Fig. 2.4).

All the gastropod shells collected from this site were identified and their widths were measured. They were all *Littorina littorea*. A total of 162 shells was collected from the 0.25 m$^2$. 125 shells were found occupied by live winkles (mean shell width 10.6 mm). Also 33 were occupied by *P. bernhardus* (mean shell width 15.3 mm). The remaining shells were unoccupied (mean shell width 15.8 mm).

This second site examined by the use of the 0.25 m$^2$ quadrat gave a very different result from the first site. The overall density was lower but the shells still occupied by the original winkle consisted of 77.16 percent of the total. Very few available empty shells (2.47%) were found, and furthermore these included no very small ones necessary for occupation by glaucothöe at settlement. This was in contrast to the mollusc occupied shells which included many small specimens.

### 2.3.1.1iii Study of large pool

Major features of the pool are shown in figure 2.5 (note that the depth profile relates to the north/south axis). Figure 2.6 also shows the depth profile and the overall abundance of hermit crabs at each of the different sampling points along the pool transect each month. Although there were differences in the monthly distribution of crabs along the fixed transect (Fig. 2.6), they were most abundant at North 4 m and South 8 m.

The hermit crabs seem to prefer being in a depth range of 9-12 cm along the northern sample line with a mean of 10.5 cm for north 4 m and a range of 2-9 cm along the southern transect where the mean preferred depth is 5.5 cm between south 4 m - south 10 m (Fig. 2.6).

It can be seen that the hermit crabs are not particularly abundant in the deeper parts of the pool.

### 2.3.1.1iv Seasonal changes in the pool population

It is immediately clear from the figure 2.3 that unlike several other intertidal crab species *P. bernhardus* at the study site at Mumbles Head, remain intertidal throughout the year rather than undergoing seasonal offshore migration.

In general throughout the period of sampling of this area, significant numbers of hermit crabs were always available in the population, although fluctuations in numbers were observed.

Monthly variation in the abundance of *Pagurus bernhardus* in the area is apparent in the histograms (Fig. 2.7) and is reflected in the number of hermit crabs collected per transect per tide (Fig. 2.8). It shows a variation in their number throughout the season. The largest number of hermit crabs was collected in the month of November 1982 (211) and the lowest was in February 1983 (98) (Table 2.1). However, these results need to be interpreted with caution. Movement of the cobbles by winter storms altered the outline of the pool reducing its size. Also it should be borne in mind that collecting winkles in 30 cm of water in cold windy weather is much more difficult than when it is fine.

Subjective assessment suggested that the distribution of hermits in the fixed transect was typical of the whole pool. Extrapolation of the densities measured suggest that the whole pool might contain in excess of 11,000 individuals.

The size frequency distribution of hermit crabs collected from the intertidal zone at Mumbles Head, during the period of sampling between November 1982-December 1983, are shown in figure 2.8. It indicates that the smallest post larval crabs (< 1.0 mm carapace width) appeared in the transect in summer, June-July 1983. The largest crabs were collected in the months of August, September and October 1983. From the figure 2.8 it can be seen that a high proportion of the hermit crab population in the area were between 2.0 and 5.0 mm carapace width. Hermit crabs larger than 1.0 mm carapace width and less than 2.0 mm were common during August. Clearly, this was the period of maximum recruitment.

The data collected during the monthly sampling of intertidal

*Pagurus bernhardus* at Mumbles Head gave some information about rate of growth. Attempts at analysing these data using the classic method of Cassie (1954) failed to produce meaningful results. It was not possible to identify and follow "real" peaks in the data through the time series. First appearance of recruits in the population was recorded, and although these were in low numbers it was possible to follow them through in later months although they quickly merged with the larger size groups. The overall impression in this respect was of a low recruitment rate to a stable population.

The frequency distribution of male and female *Pagurus bernhardus* is shown in Figure 2.9. There was no marked difference in the numbers of each sex at a particular size.

The sex-ratio of the hermit crab *P. bernhardus* at Mumbles Head sampling area indicates similarity in the monthly percentage for males and females throughout the year slightly in favour of males (Fig. 2.10) except during the months of January, February and March 1983, where the percentage of females slightly exceeded that of males. In March 1983 when the percentage of females was highest, it reached 57.8% of the sample. Figure 2.9 shows the monthly changes in the different size groups of males and females.

The result of a t-test showed that there is a significant difference between numbers of males and females ($P < 0.05$).

It was interesting to note that the females greater than 6.0 mm carapace width are absent in the site, so the largest hermit crab (> 6.0 mm CW) seen here were all males. The numbers of these however were very small indeed. They were occupying rare *Buccinum undatum* shells.

Monthly variations in the mean carapace width of males and females of *P. bernhardus* (Fig. 2.11) did not show any clear evidence of season disappearance (migration) of larger specimens apart from the absence in the pool of the few specimens occupying *Buccinum* shells after October 1983.

### 2.3.1.1v Special sampling

Following a chance observation, a special search and collection of *Pagurus bernhardus* occupying *Buccinum undatum* shells were made between the survey pool and the southern shore near low water during February 1987. Sixteen individuals were collected. Another 5 specimens were found very near low water mark at the time of spring tides; each of these was holding a smaller gastropod shell occupied by a hermit crab. Tens of thousands of *P. bernhardus* occupying smaller gastropod shells were present in the same area as these few *Buccinum* shells.

Back in the laboratory the hermits were extracted and were sexed and their shell width, carapace width etc. were measured. Shell condition was also noted. All these hermit crabs occupying *B. undatum* shells were males, the smallest was 4.0 mm carapace width and the largest was 13.8 mm. The overall mean carapace width of the sixteen hermit crabs was 8.9 mm (Table 2.2).

Figure 2.12 shows the relation between the size of carapace width and *Buccinum* shell width. The results obtained from calculating a regression line shows that increased shell width is correlated with increased size of the carapace width of *P. bernhardus* ($P < 0.01$).

The size and sex of 5 pairs of hermit crabs and the type of shell they occupied are set out in Table 2.3. It shows that the crabs occupying *Buccinum* shells were all males and the crabs occupying small gastropod shells (*Littorina littorea* and *Nucella lapillus*) were females. The overall mean size of the carapace width of the males occupying *Buccinum* shells was 11.94 mm and for the small ones was 4.76 mm.

### 2.3.1.2i Sublittoral populations of *Pagurus bernhardus*

These results arise from the trawl sampling described in the "Methods" section of this chapter. They refer to sublittoral *Pagurus bernhardus* caught at a site on the southern coast of the Gower peninsula, using a beam trawl. This was at Oxwich Bay on four occasions between October 1982 and February, March and April 1983.

Unfortunately, the numbers of crabs sampled in this way were rather small, the total number being 312. The number and size of hermit crabs in these four samples is given in Figure 2.13 and Table 2.4. It is immediately apparent that the size frequency distribution of the specimens in the first three samples is very similar and different from the fourth sample. The absence of specimens below about 10 mm carapace width in the first three samples needs explaining. It is most probably a reflection of the mesh size of the beam trawl net which was 20 mm allowing smaller specimens to pass through. The size frequency in the fourth sample is more interesting. On this occasion an extra lining net of smaller mesh size was used (9.0 mm) with the object of catching small sublittoral hermit crabs and this was clearly successful. However, it does not explain the scarcity of large hermit crabs from the catch. This may have resulted from the use of different trawl gear but it seems possible that there were very few at this sampling point perhaps because it was too shallow or because the substrate was unsuitable.

The sex ratio for each sample is shown in Fig. 2.14 and size frequency of each sex is indicated separately for each sample in Fig. 2.15. It is evident that the mean size of males is greater than that of females in each of the first three samples (Table 2.5). This is different from the situation observed in intertidal population.

Because of the small number of samples it is instructive to combine the results in various ways. If the results of the first three samples are combined (Fig. 2.16), it is possible to get a good impression of upper size limit of each sex (Table 2.4). The males are clearly larger by about 2 mm of carapace width. The largest male was 17.6 mm CW and the largest female 15.7 mm CW (Fig. 2.15).

The fourth (April) samples needs to be considered separately from the other three. About 90% of the specimens were under 10.0 mm in carapace width (see Fig. 2.15). The very few larger ones all occupied *Buccinum* shells. It is valuable to ignore these for some purpose and concentrate on the smaller specimens which made up the bulk of this collection. It is possible to determine the sex ratio of these and the size frequency distribution and mean size of the sexes separately (Table 2.6). In this case it is seen that the mean carapace size of females is, if anything, slightly larger than that of males (which is different from the case in the intertidal populations; Fig. 2.9).

For other purposes it is instructive to combine the results of all the sublittoral samples. The combined size frequency distributions are shown in Fig. 2.17. The bimodality of the distribution discussed earlier is immediately apparent. It may have little ecological significance. The extremes of size of specimens in these four collections were 2.5 mm and 17.6 mm.

### 2.3.1.2ii Hermit size related to *Littorina* shell size

A very interesting observation was made in the case of sublittoral *Pagurus bernhardus* occupying *L. littorea* shells. They appeared to be larger than those intertidal ones occupying similar sized shells.

Figure 2.18 shows the size of hermit crabs collected from the sublittoral zone compared with a sample from the intertidal rock pool at Mumbles Head. It can be seen from the histograms that the offshore hermit crabs inhabiting *L. littorea* shells had a slightly larger mean and maximum size than those on the shore.

Also the histograms show that the mean diameter of the shells of *L. littorea* occupied by the sublittoral hermit crabs was slightly larger than shells of the same species inhabited by the intertidal hermit crab.

Figure 2.19 shows the relationship between the carapace width and the shell width of the hermit crabs from both areas (littoral and sublittoral). Regression analysis indicates different values from the two sets of data.

*Littorina littorea* (littoral) $y = 0.2548x + 0.2405$; $r = 0.6034$

*Littorina littorea* (sublittoral) $y = 0.2512x + 0.3640$; $r = 0.8017$

The difference is highly significant ($P < 0.05$),

### 2.3.1.2iii Colour of integument

Colour differences between intertidal and sublittoral *Pagurus bernhardus* are on record (Marine Biological Association, 1959). Such differences were noticed during the period of the study observations. It was noted that the colour of the hermit crabs in the intertidal habitats was darker than those from sublittoral populations. Whereas in sublittoral specimens the patches of orange colouration are separated by pale or white areas (see Plate 2.2), intertidal specimens have an olive or greenish colour which partly obscures the orange (see Plate 2.2 ). These colour differences are only seen on body parts that protrude from the shell, i.e. cephalothorax and associated appendages. It appears to be superficial in the integument. Some paler individuals found intertidally appeared to be newly moulted.

### 2.3.3 Incidence of missing limbs

The number of hermit crabs (*Pagurus bernhardus*) with missing chelae during a fourteen month survey period is shown in Table 2.7. The hermit crabs showed a higher incidence of autotomy in chelae than walking limbs. Maximum autotomy observed was 10.0% (November 1982) and the minimum was 3.6% (February 1983) (see Fig. 2.20).

Figure 2.20 shows that the male hermit crabs exhibited a greater degree of both major and minor chelae autotomy than the females. The regular shape of the graph suggests that this reflects a genuine seasonal change rather than more statistical variation.

### 2.3.4 Gastropod shell species occupied by *Pagurus bernhardus*

#### 2.3.4.1 Intertidal

Table 2.8 indicates that the most usual shell for occupation by the hermit crab *P. bernhardus* in the intertidal study area is that of *Littorina littorea*. This is shown by the high percentage (78.9%) (1645 out of a total 2086 *P. bernhardus* examined) were occupying *L. littorea* shells. The second most frequented shell was that of *Nucella lapillus* (18.1%) (378 out of 2086), whilst the shells of the remaining gastropod species were infrequently occupied by the hermit crab.

Also, the monthly figures (Table 2.8) show no annual variation in the preference for shells of the two main species of gastropod. The percentage varies between 70-80% for *L. littorea* and 10-25% for *N. lapillus* throughout the period of sampling.

The size range of hermit crabs occupying shells of different species is shown in Fig. 2.21. The histogram for *L. littorea* is based on one month's sampling. The histograms for the other species are the total results for the whole period of sampling the pool.

It can be seen from the histogram that the modal size (carapace width 3.5-4.0 mm) of crabs occupying *Nucella* shells is larger than that (3.0-3.5 mm) occupying *L. littorea* (the mean and the maximum are also larger). For most of the other species of gastropod the size of occupying hermit crabs is smaller.

However, overall, the smallest crabs (< 2.0 mm CW) are more likely to be occupying shells of *L. littorea* and *N. lapillus* than any other shells.

Only in the case of the very few *Buccinum undatum* shells was the size range of occupants larger than *L. littorea* and *N. lapillus*. In terms of size and shape of gastropod shells, crabs up to 5.0 mm CW appear to have a choice between *L. littorea*, *N. lapillus*, *L. obtusata* and *G. cineraria*, but hermit crabs larger than this appear to have a more restricted choice of gastropod shells available.

### 2.3.4.2 Sublittoral

Table 2.9 shows the numbers of sublittoral hermit crabs (*Pagurus bernhardus*) inhabiting the different species of gastropod shells. Figure 2.22 indicates the relationship between carapace width and species of gastropod shell occupied. All the larger hermit crabs occupied shells of the whelk *Buccinum undatum*. Smaller hermit crabs mostly occupied shells of smaller species of gastropod. A survey of the gastropods occurring at Oxwich showed that shells of all the species there were used by hermit crabs. Choice of shell species seemed to depend mostly on the size of the hermit crabs. The shells of adult *Buccinum* have an obviously much higher internal volume than those of other species. They are preferred by hermit crabs larger than 10.0 mm carapace width. The *Buccinum* shells used by crabs below this size were small, immature specimens.

On the basis of this admittedly small sample the gastropod species can be listed in order of the mean size (carapace width) of hermits occupying them. This is most usefully done for hermits below 10.0 mm carapace width (Table 2.10). It gives the order: *Buccinum undatum* ($\bar{X}$CW = 8.11 mm), *Natica catena* ($\bar{X}$CW = 6.6 mm), *Nassarius reticulatus* ($\bar{X}$CW = 5.0 mm), *Littorina littorea* ($\bar{X}$CW = 4.9 mm), *Nucella lapillus* ($\bar{X}$CW = 4.8 mm) and *Ocenebra erinacea* ($\bar{X}$CW = 4.5 mm).

The gastropod species utilized can also be listed in order of frequency of use (again limiting the survey to "small" specimens, i.e. below 10.0 mm carapace width) (Table 2.11). This gives a different order with preference being shown for the shells of *Littorina littorea* followed by, in order: *Buccinum undatum*, *Natica catena*, *Nucella lapillus*, *Nassarius reticulatus* and *Ocenebra erinacea.*

### 2.3.5 Activity monitored by a mark and recapture experiment

Results from the mark and recapture experiment carried out at 2.1 m above low tide level are presented in Table 2.12. Over a 1 day recovery period 6.4% (8) of marked hermit crabs were accounted for (recaptured) within the original square.

This experiment was conducted to determine the extent of movement of crabs within the pool over a short space of time. Of the total hermit crabs marked, 93.7% (117) were found outside the initial square metre of release. The great majority of the marked hermit crabs had migrated out of the original square within the 24 hour period. The greatest distance moved was 21 metres. Fifty percent of the crabs had moved 5 metres or more from the original square. The maximum distance that a marked released hermit crab was found to move in 1 day was around 15-20 metres (Fig. 2.23). These results indicate that this species is highly active and this behaviour must influence its distribution on the shore at this time of year (January 1983).

### 2.3.6 Commensal fauna

In the sublittoral samples 65.7% (205) of the total gastropod shells were covered by colonies of the hydroid *Hydractinia echinata*. The highest percentage of shells covered by this hydroid was from *Buccinum* and *Natica* shells (see Table 2.13).

The larger specimens of *P. bernhardus* often carry tube-building serpulid worms, *Pomatoceros triqueter*. About 25% of the gastropod shells were carrying these tube worms in and outside the shell. In a few cases the *Pomatoceros* tubes had completely encircled the mouth of the *Buccinum* shell in such a manner that the abdomen of the crab could not have moved without breaking the tube.

Table 2.13 shows that this tube worm was found in or on *Buccinum* shells only. 78 out of 255 (30.6%) *Buccinum* shells were carrying this tube worm.

The interior associates include the errant polychaete worm, *Nereis fucata*. My records made from the examination of 312 sublittoral gastropod shells occupied by *Pagurus bernhardus* show that the worm was only associated with *Buccinum* shells. 211 out of 255 (82.8%) of *Buccinum* shells were harbouring *N. fucata*. Occasionally two worms were found associated with the hermit crab *P. bernhardus* in the same *Buccinum* shell.

A total of 2086 intertidal gastropod shells occupied by the hermit crab *Pagurus bernhardus* collected from Mumbles Head during the period of studying were searched for associated fauna. 364 out of 1645 (22.13%) *Littorina littorea* shells were associated with the local rocky barnacles *Elminius modestus* and *Semibalanus balanoides*. No *Hydractinia echinata* were recorded during the examination, also no interior associates include *Nereis fucata*. Six out of the ten *Buccinum* shells found in the pool survey were also found to be associated with the errant polychaete worm *Nereis fucata*. The rest of the gastropod shells were found not associated with animals mentioned above or any other associated fauna (apart from parasites mentioned in the Appendix).

## 2.4 DISCUSSION

Previous workers have interpreted intertidal populations of *Pagurus bernhardus* as juveniles which eventually move to the sublittoral to become adult (Yonge, 1954; Wilson, 1935). The present study failed to confirm this simplistic explanation.

The rarity of large specimens intertidally appeared to be the result of a scarcity of large shells such as *Buccinum* on the shore. Live *Buccinum* live sublittorally and although their shells are sometimes washed ashore on stony beaches, those that were found at Mumbles were not only very few but were almost invariably damaged and often unsuitable for hermit occupation. It is not known how they were damaged, but they are comparatively fragile so might easily have been broken by predators such as gulls. Their large size and whitish colour make them very conspicuous on a beach such as that at Mumbles Head. A very small number of such damaged *Buccinum*, occupied by moderate sized hermits in the survey pool, occurred in the summer but none survived there in winter on the transect.

During the winter breeding season a few (16) male hermit-occupied *Buccinum* were found scattered over a very wide area. More significantly another 5 near LWST on the south side were each holding on to a smaller hermit-occupied gastropod. The fact that these twenty-one *Buccinum* were all near low water mark suggests they had entered the intertidal for mate-seeking purposes in spite of the risk from predators. During the following summer months (outside the breeding season) no such large male *P. bernhardus* occupying *Buccinum* shells could be found on the lower shore at the times of low water of spring tides, tending to corroborate the mate seeking interpretation above.

The absence of marked seasonal variation in the intertidal population (apart from recruitment) indicated lack of season migration or seasonal mass exodus of larger specimens. On the contrary the intertidal population was remarkably stable.

A further feature of this survey which argues against the simple concept of the intertidal as a nursery area is that when suitable fine mesh trawl netting was used, plentiful small *P. bernhardus* were caught offshore. Furthermore, analysis of these tended to indicate little interchange with the intertidal populations judging from the differences in colour, the fact that commensals such as *Hydractinia* were confined to the sublittoral collections and pattern of occupancy of *Littorina littorea* shells.

This last point needs further examination. It was observed (Fig. 2.18) that for a given size of *Littorina littorea* shell, a larger size of hermit occurred sublittorally than intertidally. In practice this means that for most of the intertidal specimens the hermit could retreat almost out of sight in the shell - often only the tips of the second and third pereopods being visible. In contrast, in the case of sublittoral *L. littorea* shells used, the major chela was often fully exposed at the shell mouth. This difference was independent of shell size. It is suggested here that this argues in favour of the action of bird predators during ebb tide. Waders such as the "turnstone" (*Arenaria interpres*) are usually present in flocks of 30 or more birds throughout the winter months at Mumbles - systematically foraging amongst the cobbles. *P. bernhardus* has been recorded in its stomach contents (Cramp

1983). An exposed chela could no doubt be seized easily by such a bird. Sublittoral predators such as fish or crabs would be less well adapted to prising out the hermit.

Thus on balance it seems unlikely that there is a mass movement of *P. bernhardus* occupying winkle shells between the littoral and sublittoral.

### Autotomy

As in any other decapod Crustacea, the hermit crab, *P. bernhardus*, is able to shed any of its limbs. In general there were more hermit crabs with missing chelae than missing walking legs. During the year of study at Mumbles Head, the data (Table 2.5) show the highest incidence of autotomy in November 1982, the month in which highest numbers of hermit crabs were collected (Fig. 2.19). The possibility of encounters and interference between hermit crabs increases with higher density, particularly during shell fighting when they show their aggressive behaviour (Hazlett, 1981). Use of their chelae in fighting makes them more vulnerable to damage than the walking limbs. But the possibility of attack by bird predators is an alternative explanation.

### Density in small quadrat

Mention needs to be made of the high density recorded in the special quadrats (see section 2.3.1.1ii). These were placed to record exceptionally high densities. It seemed likely that clustering of the crab recorded and discussed by Snyder-Conn (1980, 1981) was involved in certain rock pools at Mumbles.

The significance of the slight differences in sex ratio were not satisfactorily interpreted. The slight deficiency of females intertidally cannot be because of retreat of breeders to the sublittoral since most of the intertidal females were fully breeding anyway.

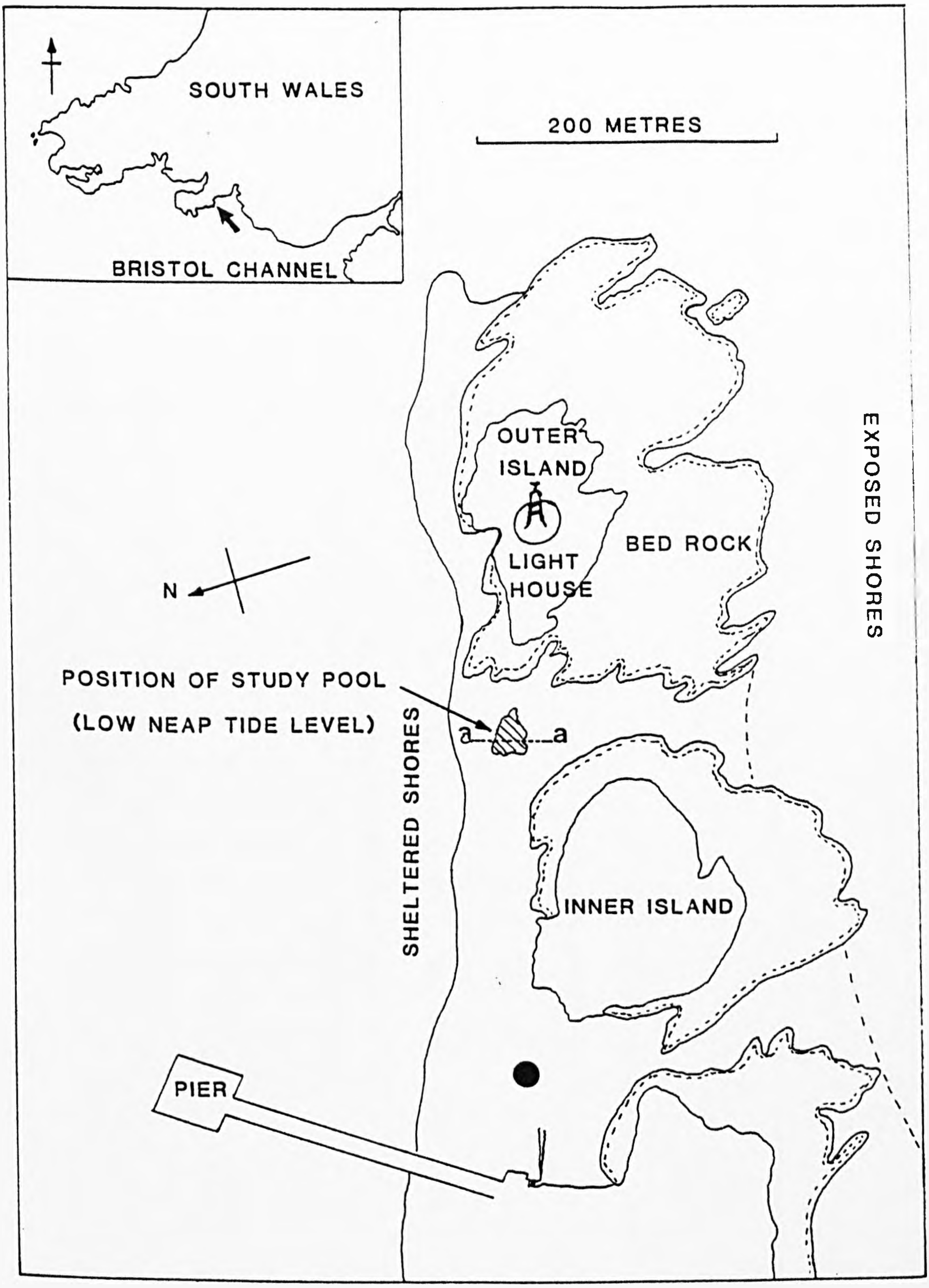
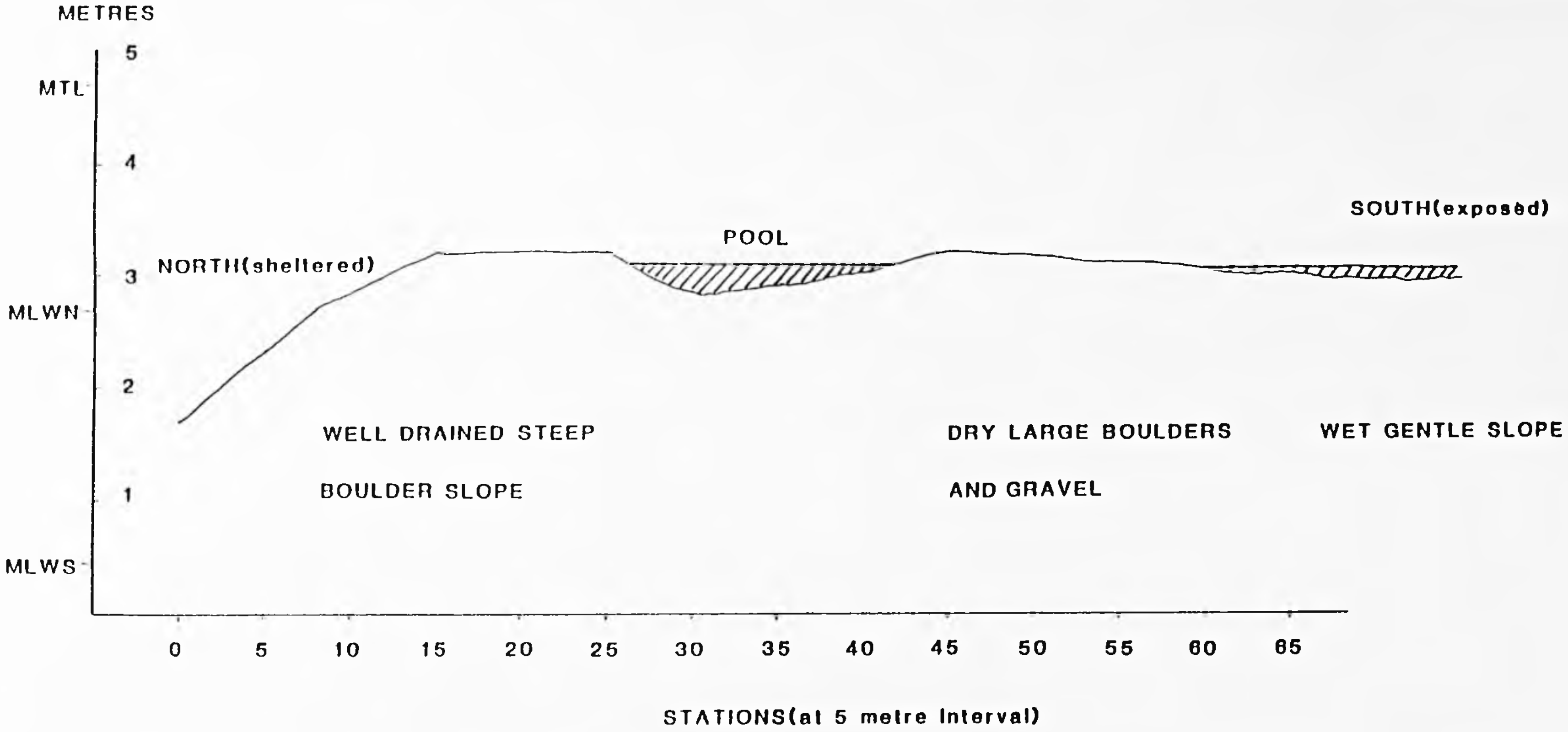

SOUTH WALES
BRISTOL CHANNEL
200 METRES
OUTER ISLAND
LIGHT HOUSE
BED ROCK
EXPOSED SHORES
N
POSITION OF STUDY POOL
(LOW NEAP TIDE LEVEL)
a
a
SHELTERED SHORES
INNER ISLAND
PIER

Figure 2.1

Map showing location of *Pagurus bernhardus* study areas at Mumbles Head; a---a transect, dark circle marks quadrat site.


METRES
5
MTL
4
3
MLWN
2
1
MLWS
NORTH(sheltered)
POOL
SOUTH(exposed)
WELL DRAINED STEEP
BOULDER SLOPE
DRY LARGE BOULDERS
AND GRAVEL
WET GENTLE SLOPE
0
5
10
15
20
25
30
35
40
45
50
55
60
65
STATIONS(at 5 metre interval)

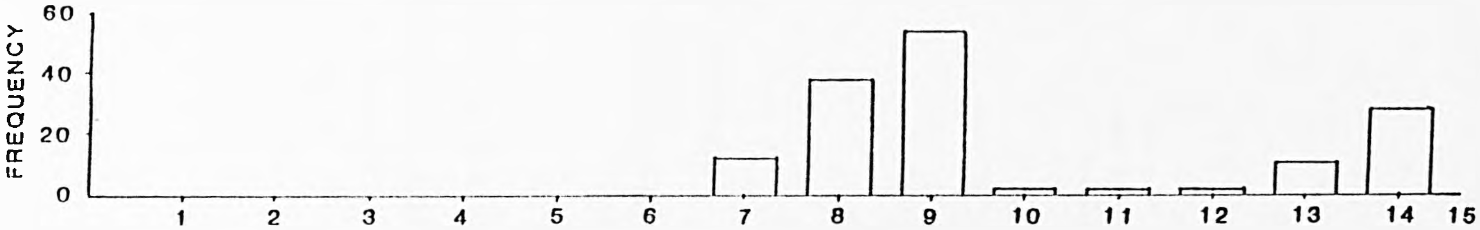

FREQUENCY
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Figure 2.2

Transect survey at a---a (see Fig. 2.1). Shore profile (above) and bar graph of hermit crab abundance.

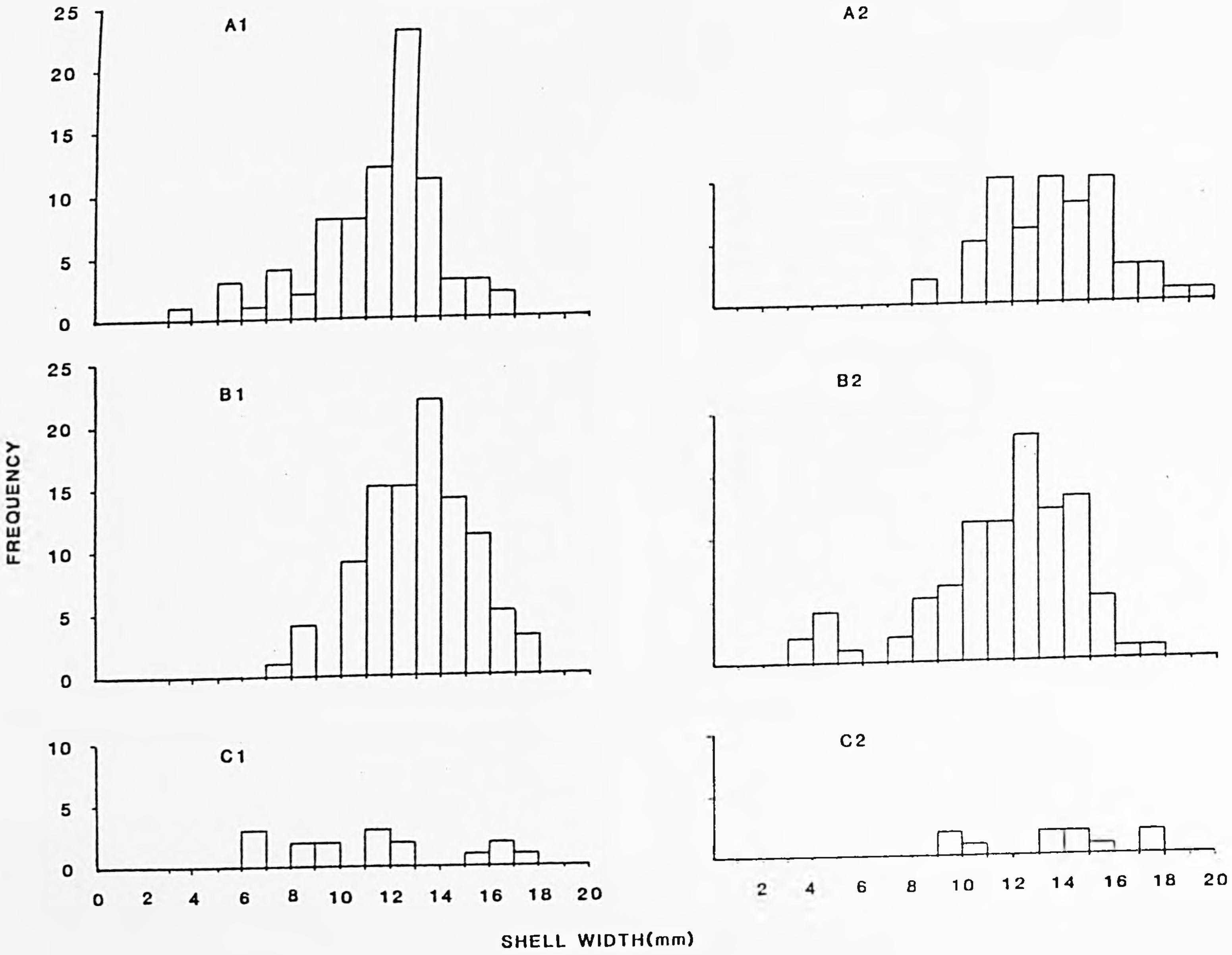

A1
A2
B1
B2
C1
C2
25
20
15
10
5
0
FREQUENCY
0 2 4 6 8 10 12 14 16 18 20
2 4 6 8 10 12 14 16 18 20
SHELL WIDTH(mm)

Figure 2.3

Occupancy of *Littorina littorea* shell from pool at Mumbles Head (black circle, Fig. 2.1). Two counts (1 & 2) from 0.25 $m^2$ quadrats.

A = *Littorina littorea* shells still containing live winkles

B = *L. littorea* shells occupied by *Pagurus bernhardus*

C = *L. littorea* shells unoccupied

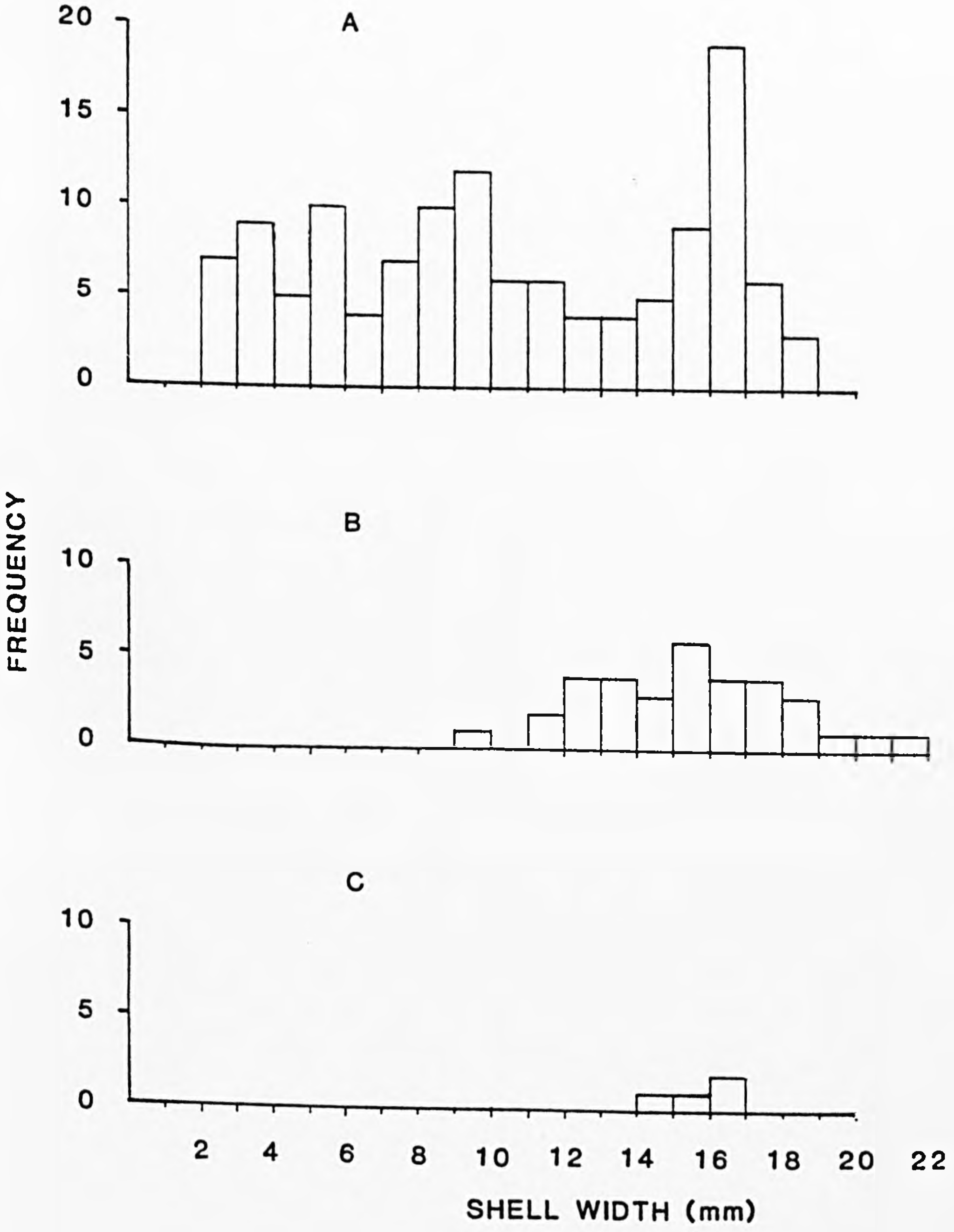

A
20
15
10
5
0
B
10
5
0
C
10
5
0
FREQUENCY
2
4
6
8
10
12
14
16
18
20
22
SHELL WIDTH (mm)

Figure 2.4

Occupancy of *Littorina littorea* shells from the edge of the main pool sampling site at Mumbles Head. Counts from 0.25 $m^2$ quadrat.

A = *Littorina littorea* shells still containing live winkles
B = *L. littorea* shells occupied by *Pagurus bernhardus*
C = *L. littorea* shells unoccupied

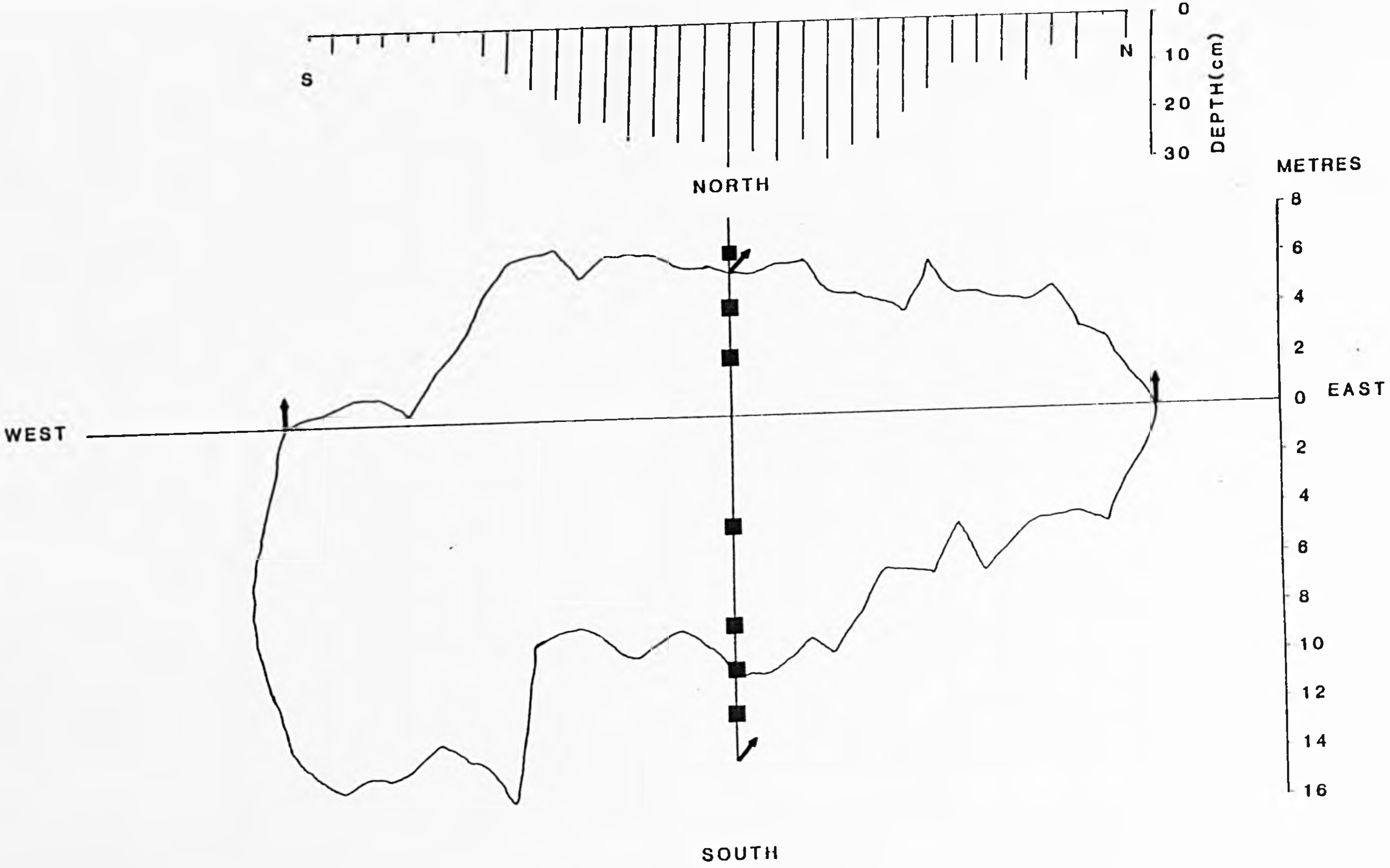

0
10
20
30
DEPTH(cm)
S
N
METRES
NORTH
WEST
EAST
SOUTH
8
6
4
2
0
2
4
6
8
10
12
14
16

Figure 2.5

Diagram of survey pool showing 1) its main outline, 2) the position of transect line across the pool (north to south) and 3) the depth profile by centimetres.

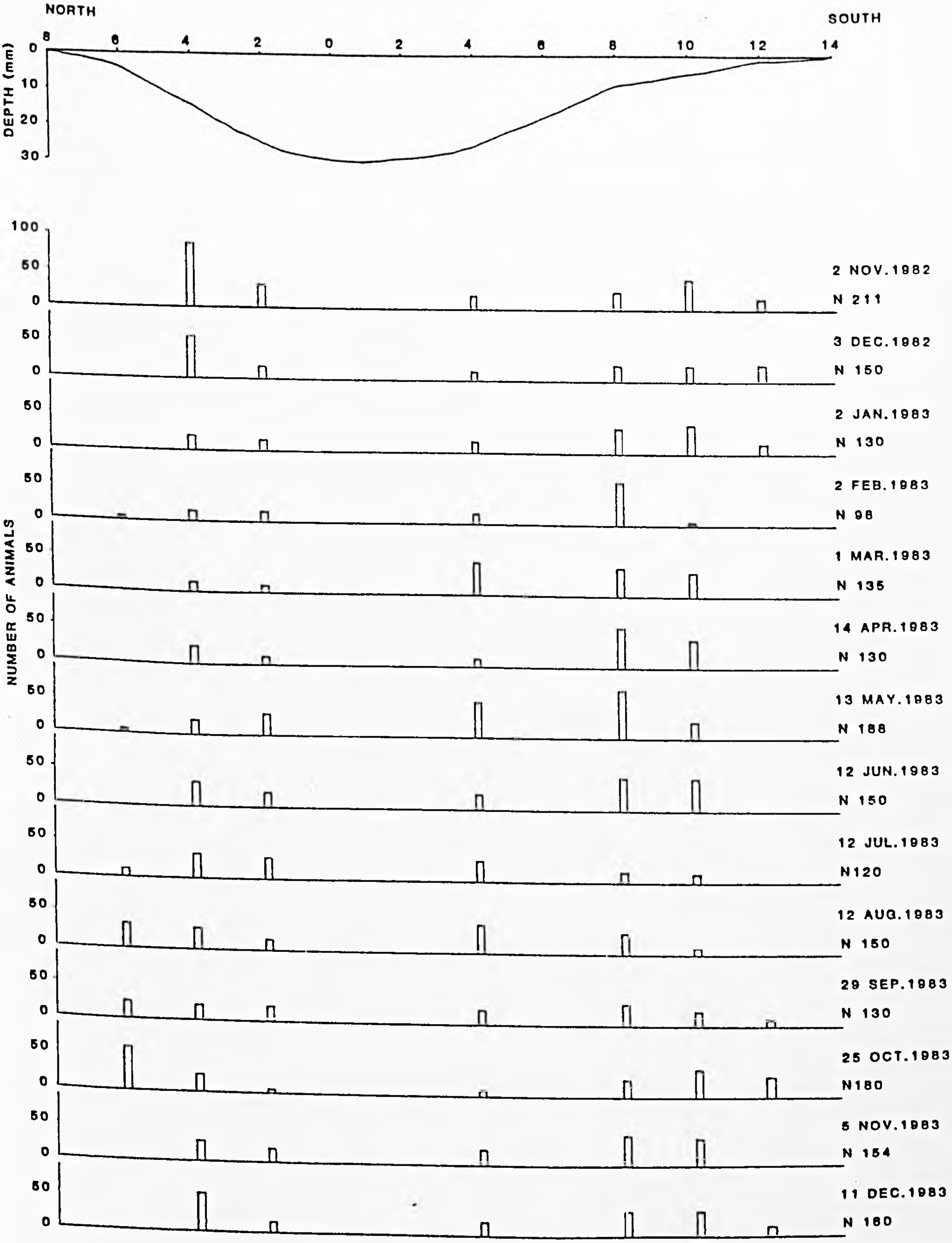

NORTH
SOUTH
8
6
4
2
0
2
4
6
8
10
12
14
DEPTH (mm)
0
10
20
30
NUMBER OF ANIMALS
100
50
0
2 NOV.1982
N 211
3 DEC.1982
N 150
2 JAN.1983
N 130
2 FEB.1983
N 98
1 MAR.1983
N 135
14 APR.1983
N 130
13 MAY.1983
N 188
12 JUN.1983
N 150
12 JUL.1983
N120
12 AUG.1983
N 150
29 SEP.1983
N 130
25 OCT.1983
N180
5 NOV.1983
N 154
11 DEC.1983
N 160

Figure 2.6

Results of monthly sampling of *Pagurus bernhardus* along the fixed transect line across intertidal pool at Mumbles Head, Swansea. Pool profile shown above (see also Figs. 2.1, 2.2 and 2.5).

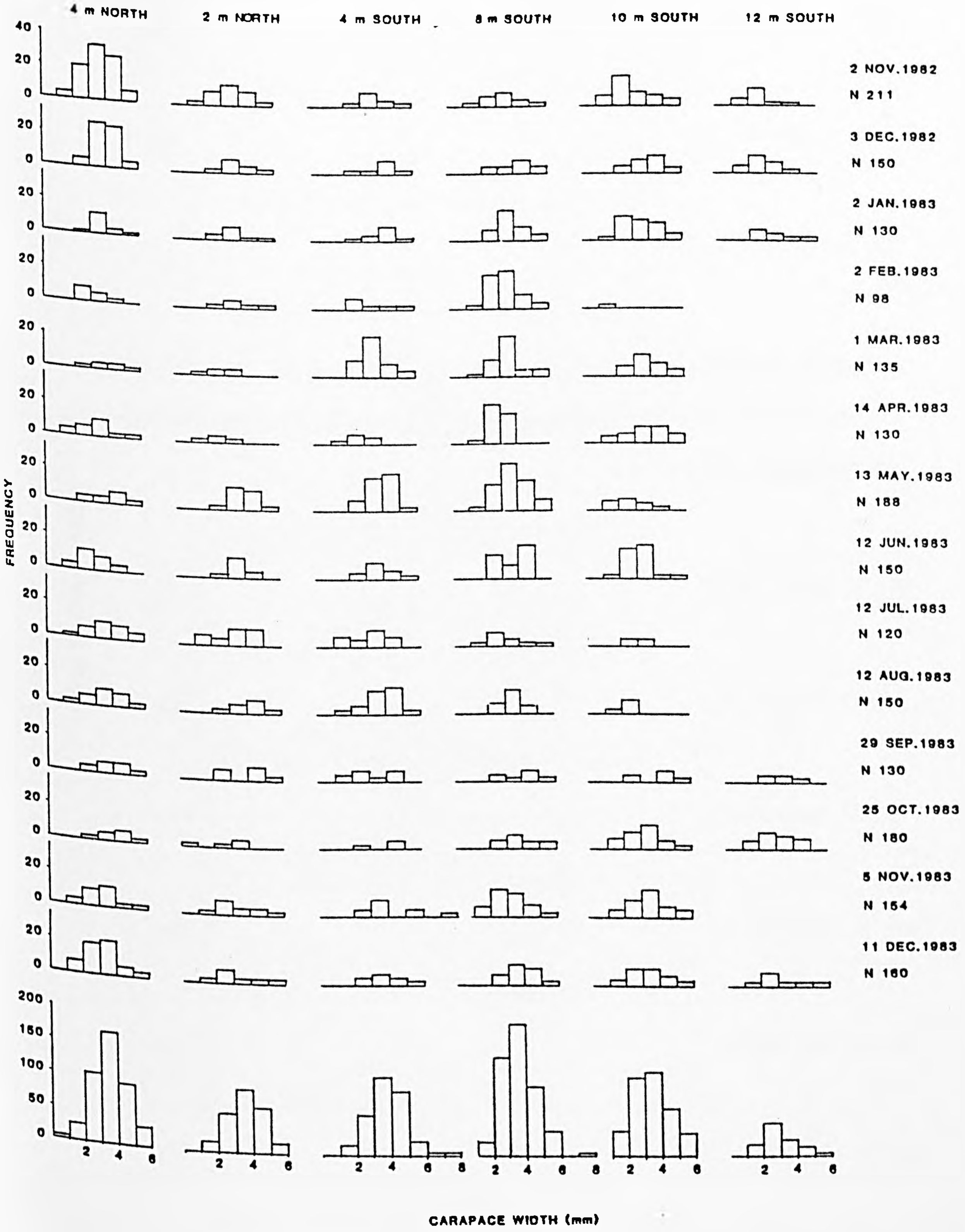

4 m NORTH
2 m NORTH
4 m SOUTH
8 m SOUTH
10 m SOUTH
12 m SOUTH
FREQUENCY
40
20
0
200
150
100
50
2 NOV.1982
N 211
3 DEC.1982
N 150
2 JAN.1983
N 130
2 FEB.1983
N 98
1 MAR.1983
N 135
14 APR.1983
N 130
13 MAY.1983
N 188
12 JUN.1983
N 150
12 JUL.1983
N 120
12 AUG.1983
N 150
29 SEP.1983
N 130
25 OCT.1983
N 180
5 NOV.1983
N 154
11 DEC.1983
N 160
2
4
6
8
CARAPACE WIDTH (mm)

Figure 2.7

Monthly size frequency histograms of *P. bernhardus* along transect (Fig. 2.5) across study pool. Bottom histogram showing the total of hermit crabs in each quadrat during sampling period.

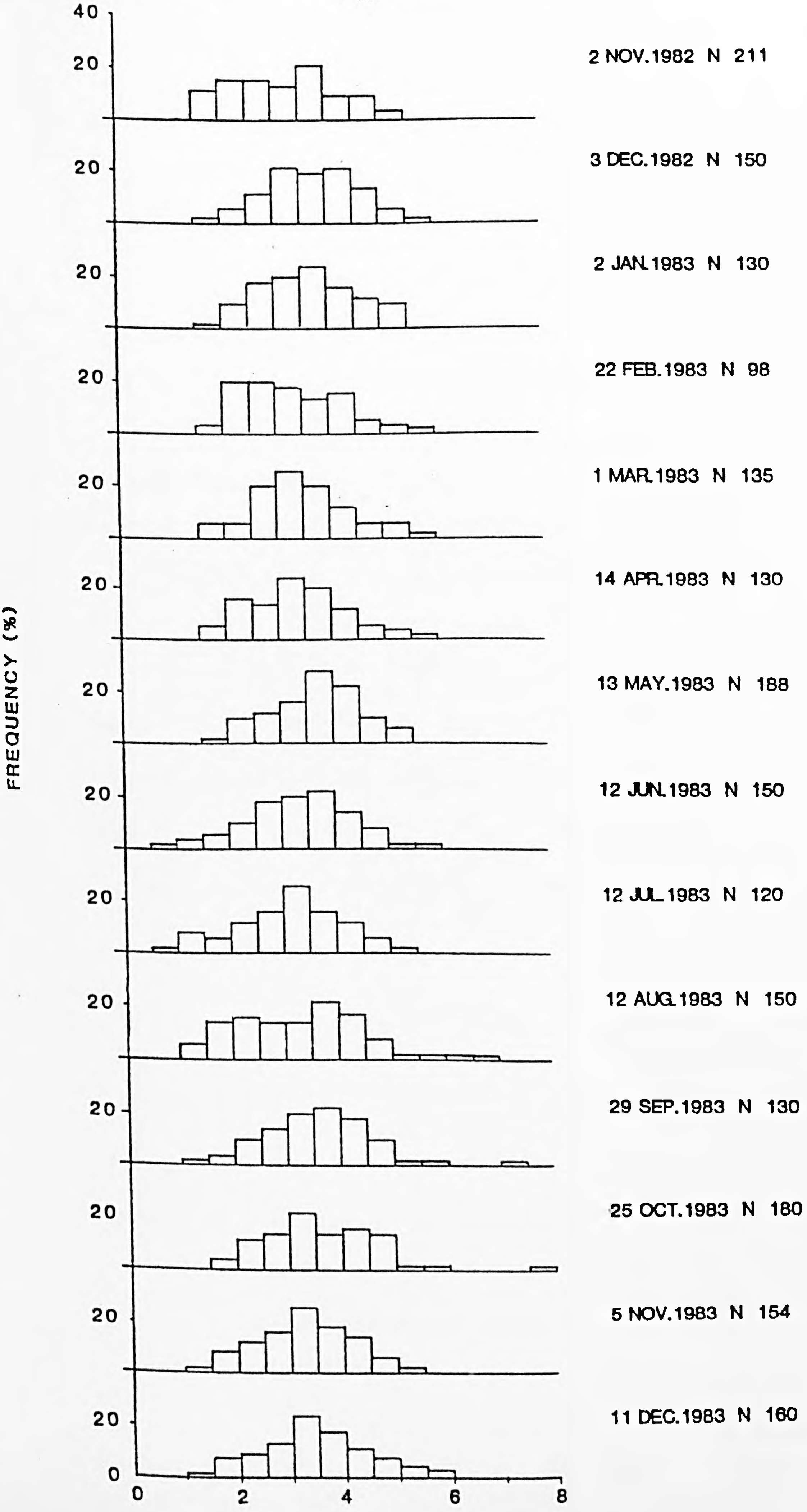

40
20
2 NOV.1982 N 211
20
3 DEC.1982 N 150
20
2 JAN.1983 N 130
20
22 FEB.1983 N 98
20
1 MAR.1983 N 135
20
14 APR.1983 N 130
20
13 MAY.1983 N 188
20
12 JUN.1983 N 150
20
12 JUL.1983 N 120
20
12 AUG.1983 N 150
20
29 SEP.1983 N 130
20
25 OCT.1983 N 180
20
5 NOV.1983 N 154
20
11 DEC.1983 N 160
0
FREQUENCY (%)
0
2
4
6
8

Figure 2.8

*Pagurus bernhardus*. Size frequency histograms of total hermits from monthly samples collected from pool transect at Mumbles Head during 1982-1983.

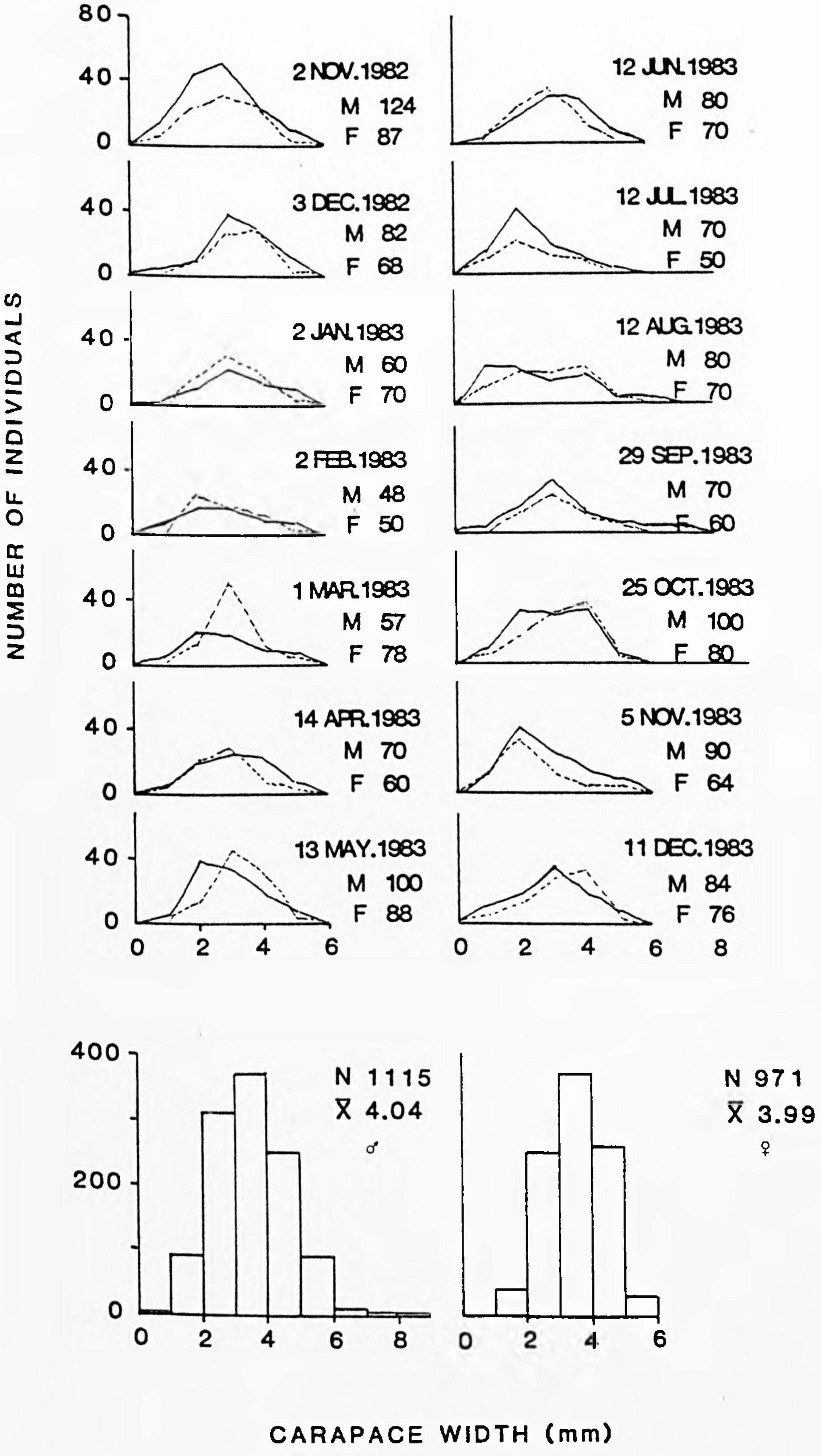

NUMBER OF INDIVIDUALS
80
40
0
2 NOV.1982
M 124
F 87
12 JUN.1983
M 80
F 70
3 DEC.1982
M 82
F 68
12 JUL.1983
M 70
F 50
2 JAN.1983
M 60
F 70
12 AUG.1983
M 80
F 70
2 FEB.1983
M 48
F 50
29 SEP.1983
M 70
F 60
1 MAR.1983
M 57
F 78
25 OCT.1983
M 100
F 80
14 APR.1983
M 70
F 60
5 NOV.1983
M 90
F 64
13 MAY.1983
M 100
F 88
11 DEC.1983
M 84
F 76
0
2
4
6
8
400
200
0
N 1115
X̄ 4.04
♂
N 971
X̄ 3.99
♀
CARAPACE WIDTH (mm)

Figure 2.9

*Pagurus bernhardus*. 1) Graphs of size groups of males and females shown separately from pool survey, and 2) histogram of total males and females for whole 14 month study.

——— males

- - - females

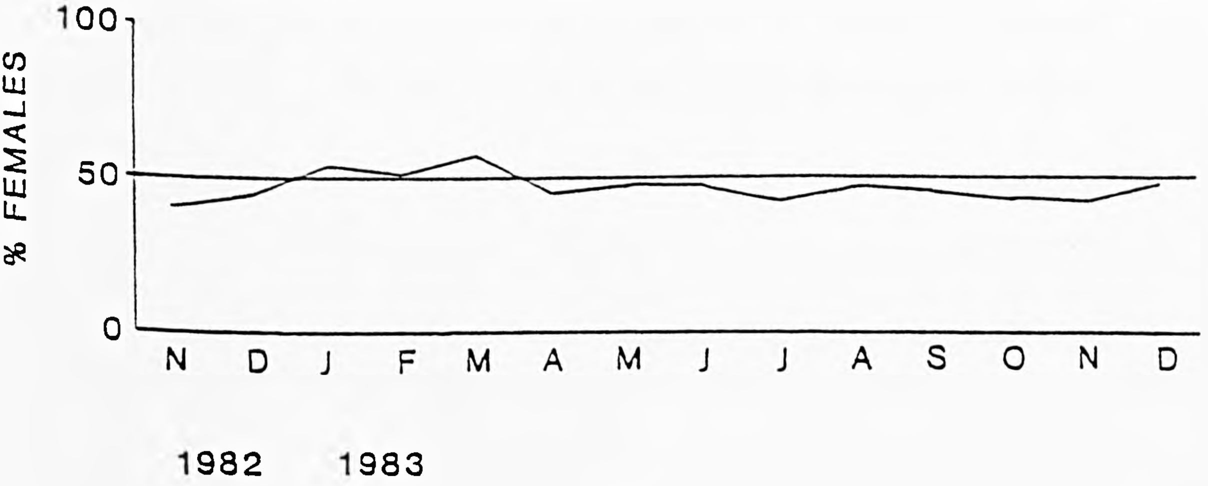

% FEMALES
100
50
0
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1982
1983

Figure 2.10

Sex ratio (% females) of *Pagurus bernhardus* from Mumbles Head.


MEAN CARAPACE WIDTH(mm)
0
2
4
N
D
J
F
M
A
M
J
J
A
S
O
N
D

Figure 2.11

Monthly variation in the mean carapace width of male and female *Pagurus bernhardus* at Mumbles Head.

▲ - females

● - males

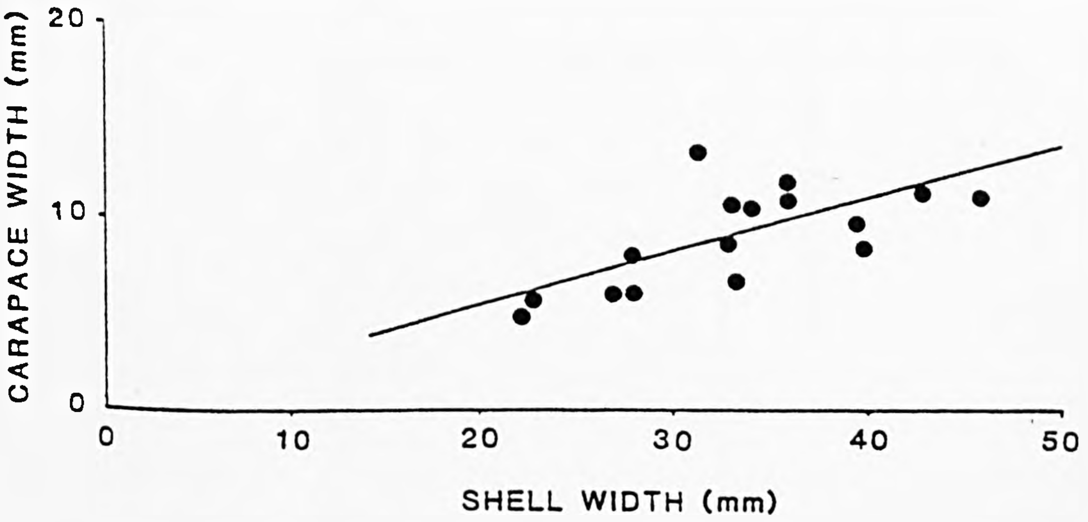

CARAPACE WIDTH (mm)
0
10
20
0
10
20
30
40
50
SHELL WIDTH (mm)

Figure 2.12

Intertidal *Pagurus bernhardus* occupying *Buccinum undatum* shells. Collected near low water February 1987. Every specimen was male, with calculated regression line.

$$y = 0.267x + 0.06;\ r = 0.692$$

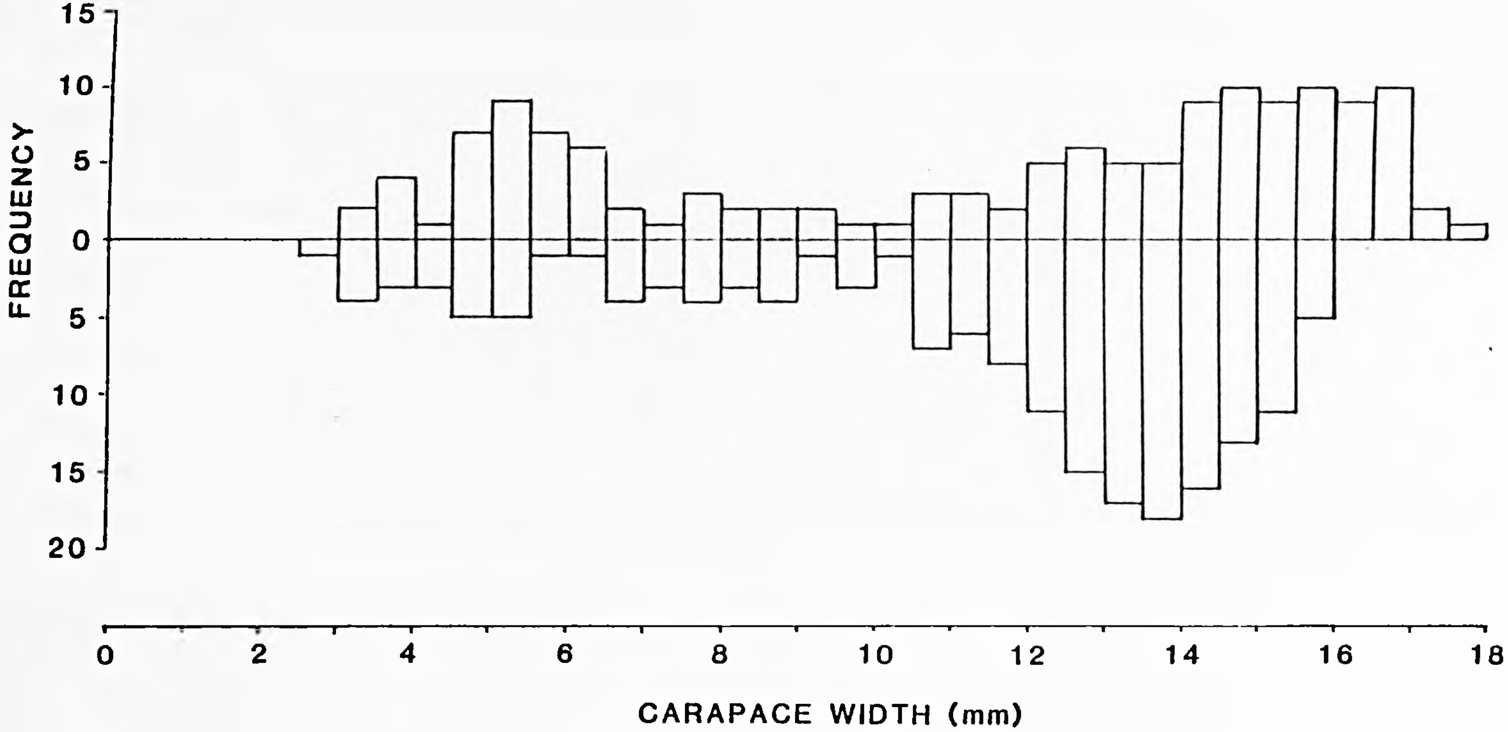

FREQUENCY
15
10
5
0
5
10
15
20
0
2
4
6
8
10
12
14
16
18
CARAPACE WIDTH (mm)

Figure 2.13

Size frequency distribution of sublittoral *Pagurus bernhardus* sampled between October 1982 and February, March and April 1983. Males above the axis and females below.

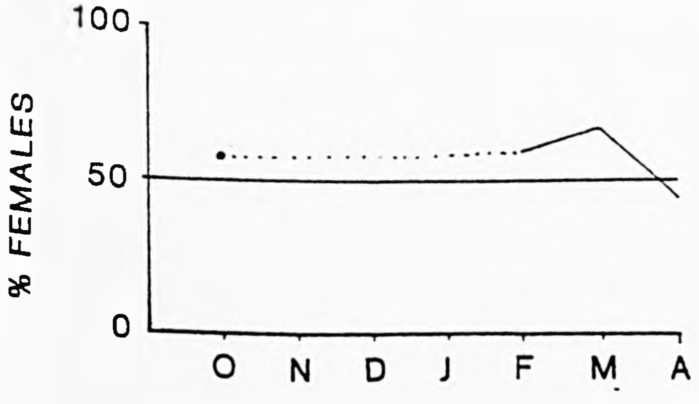

% FEMALES
100
50
0
O
N
D
J
F
M
A

Figure 2.14

Sex-ratio (% females) of *Pagurus bernhardus* from sublittoral samples.

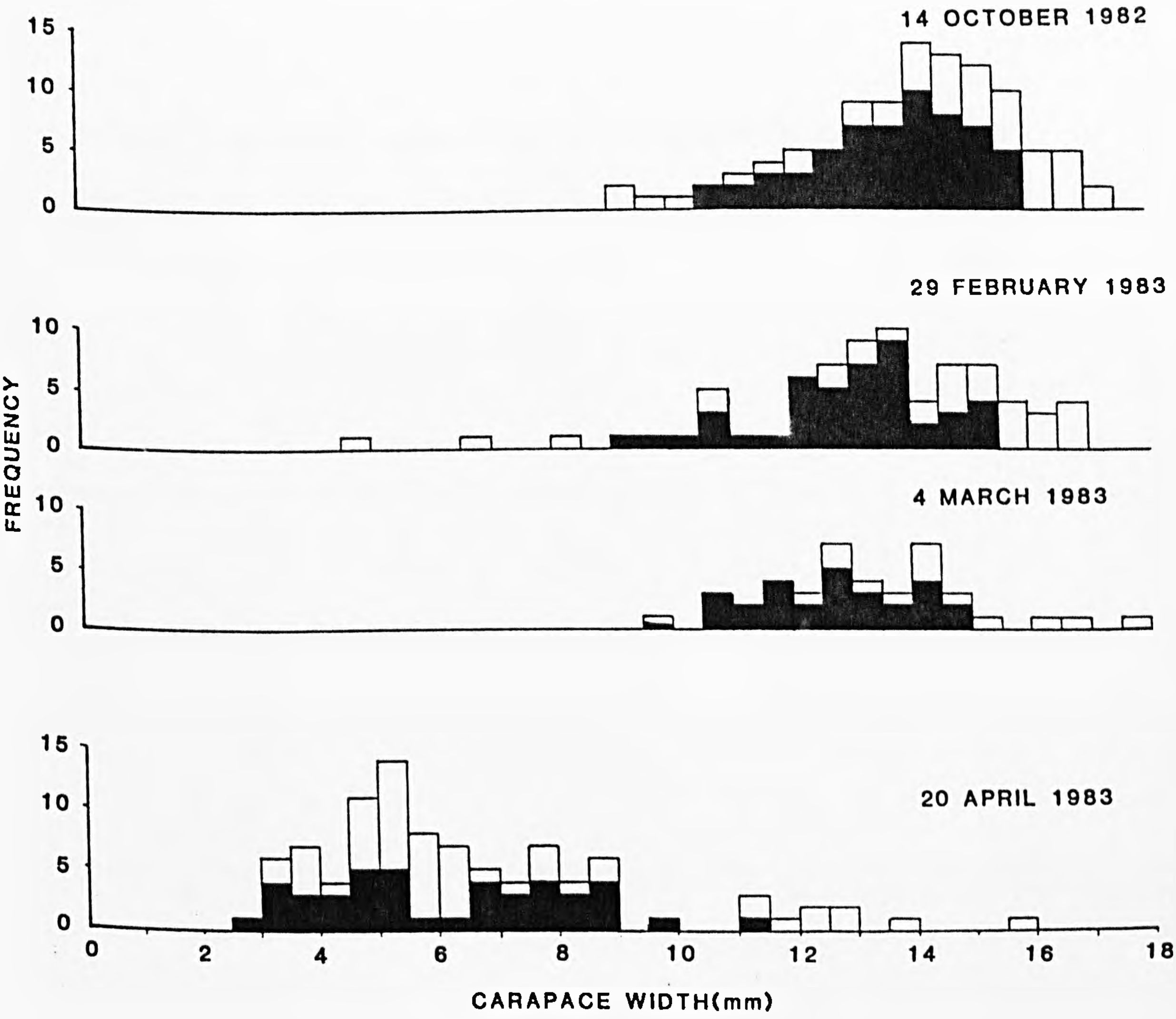

14 OCTOBER 1982
29 FEBRUARY 1983
4 MARCH 1983
20 APRIL 1983
FREQUENCY
15
10
5
0
0
2
4
6
8
10
12
14
16
18
CARAPACE WIDTH(mm)

Figure 2.15

Size frequency distribution of the few separate sublittoral sampling of *Pagurus bernhardus* at Oxwich Bay. Females in black.

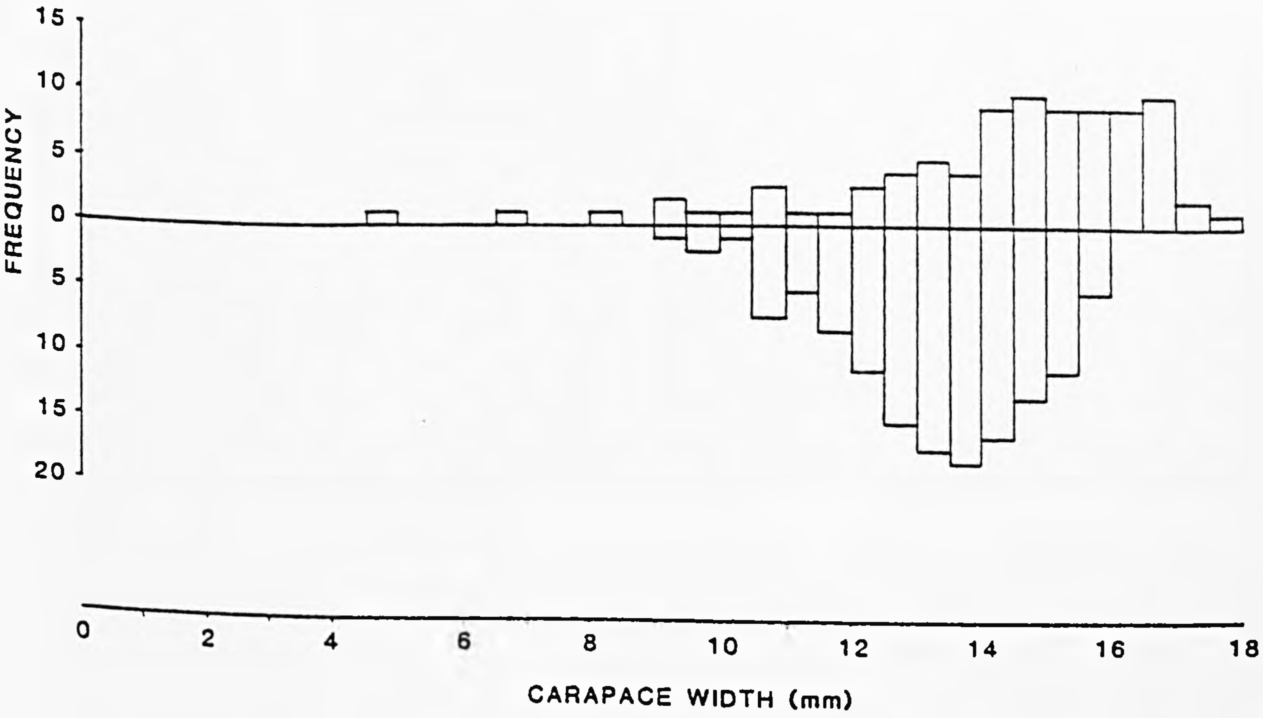

15
10
5
0
5
10
15
20
FREQUENCY
0
2
4
6
8
10
12
14
16
18
CARAPACE WIDTH (mm)

Figure 2.16

Size frequency distribution of first three sublittoral samples of *Pagurus bernhardus* combined. Males above axis and females below.

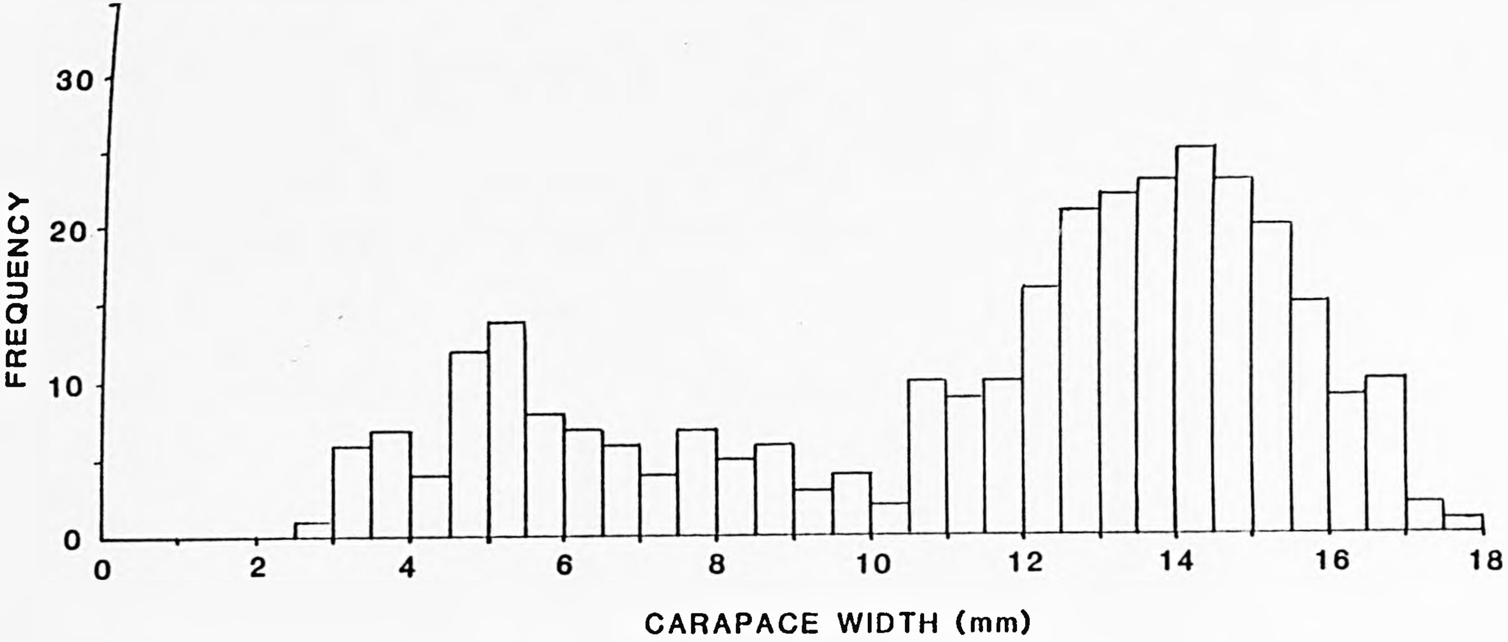

30
20
10
0
FREQUENCY
0
2
4
6
8
10
12
14
16
18
CARAPACE WIDTH (mm)

Figure 2.17

Size frequency of total *Pagurus bernhardus* collected in the sublittoral zone during the period of sampling.

N = 312.

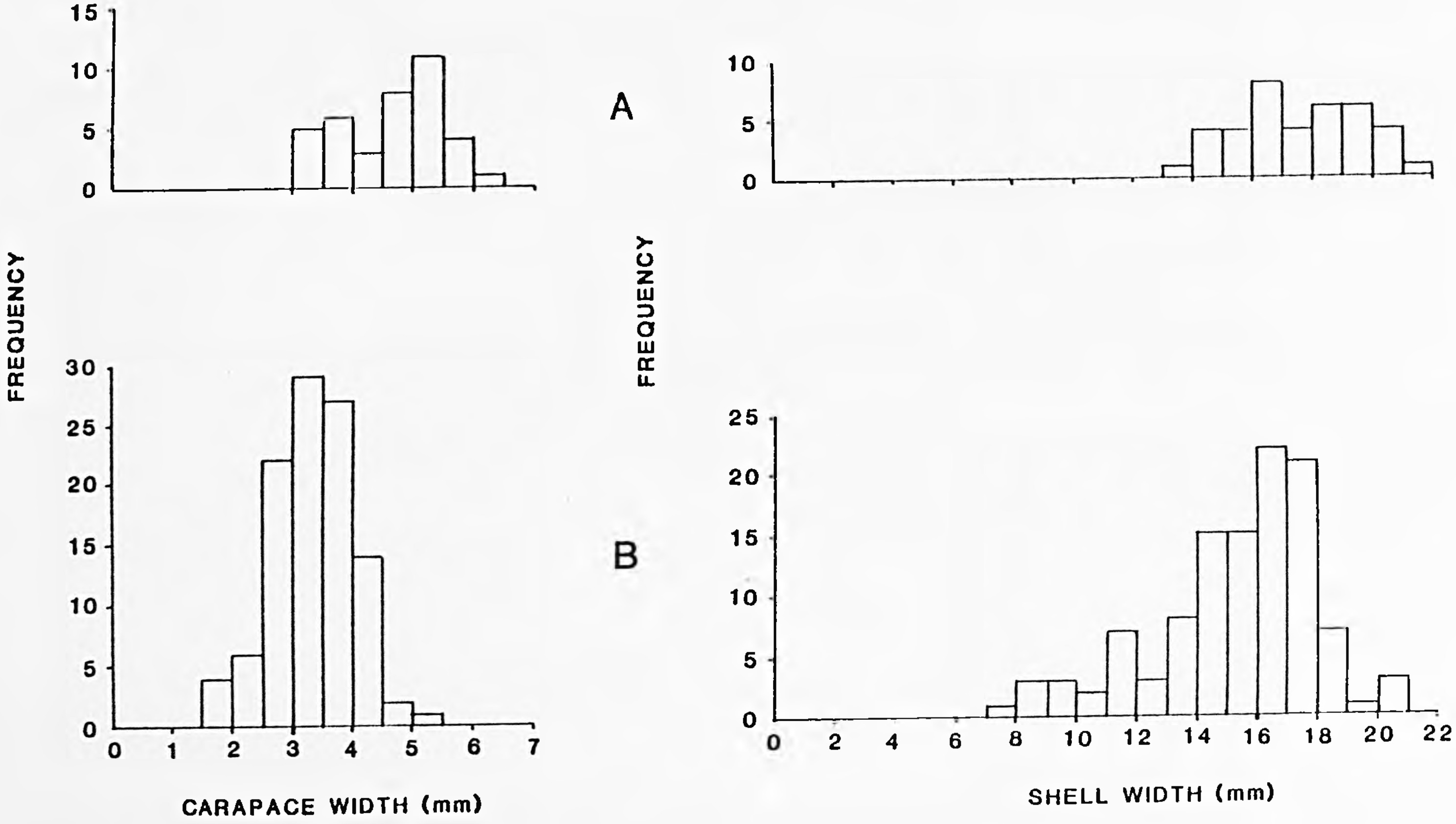

A
B
FREQUENCY
FREQUENCY
15
10
5
0
30
25
20
15
10
5
0
0 1 2 3 4 5 6 7
CARAPACE WIDTH (mm)
10
5
0
25
20
15
10
5
0
0 2 4 6 8 10 12 14 16 18 20 22
SHELL WIDTH (mm)

Figure 2.18

*Pagurus bernhardus* occupying *Littorina littorea* shells.

Comparison of littoral and sublittoral samples.

A = sublittoral

B = littoral

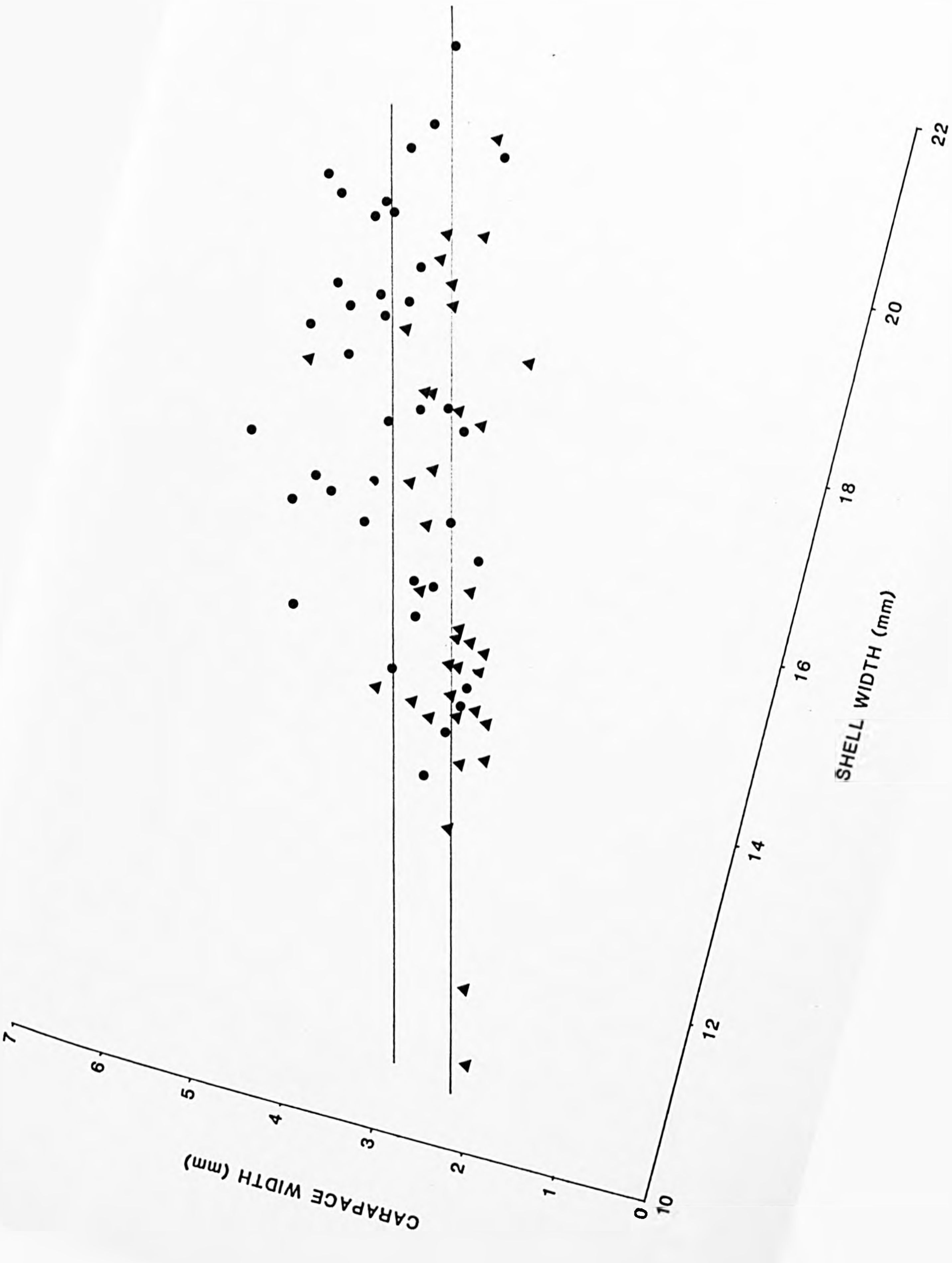
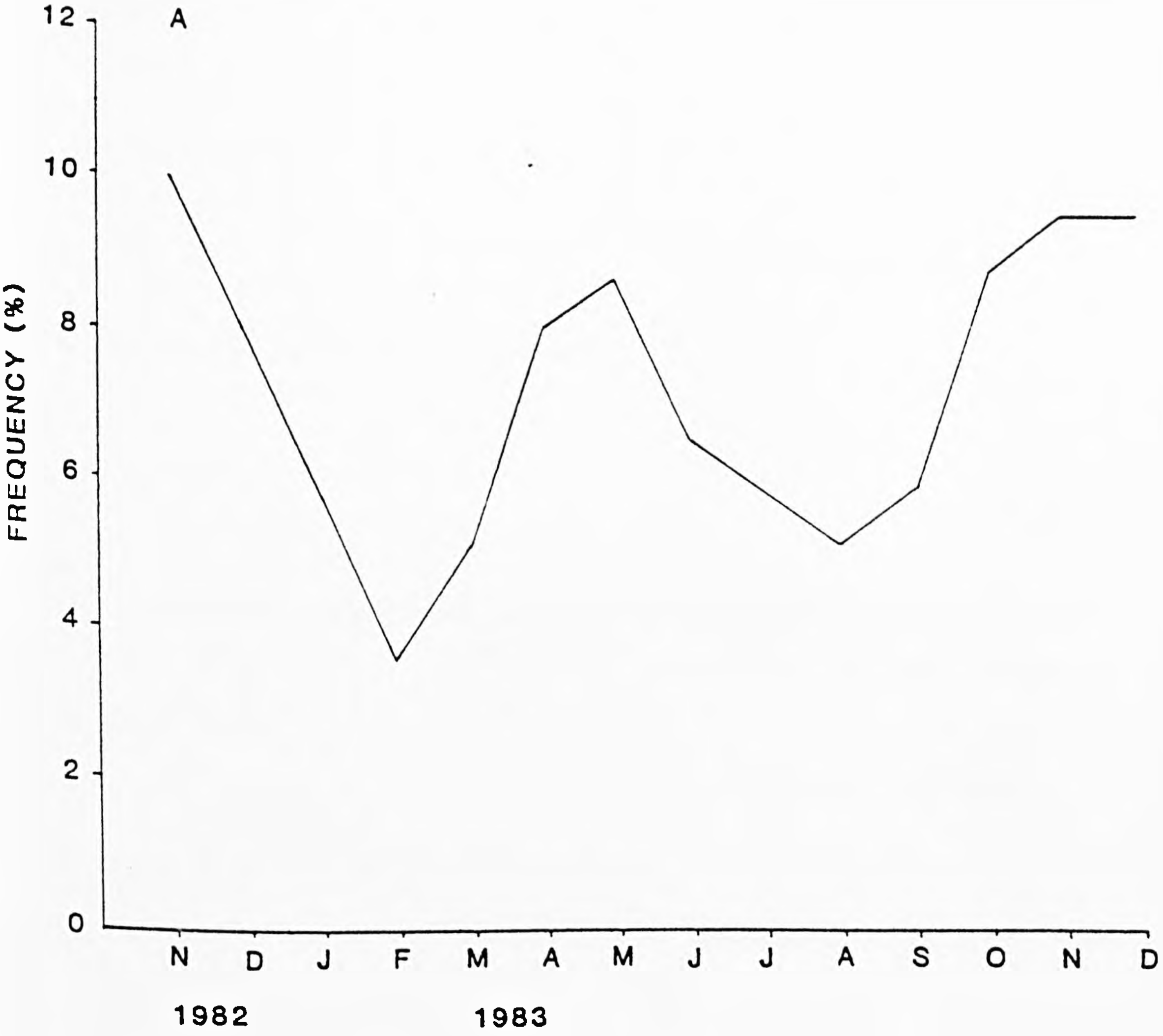

CARAPACE WIDTH (mm)
0
1
2
3
4
5
6
7
SHELL WIDTH (mm)
10
12
14
16
18
20
22

Figure 2.19

*Pagurus bernhardus*. Relationship between carapace width and size of the shell of *Littorina littorea*, with calculated regression lines.

▲ *L. littorea* (littoral) $y = 0.255x + 0.241$; $r = 0.603$

● *L. littorea* (sublittoral) $y = 0.251x + 0.364$; $r = 0.802$


A
FREQUENCY (%)
0
2
4
6
8
10
12
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1982
1983

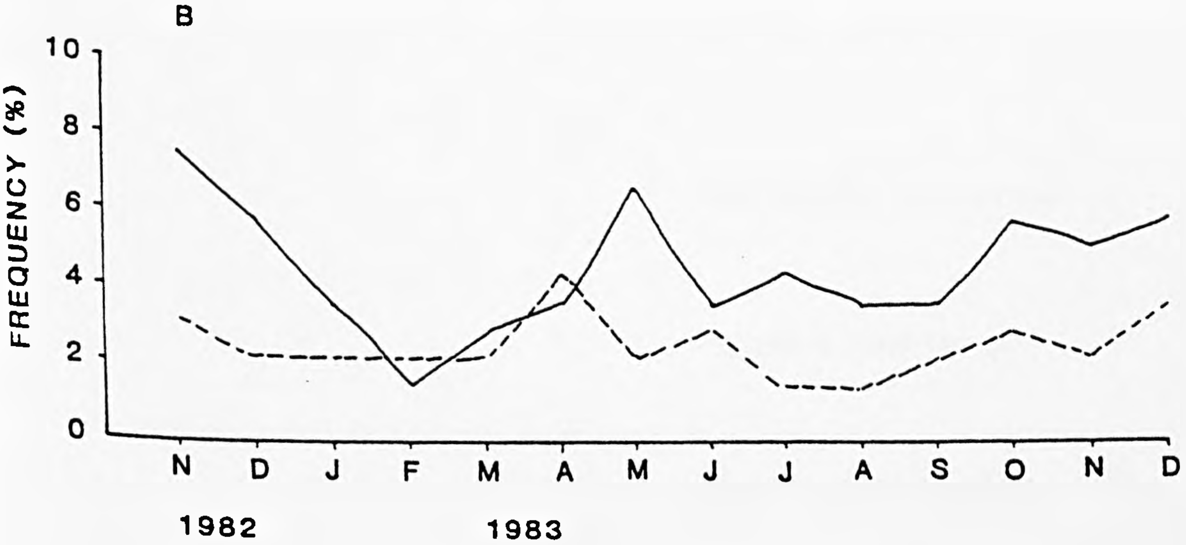

B
FREQUENCY (%)
0
2
4
6
8
10
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1982
1983

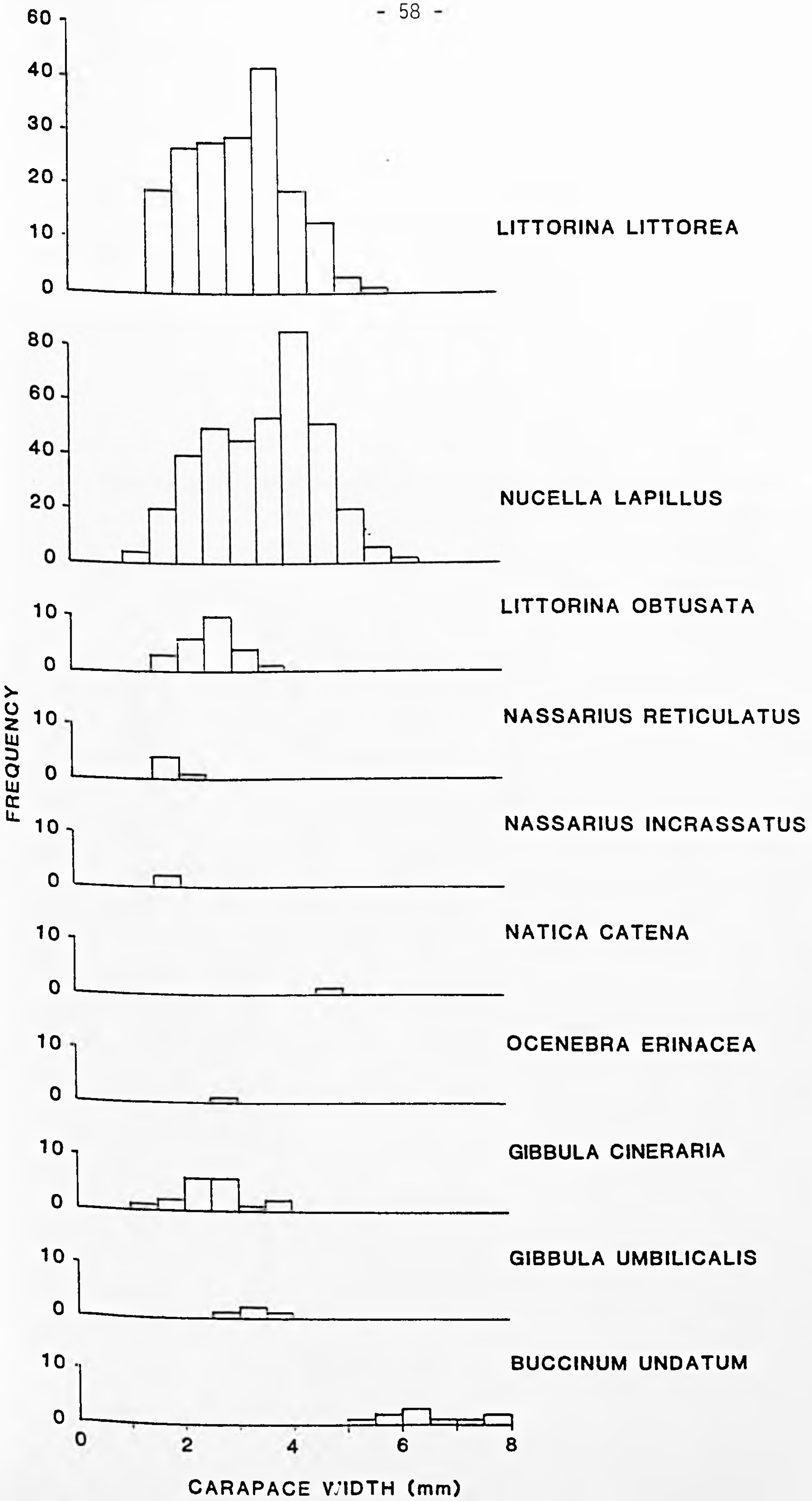
Figure 2.20

A. Percentage of hermit crabs with missing chelae.

B. Percentage of hermit crabs with missing chelae; sexes shown separately.

——— males

- - - females



60
40
30
20
10
0
LITTORINA LITTOREA
80
60
40
20
0
NUCELLA LAPILLUS
10
0
LITTORINA OBTUSATA
10
0
NASSARIUS RETICULATUS
10
0
NASSARIUS INCRASSATUS
10
0
NATICA CATENA
10
0
OCENEBRA ERINACEA
10
0
GIBBULA CINERARIA
10
0
GIBBULA UMBILICALIS
10
0
BUCCINUM UNDATUM
FREQUENCY
0
2
4
6
8
CARAPACE WIDTH (mm)

Figure 2.21

Size frequency distribution of *Pagurus bernhardus* occupying littoral gastropod shells.

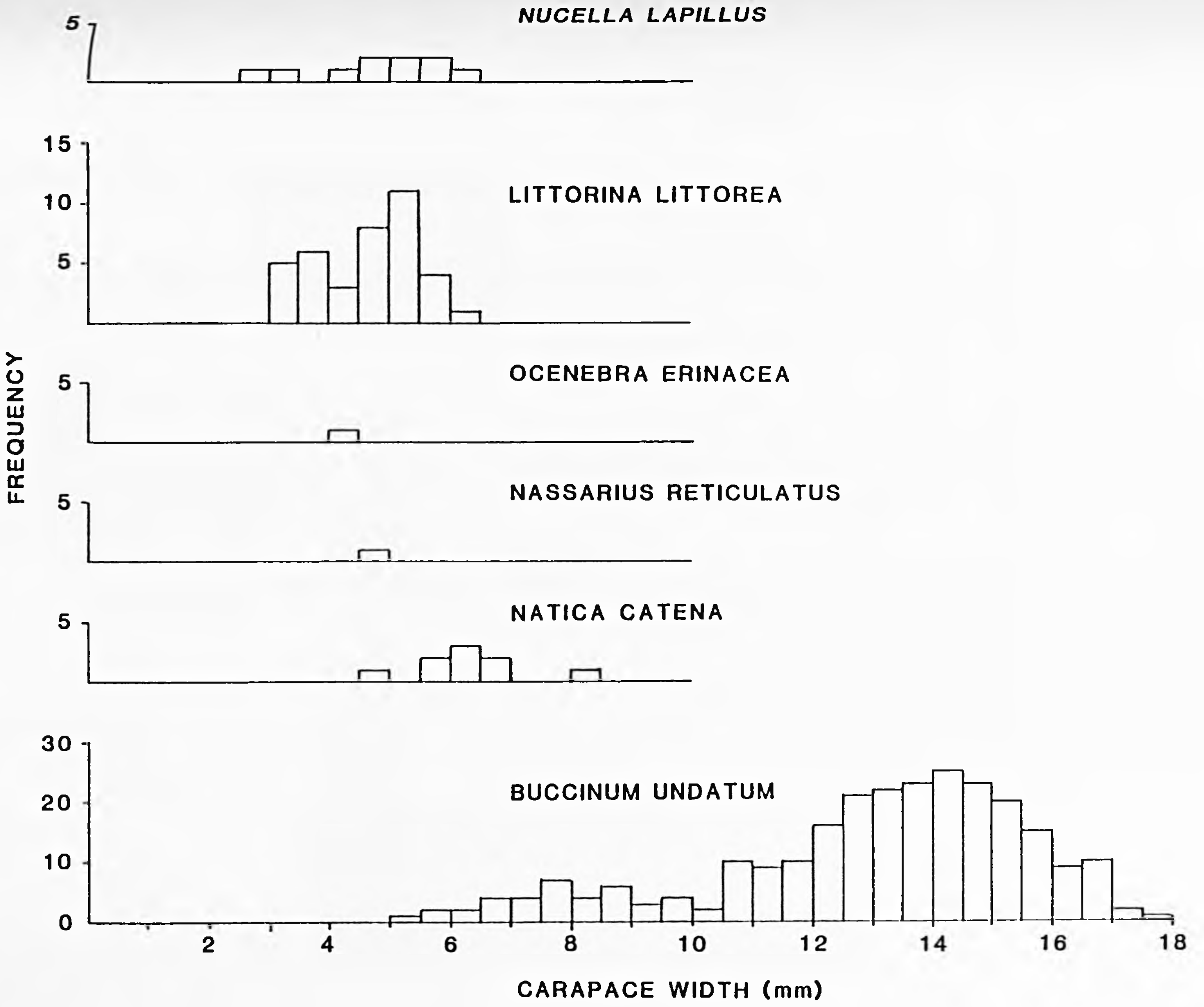

NUCELLA LAPILLUS
5
15
10
5
LITTORINA LITTOREA
FREQUENCY
5
OCENEBRA ERINACEA
5
NASSARIUS RETICULATUS
5
NATICA CATENA
30
20
10
0
BUCCINUM UNDATUM
2
4
6
8
10
12
14
16
18
CARAPACE WIDTH (mm)

Figure 2.22

Size distribution of *Pagurus bernhardus* occupying sublittoral gastropod shells.

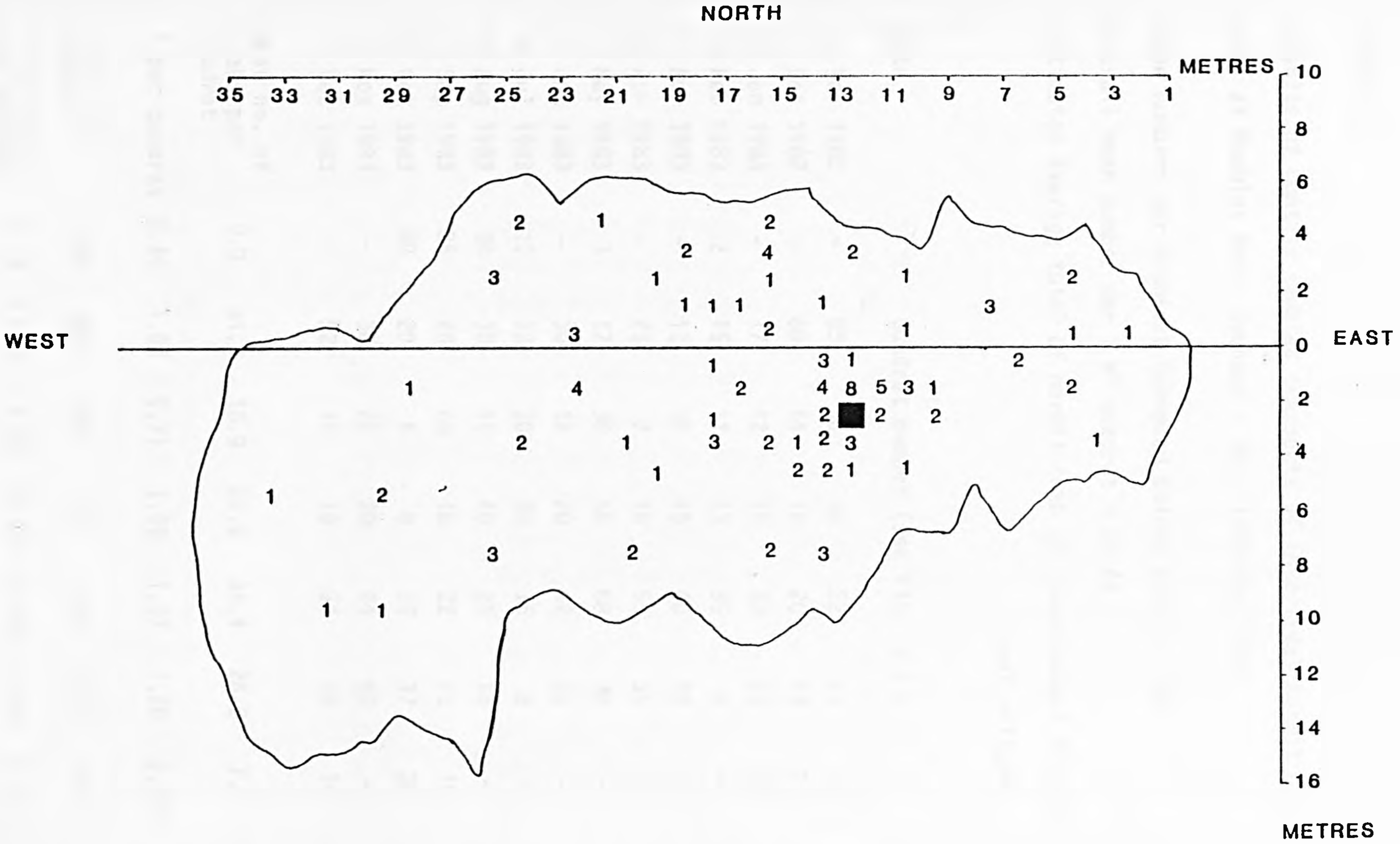

NORTH
METRES
35 33 31 29 27 25 23 21 19 17 15 13 11 9 7 5 3 1
10 8 6 4 2 0 2 4 6 8 10 12 14 16
METRES
WEST
EAST
2 1 2
2 4 2
3 1 1 1 2
1 1 1 1 3
3 2 1 1 1
1 3 1 2
1 4 2 4 8 5 3 1 2
1 2 2 2
2 1 3 2 1 2 3 1
1 2 2 1 1
1 2
3 2 2 3
1 1

Figure 2.23

Map of survey pool at Mumbles Head, showing results of mark-recapture experiment. Filled square indicates position of capture and release of marked individuals. Numbers indicate recapture square 24 hrs later.

Table 2.1

Results of monthly sampled transects of intertidal hermit crabs in pool at Mumbles Head, Swansea - Nov. 1982-Dec. 1983

Mean numbers per transect (sampled points only) = 149

Overall mean number per 1 $m^2$ quadrat = 25.44

Estimated average total of hermit crab (*P. bernhardus*) in whole pool = 11,601

| Date | Quadrat number (see Fig. 2.7 ) | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| 2 Nov 1982 | - | 85 | 30 | 16 | 22 | 41 | 17 | 211 |
| 3 Dec 1982 | - | 60 | 14 | 12 | 20 | 23 | 21 | 150 |
| 2 Jan 1983 | - | 17 | 12 | 15 | 33 | 40 | 13 | 130 |
| 2 Feb 1983 | 2 | 15 | 11 | 13 | 55 | 2 | - | 98 |
| 1 Mar 1983 | - | 12 | 10 | 45 | 40 | 28 | - | 135 |
| 14 Apr 1983 | - | 23 | 7 | 10 | 55 | 35 | - | 130 |
| 13 May 1983 | 3 | 17 | 30 | 50 | 68 | 20 | - | 188 |
| 12 Jun 1983 | - | 30 | 18 | 20 | 42 | 40 | - | 150 |
| 12 Jul 1983 | 10 | 32 | 30 | 25 | 15 | 8 | - | 120 |
| 12 Aug 1983 | 30 | 30 | 15 | 40 | 25 | 10 | - | 150 |
| 29 Sep 1983 | 25 | 20 | 20 | 18 | 22 | 15 | 10 | 130 |
| 25 Oct 1983 | 60 | 20 | 5 | 8 | 20 | 37 | 30 | 180 |
| 5 Nov 1983 | - | 30 | 20 | 20 | 44 | 40 | - | 154 |
| 11 Dec 1983 | - | 52 | 15 | 15 | 31 | 33 | 14 | 160 |
| Mean no. of crabs per quadrat | 9.3 | 31.7 | 16.9 | 22.0 | 35.4 | 26.6 | 7.6 | 2086 |
| % per quadrat | 0.45 | 1.52 | 0.71 | 1.05 | 1.57 | 1.28 | 0.36 | |
| Total per station | 130 | 443 | 337 | 307 | 492 | 372 | 105 | 2086 |
| Percentage per station | 6.23 | 21.24 | 11.36 | 14.72 | 23.58 | 17.83 | 5.03 | |
| Mean per sample | 21.7 | 31.64 | 16.93 | 21.93 | 35.40 | 26.57 | 17.5 | |

Table 2.2 Measurements of sixteen hermit crabs, *P. bernhardus* occupying *B. undatum* shells collected near low tide mark during February 1987.

| | *Buccinum undatum* | | | | |
|---|---|---|---|---|---|
| | Shell length mm | Shell width mm | Shell condition | Sex | Carapace width mm |
| 1 | 50.3 | 27.0 | Outer part missing | male | 6.0 |
| 2 | 57.7 | 27.9 | Body whorl missing | male | 7.6 |
| 3 | 53.5 | 27.9 | Body whorl missing | male | 5.9 |
| 4 | 64.5 | 39.7 | Lip missing | male | 8.3 |
| 5 | 66.2 | 42.7 | Edge of lip missing | male | 11.3 |
| 6 | 55.7 | 34.0 | Shell complete | male | 10.3 |
| 7 | 73.4 | 31.2 | Only base & columella | male | 13.4 |
| 8 | 65.2 | 46.1 | Siphonal canal missing | male | 11.4 |
| 9 | 62.6 | 39.4 | Generally chipped | male | 9.8 |
| 10 | 55.8 | 36.0 | Outer part missing | male | 11.8 |
| 11 | 59.4 | 33.0 | Lip missing | male | 10.4 |
| 12 | 30.8 | 22.8 | Small, top missing | male | 5.6 |
| 13 | 41.6 | 36.1 | Spire missing | male | 11.0 |
| 14 | 46.3 | 32.8 | Body whorl missing | male | 8.6 |
| 15 | 32.5 | 22.3 | Small, body whorl missing | male | 4.9 |
| 16 | 68.3 | 33.3 | Body whorl missing | male | 6.8 |
| | $\bar{X}$ = 55.2 | $\bar{X}$ = 33.3 | | | overall mean = 8.9 mm |

Table 2.3 Intertidal *Pagurus bernhardus* occupying *Buccinum undatum* shells.

Instances in which the hermit was holding smaller shells occupied by smaller hermit.

(All collected low on shore, near MLWS).

| | *B. undatum* | *P. bernhardus* | | Other Gastropod | | *P. bernhardus* | |
|---|---|---|---|---|---|---|---|
| | length x breadth (mm) | Sex | Size (CW in mm) | Species | length x breadth (mm) | Sex | Size (CW in mm) |
| 1 | 64.0 x 41.0 | ♂ | 12.9 | *N. lapillus* | 32.2 x 20.3 | ♀ | 4.6 |
| 2 | 69.0 x 38.9 | ♂ | 12.5 | *L. littorea* | 26.6 x 21.0 | ♀ | 4.9 |
| 3 | 55.4 x 33.3 | ♂ | 11.8 | *N. lapillus* | 31.9 x 18.8 | ♀ | 4.7 |
| 4 | 64.8 x 40.3 | ♂ | 10.7 | *L. littorea* | 28.6 x 20.7 | ♀ | 4.9 |
| 5 | 64.8 x 38.5 | ♂ | 11.8 | *N. lapillus* | 28.1 x 18.2 | ♀ | 4.7 |
| Mean = | 63.6 38.4 | | 11.94 | | 29.48 19.8 | | 4.76 |

Table 2.4

Total numbers of males and females of sublittoral *Pagurus bernhardus* collected trawling from Oxwich Bay during the period between October 1983 and February, March and April 1984, and their percentages.

| | No. of males | No. of females | Total | % age | |
|---|---|---|---|---|---|
| | | | | Males | Females |
| 14 Oct. 1982 | 44 | 58 | 102 | 43.1 | 56.9 |
| 29 Feb. 1983 | 30 | 44 | 74 | 40.5 | 59.5 |
| 9 Mar. 1983 | 13 | 28 | 41 | 31.7 | 68.3 |
| 20 Apr. 1983 | 52 | 43 | 95 | 54.7 | 45.3 |
| Total | 139 | 173 | 312 | | |

Table 2.5

Mean size of the carapace width of *P. bernhardus* from sublittoral samples of three months combined (Oct. 82, Feb. and March 83).

Males N = 87
Females N = 130

| Sex | Mean carapace width |
|---|---|
| Males | 14.54 mm |
| Females | 13.46 mm |

Sex ratio = (m/f)
1/1.49

Table 2.6

Mean size of the carapace width of hermit crabs less than 10.0 mm CW sampled sublittorally during the month of April 1983.

Males N = 43
Females N = 42

| Sex | Mean carapace width |
|---|---|
| Males | 5.88 mm |
| Females | 6.23 mm |

Sex ratio = (m/f)

1/0.98

Table 2.7

*Pagurus bernhardus* with loss of one or both chelae.

| Date | No. examined | No. with missing chelae | % age of total |
|---|---|---|---|
| 2 Nov. 1982 | 211 | 14 | 10.0 |
| 3 Dec. 1982 | 150 | 11 | 8.0 |
| 2 Jan. 1983 | 130 | 8 | 5.8 |
| 2 Feb. 1983 | 98 | 5 | 3.6 |
| 1 Mar. 1983 | 135 | 7 | 5.1 |
| 14 Apr. 1983 | 130 | 11 | 8.0 |
| 13 May 1983 | 188 | 12 | 8.6 |
| 12 Jun. 1983 | 150 | 9 | 6.5 |
| 12 Jul. 1983 | 120 | 8 | 5.8 |
| 12 Aug. 1983 | 150 | 7 | 5.1 |
| 29 Sep. 1983 | 130 | 8 | 5.8 |
| 25 Oct. 1983 | 180 | 12 | 8.7 |
| 5 Nov. 1983 | 154 | 13 | 9.4 |
| 11 Dec. 1983 | 160 | 13 | 9.4 |
|  | 2086 | 138 |  |

Table 2.8 Species of gastropod shells inhabited by *Pagurus bernhardus* at Mumbles Head during sampling period.

| | 2 Nov. 1982 | 3 Dec. 1982 | 2 Jan. 1983 | 2 Feb. 1983 | 1 Mar. 1983 | 14 Apr. 1983 | 13 May 1983 | 12 Jun. 1983 | 12 Jul. 1983 | 12 Aug. 1983 | 29 Sep. 1983 | 25 Oct. 1983 | 5 Nov. 1983 | 11 Dec. 1983 | Total | % age |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Littorina littorea* | 181 | 123 | 101 | 83 | 111 | 97 | 146 | 117 | 85 | 119 | 99 | 155 | 108 | 120 | 1645 | 78.86 |
| % age | 85.78 | 82 | 77.7 | 84.7 | 82.2 | 74.6 | 77.7 | 78 | 70.8 | 79.3 | 76.2 | 86 | 70 | 75 | | |
| *Littorina obtusata* | - | - | 1 | 1 | 3 | 3 | 2 | - | - | 6 | - | - | 5 | 1 | 22 | 1.06 |
| *Nucella lapillus* | 24 | 27 | 25 | 14 | 20 | 28 | 39 | 33 | 30 | 20 | 27 | 19 | 35 | 37 | 378 | 18.12 |
| % age | 11.4 | 18 | 19 | 14.3 | 14.8 | 21.5 | 20.7 | 22 | 25 | 13 | 20.8 | 10.6 | 22.7 | 23 | | |
| *Nassarius reticulatus* | - | - | - | - | - | - | - | - | - | 3 | - | - | 2 | - | 5 | 0.24 |
| *Nassarius incrassatus* | 2 | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | 0.096 |
| *Natica catena* | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 1 | 0.048 |
| *Ocenebra erinacea* | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 1 | 0.048 |
| *Gibbula cineraria* | 2 | - | 2 | - | 1 | 2 | - | - | 5 | 1 | - | 2 | 2 | 1 | 18 | 0.86 |
| *Gibbula umbilicalis* | 2 | - | - | - | - | - | 1 | - | - | - | - | 1 | - | - | 4 | 0.19 |
| *Buccinum undatum* | - | - | 1 | - | - | - | - | - | - | - | 4 | 2 | 2 | 1 | 10 | 0.48 |
| | 211 | 150 | 130 | 98 | 135 | 130 | 188 | 150 | 120 | 150 | 130 | 180 | 154 | 160 | 2086 | |

Table 2.9 Species of Gastropoda shell inhabited by sublittoral hermit crab, *Pagurus bernhardus* (L.) at Oxwich Bay during 1982/1983.

| | 14 Oct. 1982 | 29 Feb. 1983 | 9 Mar. 1983 | 20 Apr. 1983 | Total |
|---|---|---|---|---|---|
| *Littorina littorea* | 0 | 0 | 0 | 38 | 38 |
| *Natica catena* | 0 | 3 | 0 | 6 | 9 |
| *Nucella lapillus* | 0 | 0 | 0 | 8 | 8 |
| *Nassarius reticulatus* | 0 | 0 | 0 | 1 | 1 |
| *Ocenebra erinacea* | 0 | 0 | 0 | 1 | 1 |
| *Buccinum undatum* | 100 | 71 | 44 | 40 | 255 |
| | 100 | 74 | 44 | 94 | 312 |

Table 2.10

Species of gastropod shells occupied by *Pagurus bernhardus* collected by trawling from Oxwich Bay, listed in order according to the mean carapace width of the hermit crab.

| Shell type | Mean carapace width |
|---|---|
| *Buccinum undatum* | 8.11 mm |
| *Natica catena* | 6.56 mm |
| *Nassarius reticulatus* | 5.0 mm |
| *Littorina littorea* | 4.89 mm |
| *Nucella lapillus* | 4.75 mm |
| *Ocenebra erinacea* | 4.5 mm |

Table 2.11

Species of gastropod shells occupied by the hermit crab *Pagurus bernhardus*, collected by trawling from Oxwich Bay, listed in order according to the frequency of use.

| Type of shells | Frequency |
|---|---|
| *Littorina littorea* | 38 |
| *Buccinum undatum* | 37 |
| *Natica catena* | 9 |
| *Nucella lapillus* | 8 |
| *Nassarius reticulatus* | 1 |
| *Ocenebra erinacea* | 1 |

Table 2.12 Summary of results of mark-recapture experiment on *Pagurus bernhardus* in pool at Mumbles Head. All the experimental shells were marked with a spot of white paint (see text).

| Species of occupied shell | No. used | Recaptures within original square | | Recaptures outside original square | |
|---|---|---|---|---|---|
| | | No. | % | No. | % |
| *Littorina littorea* | 119 | 8 | 6.4 | 111 | 88.8 |
| *Nucella lapillus* | 6 | - | - | 6 | 4.8 |
| | 125 | | | 117 | 93.6 |

Table 2.13 The number and percentage of associated animals on gastropod shells inhabited by *P. bernhardus* from the sublittoral area which is mentioned in the Methods of Chapter 2.

| | No./Total | % with *Hydractinia* | No./Total | % with *Nereis fucata* | No./Total | % with *Pomatoceros* |
|---|---|---|---|---|---|---|
| *Nucella lapillus* | 2/8 | 25 | - | - | - | - |
| *Littorina littorea* | 21/38 | 55.3 | - | - | - | - |
| *Ocenebra erinacea* | 1 | - | - | - | - | - |
| *Nssarius reticulatus* | 1 | - | - | - | - | - |
| *Natica catena* | 6/9 | 66.7 | - | - | - | - |
| *Buccinum undatum* | 176/255 | 69.3 | 211/255 | 82.8 | 78/255 | 30.6 |

Plate 2.1

The sample site at Mumbles Head from where the hermit crab *Pagurus bernhardus* (L.) were collected.

Plate 2.2

*Pagurus bernhardus*, occupying two shells of *Littorina littorea*, the dark greenish crab belongs to the intertidal population and the other to the sublittoral.

# CHAPTER 3

# Taxonomic status of the intertidal populations

## 3.1 INTRODUCTION

Preliminary studies of the local populations of what was thought to be the one species, *Pagurus bernhardus*, revealed considerable differences between the intertidal specimens and those caught by trawling sublittorally. Not only did the intertidal specimens have a smaller mean size but they showed different patterns of shell occupancy and considerable differences in colour.

Careful examination of the appendages etc. however, revealed no morphological differences other than those associated with allometric growth.

In order to resolve this problem it was decided to submit some representative specimens of each population to examination by enzyme electrophoresis.

The use of the technique of enzyme electrophoresis in helping to solve taxonomic problems involving closely related animals has been well documented (Avise, 1974; Thorpe, 1979). There is now a considerable amount of published data from a wide variety of plant and animal species to show that, on average, specimens from two separate (allopatric) populations of the same species show enzyme differences at very few gene loci. The proportion is usually less than 10%. Separate species on the other hand, even if closely related sibling species, show far greater differences (usually about 50%).

The technique has been used not only to identify the presence of "cryptic" species in which the morphological differences are minimal but also to resolve the true status of populations with divergent characteristics such that the existence of separate species cannot be ruled out. In some such cases the divergent population has been shown to be an ecotype of the species with negligible genetic difference. An example of this is the winkle, *Littorina obtusata*, in which a local population had been given the specific name *L. aestuarii*, but enzyme electrophoresis revealed its status as an ecotype (Moyse, Thorpe and Al-Hamadani, 1982).

The differences between the intertidal and sublittoral *Pagurus bernhardus* were such that morphological methods could not with certainty resolve their status. Of the other methods available, enzyme electrophoresis was the quickest and most reliable.

## 3.2 MATERIALS AND METHODS

Samples of hermit crabs were collected from the intertidal zone at Mumbles Head, and also by trawling sublitorally at Oxwich Bay. They were kept alive in the Zoology aquarium in a polythene tray through which seawater was circulated. They were held here for six days (May 1987) prior to the experiment. Two specimens from each population were selected for the experiment. The two intertidal specimens selected were the largest available. The two sublittoral specimens used were somewhat larger. The sex of the specimens used was not recorded. On the morning of the experiment the four hermit specimens were removed alive from their gastropod shells and each was measured. Each was then placed individually in one stoppered specimen tube.

Electrophoretic assay of the two types was carried out at the Department of Genetics, School of Biological Sciences, Swansea, by courtesy of Dr. Skibinski and his post-graduate students. (They had specified that 2 only specimens of each population would be enough and that their sex was unimportant.)

I was told that the methods used for these analyses were those described long ago by Shaw and Prasad (1970), and later by Ahmed, Skibinski and Beardmore (1977). Table 3.1 indicates the enzyme loci that were examined by those methods.

## 3.3 RESULTS

The results are set out in Table 3.2. About 27 gene loci were examined and all but 2 gave useful results. In every such case the enzyme activity of the types of crabs was identical. According to Dr. Skibinski, these results indicate that the two types of crab appear to be identical.

## 3.4 DISCUSSION

The absence of differences between the enzymes of the two populations is strong evidence that they are the same species. If they had been different, but closely related species, some differences in enzyme activity would have been expected in a sample of 27 loci.

In the present investigation of *Pagurus bernhardus*, it was now possible to proceed in the knowledge that the different stocks are indeed components of the same species.

Table 3.1

A list of 16 enzyme loci used in this investigation.

| Abbreviations | Full name of enzyme |
|---|---|
| Ap | Amino peptidase |
| Adh | Alcohol dehydrogenase |
| Me | Malic enzyme |
| 6 Pgdh | 6-phosphogluconate dehydrogenase |
| α Gpdh | Alpha-Glycerophosphate dehydrogenase |
| Pgm | Phosphoglucomutase |
| Ldh | Lactate dehydrogenase |
| Mdh | Malate dehydrogenase |
| Got | Glutamate oxaloacetate transaminase |
| Est | Esterase (1,2) |
| Idh | Isocitrate dehydrogenase |
| Tpi | Triosephosphate isomerase |
| Lap | Leucine aminopeptidase |
| Ndh | Nothing dehydrogenase (No substrate) |
| Pgi | Phosphoglucose isomerase |
| G 6 pdh | Glucose-6-phosphate dehydrogenase |

Table 3.2

List of enzymes used in two different types of tissue from the muscle and the abdomen of the hermit crabs.

| Muscle | | Abdomen | |
|---|---|---|---|
| Ap-1 | Identical | Got-1 | Identical |
| Ap-2 | " | Got-2 | " |
| Adh-1 | " | Est-1 | " |
| Adh-2 | " | Est-2 | " |
| Adh-3 | " | 6 Pgdh-1 | " |
| Me-1 | " | Mdh-1 | " |
| Me-2 | " | Mdh-2 | " |
| 6 Pgdh | " | Pgm-1 | " |
| G 6 Pdh | " | Pgi-1 | " |
| α Gpdh-1 | " | Idh-1 | " |
| α Gpdh-2 | ? | Tpi-1 | " |
| Pgm-1 | Identical | Lap-1 | " |
| Ldh-1 | ? | Lap-2 | " |
| Ldh-2 | Identical | Ndh-1 | " |
| Mdh-1 | " | | |
| Mdh-2 | " | | |

# CHAPTER 4

## Field studies of *Diogenes pugilator* (Roux)

## 4.1 INTRODUCTION

The ecology of *Diogenes pugilator* in North Wales has been the subject of close attention in several recent unpublished M.Sc. theses (O'Sullivan, 1977; Widdop, 1979; Sabar, 1980). These workers have been particularly concerned with its niche separation from *Pagurus bernhardus*. Sabar (1980) reported results of a sublittoral survey off the south west coast of Anglesey on surf washed sandy beaches where *D. pugilator* is abundant at low tide. He showed that *D. pugilator* occurring in the surf zone is replaced quite abruptly at depths ranging from 2.5 to 5.0 metres below chart datum by *P. bernhardus*. Sabar (1980) showed that the different distribution of these two species on such sandy bottoms cannot be linked to measured differences in their abilities to tolerate reduced salinity or oxygen levels. In laboratory experiments Sabar demonstrated that the two species had rheotactic responses to different current velocities which did not differ significantly. He concluded that behavioural domination of *Diogenes* by *P. bernhardus* observed in laboratory experiments was important. He suggested that this domination decreases on a fine sand substratum because of the burying behaviour of *Diogenes*.

The burying behaviour of hermit crabs has already been examined by previous workers. Balss (1955) noted several species of hermit crabs, including *D. pugilator*, even though they are already protected by a gastropod shell may dig into the substratum. They do not bury deeply - retaining contact with the surface for the purpose of respiratory exchange. Rebach (1974), suggests that *Pagurus longicarpus* migrates into deeper water to overwinter, there they partially bury themselves in fine sand. It is assumed (Rebach, 1974) that this burying helps decrease the rate of predation on the crabs by benthic predators while the locomotor activities of the hermit crabs are reduced by the low ambient temperature.

Burial (according to Balss, 1955) is achieved as follows. The left (major) cheliped is pushed into the substrate, presumably to act as an anchor. The ambulatory limbs are then used to push sand out from under the shell, and in some cases, to heap sand on top of it. The right (minor) cheliped is used concurrently to throw sand up over the shell. In many cases, the major cheliped is also to push the sediment into a position easily accessible to the minor cheliped. While these movements are being carried out, the shell is rocked back and forth laterally until buried, the only part left exposed being a small section of the rim of the aperture. The only parts of the *Diogenes pugilator* left uncovered were the eyes, antennae and the mouth parts (Widdop, 1979).

It was also noted by Widdop that the subjects spend by far the greater proportion of their time buried in preferred substrate, whereas in non-preferred substrates, the crabs appeared to spend more time actively moving around (Rebach, 1974; Widdop, 1979). Widdop also observed the behaviour of *Diogenes pugilator* in the surf zone of the beach during the summer. He noted that during the receding tide they braced themselves against breaking waves but allowed themselves to be washed down shore by the back wash. The ecology of *Diogenes pugilator* is clearly in sharp contrast to that of *Pagurus bernhardus*, but it has in common a distribution which overall spans the intertidal/sublittoral boundary so comparisons may be of value in studying the relationships between intertidal and sublittoral populations of *Pagurus bernhardus*. The object of the present study was to examine the local population of *Diogenes pugilator* at Rhossili, Gower with regard to those features which were the subject of study in the case of *Pagurus bernhardus*. In particular seasonal and shorter term changes in the distribution seemed to be of interest.

### 4.1.1 The study area

Rhossili Bay, Gower, South Wales (Grid Reference SS403918) is a very long wide beach with flat hard packed sand, about 4 kilometres long. The beach faces west and is bounded by sand dunes which quickly give way to steep ground. To the south is the long promontory of Worm's Head, and the tidal island of Burry Holm is to the north (Plate 4.1 and Fig. 4.1). This littoral zone consists of batches of ripple-marked muddy sand interspersed with batches of very loosely packed sand. The beach slope is not uniform, being greatest near high water mark. Some batches of pebbles are present near high water. Since the beach faces due west it receives the full impact of the Atlantic swell. More detail about the area is available in Nelson-Smith and Bridges (1976).

The maximum tidal range at Rhossili is about 10 m. There are about 800 m of exposed sand between high water and low water spring tides. The degree of wave action varies from relatively moderate to heavy. The substrate is suspected to be rather unstable, and prone to large scale movement. The site is completely exposed to frequent strong westerly wind.

Qualitative observations were made of the relatively rich fauna present at this sandy area in addition to *D. pugilator*. The following invertebrates were observed alive or dead (d = dead only) in large numbers at Rhossili bay: the crabs *Corystes cassivelaunus* (Pennant), *Liocarcinus marmoreus* (Leach), the brittle star, *Ophiura texturata* Lamarck; Lamellibranchs: *Donax vittatus* (da Costa), *Pharus legumen* (L.) (d), *Mactra corallina* (L.) (d) and the gastropods *Natica catena* (da Costa) and *Acteon tornatilis* (L.). Apart from these forms evident at the surface, there was known to be a considerable population of polychaete tube worms and other buried animals.

## 4.2 MATERIALS AND METHODS

Monthly sampling of the intertidal population of the hermit crab, *Diogenes pugilator* (Roux), was carried out at Rhossili Bay, South Wales from April 1983 to December 1984. It is only possible to sample satisfactorily during relatively calm periods at times of low water. During even moderately rough weather, fewer hermit crabs are to be found even if the collector is suitably dressed (in a wet suit) to work in the breaking waves. Usually the crabs were sought visually and collected by hand. Another method of sampling was tested, namely a long handled net with a triangular, frame-held bag (side 30 cm). This net, with a mesh size of 2-3 mm, was pulled along the beach such that one edge cut into the surface of the sand. Quite large areas covered by opaque, sand-laden breakers could be sampled quite quickly by this means.

During the 1983 season, samples were taken at various different points along the length of Rhossili Bay in an attempt to locate variation in density along the Bay. In 1984, sampling was carried out at a more consistently determined point towards the northern end of the Bay, where a "good" catch could generally be relied on.

For the general routine monthly collection, it was initially intended to take a standard 20 minute collection in the belief that this would produce a statistically useful size sample of say between 150 and 200 hermits. In practice, it was found that during the high summer months (July and August) in calm weather conditions, it was often possible for one person to collect hundreds of crabs in 20 minutes. On many other occasions because of rough weather (much more usual), it was not possible to collect the predetermined satisfactory minimum of 100 crabs within the whole of the available low tide period.

On one occasion a special study was made to attempt to follow the movement of the crabs down the beach with the tide. For this purpose a transect line was staked down the shore. Across the shore-width, observations were made at half hourly intervals starting 3 hours before the predicted time of low tide. Any hermit crabs were collected at each station. The upper and lower limit of waves at each station was recorded. A plastic kitchen strainer was used to quickly seek out buried hermit crabs. A ten minute collection was made at each station.

On certain occasions during sampling, pairs of hermit crabs were encountered. To verify that the pairs were male and female and to look for spermatophores deposited on the female, a number of such pairs found holding on to each other, were collected and kept isolated in small screw-top jars for further study.

All hermit crabs collected during a sampling day were transported to the laboratory alive in vessels containing seawater. Care had to be taken or some of the crabs would not survive the duration of the journey back to the laboratory. Such mortality of crabs in capture could mainly be attributed to increases in temperature and over-crowding of the vessels.

To investigate what happens to hermits in winter, trawling was carried out in the Bay by the research vessel of U.C. Swansea, the "Venturous". Because the beach slopes so gently, the minimum distance from the shore at which it could operate safely (depthwise) was more than one kilometre at low tide.

In the laboratory all the hermit crabs were examined by the same methods as are described for *Pagurus bernhardus* (see Chapter 2).

Statistical analysis as t-test and chi-square ($\chi^2$) were used to see the relationship between numbers of males and females. The tests were conducted at two levels of significance, 5% and 1%.

### 4.2.1 Burying behaviour

The sequence of movement involved in self burial by the hermit crab *D. pugilator* was recorded by observation of a few individuals each burying itself a number of times in the substrate in a small tank, as well as many observations made at various times in the field.

In a separate laboratory experiment forcible burying of specimens of both *D. pugilator* and *P. bernhardus* in sand in a small aquarium was performed.

Individuals were either heavily sprinkled with sand or pressed down into the sand until out of sight and the reactions noted.

## 4.3 RESULTS

### 4.3.1 Season of intertidal occurrence

Figures 4.2 and 4.3 show that in both years, the hermit crab, *D. pugilator*, appeared in the sampling area starting in April and continued to be present until November.

### 4.3.2 Tidal migration

The results of the transect conducted on a falling tide are given in Fig. 4.4. It shows that some *D. pugilator* occur in the edge of the surf over $1\frac{3}{4}$ hours and 300 metres before low tide is reached. Since it is rare for *D. pugilator* to be left stranded, clearly they move down with the falling tide. It follows that they also move up with the rising tide. It may however be only a minority of the population that behaves in this way.

### 4.3.3 Size range and variation

The size frequency distribution of the hermit crab, *D. pugilator*, collected from Rhossili beach, during the period of sampling between April 1983-October 1984, are shown in Figures 4.2 and 4.3.

The histogram in Fig. 4.3 indicates that the smallest hermit crab (< 1.0 mm carapace width) was collected in August 1984. The largest hermit crabs were collected in the months of April, July and October 1983 and in September 1984. From the figure, it can be seen that a high proportion of the hermit crab population in this area ranged between 2.0 and 4.0 mm carapace width.

The frequency distribution of male and female *D. pugilator* is shown in Figures 4.2 and 4.3.

Post-larval hermit crabs (< 1.5 mm CW) were present only during the period August to October (Fig. 4.2). No hermit crabs were greater than 5.0 mm carapace width and the largest hermit crab (> 4.5 mm CW) seen here were all males. The numbers of these however were small.

Figure 4.5 shows the size distribution of males and females combined from all the monthly collections made in 1983 and 1984 compared with additional single sample made in July 1987. In all collections the maximum size of males is greater than females. The 1987 sample shows two clear peaks to the distribution of females. These could possibly represent two year groups (one and two year old). On this interpretation the males in the same sample appear to belong mostly to only one year group, probably three years old. The combined samples for 1983 and 1984 show a closer balance in size between males and females and probably represent a combination of ages no more than four years old.

### 4.3.4 Sex ratio

In the course of the study, observations were made on the sex ratios in the population.

In Table 4.1, the sex ratio is recorded for each collection from Rhossili on different dates (Fig. 4.6). Although there are some cases which show a sex ratio of 1:1, in most cases there is a statistically significant deviation from this. The statistical tests show that there was a highly significant difference in the relation between the numbers of males and females ($P < 0.01$).

### 4.3.5 Gastropod shell species occupied by *Diogenes pugilator*

Table 4.2 indicates that the most preferred shell for occupation by the hermit crab, *D. pugilator*, in the study area is that of *Littorina littorea*. This is shown by the high percentage (42.8%) (787 out of a total 1840 *L. littorea* shells examined) being inhabited by the hermit crab, *D. pugilator*. The second most frequented shells were those of *Nucella lapillus* and *Natica catena*, whilst the shells of the remaining gastropod species were infrequently occupied by this hermit crab.

The size range of hermit crabs occupying shells of different species is shown in Fig. 4.7. The histograms for species of gastropod are based on the total results for the whole 13 months' sampling.

It can readily be seen from the histograms that the carapace width (between 3.0-4.0 mm) of *D. pugilator* occupying *L. littorea* shells is larger than that occupying *Nucella* shells.

The smallest hermit crabs (< 1.0 mm CW) were occupying shells of *Rissoa parva* rather than any other species.

### 4.3.6 Sublittoral sampling

No *Diogenes pugilator* were collected during the winter trawling around Rhossili Bay. A few *P. bernhardus* were however caught. This negative result suggests that the vessel "Venturous" was trawling too far away from the shore, below where the hermit crabs may be buried.

### 4.3.7 Burying behaviour

Broadly speaking it was observed that *Diogenes pugilator* buried themselves in the same way as described by Balss (1955) and Rebach (1974). All movements in the burial procedure are carried out vigorously, and a healthy specimen could usually bury itself within 8 to 10 seconds.

In the forced burial experiment the specimens of *Diogenes pugilator* rapidly orientated themselves within the sand and settled down with only the eyes and antennae protruding. *P. bernhardus* specimens on the other hand, struggled to the surface within a few seconds. This species showed considerable distress and quickly started to evacuate sand from its shell by standing on the chelae and legs and lifting the shell so that sand drained out. The shell was repeatedly moved up and down by the abdomen for this purpose.

## 4.4 DISCUSSION

### 4.4.1 Shell occupancy

Controlled laboratory experiments on shell selection by *Diogenes pugilator* by Widdop (1979) demonstrated some preference for species of *Littorina* and *Nassarius incrassatus*. Field tests on the other hand, showed that occupancy reflected availability (Widdop, 1979). There is no reason to believe otherwise of the Rhossili population.

### 4.4.2 Sex ratios

Observed sex ratios in *Pagurus bernhardus* remained close to 50/50 (1:1). Those of *Diogenes pugilator* did not. A variety of explanations is possible for the wide fluctuations observed. Selective mortality of one sex is improbable because it would take years to correct. Non-randomness of the samples is much more probable. MacDonald *et al.* (1957) suggested females incubating late stage eggs might remain in the sublittoral. Data on breeding (in the present study) do not bear this out. Behaviour differences between the sexes, associated with moulting might contribute. Tendency to different seasonal moulting as occurs in *Carcinus maenas* (males in spring, females in autumn; see Crothers, 1967) are a possibility but again the data are not consistent with this hypothesis.

A more satisfactory explanation is mechanical sorting by wave action. Balss (1955) demonstrated that the major chela may be used as an anchor against wave action. The very small major chela of *Diogenes pugilator* represents a much less efficient anchor than that of the male. Resulting differential transport rates can be expected to result in sexual sorting sufficient to explain observed diverse sex ratios.

### 4.4.3 Seasonal migration of *Diogenes pugilator*

Although not referred to by MacDonald *et al.* (1957) and apparently unknown to Widdop (1979) and Sabar (1980), *Diogenes pugilator* in the British Isles only appears in the intertidal surf during the summer months, April to October. Repeated autumn, winter and spring sampling at Rhossili in the present survey showed this to be absolute and regular. This mirrors a similar offshore seasonal migration seen in other intertidal decapods, for instance *Carcinus maenas* (see Naylor, 1958; Abbas, 1984). As in the case of *C. maenas* *D. pugilator* appears to pass the winter not far below chart datum, judging by the total absence of deeper records. Here (unlike *Carcinus*) it probably remains buried. The best survey was that of O'Sullivan (1977) using a van Veen dredge off Anglesey, who reported it at a maximum depth of 10 metres below chart datum. Such behaviour of staying in the sublittoral is a means of avoiding the coldest winter conditions associated with the ebb and flow of tides over frosted sand flats. However, it is possible that some other cue than temperature rise may initiate return to the intertidal zone in spring.

### 4.4.4 Tidal migration

As with seasonal migration, tidal movement of *Diogenes pugilator* up and down the shore during the summer months, is not specifically described by MacDonald *et al.* (1957), Widdop (1979) nor Sabar (1980). In the present study, it was deduced by various lines of evidence. Firstly, the presence of large numbers of *D. pugilator* in the edge of the surf at the time of low water both during extreme spring and mean spring tides. Such low tides were separated by 100 metres or more on the very gently sloping beach. Secondly, a few live specimens were often to be found stranded even further up the beach above the level of low water of neap tides. Furthermore, as even Widdop (1979) describes, the hermit's behaviour is designed to carry them down shore on a falling tide; it follows that they have travelled up on the rising tide. Indeed, it seems highly possible (see Fig. 4.4) that at the time of high tide many *Diogenes pugilator* may be foraging as high as mid tide level.

The functional significance of this tidal migration is somewhat obscure. Presumably it relates to better feeding conditions on the low littoral sand flats, but escape from sublittoral predators or competitor are other possibilities. Clearly it must be very important to the animals since it involved them spending so much time in the obviously hostile conditions associated with the action of the surf. Whilst in this zone the animals' preoccupation appears to be with maintaining station and avoiding being stranded. What are the compensatory advantages? Widdop (1979) described how *D. pugilator* will anchor to avoid being washed too far up the shore by a breaking wave. He also refers to hermits allowing themselves to be taken down the shore by being passively rolled by backwash. In the present study it was further noted that such animals will often "spread eagle" their pereopods apparently to create maximum drag effect in such a backwash situation. This was observed on many occasions and appeared to be most effective for taking the animal down the shore. Altogether these behaviour patterns appear to be designed to keep the animals in the surf but at the same time to avoid stranding.

### 4.4.5 Niche separation from *Pagurus bernhardus*

In laboratory tests, Widdop (1979) demonstrated a preference, by *D. pugilator*, for sands with a relatively large mean particle size (0.25-0.35 mm diameter). However, they did not discriminate between such artificially sorted sands and mixed sands from their natural habitat containing such large particles. The presence of large particles, rather than a large mean size seemed to be the important factor. *Pagurus bernhardus* did not discriminate between sands in Widdop's laboratory tests.

In attempting to understand the different habitat requirements of the two crabs, certain features of their distribution need to be borne in mind. Neither species occurs in estuarine conditions such as the extensive sand flats of the Burry Inlet to the north of Gower perhaps because of lowered salinity. In Rhossili Bay, *Diogenes pugilator* is replaced by *Pagurus bernhardus* at the sheltered southern end of this sandy bay, just north of the Worm's Head. There is virtually no overlap in the population of the two species. The horizontal separation has similarities to the vertical separation recorded by Sabar (1980).

It is instructive to consider conditions in the two extremes and reasons for the absence of one species in each.

The absence of *Diogenes* from the southern end of Rhossili Bay and from deeper water over sand is unlikely to be a direct result of absence of surf. Outside the British Isles, *D. pugilator* occurs in the Bitter Lakes for instance. These are an integral part of the Suez Canal and being inland are virtually devoid of wave action, certainly not surf. Competitive exclusion by the larger more aggressive species, *Pagurus bernhardus*, is a plausible explanation. Driven from their shells by the dominant species, *D. pugilator*, here would fall foul of predators.

Absence of *P. bernhardus* from the surf zone of Rhossili Bay needs a quite different explanation. Competitive exclusion here does not apply since the demonstrated agonistic dominance operates in the wrong direction (Sabar, 1980). Explanations based on substrate preference, salinity or oxygen level tolerance are equally unacceptable as pointed out by Sabar (1980). Furthermore, different toleration of high current velocity is not sufficient to explain their exclusion.

A new hypothesis is offered here. It is suggested that, unlike *D. pugilator*, *P. bernhardus* is unadapted to deal with large quantities of water borne sand particles. As described by various authors, the whole body of *Diogenes* is thickly clothed in fine hairs, which bridge the gap between body and carcinoecium. Such hairs are quite sparse in *P. bernhardus* and unlike the condition in *Diogenes* do not prevent suspended sand entering. The experiment described earlier (4.2.1 and 4.3.7) revealed the great sensitivity of *P. bernhardus* to sand inside its shell. This species probably avoids areas where surf is sufficient to cause frequent suspension of large quantities of sand in the water column.

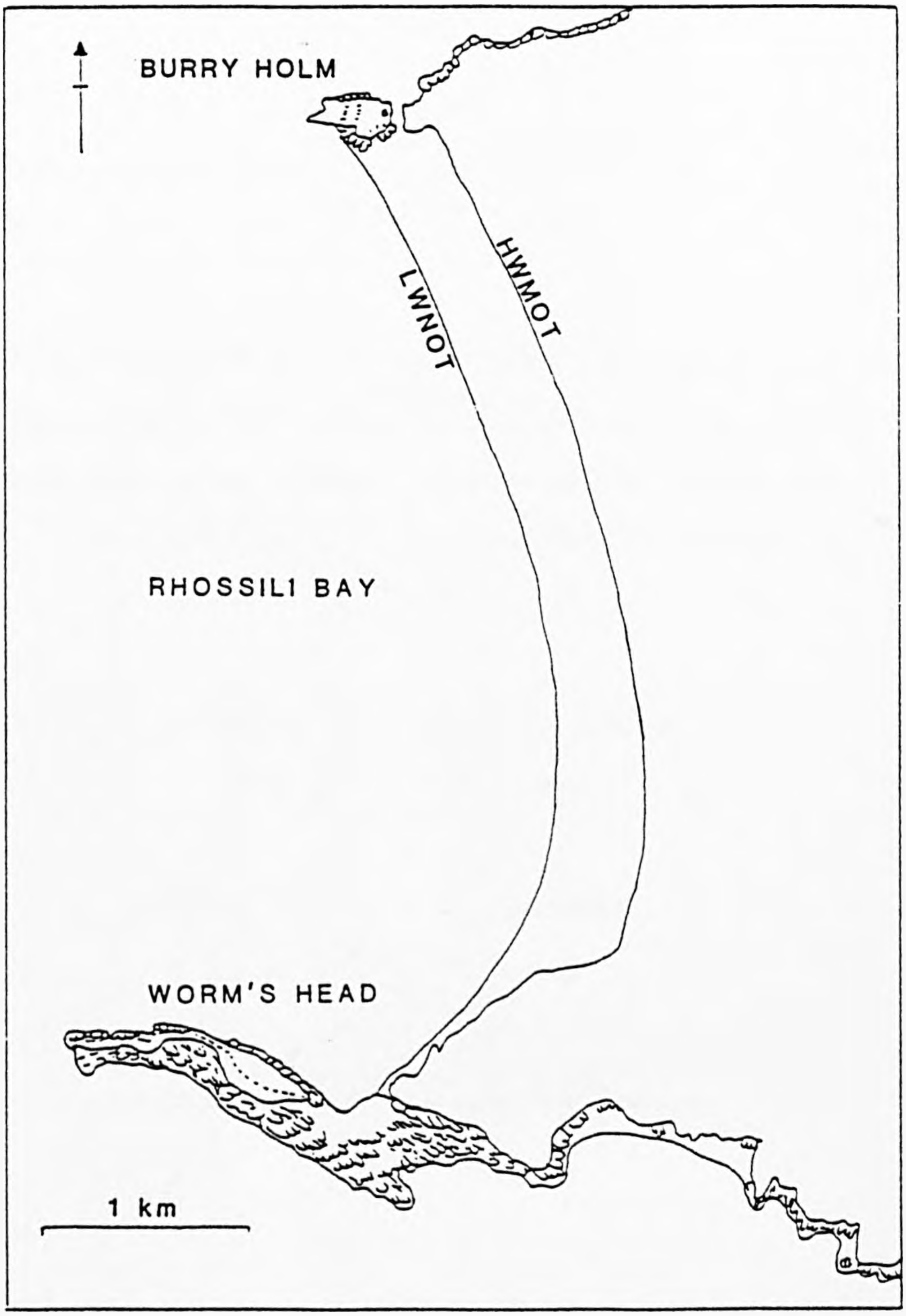

BURRY HOLM
HWMOT
LWNOT
RHOSSILI BAY
WORM'S HEAD
1 km

Figure 4.1

Map showing area where *D. pugilator* was studied.

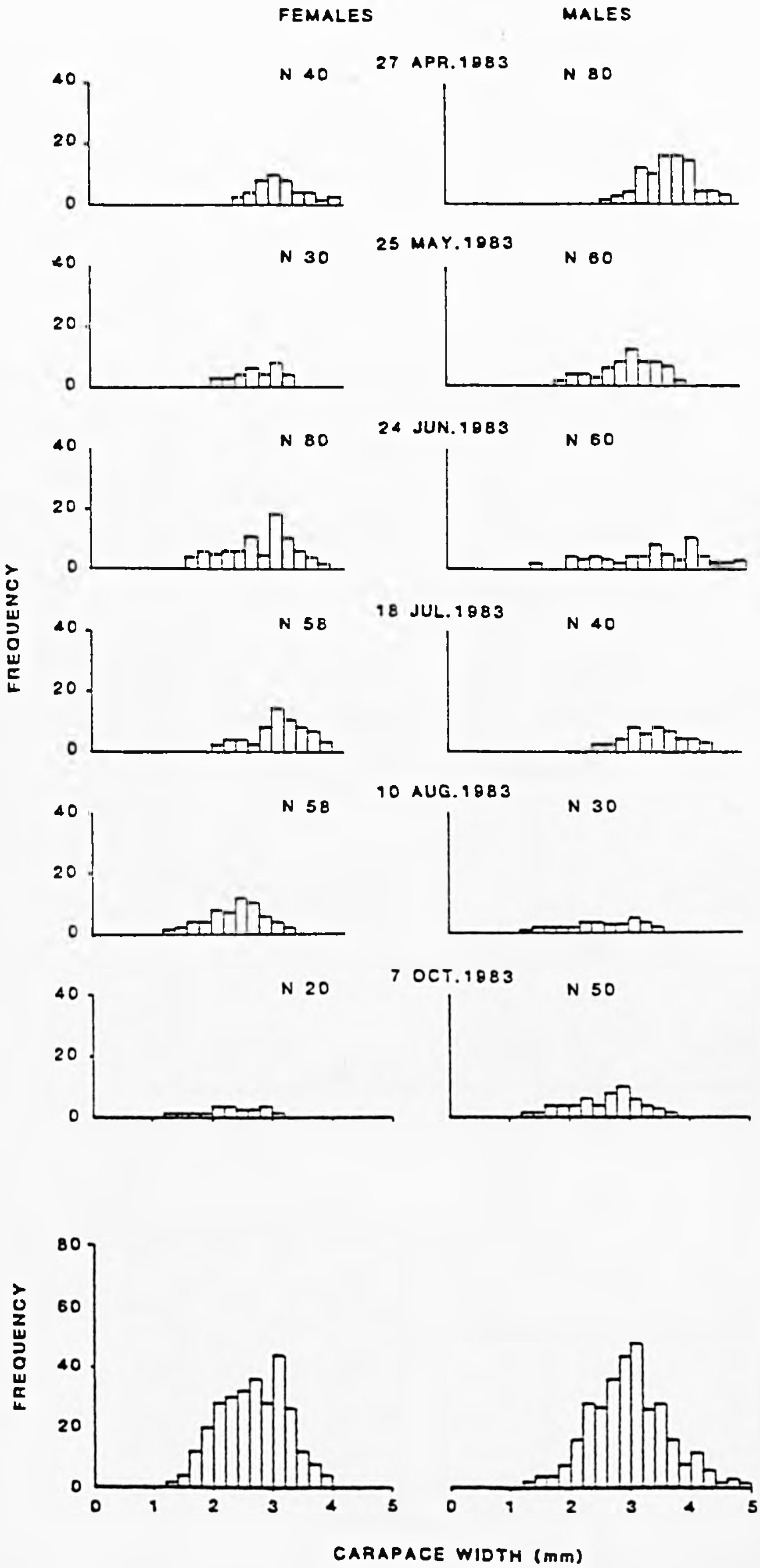

FEMALES
MALES
27 APR.1983
N 40
N 80
25 MAY.1983
N 30
N 60
24 JUN.1983
N 80
N 60
18 JUL.1983
N 58
N 40
10 AUG.1983
N 58
N 30
7 OCT.1983
N 20
N 50
40
20
0
FREQUENCY
80
60
40
20
0
0
1
2
3
4
5
CARAPACE WIDTH (mm)

Figure 4.2

*Diogenes pugilator*. Histograms of size frequency of both sexes separately from monthly samples, collected intertidally from Rhossili Bay during 1983. Monthly values added in bottom histogram.

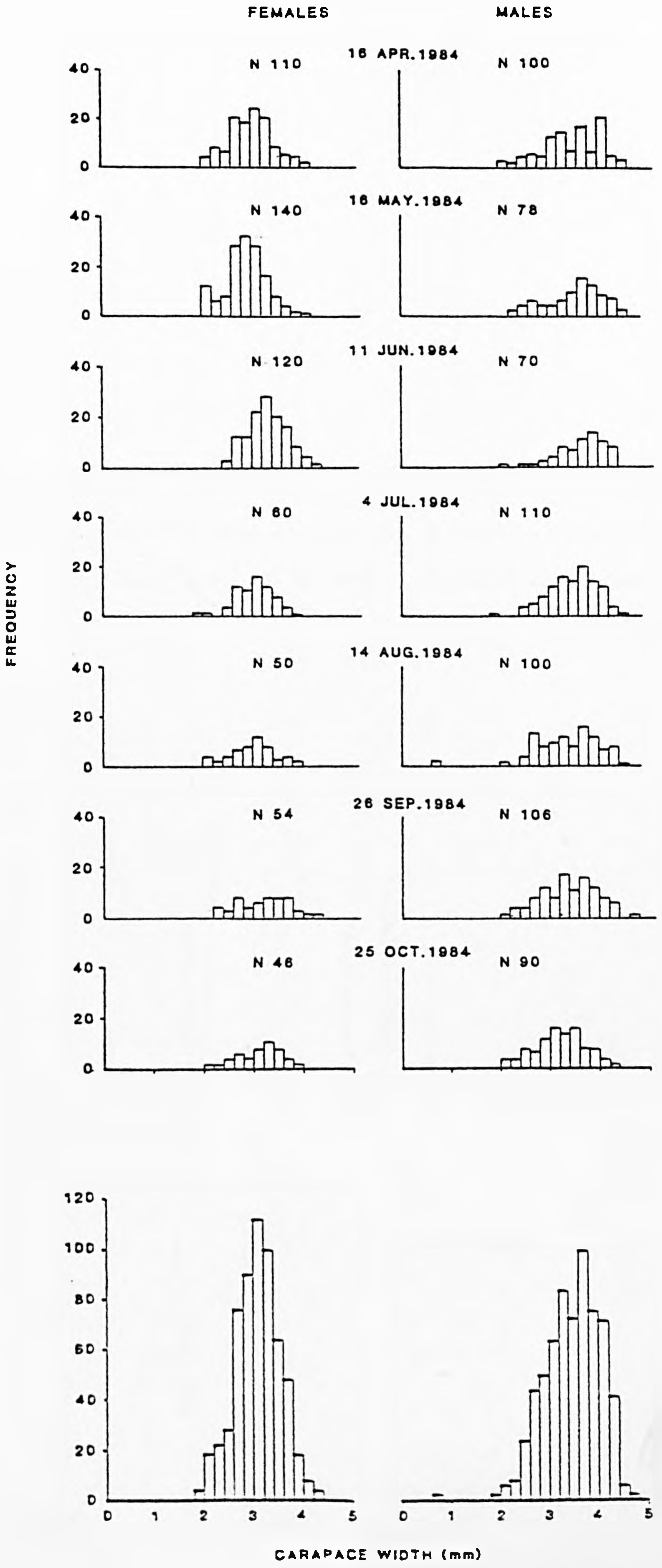

FEMALES
MALES
16 APR.1984
N 110
N 100
16 MAY.1984
N 140
N 78
11 JUN.1984
N 120
N 70
4 JUL.1984
N 60
N 110
14 AUG.1984
N 50
N 100
26 SEP.1984
N 54
N 106
25 OCT.1984
N 46
N 90
0
20
40
60
80
100
120
FREQUENCY
0
1
2
3
4
5
CARAPACE WIDTH (mm)

Figure 4.3

*Diogenes pugilator*. Histograms of size frequency of both sexes separately from monthly samples, collected intertidally from Rhossili Bay during 1984. Monthly values added in bottom histogram.

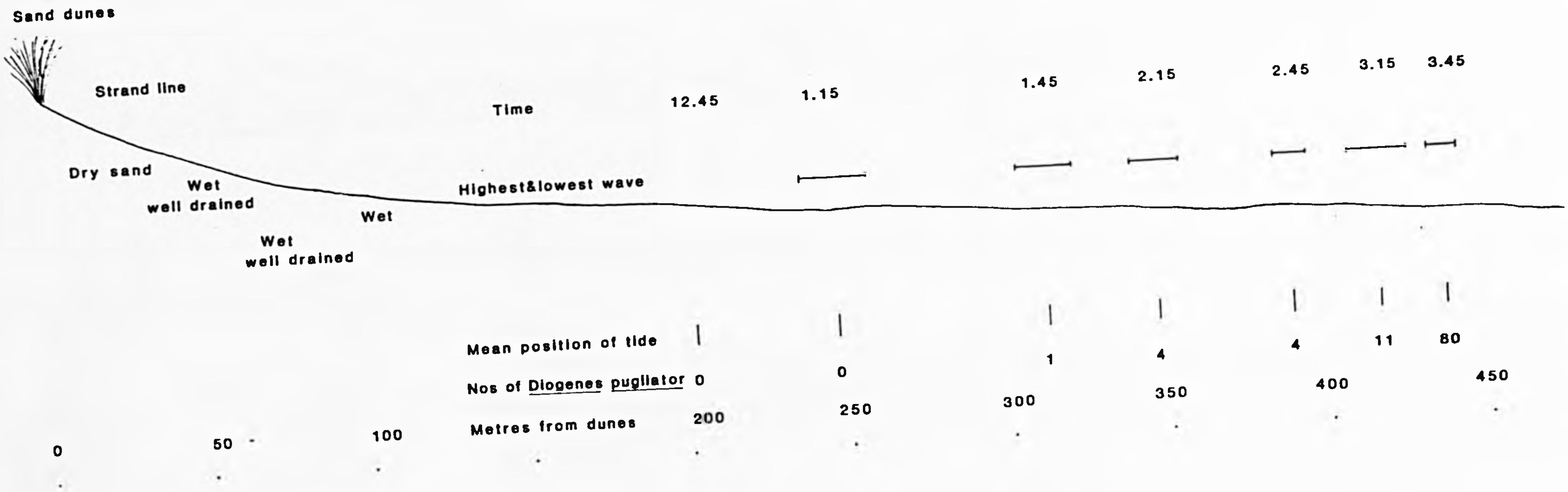

Sand dunes
Strand line
Dry sand
Wet
well drained
Wet
well drained
Wet
Time
12.45
1.15
1.45
2.15
2.45
3.15
3.45
Highest&lowest wave
Mean position of tide
Nos of Diogenes pugilator
0
0
1
4
4
11
80
Metres from dunes
0
50
100
200
250
300
350
400
450

Figure 4.4

Transect across Rhossili Beach. Observations made at half hour intervals recording position of edge of tide, wave and presence of *D. pugilator*. Time of low tide 15:45 B.S.T. (spring tide).

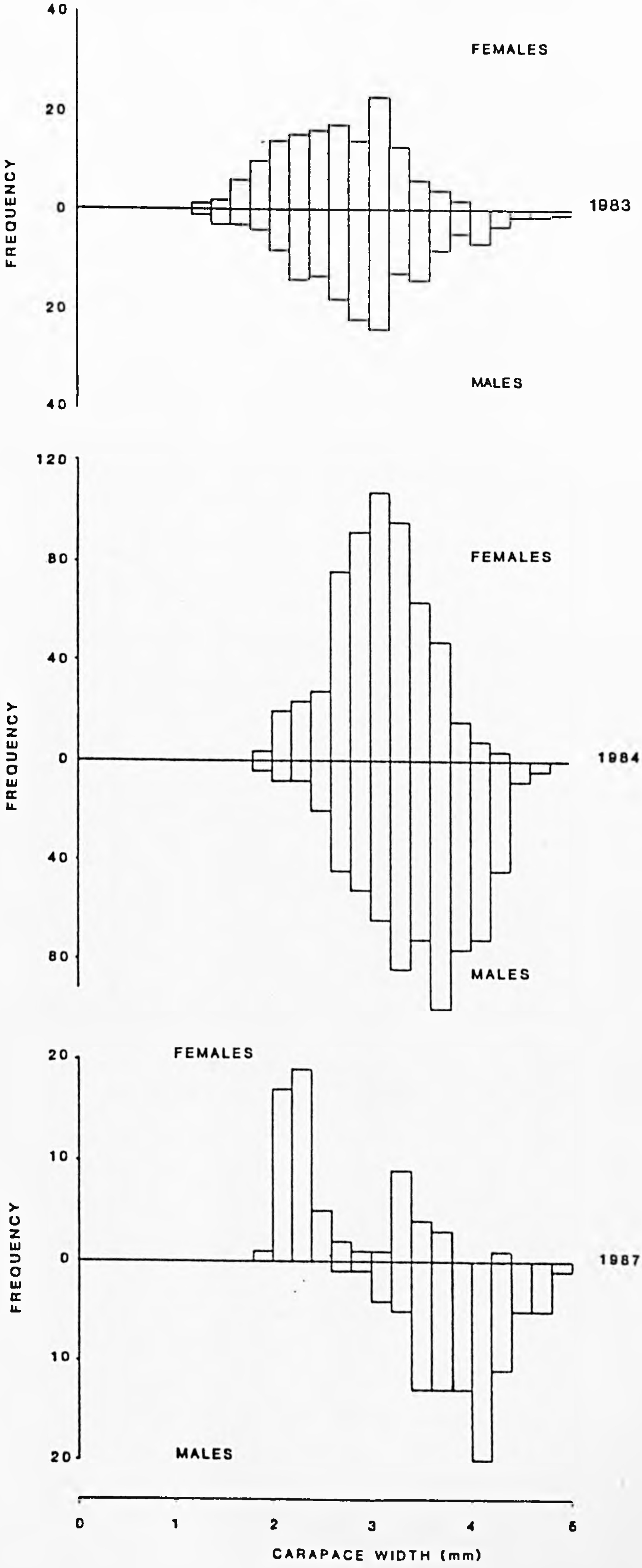

40
20
0
20
40
FREQUENCY
FEMALES
MALES
1983
120
80
40
0
40
80
FREQUENCY
FEMALES
MALES
1984
20
10
0
10
20
FREQUENCY
FEMALES
MALES
1987
0
1
2
3
4
5
CARAPACE WIDTH (mm)

Figure 4.5

*Diogenes pugilator*. Size frequency distributions. Histograms for 1983 and 1984 represent monthly valued added together. 1987 histogram represents a single sample taken in July.

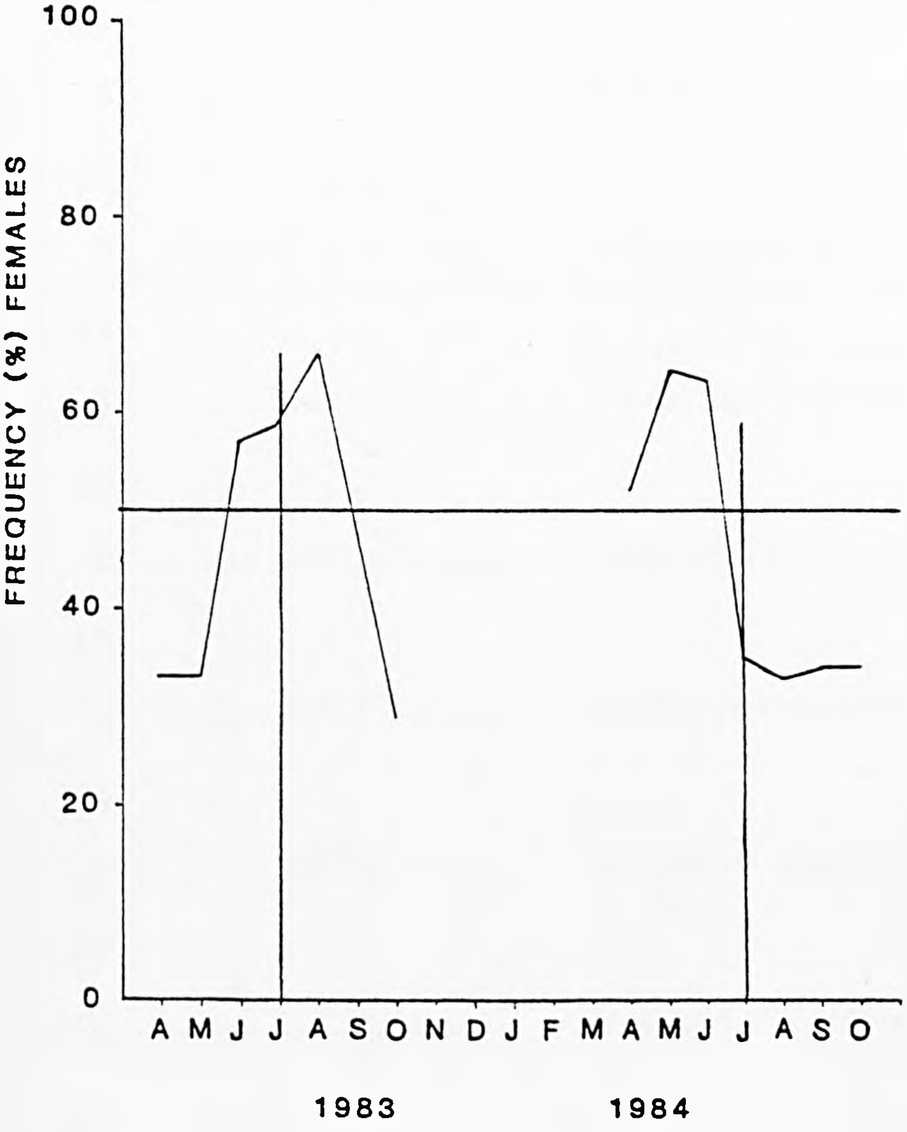

FREQUENCY (%) FEMALES
100
80
60
40
20
0
A M J J A S O N D J F M A M J J A S O
1983
1984

Figure 4.6

*Diogenes pugilator*. Monthly variations of sex ratio (% females).

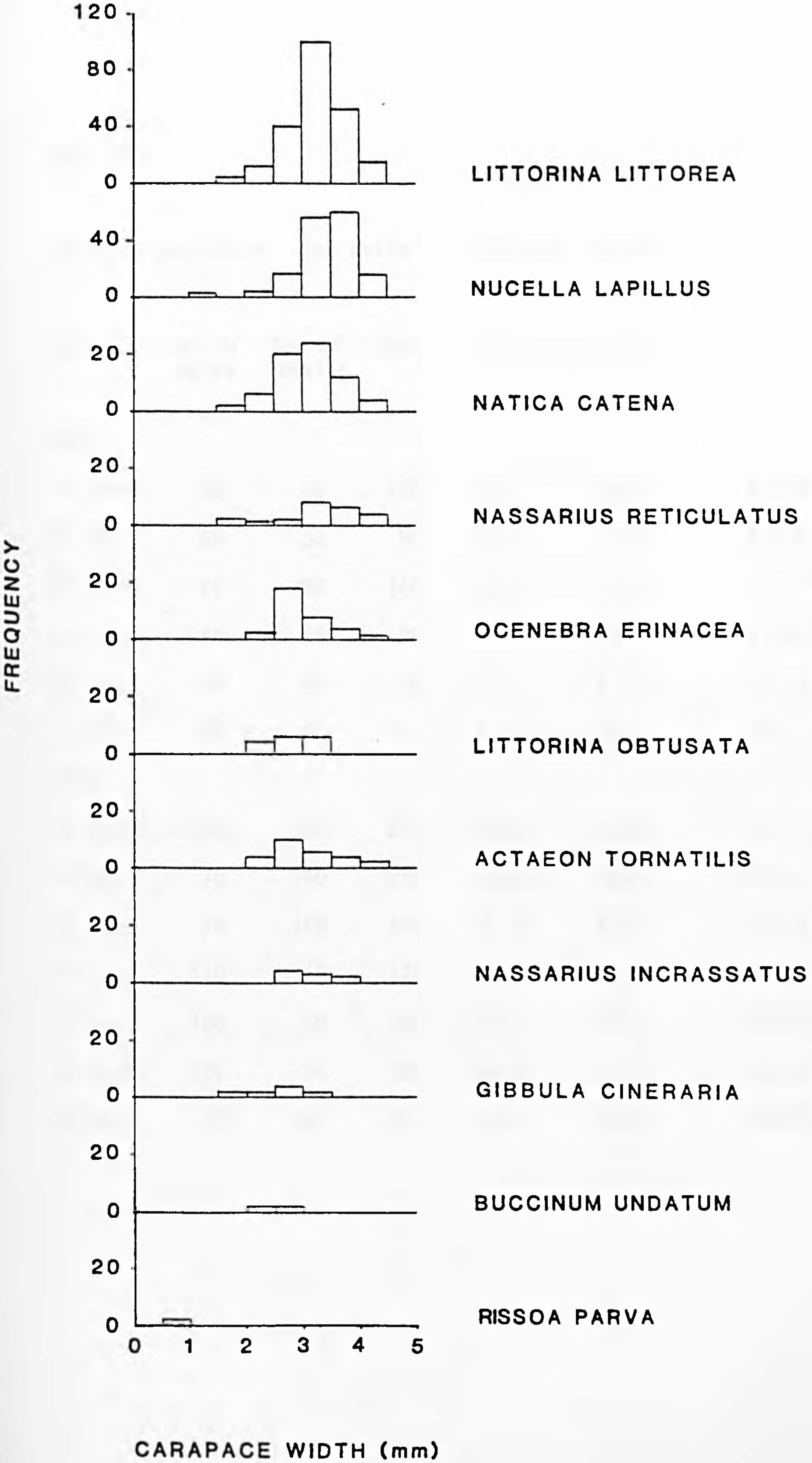

120
80
40
0
LITTORINA LITTOREA
40
0
NUCELLA LAPILLUS
20
0
NATICA CATENA
20
0
NASSARIUS RETICULATUS
20
0
OCENEBRA ERINACEA
20
0
LITTORINA OBTUSATA
20
0
ACTAEON TORNATILIS
20
0
NASSARIUS INCRASSATUS
20
0
GIBBULA CINERARIA
20
0
BUCCINUM UNDATUM
20
0
RISSOA PARVA
0
1
2
3
4
5
FREQUENCY
CARAPACE WIDTH (mm)

Figure 4.7

Size frequency distribution of *Diogenes pugilator* occupying littoral gastropod shells.

Table 4.1

*Diogenes pugilator*. Sex ratio in individual samples.

| Date | No. of males | No. of females | Total | % males | % females | Sex-ratio (♂/♀) |
|---|---|---|---|---|---|---|
| 1983 | | | | | | |
| 27 April | 80 | 40 | 120 | 66.7 | 33.3 | 1:0.5 P |
| 26 May | 60 | 30 | 90 | 66.7 | 33.3 | 1:0.5 P |
| 24 June | 60 | 80 | 140 | 42.9 | 57.1 | 1:1.3 P |
| 18 July | 40 | 58 | 98 | 40.8 | 59.2 | 1:1.6 P |
| 10 Aug. | 30 | 58 | 88 | 34.1 | 65.9 | 1:1.9 P |
| 7 Oct. | 50 | 20 | 70 | 71.4 | 28.6 | 1:0.4 P |
| 1984 | | | | | | |
| 16 April | 100 | 110 | 210 | 47.6 | 52.4 | 1:1.1 P |
| 15 May | 78 | 140 | 218 | 35.8 | 64.2 | 1:1.8 P |
| 11 June | 70 | 120 | 190 | 36.8 | 63.2 | 1:1.7 P |
| 4 July | 110 | 60 | 170 | 64.7 | 32.3 | 1:0.5 P |
| 14 Aug. | 100 | 50 | 150 | 66.7 | 33.3 | 1:0.5 P |
| 26 Sept. | 106 | 54 | 160 | 66.2 | 33.8 | 1:0.5 P |
| 25 Oct | 90 | 46 | 136 | 66.2 | 33.8 | 1:0.5 P |

Table 4.2 Species of gastropod shells inhabited by *Diogenes pugilator* (Roux) at Rhossili Bay during sampling period.

| | April 83 | May 83 | June 83 | July 83 | Aug. 83 | Sept. 85 | Oct. 83 | April 84 | May 84 | June 84 | July 84 | Aug. 84 | Sept. 84 | Oct. 84 | Total | % age | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Littorina littorea* | 30 | 32 | 49 | 35 | 50 | - | 22 | 140 | 98 | 80 | 72 | 65 | 69 | 45 | 787 | 42.8 | (1) |
| % age | 25 | 35.6 | 35 | 35.7 | 56.8 | | 31.4 | 66.7 | 45 | 42.1 | 42.4 | 43.3 | 43.1 | 33.1 | | | |
| *Littorina obtusata* | 0 | 4 | 7 | 7 | 1 | - | 2 | 5 | 0 | 2 | 5 | 7 | 8 | 10 | 58 | 3.2 | (6) |
| *Nucella lapillus* | 59 | 27 | 38 | 23 | 25 | - | 17 | 35 | 68 | 64 | 43 | 32 | 38 | 54 | 523 | 28.4 | (2) |
| % age | 49.2 | 30 | 27.1 | 23.5 | 28.4 | | 24.3 | 16.7 | 31.2 | 33.7 | 25.3 | 21.3 | 23.4 | 39.7 | | | |
| *Nassarius reticulatus* | 7 | 6 | 4 | 5 | 2 | - | 8 | 0 | 9 | 5 | 15 | 14 | 14 | 7 | 96 | 5.2 | (4) |
| *Nassarius incrassatus* | 0 | 2 | 0 | 2 | 1 | - | 2 | 1 | 15 | 7 | 2 | 0 | 0 | 2 | 34 | 1.8 | (8) |
| *Natica catena* | 23 | 10 | 23 | 11 | 7 | - | 7 | 23 | 23 | 19 | 19 | 12 | 15 | 12 | 204 | 11.1 | (3) |
| % age | 19.2 | 11.1 | 16.4 | 11.2 | 8 | | 10 | 11 | 10.6 | 10 | 11.2 | 8 | 9.4 | 8.8 | | | |
| *Ocenebra erinacea* | 1 | 4 | 5 | 4 | 1 | - | 9 | 4 | 3 | 11 | 11 | 13 | 13 | 2 | 81 | 4.4 | (5) |
| *Actaeon tornatilis* | 0 | 5 | 11 | 9 | 1 | - | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 42 | 2.3 | (7) |
| *Gibbula cineraria* | 0 | 0 | 2 | 1 | 0 | - | 1 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 10 | 0.5 | (9) |
| *Buccinum undatum* | 0 | 0 | 1 | 1 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0.2 | (10) |
| *Rissoa parva* | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0.1 | (11) |
| Total = 1840 | 120 | 90 | 140 | 98 | 88 | | 70 | 210 | 218 | 190 | 170 | 150 | 160 | 136 | | | |

Plate 4.1

The views of Rhossili Bay at low water. *Diogenes pugilator* were found to be abundant at this site.

Plate 4.2

A group of hermit crabs uncovered by a wave.

# CHAPTER 5

## Growth studies

## 5.1 INTRODUCTION

In arthropods, growth always occurs as a series of steps at each of which a new larger exoskeleton is produced. Each step or moult is a hazardous but necessary event in crustacean life (Passano, 1960). In addition to growth, moulting performs other functions such as the repair of damaged appendages, removal of metabolites, and preparation for incubation (Hartnoll, 1982) changes in the relative size of appendages etc., related to maturity, may occur.

For a hermit crab, moulting and growth pose special problems. It is assumed that when moulting the hermit crab must divest itself of its exoskeleton while in the restricted space of its shell and must remain in the shell until the new exoskeleton hardens. The increase in size that follows moulting requires the hermit crab to find a new larger shell to accommodate its larger body. This leads to a high level of shell exchange between hermit crabs and to a high demand for new shells. The soft body of the hermit crab must be protected at all times, especially from predators, and the hermit crab must choose the safest time and place in which to undergo a moult.

Growth rate of crustaceans is a function of moulting rate and the increase in size attained at each moult. Unlike fish where periodic markings on skeletal structures can be used for precise and accurate ageing (Menon, 1950; Bagenal, 1974), the age and growth of decapod crustaceans is very difficult to estimate reliably because most of the calcareous structures are shed during moulting. Methods that have been used to estimate growth and related factors such as mortality, migration and recruitment in crustaceans are:-

(a) rearing individuals in captivity (Forster, 1970; Chittleborough, 1976; Hartnoll, 1978).

(b) mark and recapture (Lindner and Anderson, 1956; Penn, 1975, 1976; Bennett, 1979; Edwards, 1979).

(c) analysis of size frequency data (Poole, 1967; Thomas, 1979; Pauly *et al*, 1984; Naylor, 1962).

Although numerous studies have been carried out on the physiology of moulting and the population dynamics of decapod crustaceans (typical papers can be found in Waterman, 1960, 1961; Cole, 1965; Thomas, 1979; Cobb and Phillips, 1980a, b; Gulland and Rothschild, 1984c), few data are available on the growth and related vital parameters of pagurid crabs.

McLay (1985), in his recent study of the moulting and growth in *Pagurus traversi* and *P. novizealandiae* and the effects of neighbours, reported that moulting probability decreased with increased size. Moult increments were independent of pre-moult size for both species and ranged from 29% for small animals to 2.9% for large animals. Male and female moult increments of *P. traversi* and *P. novizealandiae* were not significantly different. Both species had similar moult increments. Also he suggests that *P. traversi* are fast-growing, shorter-lived, small hermit crabs. Whereas *P. novizealandiae* are slower growing, longer-lived, large hermit crabs. Median and maximum life spans are: *P. traversi* males - 1.5, 4.9Y, females - 0.4, 2.2Y; *P. novizealandiae* males - 1.6, 10.9Y; females - 1.0, 6.5Y.

Other studies have shown that shell size affects moulting in hermit crabs. Markham (1968) investigated the effects of smaller and larger than normal shells on *Pagurus bernhardus* and found that animals given larger shells increased in size more at each moult and had shorter intermoult intervals. Fotheringham (1976 ) observed that growth of both *P. longicarapus* and *P. pallicarpus* decreased at each moult when given smaller shells. Growth of male *Clibanarius albidigitus* is affected by shell volume and weight (Bertness, 1981 ) and inadequate shells results in more energy being devoted to reproduction rather than growth (Bertness, 1981 ). Social dominance may also affect moulting. Mainardi and Rossi (1972) found that dominant individuals of *Diogenes pugilator* and *Dardanus arrosor* always moult first and their moulting was more frequent than other individuals. Dominance was usually associated with larger size. These studies suggest that availability of larger shells as well as the presence of other hermit crabs will have an important influence on growth.

Drapkin (1963), commenting on the effects of the introduction of the large Japanese prosobranch *Rapana bezear* to the Black Sea, notes that the hermit crabs *Clibanarius misanthropus* (Risso) and *Diogenes varians* Costa were both known only as dwarf races in the Black Sea before *Rapana* was introduced. Thereafter, individuals of both species were found which had attained the maximum size known in the Mediterranean, where larger gastropods occur naturally; further, *Diogenes* reared in the laboratory with access to *Rapana* shells reached the maximum size reported from the Mediterranean. Drapkin, however, gives no indication of the growth rate recorded under these conditions or when this crab had access only to native Black Sea snail shells.

Pike and Williamson (1959) raised individuals of *P. bernhardus* from larvae through a few post-larval stages. After giving some general figures on the size and duration of the first post-larval instars, they concluded (op. cit., p. 556) that "there is considerable difference both in frequency of moult and the growth at each moult, even between specimens kept under apparently identical conditions" and that thus "it is not possible to estimate the age of larger individuals".

Apart from absolute growth in size it is useful to examine relative or allometric growth in which the proportions of different structures change with each moult. In such morphometric studies the linear dimensions of different structures or weight are the most usual parameters studied. It might be thought that the stepwise growth of crustaceans might complicate such considerations. In fact, the separation of growth into distinct instars simplifies their study. It is easy to make accurate measurements of the rigid integument. Crustacea received considerable attention by early workers on relative growth (Huxley, 1924, 1927, 1932; Huxley and Richards, 1931). Studies were actually carried out on *Pagurus* (=*Eupagurus*) species at about that time. Bush (1930) examined the relative growth involved in the assymetry of *Pagurus prideauxi* and Bush and Huxley (1930) extended this to *P. bernhardus*. Each pereopod was found to have a slightly different growth rate.

Otherwise, changes in the allometry of growth are associated with onset of maturity or of growth phases (Hartnoll, 1982).

The object of the present study was to compare the growth characteristics of *Pagurus bernhardus* from intertidal and sublittoral populations including the onset of allometry of chela growth, and to attempt to determine the relationship between size and age. *Diogenes pugilator* was to be studied similarly as a comparison.

## 5.2 MATERIALS AND METHODS

### 5.2.1 Morphometric relationships

The relationships between various linear body measurements, e.g. carapace width, carapace length, chela length and weight of the hermit crabs, *Pagurus bernhardus* (L.) and *Diogenes pugilator* (Roux) were plotted, and their regression growth equations calculated.

The measurements used for this purpose were derived from specimens being examined as part of the monthly sampling programmes.

### 5.2.2 Laboratory growth studies

Hermit crabs were collected from the same three sampling sites around the Gower area used in other aspects of this study; *Diogenes pugilator* from Rhossili Bay at low tide, small specimens of *Pagurus bernhardus* intertidally from Mumbles Head, and large specimens of the same species from Oxwich Bay by trawling (see Chapter 2).

In the laboratory, individual specimens (10 male and 10 female) of *D. pugilator* were placed in plastic containers measuring 9.5 cm diameter and 5.5 cm depth. Sea water on tap was piped along a main tube and through smaller secondary tubes leading to individual containers (Fig. 5.1A) from which it overflowed via four small holes in the side of each container (Fig. 5.1B). The experiment with *D. pugilator* was commenced on 31st July 1985 and terminated on 29th June 1986.

The same apparatus and technique was used for 10 males and 10 females of *Pagurus bernhardus* (small intertidal specimens), commencing on 31st July 1985 and terminated on 30th June 1986.

Another ten hermit crabs were selected randomly from Mumbles Head, and they were reared in the marine science laboratory for about nine months. All ten hermit crabs were offered larger shells such as *Natica catena* and small *Buccinum* shells.

Large specimens of *P. bernhardus* (10 males and 10 females) were kept individually in a similar apparatus but using large plastic containers (22 cm length, 15 cm width and 14.5 cm depth) (Fig. 5.1C). The experiment with large specimens of *P. bernhardus* was run simultaneously to that with small specimens. All of the hermit crabs in these experiments were offered an unrestricted supply of *Mytilus edulis* L. as food. The crabs were inspected daily for moulted exuviae. Any of these were collected and preserved in 4% sea-water formalin. The carapace width and length were measured from the cast exoskeleton for the small crabs, and from the live crab for the large ones.

Temperature, salinity and pH of the recirculating seawater were recorded daily.

## 5.3 RESULTS

The results in this chapter fall into 2 groups. The first group represents data derived from field samples. The second comes from laboratory experiments.

### 5.3.1 Relation between carapace length and carapace width (field samples)

The relationship between carapace length and carapace width of combined males and females of *Pagurus bernhardus* collected intertidally is shown in Figure 5.3. It can be seen that there is a very strong relationship between the two variables, and that they are linearly related. The regression line is a straight $P < 0.01$.

The sublittoral *P. bernhardus* showed the same relation between carapace length and width for both sexes together (Fig. 5.4).

The relationship between carapace length and carapace width for the hermit crab, *Diogenes pugilator*, is shown in Figure 5.5. These results were obtained from the monthly samples, and show a very strong linear relationship between these two variables at $P < 0.01$.

### 5.3.2 Weight and size

Rough wet weights of whole hermit crabs (removed from their shells) were recorded for both *P. bernhardus* and *D. pugilator*. These were plotted against carapace length or carapace width.

Figure 5.6 represents the raw data from a random collection of intertidal *Pagurus bernhardus*. These showed the size range typical of intertidal specimens and the weights are plotted against carapace width. Different symbols are used for gravid and non-gravid females and for males. It can be seen that for any given size, males are heavier than non-gravid females but heaviest are gravid females (including their eggs).

It can be seen from Figure 5.6 that the data follow an exponential path. In Fig. 5.9 another set of weight data is plotted on a log-log base where they conform to a fitted straight line distribution.

In the case of *Diogenes pugilator*, raw wet weight data were again plotted against carapace width with different symbols for gravid and non-gravid females and males (Figure 5.7). These hermits were collected at Rhossili Bay in July 1987 when the random sample was unbalanced - with very small females and large males. The sample is described in Chapter 4. The overall weight distribution is plotted in Figure 5.8.

Despite the imbalance in the sample it is clear that for a given carapace width, gravid females are heavier than non-gravid and males are heavier still. The data clearly fall on an exponential curve. A set of grouped data was plotted on a log-log base for males and females separately and they showed agreement to a fitted straight line distribution.

It is of interest to note that the smallest gravid specimen weighed < 0.1 g. The heaviest *D. pugilator* (4.7 mm carapace width) weighed c. 0.8 g.

### 5.3.3 Relation between major chela length and carapace width

Initially the data for chela length and carapace width were plotted on an arithmetic grid. Figure 5.11 gives a computer plot of raw data of a sample of intertidal males and females together with data from a sublittoral sample. It was evident that chelae of the largest males exhibited faster growth. Using additional data from sublittoral samples that included small specimens, grouped data were used and it became evident that there was a change in the chela growth rate of males at a carapace width of about 12 mm. The data were now subjected to analysis by the allometric growth curve equation using a Casio fx 7000G calculator and the programme for power regression. Separate plots were made for the calculated regression lines for the different subgroups namely: intertidal males, intertidal females, sublittoral females, sublittoral males less than 12 mm carapace width and sublittoral males over 12 mm carapace width. The values were plotted on log-log graph paper and are given in Figure 5.12, which also gives the growth constants A and B for each plot. It can be seen that the values for the growth of sublittoral female hermits (5) and males under 12 mm (3) are very similar. Intertidal males (1) and females (2) on the other hand, are divergent. This is also shown in fig. 5.12B.

In *Diogenes pugilator* the relationship between the length of the major chela and the carapace width was shown for both males and females in figures 5.13 and 5.14. It has been noted during the period of study in the field and during the examination of the hermit crabs in the laboratory that the males of *D. pugilator* have a larger major chela than the female. The maximum value for male major chela was greater than 25.0 mm and 17.0 mm for female. The minimum 9.0 mm for males and 7.0 mm for females. Figure 5.14 also shows the difference between the length of the major chela and the size of the carapace for both sexes, with calculated regression lines ($P < 0.01$).

### 5.3.4 Laboratory Growth Studies

#### 5.3.4.1i *Pagurus bernhardus*

The results of the laboratory growth studies on *P. bernhardus* are given in figures 5.15-5.17 and Tables 5.1, 5.2, 5.3 and 5.7.

The hermits survived well, and exhibited growth in size in the experimental assembly. They frequently accepted a new gastropod shell offered and moved into it. Some of the hermits survived in captivity until the end of the experiment (up to one year). Data relating to 71 moults in captivity were recorded. Positive growth in size was recorded at every moult.

Tables 5.1, 5.2 and 5.3 record the data for individual hermits, and Figures 5.15, 5.16 and 5.17 set these out graphically. As seen from Table 5.7 moults occurred in most months of the year with no clear seasonal peaks in the moulting rate either in the combined results or for each sex separately. The mean number of moults survived per crab was more than 2.0. The maximum number of moults of a hermit in these experiments was four. The results obtained from intertidal and sublittoral crabs, which also represent two different size groups, were either recorded separately or together as appropriate.

The relationship between premoult and postmoult carapace size for both sexes of *P. bernhardus* are shown in figure 5.19. There was a linear relationship between these two variables for both sexes.

#### 5.3.4.1 Growth increment

The growth increment at a moult was measured in millimetres difference between premoult and postmoult carapace width. This was recorded for every moulting hermit and plotted in figure 5.26 against premoult carapace width. The data for both the intertidal and sublittoral series are plotted together. The mean figure for the intertidal hermit was 0.425 mm. The mean for males was 0.42 mm and females 0.43 mm. The minimum increment for both males and females was 0.2 mm. The maximum increment for males was 0.7 mm and 0.6 mm for females. The corresponding data for the sublittoral crabs was as follows: The mean figure for the sublittoral hermits was 0.64 mm. The minimum increment for males was 0.3 mm and 0.2 mm for females. The maximum increment for males was 0.9 mm and 1.0 mm for females. For the intertidal crabs offered larger shells, the mean growth increment was larger (0.78 mm) and the maximum growth increment was 1.2 mm.

### 5.3.4.1ii <u>Growth factor</u>

Growth factor relates the growth increment to the premoult carapace width as a percentage increase in size. This is plotted in figure 5.22 with the overall mean value for intertidal hermits of 10.1% and for sublittoral 5.2%. The means, maximum and minimum for males and females separately is as follows: males, mean 8.9%. Males maximum 13.7%, minimum 4.3%. Females means 10.6%, maximum 16.2%, minimum 5.1%. For sublittoral hermits the corresponding figures are as follows: Males, mean 5.3%. Males maximum 7.6%, minimum 2.3%. Females mean 5.9%, maximum 10.9%, minimum 1.8%. Intertidal hermits offered larger shells gave a mean growth increment of 14.6 mm and a maximum of 22.0%.

### 5.3.4.1iii Intermoult duration

The duration of the intermoult in days had an overall mean value of 73.4 days. There was little difference between the value for the intertidal specimens and the sublittoral ones (5.24).

### 5.3.4.1iv Increment per week

Finally, the increment in terms of growth (mm of carapace width) per week was plotted against premoult carapace width. This value proved to be very variable (see figure 5.28). The mean value for sublittoral hermits, 0.061 mm/wk, was slightly higher than for intertidal animals, 0.053 mm/wk. There was wider spread for females than males both for the intertidal and sublittoral hermits. For intertidal *P. bernhardus* offered larger shells the values were:- mean 0.87 mm. Extreme values can be seen from the figures.

The data from these various studies on growth were used to construct a hypothetical growth curve (Fig. 5.30).

### 5.3.4.2 *Diogenes pugilator*

Results obtained from the laboratory growth studies on *D. pugilator* are shown in figure 5.18 and Tables 5.6 and 5.7.

A few of the hermit crabs died within three months of starting the experiment. The rest of them survived well, and they exhibited growth in size in this experiment. Between moults they were offered a new gastropod shell and moved into it. Some of the specimens survived until the end of the experiment. Data relating to 31 moults in captivity were recorded. At each moult the increase in size of the crab carapace width was recorded.

Table 5.6 recorded the data of individual hermits and figure 5.18 set this out graphically. Table 5.7 shows two peaks, one in spring between March and June, and the other in late summer between August and October. No moults occurred during January and February. The mean number of moults survived per hermit crab was 1.94. The maximum number of moults by a hermit in these experiments was three.

The relationship between premoult and postmoult carapace width of *D. pugilator* is shown in figure 5.20.

### 5.3.4.2i Growth increment

The growth increment at each moult was measured in millimetres difference between premoult and postmoult carapace width. These data were recorded for every moulting hermit crab and plotted in figure 5.27 against premoult carapace width. The mean increment for these hermit crabs was 0.35 mm. The mean for males was 0.34 mm and females 0.36 mm. The minimum increment for both males and females was 0.2 mm. The maximum increment for both males and females was 0.5 mm.

### 5.3.4.2ii Growth factor

Growth factor relates the growth increment to the premoult carapace width as a percentage increase in size. This is plotted in figure 5.23 and shows an overall mean value 10.2%. The means, maximum and minimum for males and females separately is as follows: Males, mean 9.2%, males maximum 14.3%, minimum 5.0%. Females 11.2%, maximum 16.9%, minimum 5.7%.

### 5.3.4.2iii Intermoult duration

The duration of the intermoult in days had an overall mean value of 118.5 days. This was plotted in figure 5.25.

### 5.3.4.2iv Increment per week

Finally, the increment in terms of growth (mm of carapace width) per week was plotted against premoult carapace width (see figure 5.29). The mean value for both sexes was 0.018 mm/wk.

The data which were obtained from these various studies on growth were used to derive a hypothetical growth curve (Fig. 5.30).

## 5.4 DISCUSSION

### 5.4.1 Morphometric analysis

#### 5.4.1.1 Carapace size and weight

The relationship between length and width of the carapace is seen to be a simple isometric one for both intertidal and sublittoral populations of *Pagurus bernhardus*. Very similar values were obtained for the regression constants for both populations. Either parameter is a good measure of size. A similar relationship held for the carapace dimensions of *Diogenes pugilator*.

Body weight data were not available for sublittoral *P. bernhardus*. For the intertidal population there was a straight line relationship when weight was plotted against carapace length on a log-log base. This is similar to other crustaceans (see, for instance, Choy, 1986). Again, the same was true for *Diogenes pugilator* for the few weight data available.

The greater weight difference between males and females of *D. pugilator* is probably a result of the males having a much larger major chela than does *P. bernhardus*.

#### 5.4.1.2 Chela size

The whole subject of allometric growth of the limbs of the hermit crab, *Pagurus prideauxi*, was investigated very thoroughly by Bush (1930) working under the supervision of Julian S. Huxley who had made a special study of relative growth (Huxley, 1924, 1932). Huxley consolidated the use of the equation $Y = AX^B$ for allometric growth. Bush examined the asymmetrical growth rates of left and right side limbs and compared rates of growth of neighbouring limbs. He even studied the rates of growth of individual articles of a single limb. Bush (1930) paid particular attention to the chelae, both left and right, of male and female. However, there were limitations to his study; he gave very few examples of the value of the constant B; the smallest of the size groups in his study consisted of crabs of carapace length 8.8-9.7 mm; also he was clearly unaware of the size at which puberty occurred in these hermits.

There was no need or intention to make such a thorough study of relative growth in *P. bernhardus* in the present work. Attention was confined to total length of major chelae of male and female at different sizes, intertidally and sublitorally. *P. bernhardus* is closely related to *P. prideauxi* so similarities in growth form are to be expected.

Plots of chela length against carapace size of *Pagurus bernhardus* were complex but consistent. The most marked feature was a change from slightly negative (B = 0.922) to strongly positive (B = 1.701) allometric growth of the major (right) chela in the largest male sublittoral crabs. Such a change was also seen in *P. prideauxi* by Bush (1930, page 64) at a carapace length close 11.36 mm although in that species the rate was slightly positive before the change. It occurred in *P. bernhardus* at about 12.0 mm carapace width. There was no similar increase in the growth rate of the major chela of sublittoral females which remained slightly negative (B = 0.869) unlike *P. prideauxi* in which it was almost isometric. Two points of special interest need to be discussed here. Firstly, it should be stressed that the start of this positive allometry in *P. bernhardus* is not associated with puberty as it often is in crabs and as Bush

(1930) presumed it was in *P. prideauxi*. Puberty in both sexes of *Pagurus bernhardus* occurs at a very small size (see Chapter 6). The second point concerns the nature of the allometry. Hartnoll (1982) points out that allometry of size can resemble allometry of growth, particularly when allometry of size is associated with terminal ecdysis. There is no published work on the incidence of terminal ecdysis in hermit crabs. Some species, e.g. *Birgus*, occasionally grow to a very large size suggesting that growth is not so limited. On the other hand, for a species such as *Pagurus bernhardus*, there is an upper size limit set by the availability of large *Buccinum* shells. But it is argued elsewhere that the available gastropod shells might set the size limits to hermit growth. Arguing against allometry of size as the correct interpretation is the wide carapace size range involved (12-18 mm+). On balance, this seems to be an example of allometry of growth.

The function of very large male major chela in hermit crabs has been extensively studied and is usually quite clearly involved in promoting success of males in agonistic encounters over shell ownership and insemination of females (Hazlett, 1970). Its very late onset in *P. bernhardus* well separated from puberty, could be evidence of a function associated with competition for the largest available shells. Suitable large *Buccinum* are likely to be a limiting resource.

Growth curves of major chelae of all the sublittoral females and of those sublittoral males under 12.0 mm carapace width are very similar and parallel (see 3 and 5, Fig. 5.12). The calculated lines in this figure (5.12) are based on 63 and 61 specimens for males and females respectively, both indicate slightly negative allometric growth, with growth constant B valued at 0.862 and 0.869 respectively. This seems to be in contrast with *P. prideauxi*. Bush's (1930) results do not indicate a phase in which the male chela growth is isometric, let alone negatively allometric, although as mentioned earlier, this could be partly explained by the restricted size range of the material available to him.

The major chelae of intertidal *Pagurus bernhardus* unlike those of the smaller sublittoral specimens, show a difference between the sexes. Chelae of intertidal males grow faster than those of intertidal females (1 and 2, Fig. 5.12). Thus the larger intertidal male *Pagurus bernhardus* have larger chelae than similar sized females. When handling them, even on the beach the sexes can be distinguished by this difference. Sublittoral crabs of this size have similar sized chelae in male and female and sexes cannot be told apart so easily. This difference has been checked on several samples of intertidal hermits in addition to those figured (Fig. 5.12A and 5.12B).

A striking comparison can be made between intertidal and sublittoral males. In both cases the largest males (intertidal ones in *Littorina littorea* shells and sublittoral ones in *Buccinum* shells) have much larger major chelae than the same sized females, a difference between the sexes which does not apply to small (say 5 mm) sublittoral hermits. Investigation of the growth mechanism involved is beyond the scope of this study. Two possibilities spring to mind. Perhaps the onset of positive allometry of chela growth is related to a particular instar and that telescoped growth of intertidal hermits results in the start of positive allometry occurring in much smaller crabs. More likely male chela growth is ecotypically related to competition for scarce large shells as carcinoecia.

The generally smaller size of chelae in both males and females of intertidal hermits (see Fig. 5.12) is strange but appears adaptive if it is accepted that these intertidal crabs are restricted in growth by lack of larger shells.

Altogether the revealed patterns of chela growth indicate and confirm profound differences between intertidal and sublittoral stocks, especially when specimens of the same carapace size are compared. This adds weight to the hypothesis that intertidal and sublittoral stocks are normally discrete and do not intermix. A full explanation in terms of growth patterns or adaptive significance can only be speculative.

Major chela growth patterns in *Diogenes pugilator* are consistently different between male and female. Larger size of the male chela results from a faster growth rate which starts at a young age perhaps related to puberty.

### 5.4.2 Growth rate studies

The most sophisticated growth rate studies so far reported on hermit crabs are those of McLay (1985) on two species in New Zealand. Moulting was monitored amongst hermits maintained in individual compartments in circulating seawater at temperatures of 17-20°C over a period of only two months. Data on probability of moulting were used to calculate a mean intermoult duration for each sex of both species, in an experiment involving 127 specimens. There was a fairly wide scatter to his results much as in the present study. The mean values obtained were used to produce growth curves. McLay deduced that the females of both of his species grew faster than the males and thereby took considerably less time to reach maximum size. For one of his species, *Pagurus novizealandiae*, he calculated a life span of 6.5 and 10.9 years for females and males respectively, and for the other species, *P. traversi*, 2.2 and 4.9 years for females and males. These values seem somewhat excessive for such decapods at these latitudes and should be treated with caution. His assumption that growth rate observed over a two month period was typical of all seasons, is open to criticism. However, McLay is probably correct in concluding that the growth format (Hartnoll, 1982) of these hermit crabs is indeterminate and that the overall growth curve is exponential.

In the older study of Markham (1968), it was concluded that the growth rate of *Pagurus bernhardus* depended on the availability of alternative gastropod shells. Growth was depressed if larger shells were not available. Markham's studies were carried out with hermits in the size range 4.7-9.2 mm carapace length, and mostly in the 6-7 mm range. His results also showed a very wide spread even within one treatment. The maximum growth factor he reported was 18.7% (Fig. 5.21). His mean intermoult duration was 95.2 days. Markham concluded that the males of *P. bernhardus* had a faster growth rate than females.

Other estimates of the growth rate of *P. bernhardus* include those of Pike and Williamson (1959) who concluded that intertidal specimens inhabiting *Littorina littorea* shells were probably under two years old.

In the present study of *P. bernhardus* a similar wide spread of results was obtained. Two separate experiments using the small, intertidal hermits, gave some corroboration of Markham's findings on the influence of shell size on growth rate. Several points of particular interest are apparent in the results. When intertidal hermits were provided with a suitable larger shell, more than 50% of them moulted within seven days putting on a relatively small increment. This did not seem to be a seasonal moult but two other explanations are possible. Perhaps this was a moult which had been 'held back' in the absence of a larger shell or secondly perhaps it was a moult intended to end a slow growth phase in preparation to begin a faster growth rate. Two exceptionally high values for increment in terms of mm per week need comment. They could be the result of experimental error. However, both arise as a result of a combination of high growth factor and low intermoult duration neither of which were in themselves exceptional.

A notable feature of these experiments was that the moulting rate of larger hermits was very similar to that of small ones. The growth factor was however reduced. When the calculated mean values of increment in terms of mm/week were converted, annual values in the order of 2.5 or 4.5 mm per annum were found. The higher value applied when larger gastropod shells were available and in these circumstances the growth of males was faster than females.

In the estimated growth curves (Fig. 5.30) two types of information have been used. Firstly, growth rates as discussed above and secondly field data about recruitment. The curves originate at the time of peak recruitment and use the mean size of the observed recruits. The observed size of the smallest gravid females gives an indication of actual growth in the field during the first year of life. Three curves are given for *P. bernhardus*, one represents growth rate based on the low values achieved when larger shells are not available; the second and third (male and female) indicate the higher rates of growth that occur when they are present. It is postulated that these rates of growth are those that apply intertidally and sublittorally respectively. Although these results need to be treated with caution they suggest that intertidal crabs may attain an age of at least three years and that the largest sublittoral specimens are probably at least four or five years old.

A growth curve for *Diogenes pugilator* has been produced in the same way. A seasonalised growth curve is added in this case. *Diogenes* is seen to be a slow growing hermit. Field data (Fig. 4.5) of this species add some corroboration for the age span suggested, namely three and sometimes four years.

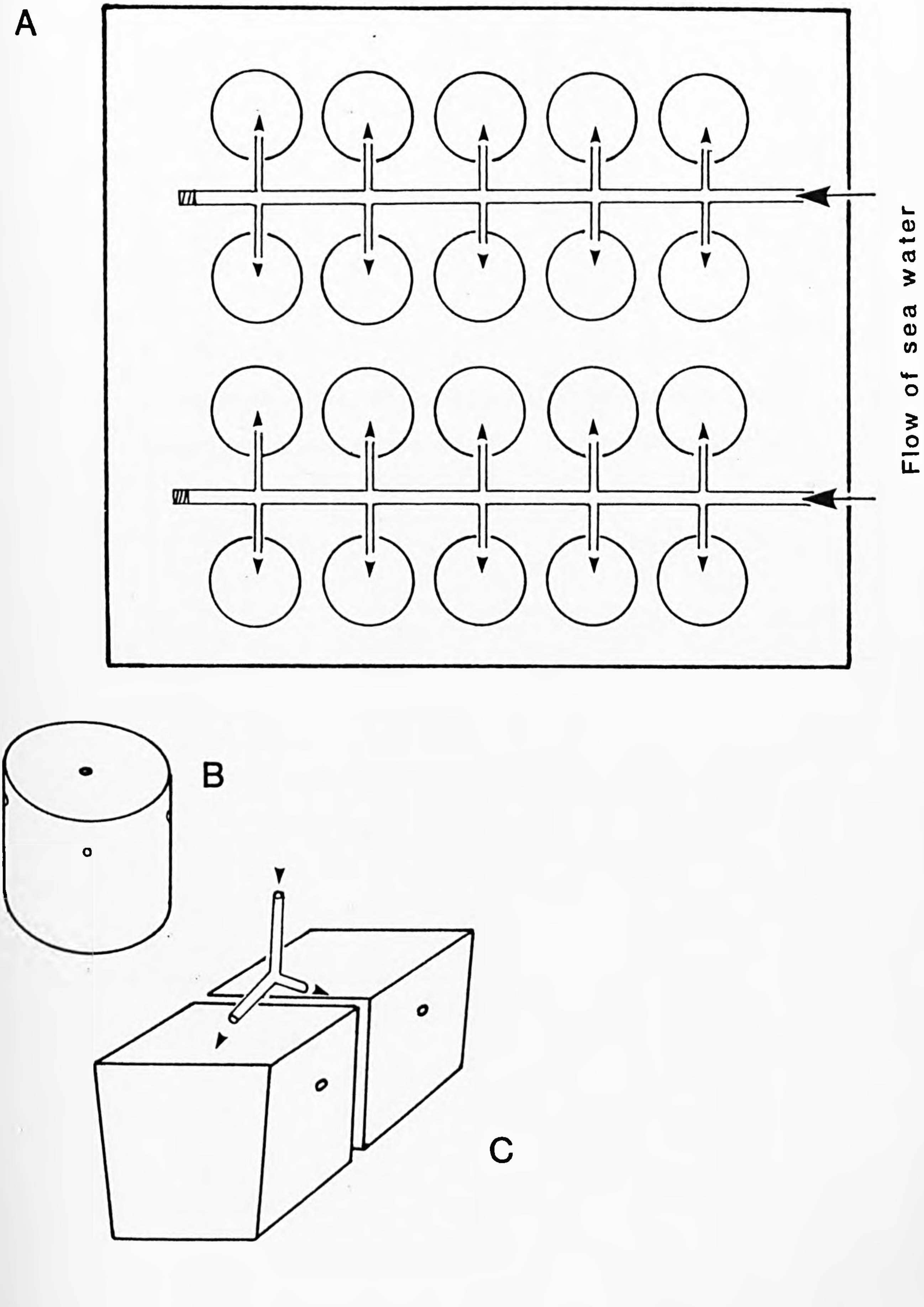

A
Flow of sea water
B
C

Figure 5.1

A Diagram showing compartments used to hold hermit crabs during growth experiments. Arrows indicate direction of seawater flow.

B View of one of the compartments with holes setting the level of seawater.

C View of two plastic ice-cream containers used to hold large hermit crabs during the experiment.

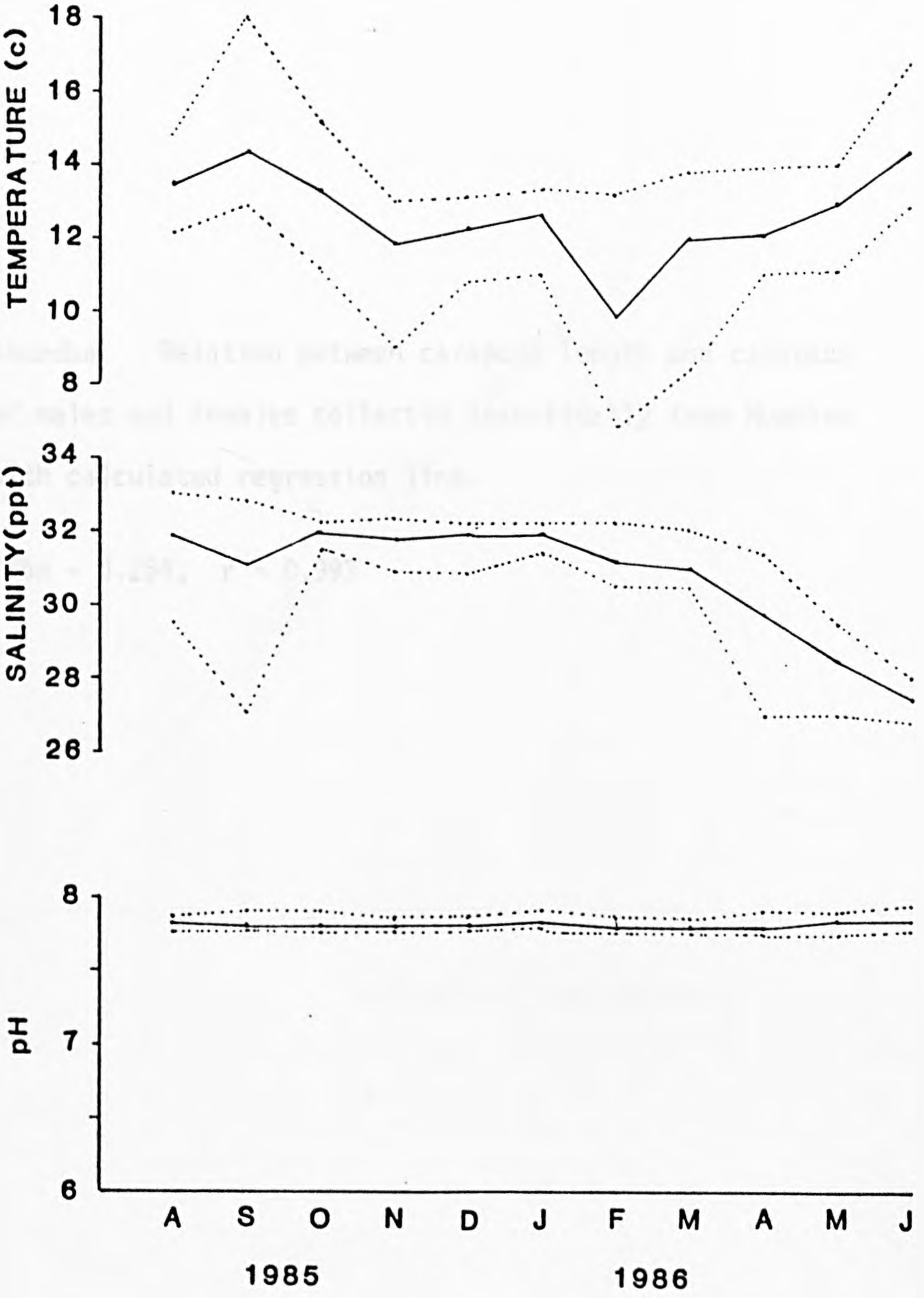

TEMPERATURE (c)
8
10
12
14
16
18
SALINITY(ppt)
26
28
30
32
34
pH
6
7
8
A
S
O
N
D
J
F
M
A
M
J
1985
1986

Figure 5.2

Monthly variation in temperature, salinity and pH of the recirculating seawater in which hermit crabs were reared during 1985-1986.

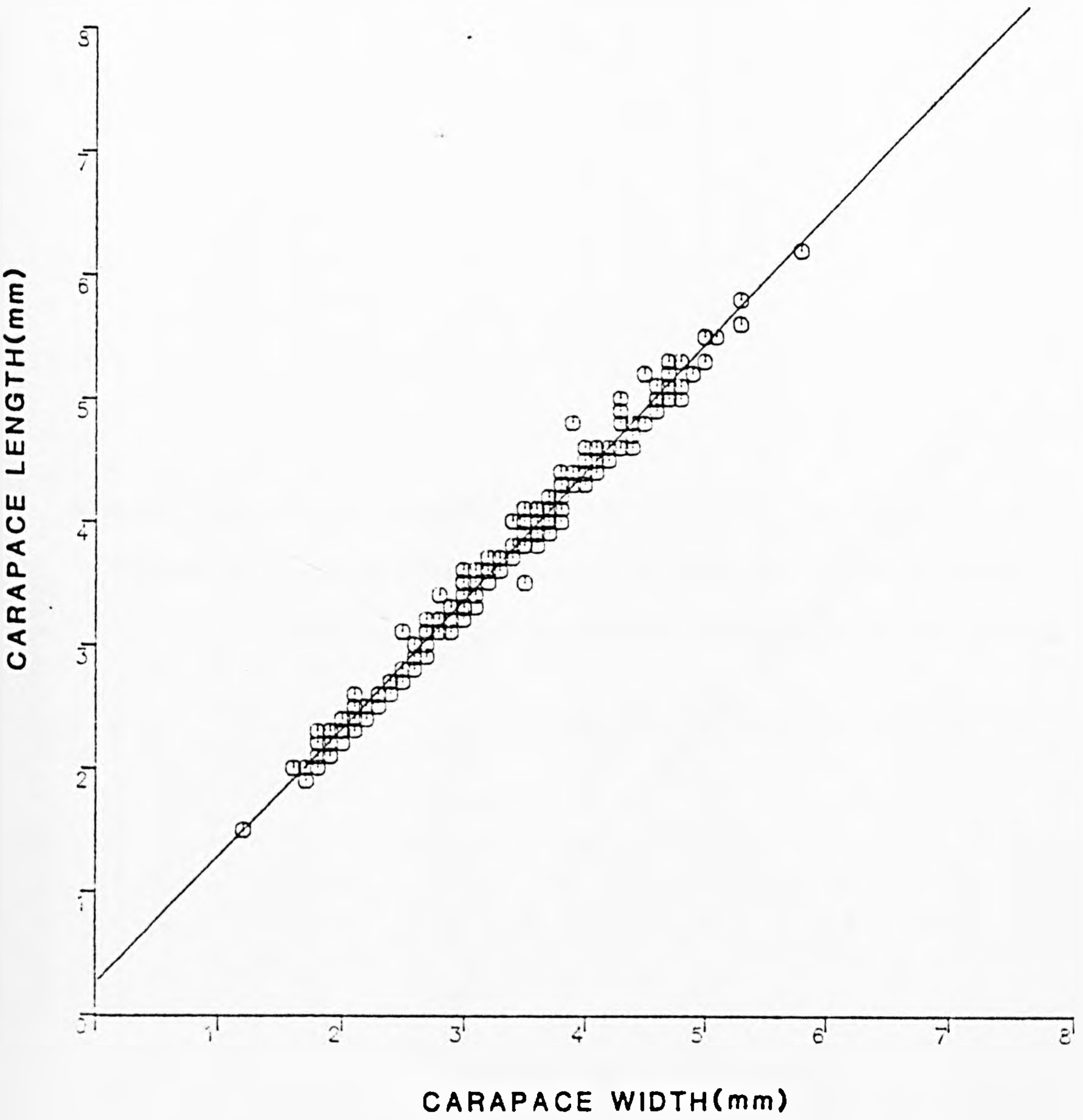

CARAPACE LENGTH(mm)
CARAPACE WIDTH(mm)
0
1
2
3
4
5
6
7
8
1
2
3
4
5
6
7
8

Figure 5.3

*P. bernhardus*. Relation between carapace length and carapace width of males and females collected intertidally from Mumbles Head, with calculated regression line.

$y = 1.036x + 0.254$; $r = 0.993$

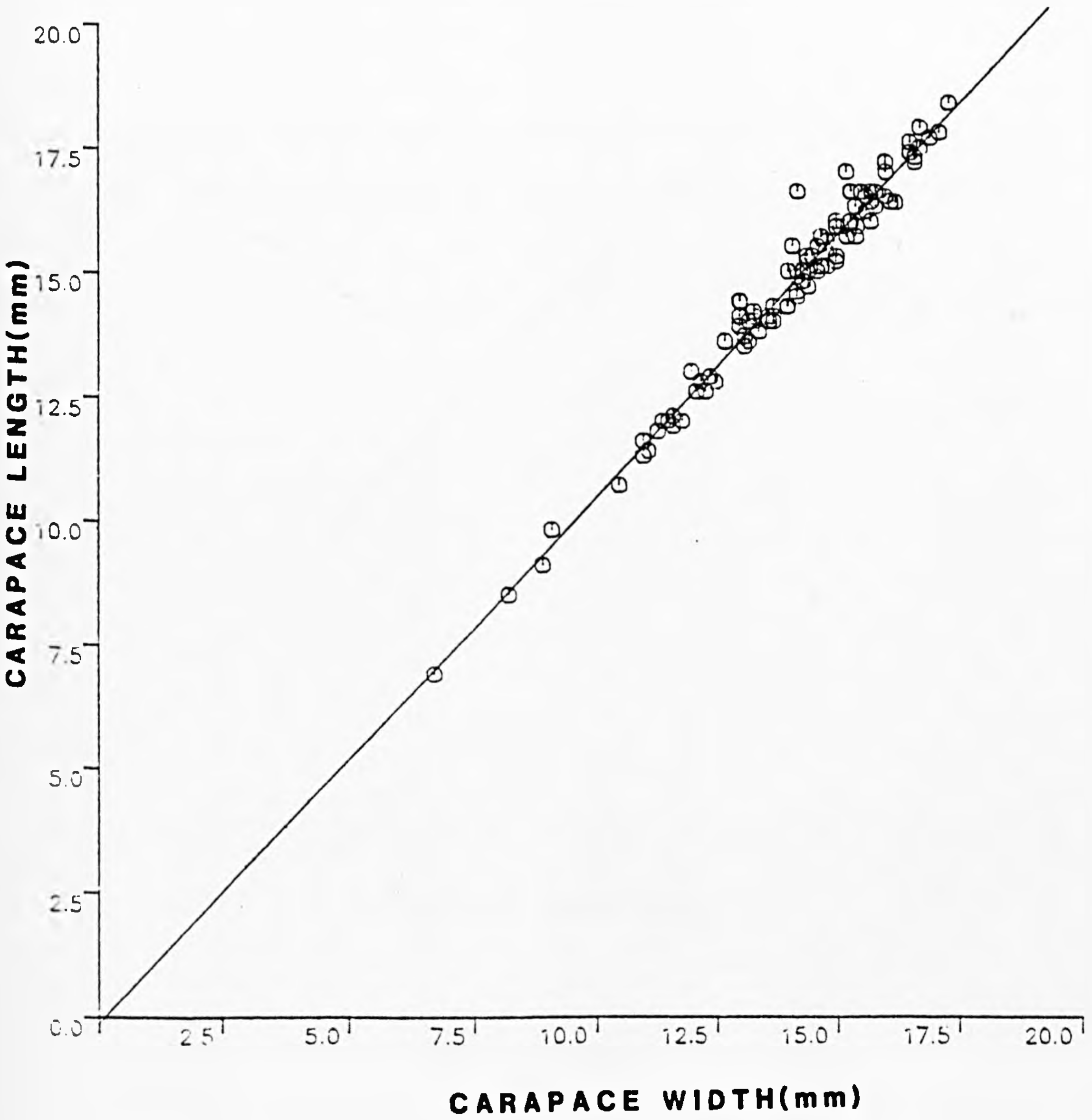

CARAPACE LENGTH(mm)
20.0
17.5
15.0
12.5
10.0
7.5
5.0
2.5
0.0
2.5
5.0
7.5
10.0
12.5
15.0
17.5
20.0
CARAPACE WIDTH(mm)

Figure 5.4

*P. bernhardus*. Relation between carapace length and carapace width of males and females collected sublitorally by dredging from Oxwich Bay, with calculated regression line.

$y = 1.057x - 0.128$; $r = 0.986$

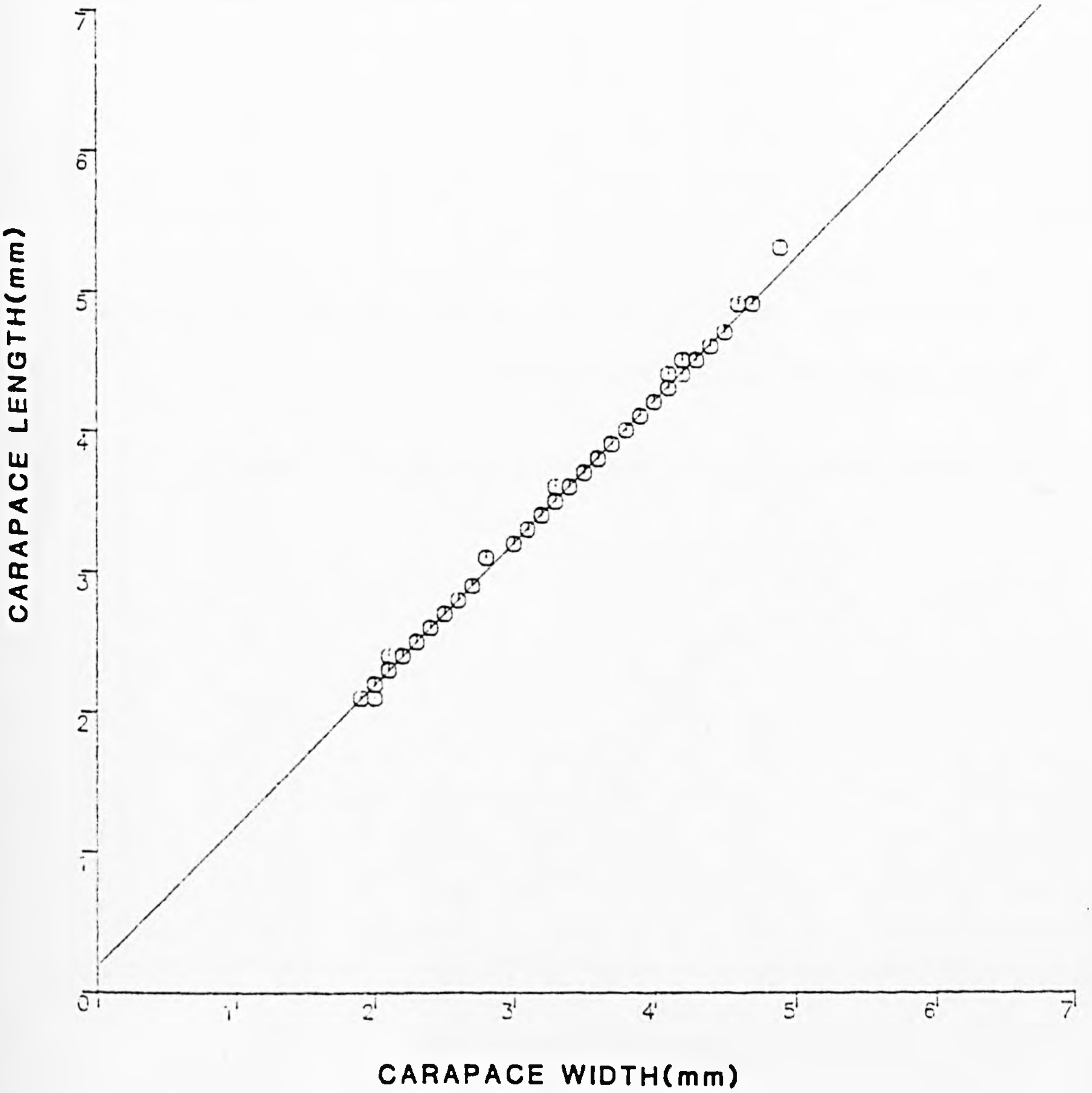

CARAPACE LENGTH(mm)
CARAPACE WIDTH(mm)
0
1
2
3
4
5
6
7

Figure 5.5

*D. pugilator*. Relation between carapace length and carapace width of males and females, with calculated regression line.

$y = 0.182 + 1.007x$; $r = 0.999$

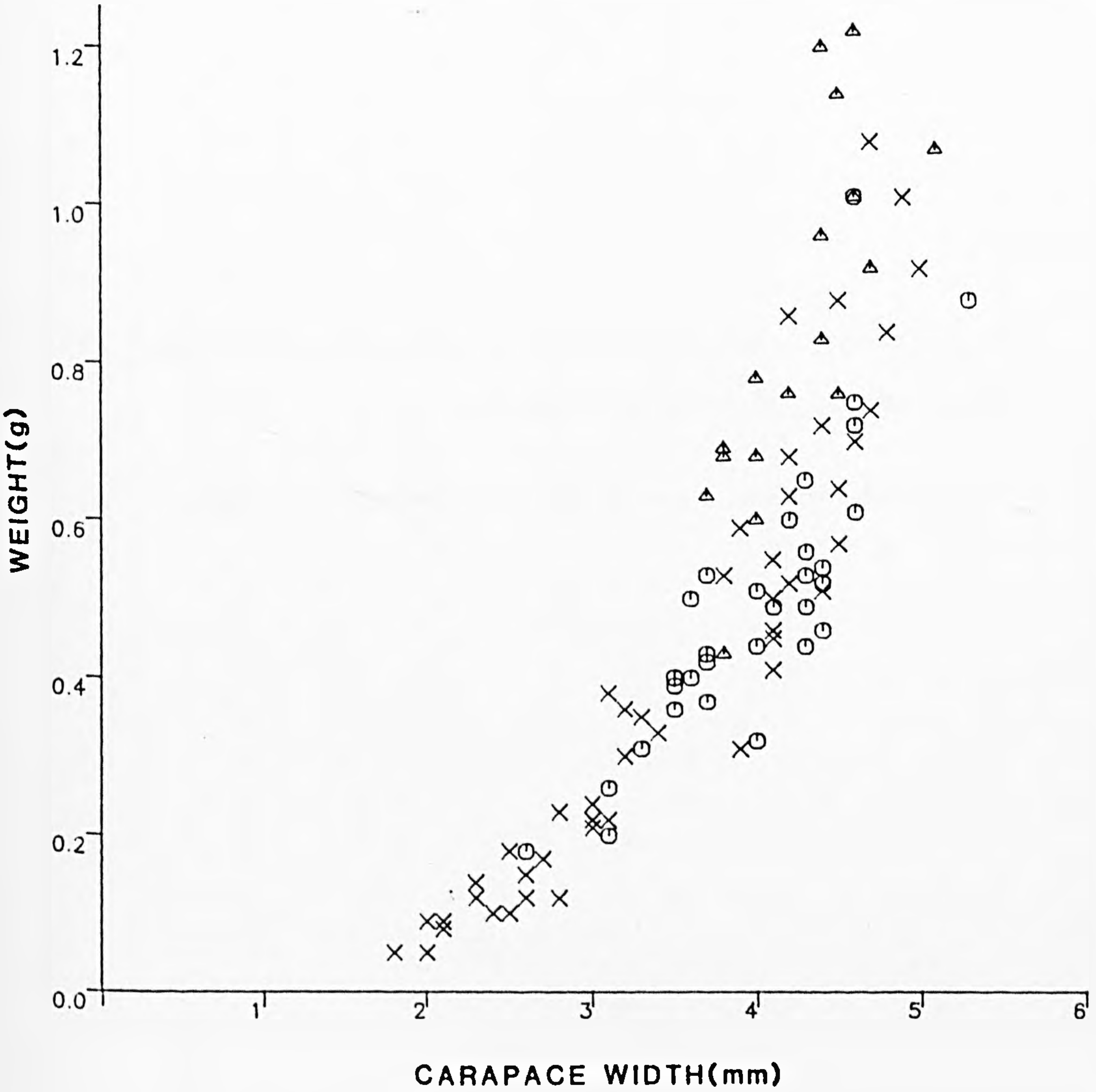

1.2
1.0
0.8
0.6
0.4
0.2
0.0
WEIGHT(g)
1
2
3
4
5
6
CARAPACE WIDTH(mm)

Figure 5.6

*P. bernhardus*. Relation between weight and carapace width of males, gravid and non-gravid females.

Δ = gravid female; o = non-gravid female; X = male

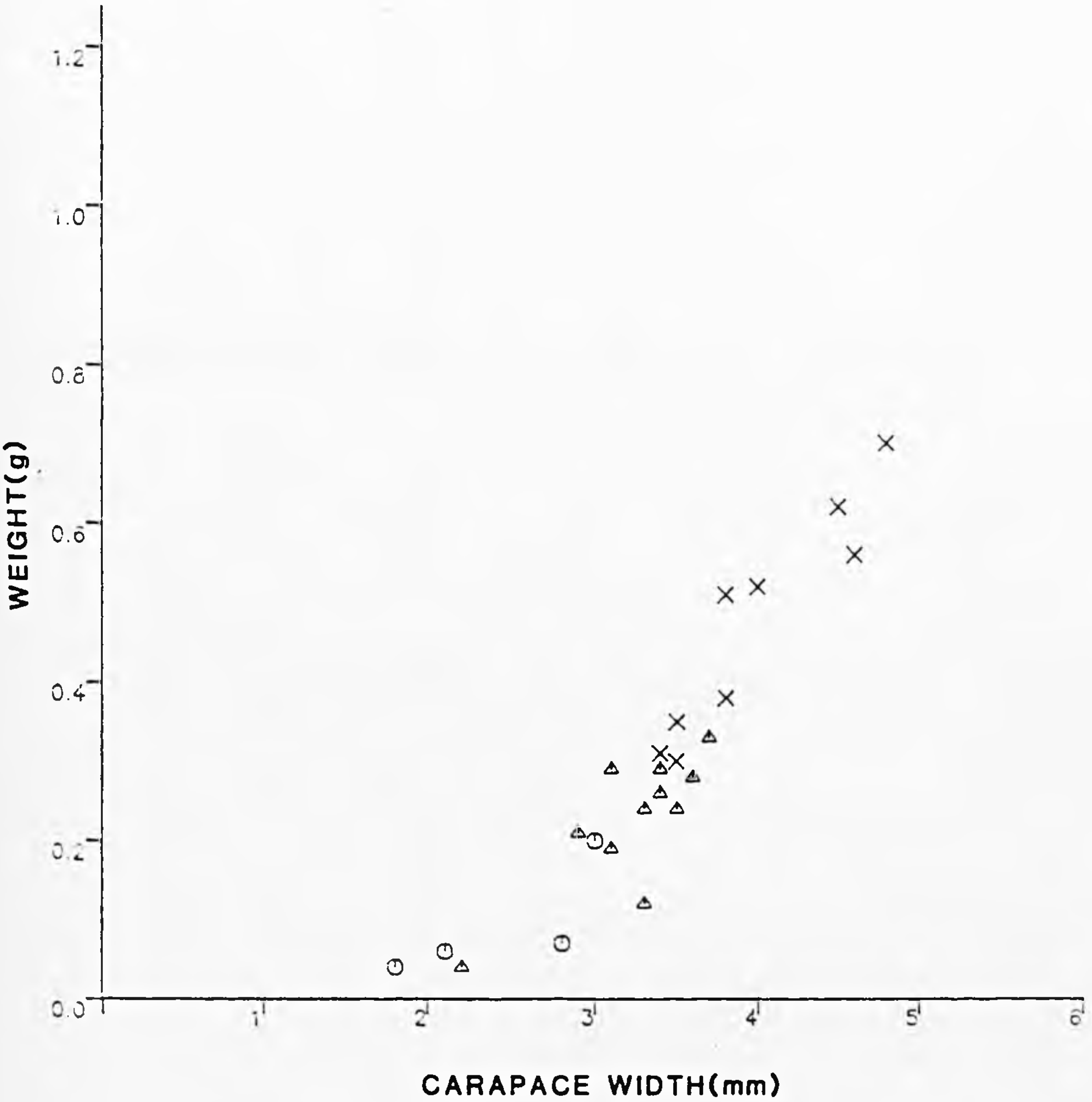

WEIGHT(g)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
CARAPACE WIDTH(mm)

Figure 5.7

*D. pugilator*. Relation between weight and carapace width of males, gravid and non-gravid females.

Δ = gravid females; o = non-gravid females; x = males

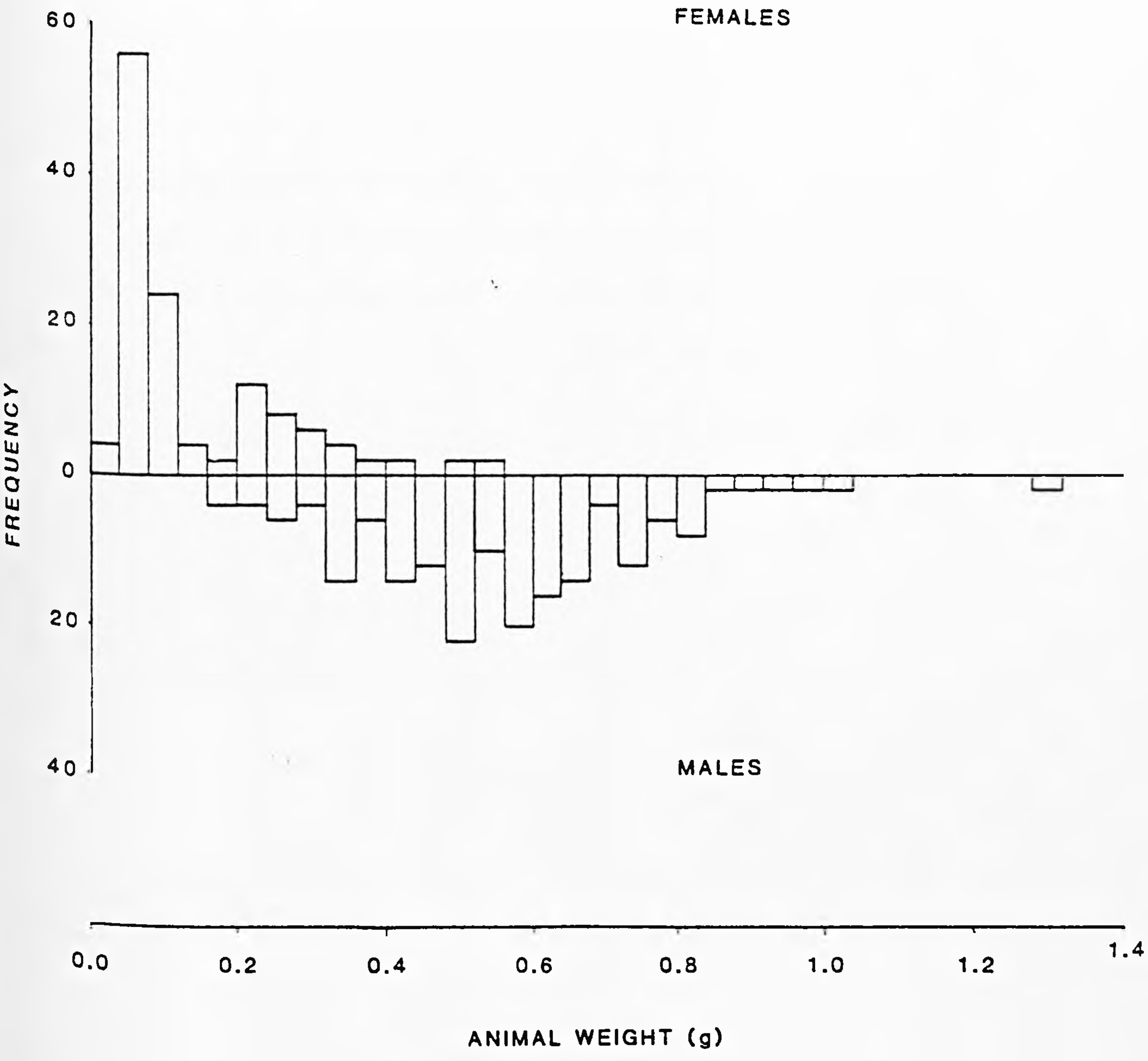

FEMALES
MALES
FREQUENCY
60
40
20
0
20
40
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
ANIMAL WEIGHT (g)

Figure 5.8

*Diogenes pugilator*. Whole animal wet weight of a random sample collected at Rhossili, July 1987.

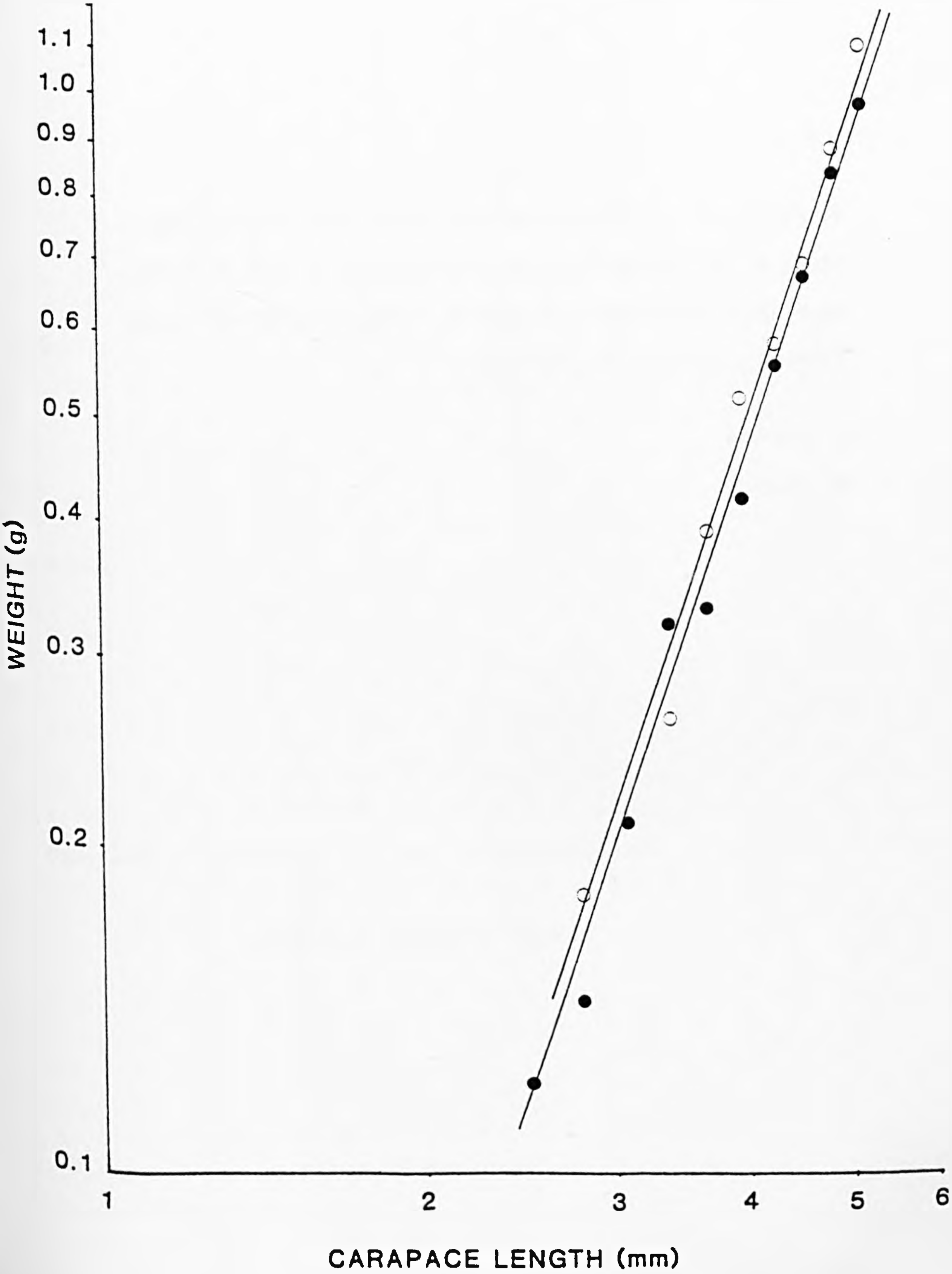

1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
WEIGHT (g)
1
2
3
4
5
6
CARAPACE LENGTH (mm)

Figure 5.9

*P. bernhardus*. Relation between weight and carapace length, based on results obtained from Mumbles Head on 27th May 1987. Each point represents the mean of 5 measurements with lines fitted by eye (log-log scale).

○ = females

● = males

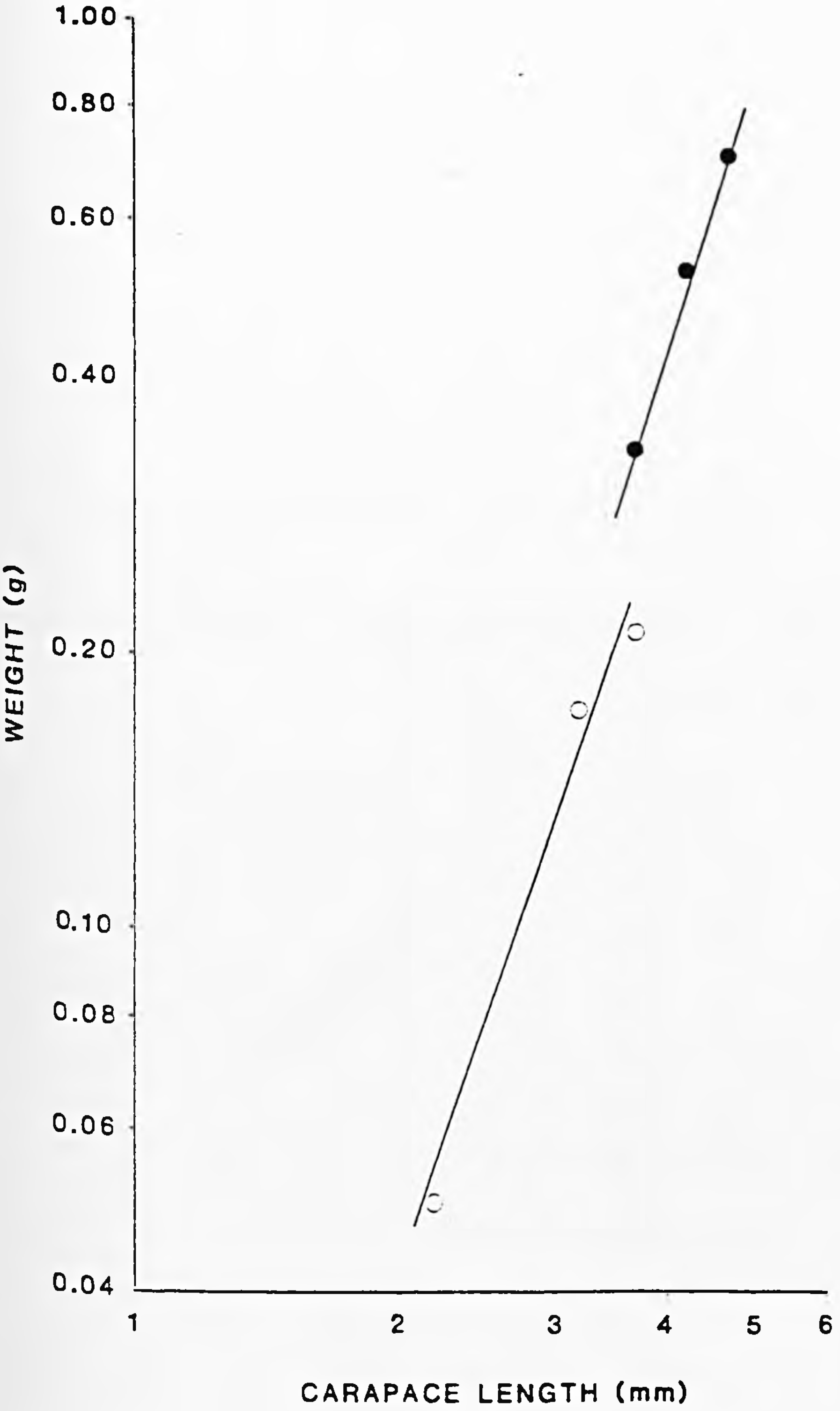

1.00
0.80
0.60
0.40
0.20
0.10
0.08
0.06
0.04
WEIGHT (g)
1
2
3
4
5
6
CARAPACE LENGTH (mm)

Figure 5.10

*D. pugilator*. Relation between weight and carapace length, based on data collected from Rhossili Bay on 15th June 1987. Each point represents the mean of 5 measurements with lines fitted by eye (log-log scale).

○ = female

● = male

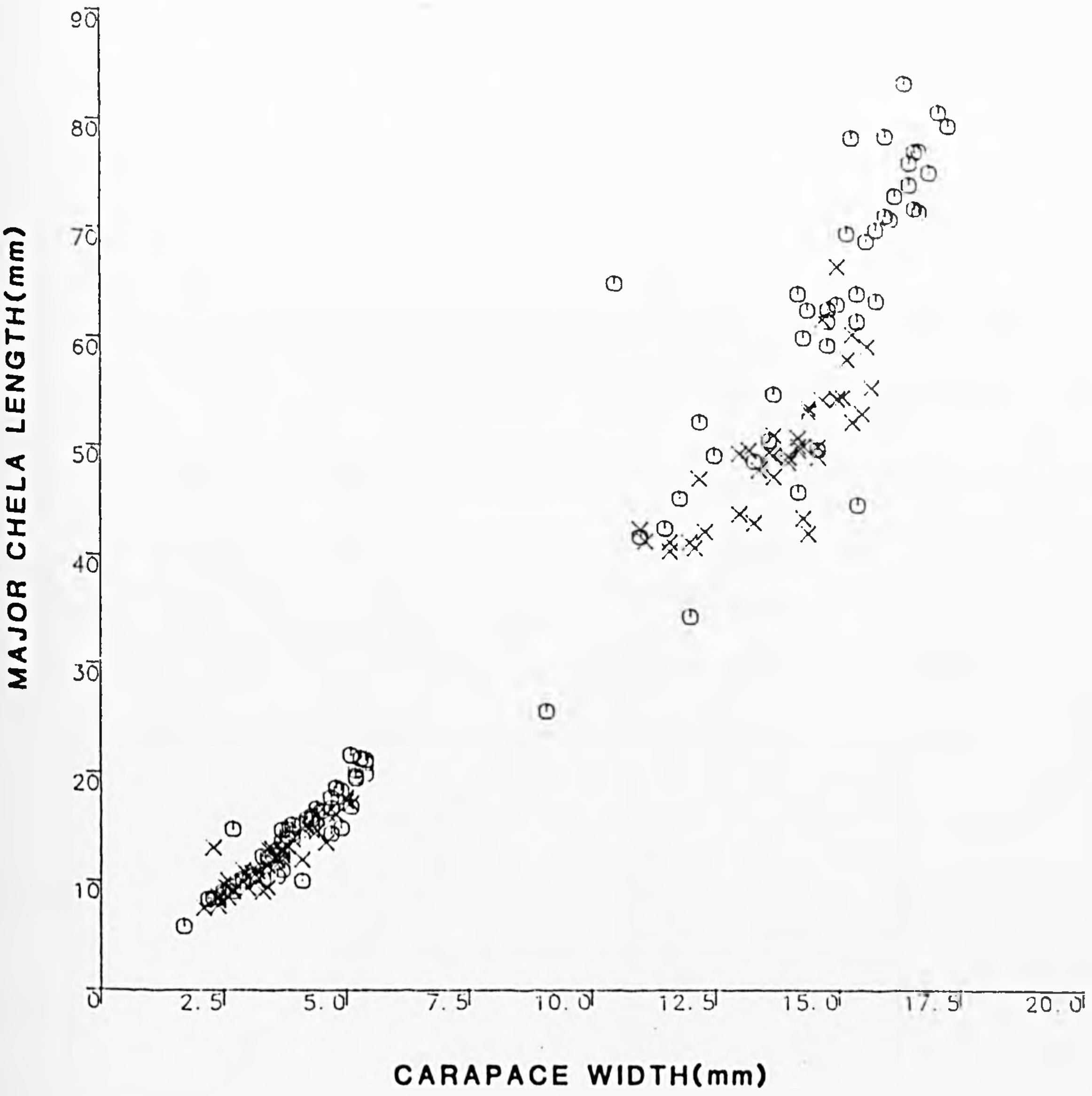

MAJOR CHELA LENGTH(mm)
0
10
20
30
40
50
60
70
80
90
2.5
5.0
7.5
10.0
12.5
15.0
17.5
20.0
CARAPACE WIDTH(mm)

Figure 5.11

*P. bernhardus*. Relation between major chela length and carapace width of males and females of both intertidal and sublittoral populations raw data (excludes small sublittoral specimens caught, April 1983).

x = female

o = male

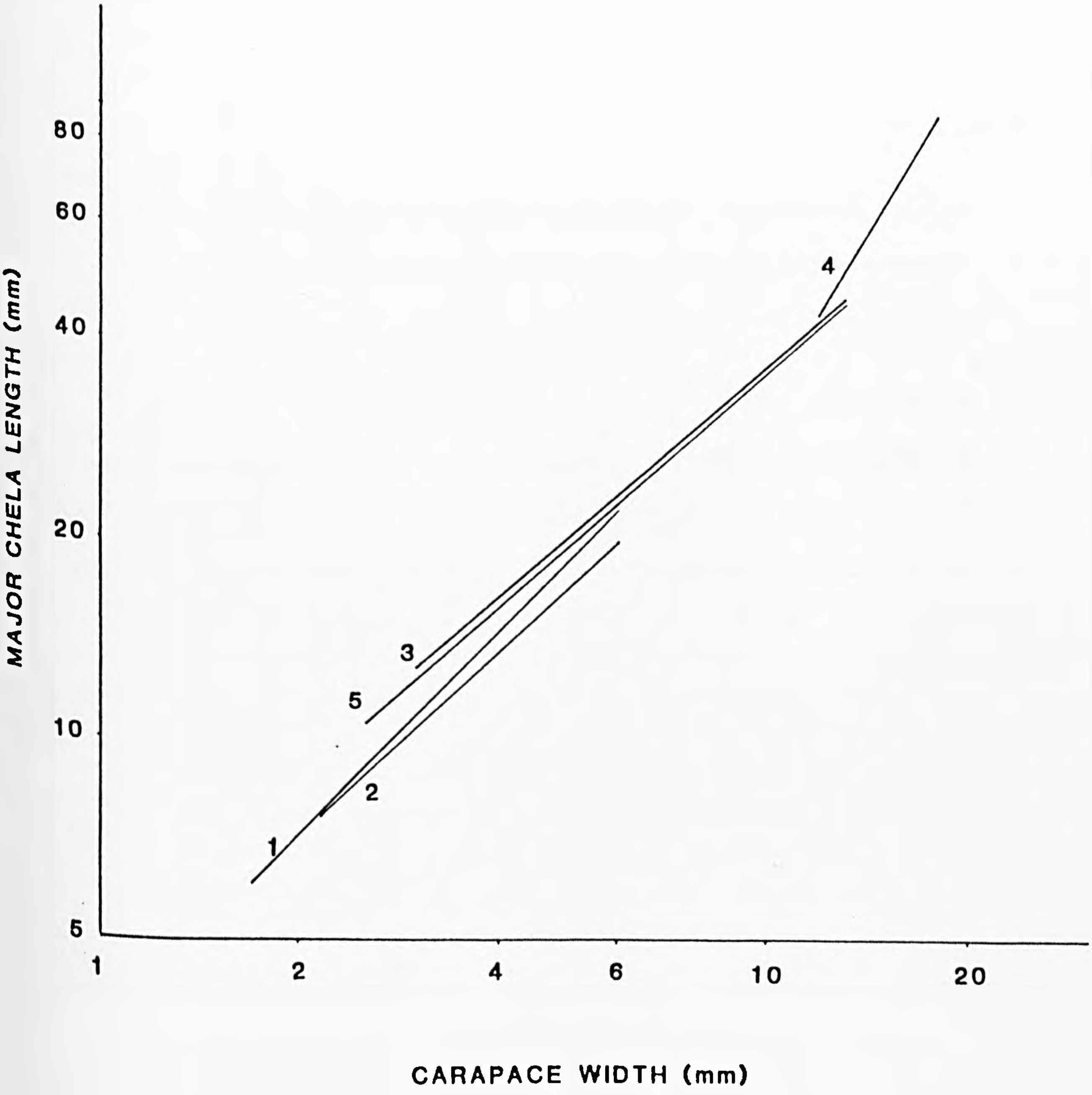

80
60
40
20
10
5
MAJOR CHELA LENGTH (mm)
1
2
4
6
10
20
CARAPACE WIDTH (mm)
1
2
3
4
5

Figure 5.12 A

*Pagurus bernhardus*. Calculated growth lines for major chela length plotted against carapace width.

1. Intertidal males $B = 1.053$, $A = 3.455$ and $r = 0.995$
2. Intertidal females $B = 0.922$, $A = 3.826$ and $r = 0.995$
3. Sublittoral males up to 12 mm $B = 0.862$, $A = 5.0$ and $r = 0.967$
4. Sublittoral males above 12 mm $B = 1.701$, $A = 0.981$ and $r = 0.98$
5. Sublittoral females $B = 0.869$, $A = 4.825$ and $r = 0.980$

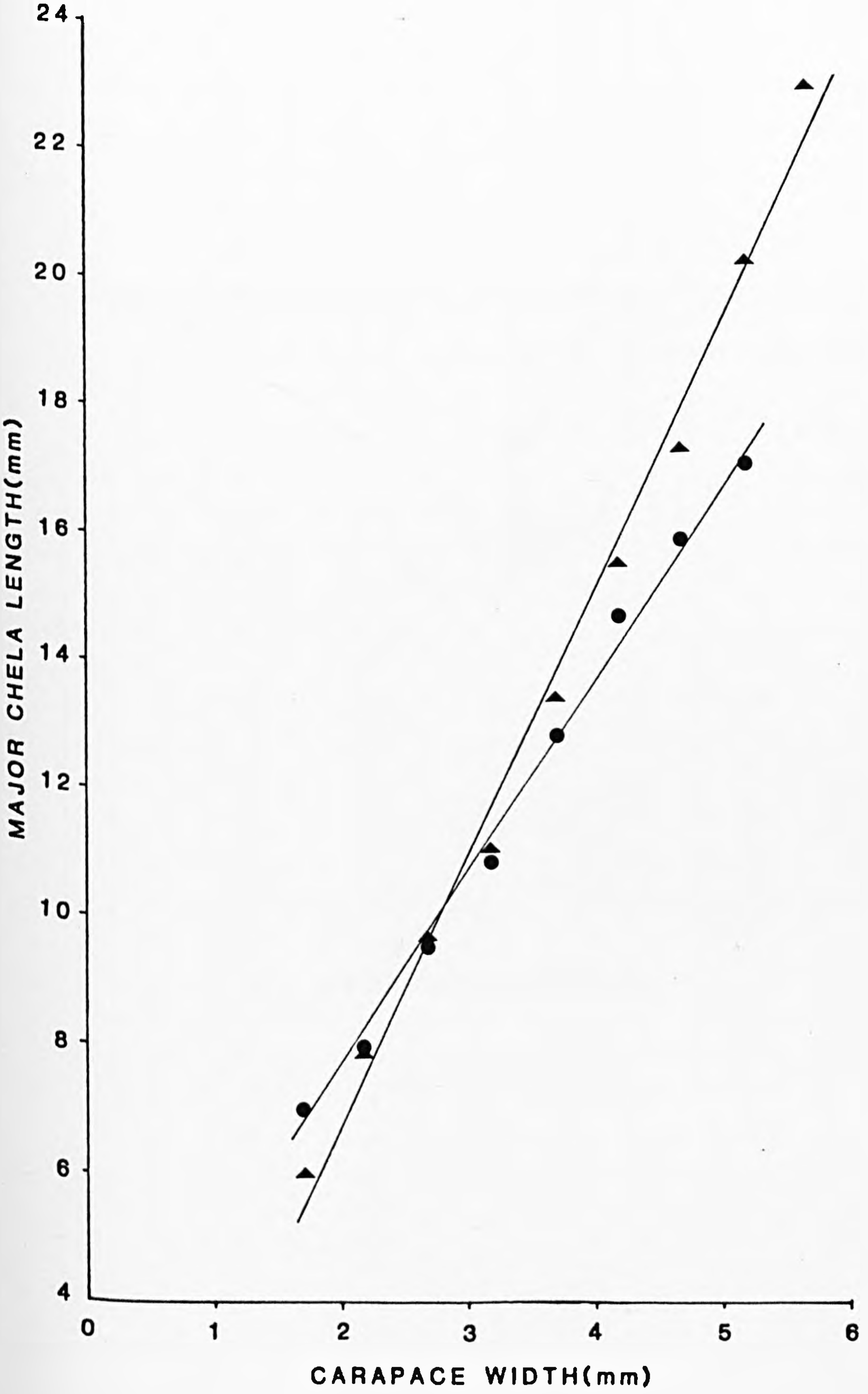

24
22
20
18
16
14
12
10
8
6
4
MAJOR CHELA LENGTH(mm)
0
1
2
3
4
5
6
CARAPACE WIDTH(mm)

Figure 5.12 B

*Pagurus bernhardus.* Relation between major chela length and carapace width of intertidal males and females, grouped data, with lines fitted by eye.

▲ = males (n = 241)

● = females (n = 270)

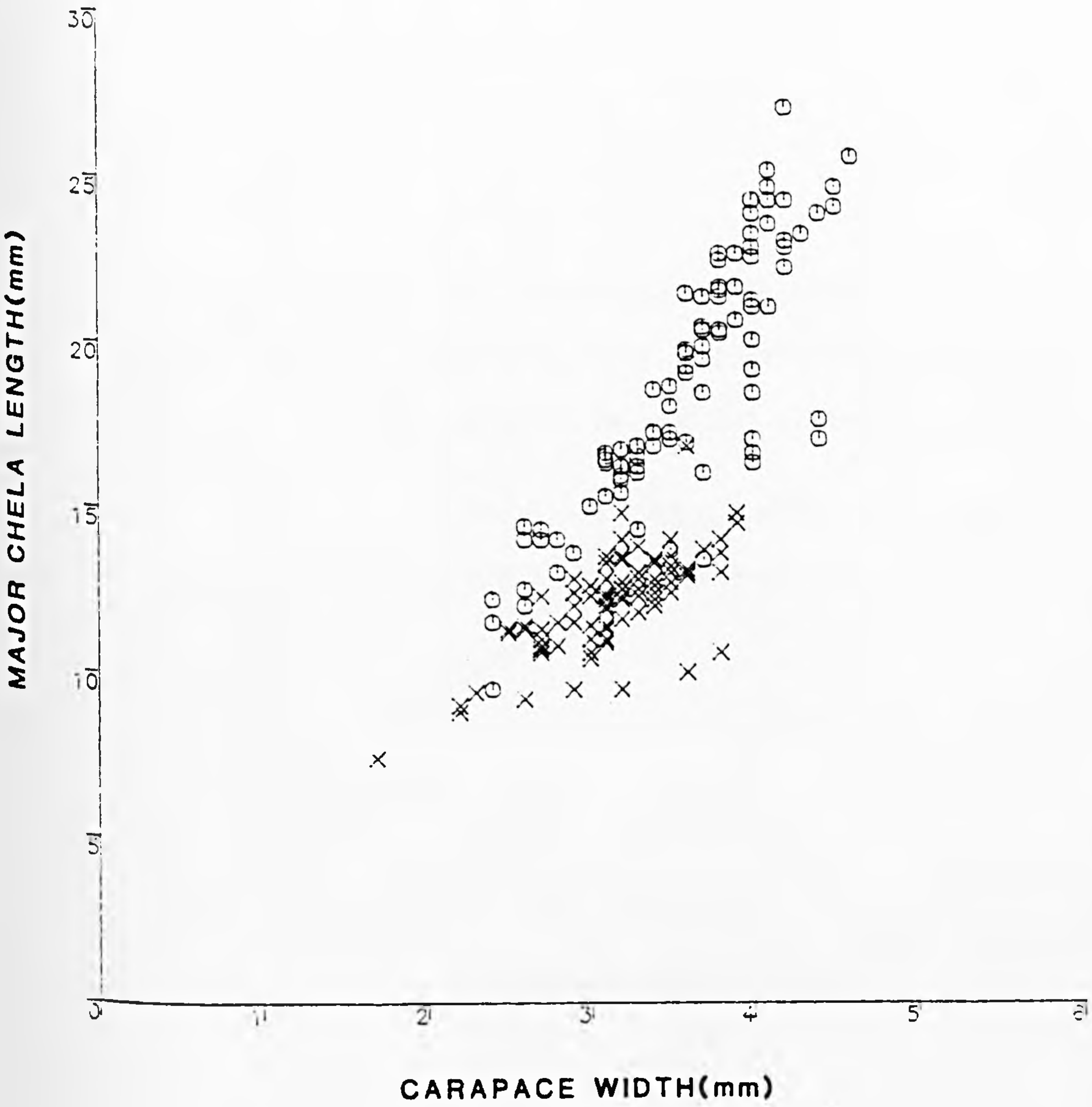

MAJOR CHELA LENGTH(mm)
30
25
20
15
10
5
0
1
2
3
4
5
6
CARAPACE WIDTH(mm)

Figure 5.13

*D. pugilator*. Relation between major chela length and carapace width of males and females, raw data.

x = female

⊙ = male

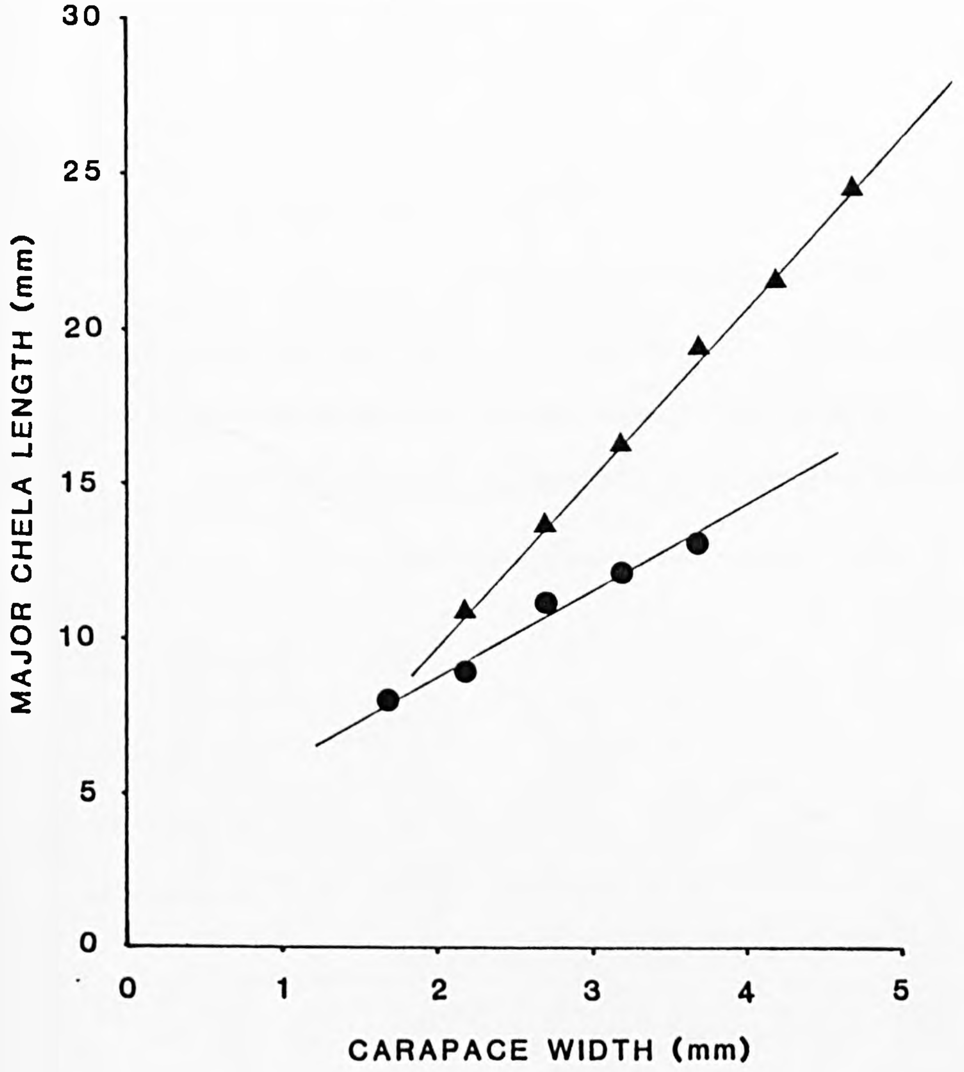

30
25
20
15
10
5
0
MAJOR CHELA LENGTH (mm)
0
1
2
3
4
5
CARAPACE WIDTH (mm)

Figure 5.14

*D. pugilator*. Relation between major chela length and carapace width for males and females, with calculated regression lines. Each point represents the mean of 20 measurements.

● = female $y = 2.86x + 3.04$; $r = 0.999$

▲ = male $y = 5.45x - 1.02$; $r = 0.999$

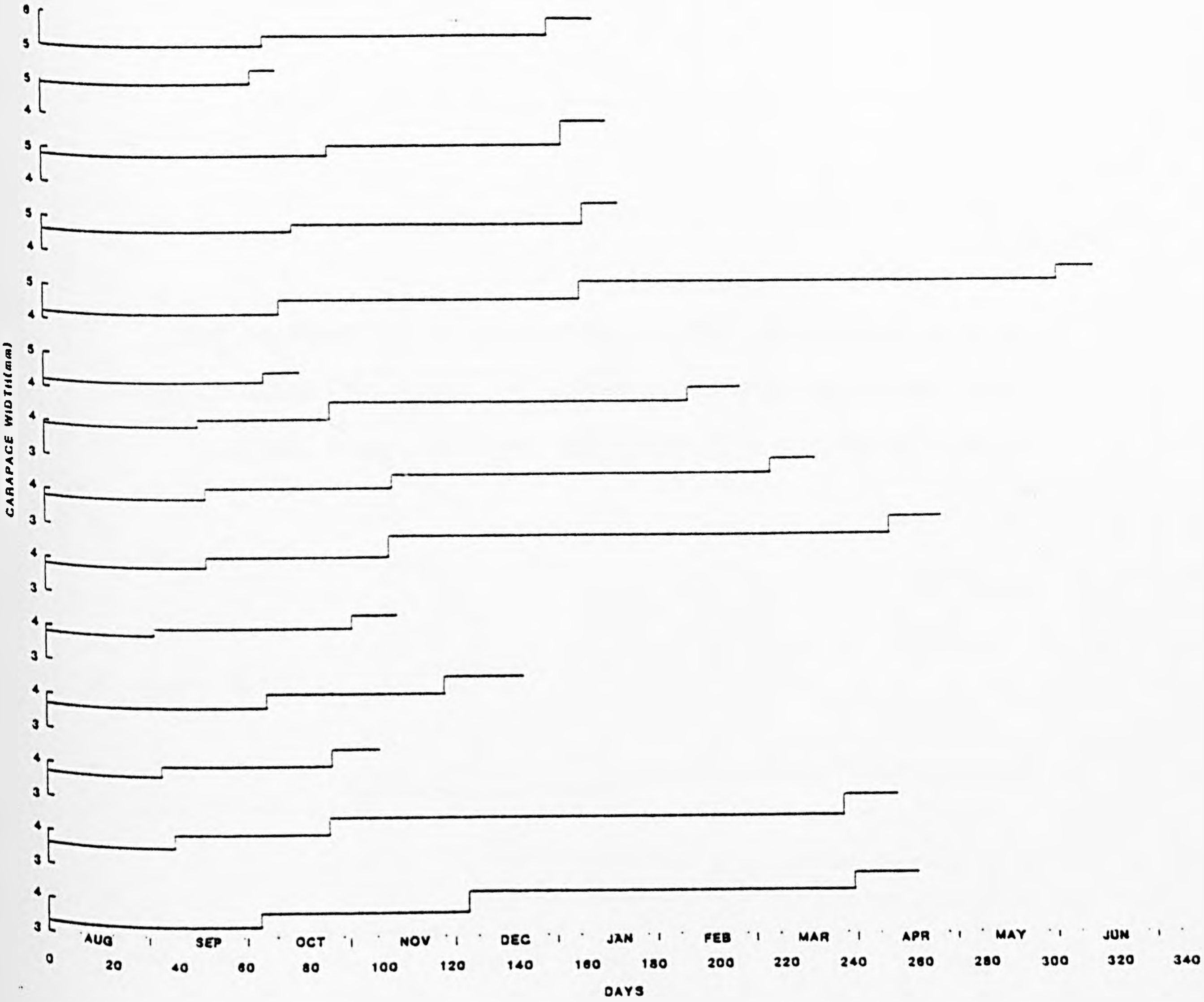

CARAPACE WIDTH(mm)
6
5
4
3
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
340
DAYS

Figure 5.15

*P. bernhardus*. Growth chart showing size increment at each moult and duration between moults for individual hermits, collected intertidally and reared in the laboratory.

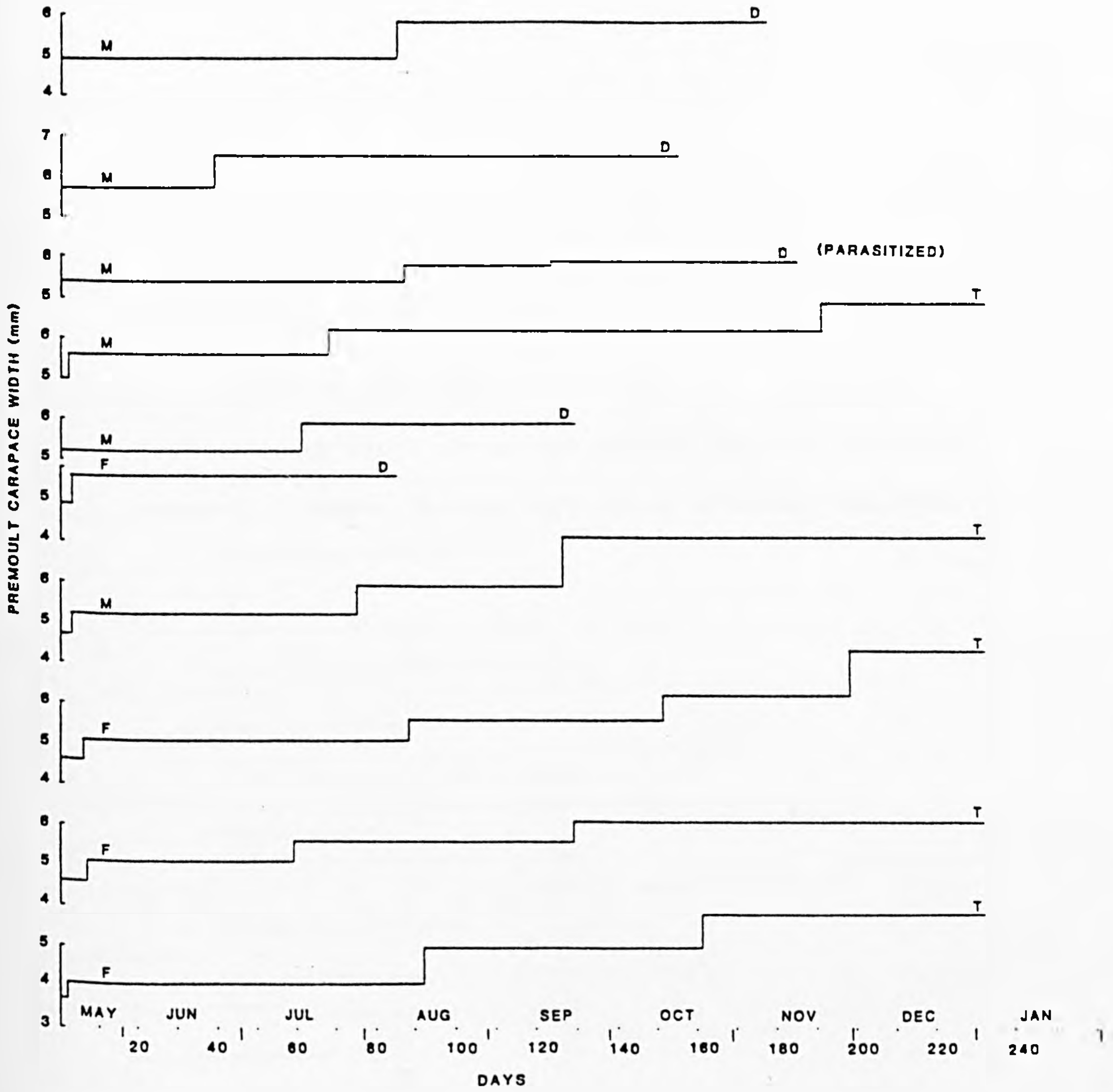

PREMOULT CARAPACE WIDTH (mm)
DAYS
M
F
D
T
(PARASITIZED)
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
20
40
60
80
100
120
140
160
180
200
220
240
3
4
5
6
7

Figure 5.16

*Pagurus bernhardus*. Growth chart showing increment at each moult and duration between moults for individual hermits reared in the laboratory with access to large gastropod shells.

M = males

F = females

D = dead

T = terminated

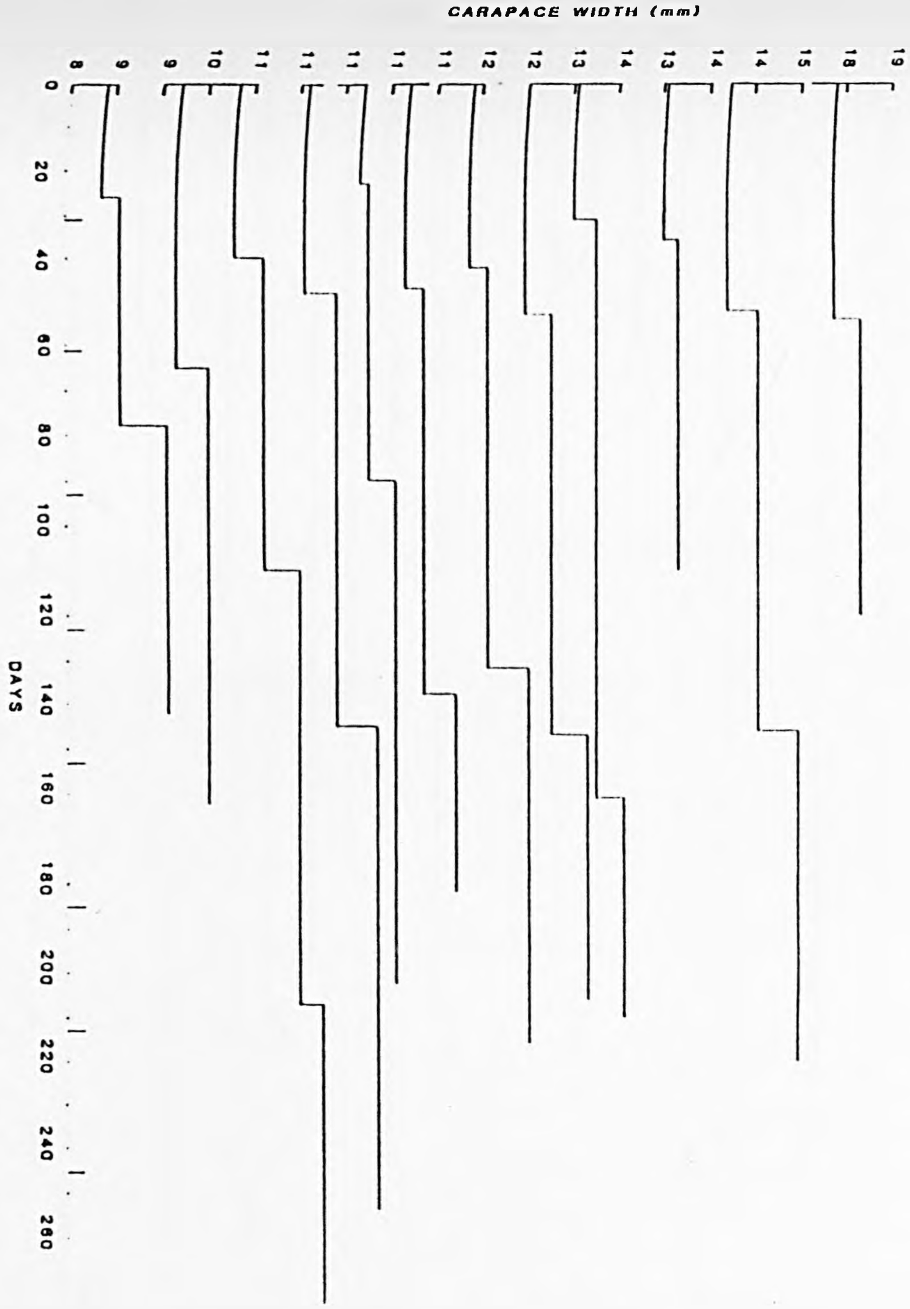

CARAPACE WIDTH (mm)
8
9
9
10
11
11
11
11
11
12
12
13
14
13
14
14
15
18
19
0
20
40
60
80
100
120
140
160
180
200
220
240
260
DAYS

Figure 5.17

*P. bernhardus*. Growth chart showing size increment at each moult and duration between moults for individual hermits, collected sublitorally, plotted against premoult carapace width.

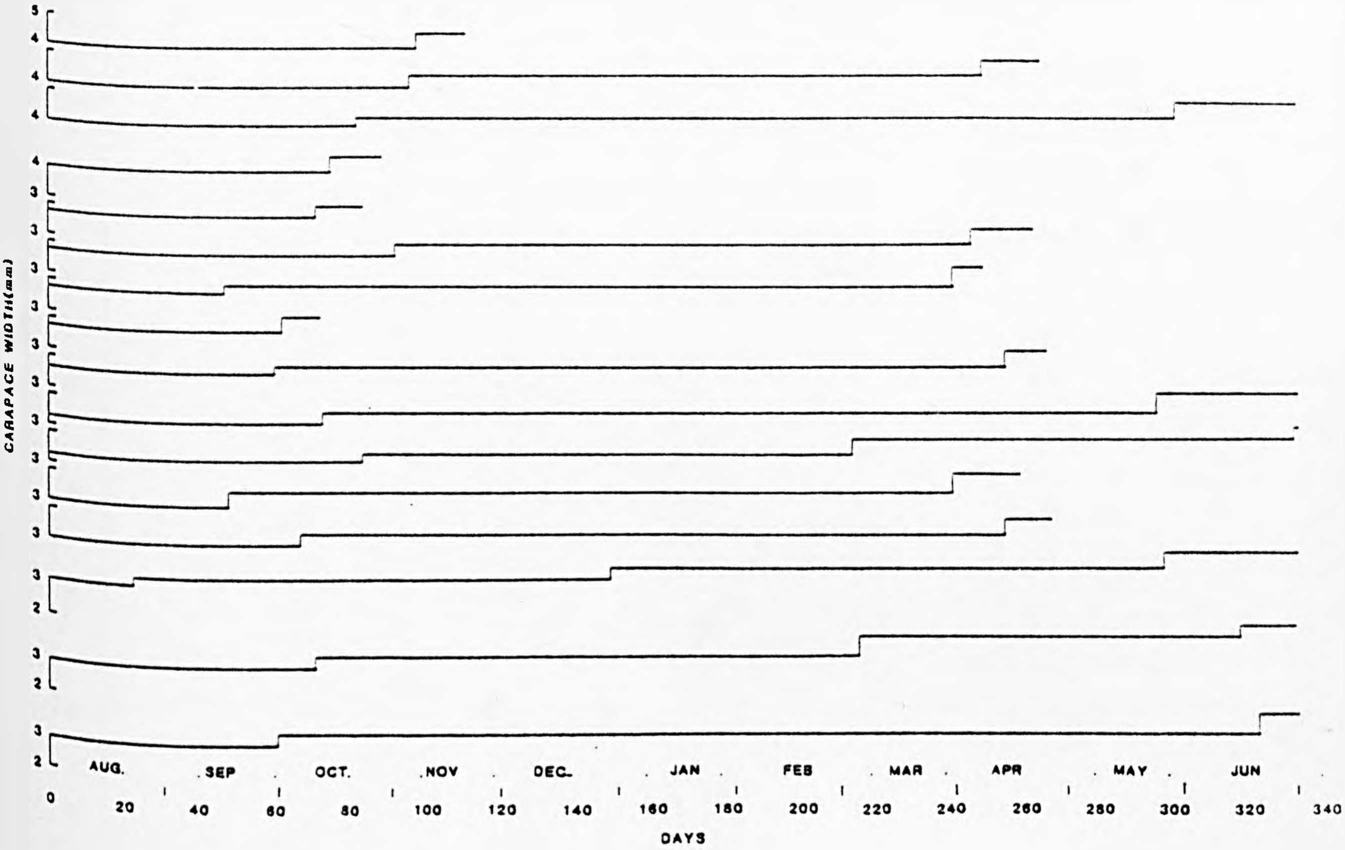

CARAPACE WIDTH(mm)
5
4
3
2
AUG.
SEP
OCT.
NOV
DEC.
JAN
FEB
MAR
APR
MAY
JUN
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
340
DAYS

Figure 5.18

*D. pugilator*. Growth chart showing size increment at each moult and duration between moults for males and females.

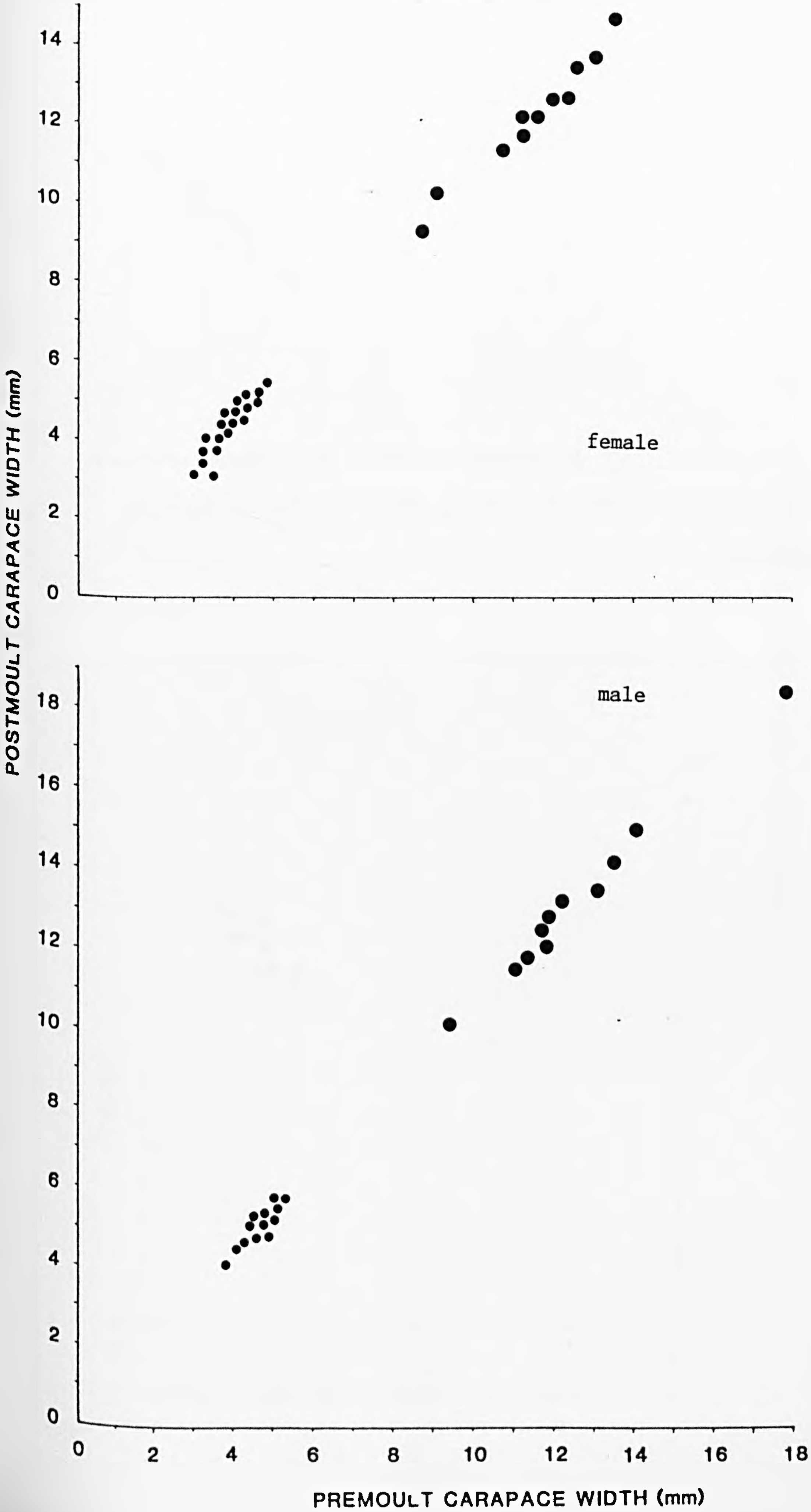

POSTMOULT CARAPACE WIDTH (mm)
PREMOULT CARAPACE WIDTH (mm)
female
male
0
2
4
6
8
10
12
14
16
18

Figure 5.19

*P. bernhardus.* Relation between postmoult and premoult carapace width obtained by rearing individuals at the Marine Science Laboratory.

• = intertidal

● = sublittoral

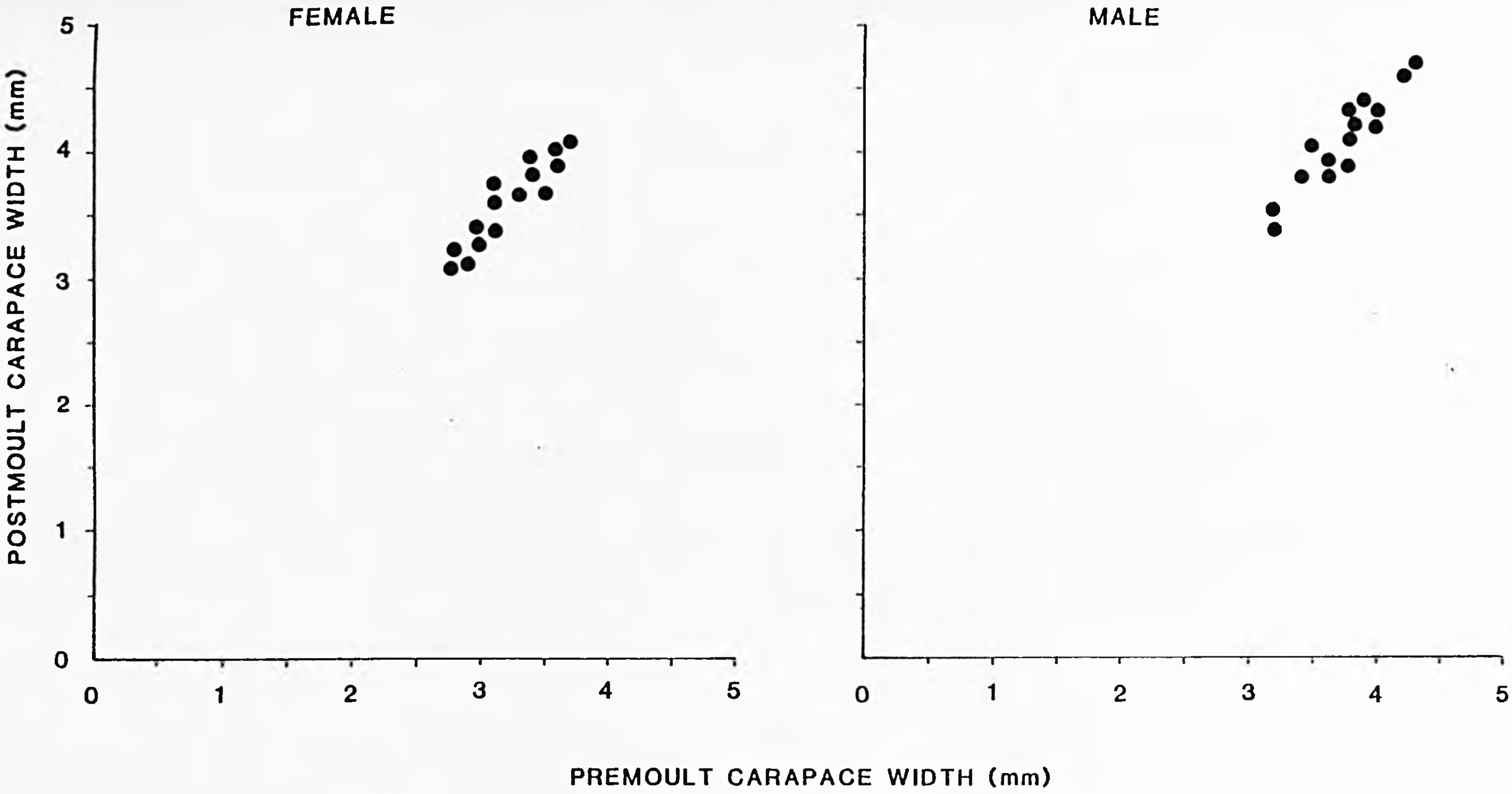

FEMALE
MALE
POSTMOULT CARAPACE WIDTH (mm)
PREMOULT CARAPACE WIDTH (mm)
0
1
2
3
4
5

Figure 5.20

*D. pugilator*. Relation between postmoult and premoult carapace width, obtained by rearing individuals at the Marine Science Laboratory.

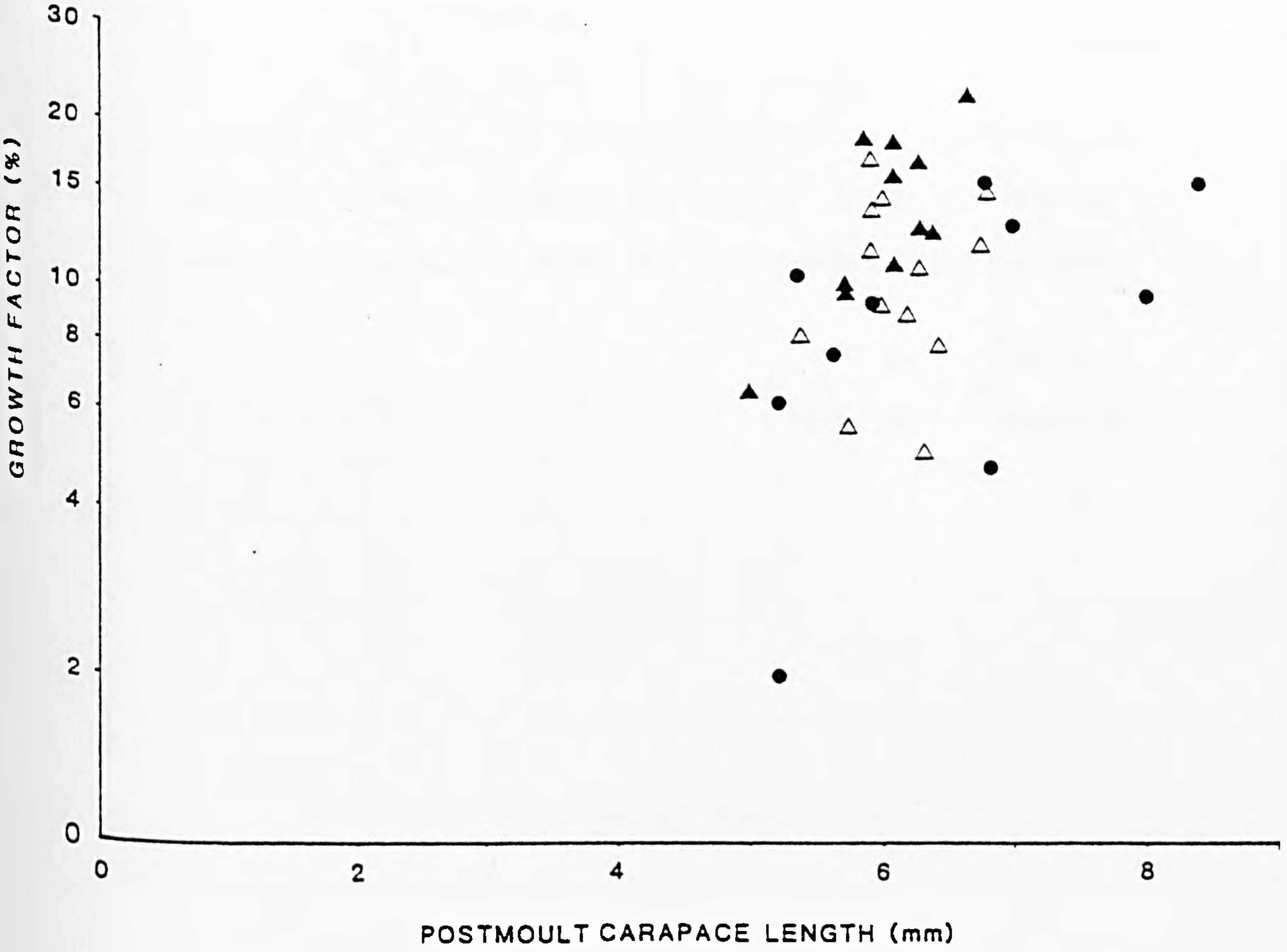

GROWTH FACTOR (%)
30
20
15
10
8
6
4
2
0
0
2
4
6
8
POSTMOULT CARAPACE LENGTH (mm)

Fig. 5.21

*P. bernhardus.* Relation between growth factor (percentage increment at moult) on semi-log graph and postmoult carapace length, based on results of Markham (1968).

● = same
Shell size ▲ = larger
△ = smaller

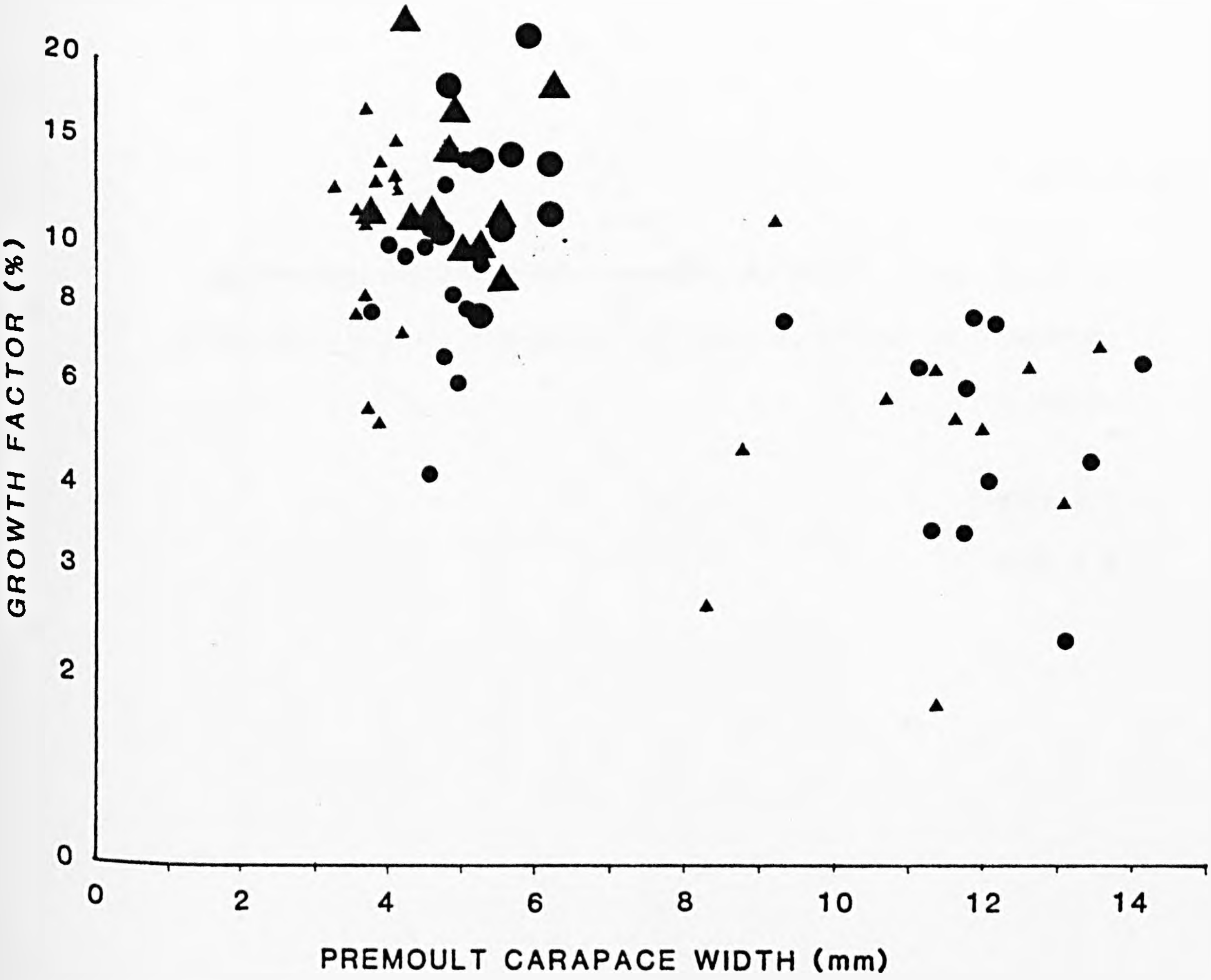

20
15
10
8
6
4
3
2
0
GROWTH FACTOR (%)
0
2
4
6
8
10
12
14
PREMOULT CARAPACE WIDTH (mm)

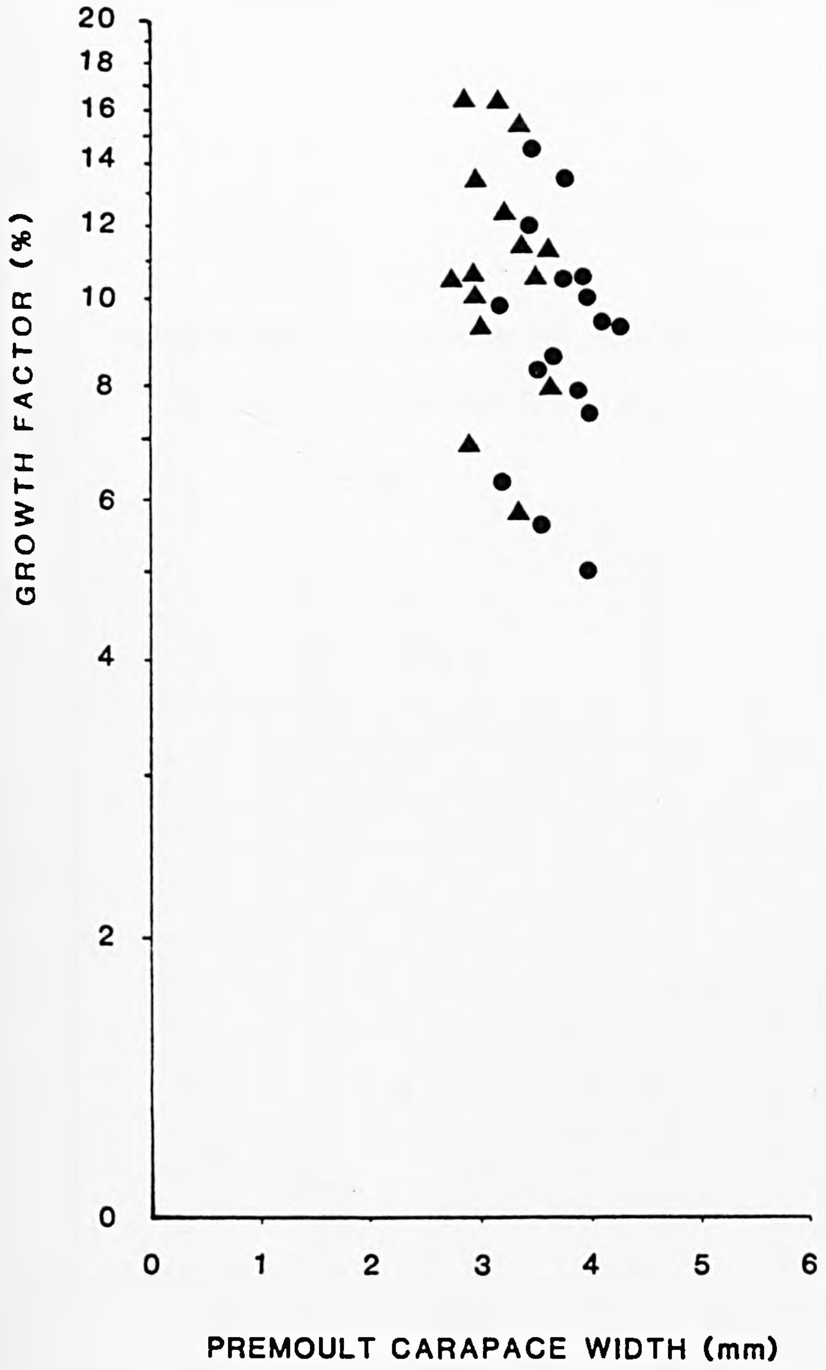
Figure 5.22

*P. bernhardus*. Relation between growth factor (percentage increment at moult) on semi-log graph and premoult carapace width of small (intertidal) and large (sublittoral) hermits.

▲ = female ▲

hermit crabs offered large shells

● = male ●


GROWTH FACTOR (%)
20
18
16
14
12
10
8
6
4
2
0
0
1
2
3
4
5
6
PREMOULT CARAPACE WIDTH (mm)

5.23

Figure 5.23

*D. pugilator.* Relation between growth factor (percentage increment at moult) on semi-log **graph** and premoult carapace width.

▲ = female

● = male

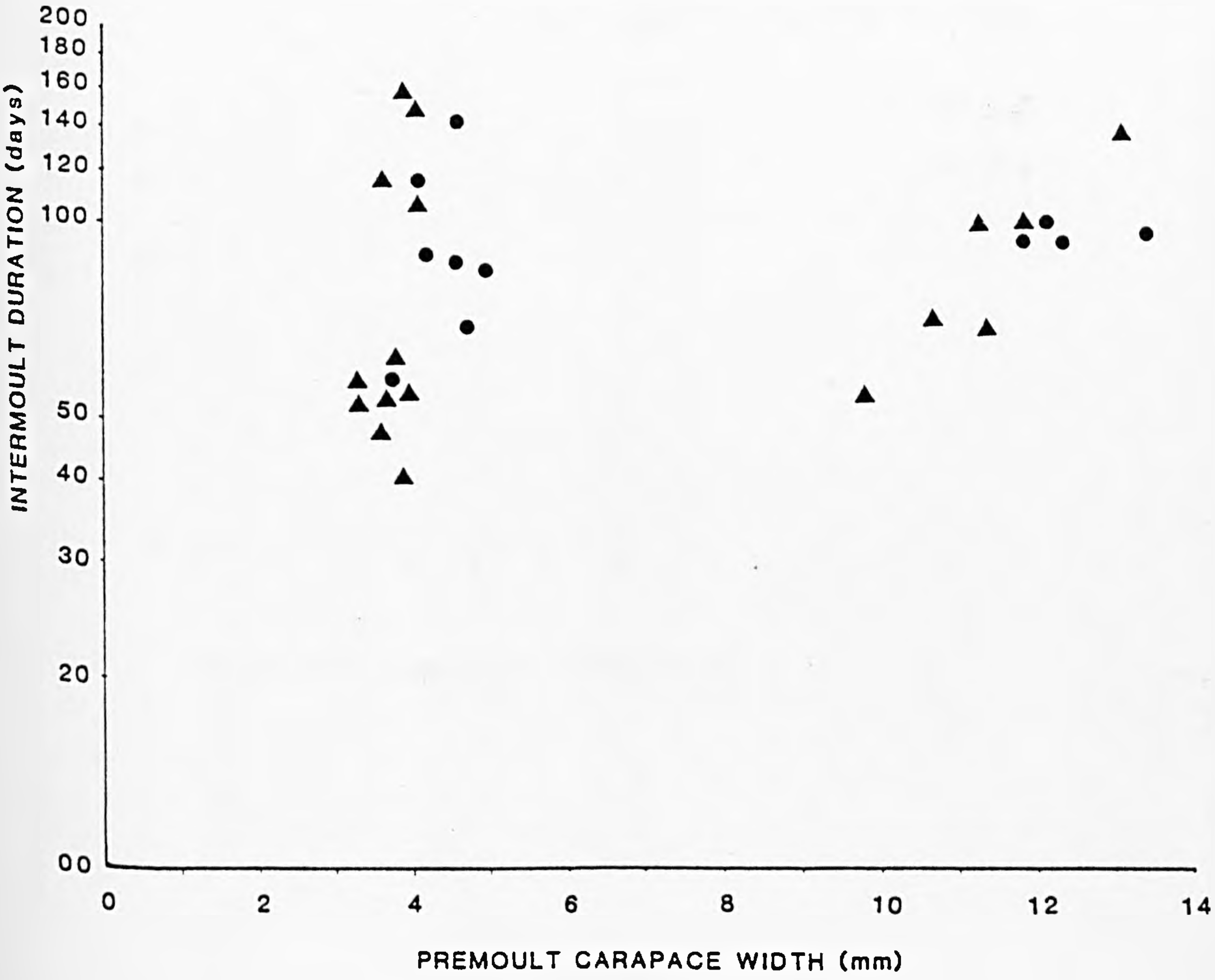

INTERMOULT DURATION (days)
200
180
160
140
120
100
50
40
30
20
00
0
2
4
6
8
10
12
14
PREMOULT CARAPACE WIDTH (mm)

Figure 5.24

*P. bernhardus.* Relation between intermoult duration on semi-log **graph** and premoult carapace width for both populations.

▲ = female

● = male

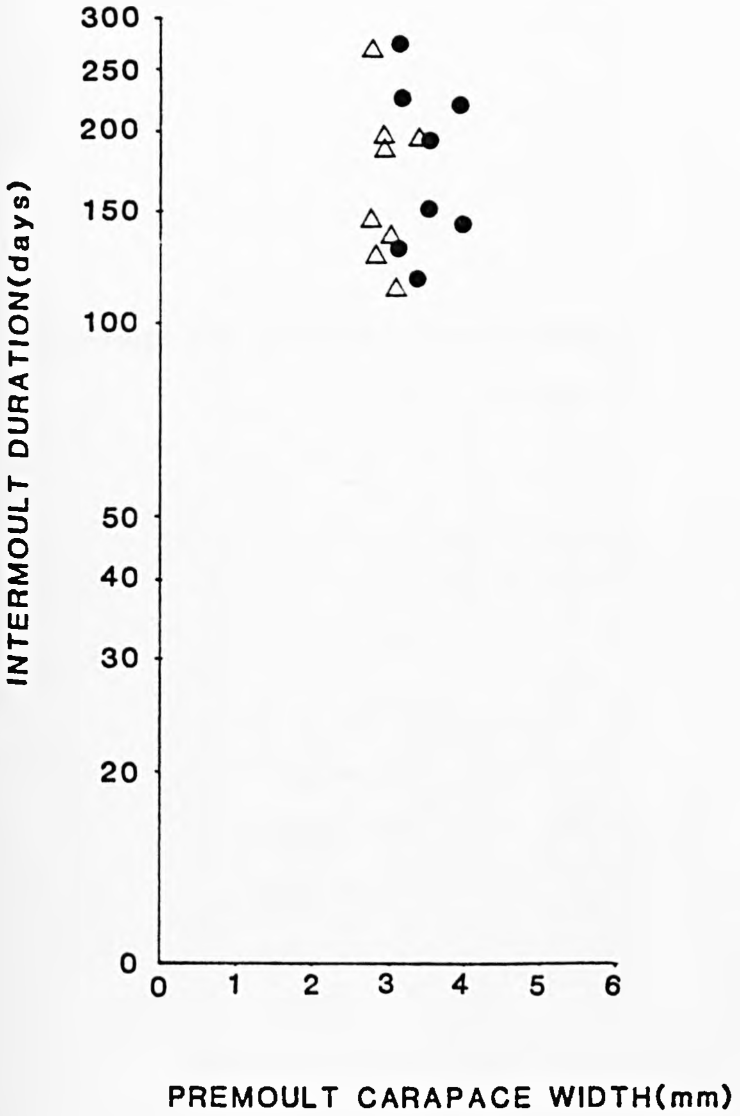

INTERMOULT DURATION(days)
300
250
200
150
100
50
40
30
20
0
0
1
2
3
4
5
6
PREMOULT CARAPACE WIDTH(mm)

Figure 5.25

*D. pugilator*. Relation between intermoult duration on semi-log graph and premoult carapace width.

▲ = female

● = male

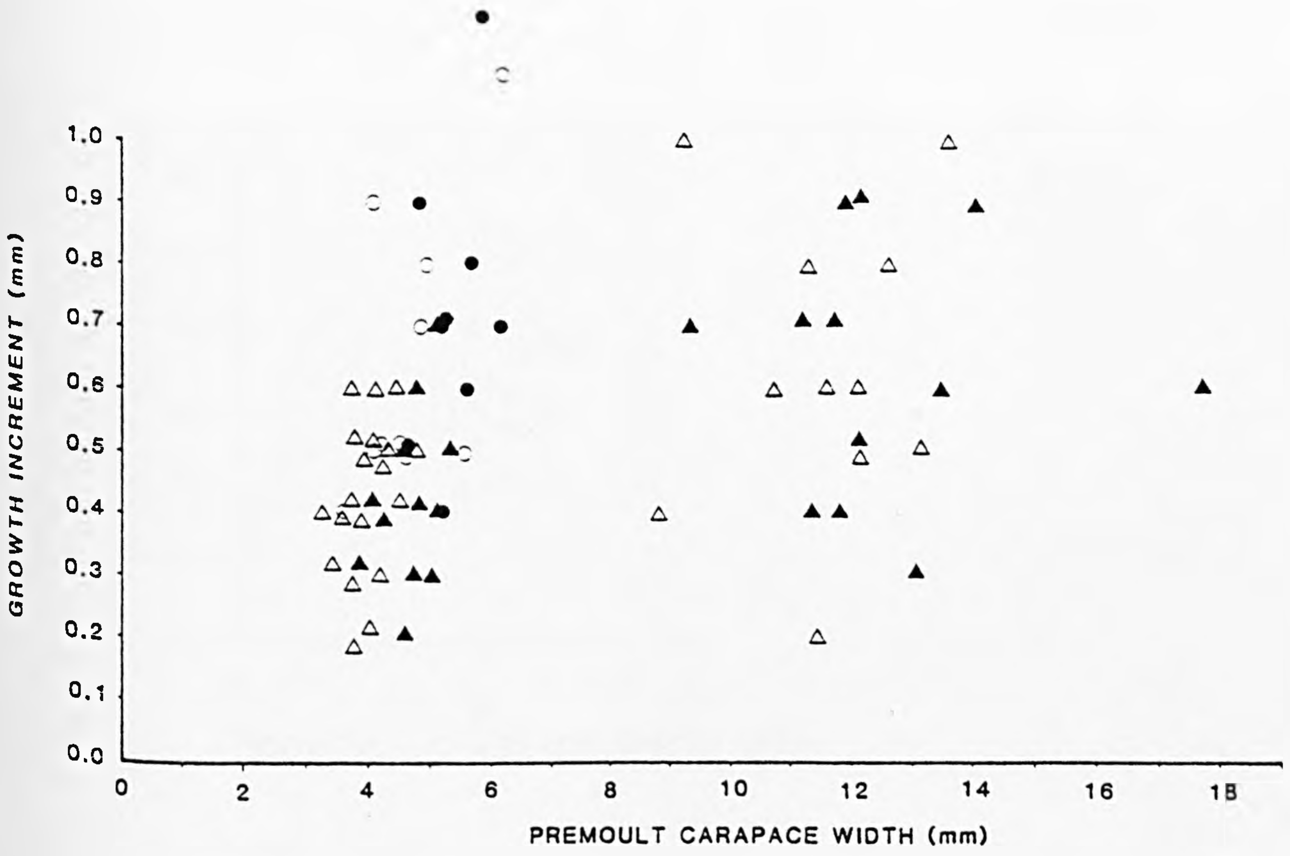

GROWTH INCREMENT (mm)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
12
14
16
18
PREMOULT CARAPACE WIDTH (mm)

Figure 5.26

*P. bernhardus*. Relation between growth increment and premoult carapace width for both populations.

△ = female o
circle symbols for hermit crabs offered large she
▲ = male ●

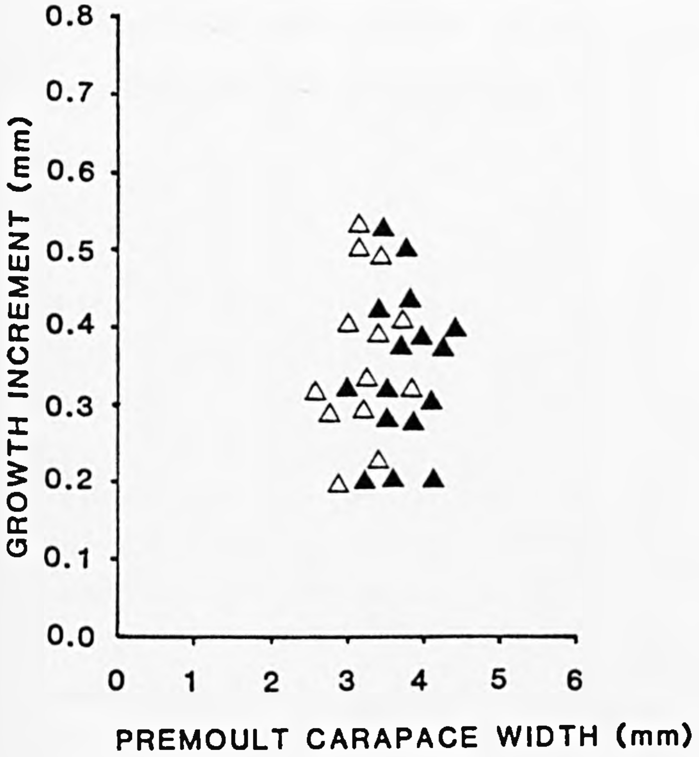

GROWTH INCREMENT (mm)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
PREMOULT CARAPACE WIDTH (mm)
0
1
2
3
4
5
6

Figure 5.27

*D. pugilator*. Relation between growth increment and premoult carapace width.

△ = female

▲ = male

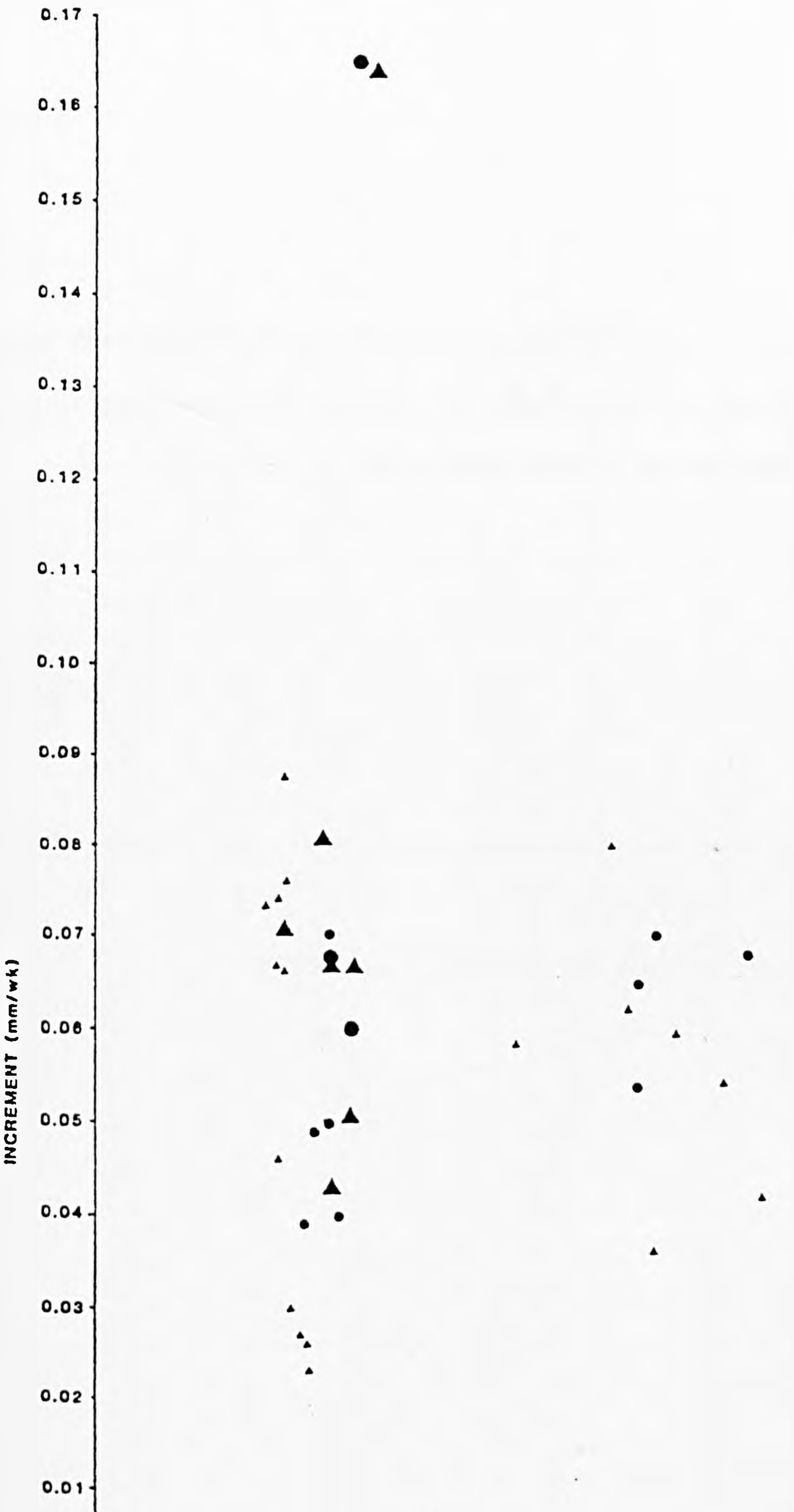

INCREMENT (mm/wk)
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.10
0.11
0.12
0.13
0.14
0.15
0.16
0.17
0
2
4
6
8
10
12
14
PREMOULT CARAPACE WIDTH (mm)

Figure 5.28

*P. bernhardus*. Relation between growth increment per week and premoult carapace width, based on results from individuals reared at the Marine Science Laboratory on log-log scale.

▲ = female ▲

● = male ●

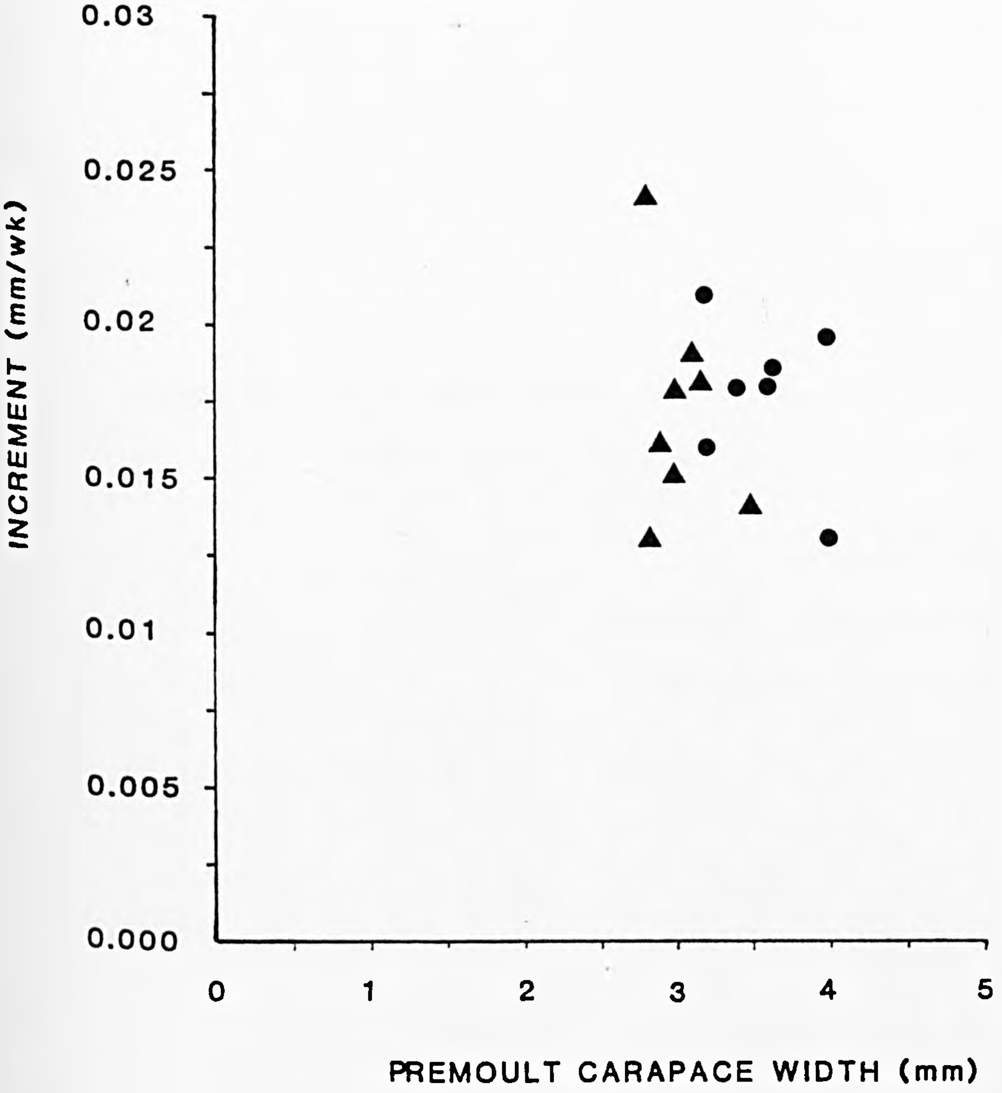

0.03
0.025
0.02
0.015
0.01
0.005
0.000
INCREMENT (mm/wk)
0
1
2
3
4
5
PREMOULT CARAPACE WIDTH (mm)

Figure 5.29

*D. pugilator*. Relation between growth increment per week and premoult carapace width, based on results from individuals reared at the Marine Science Laboratory.

▲ = female

● = male

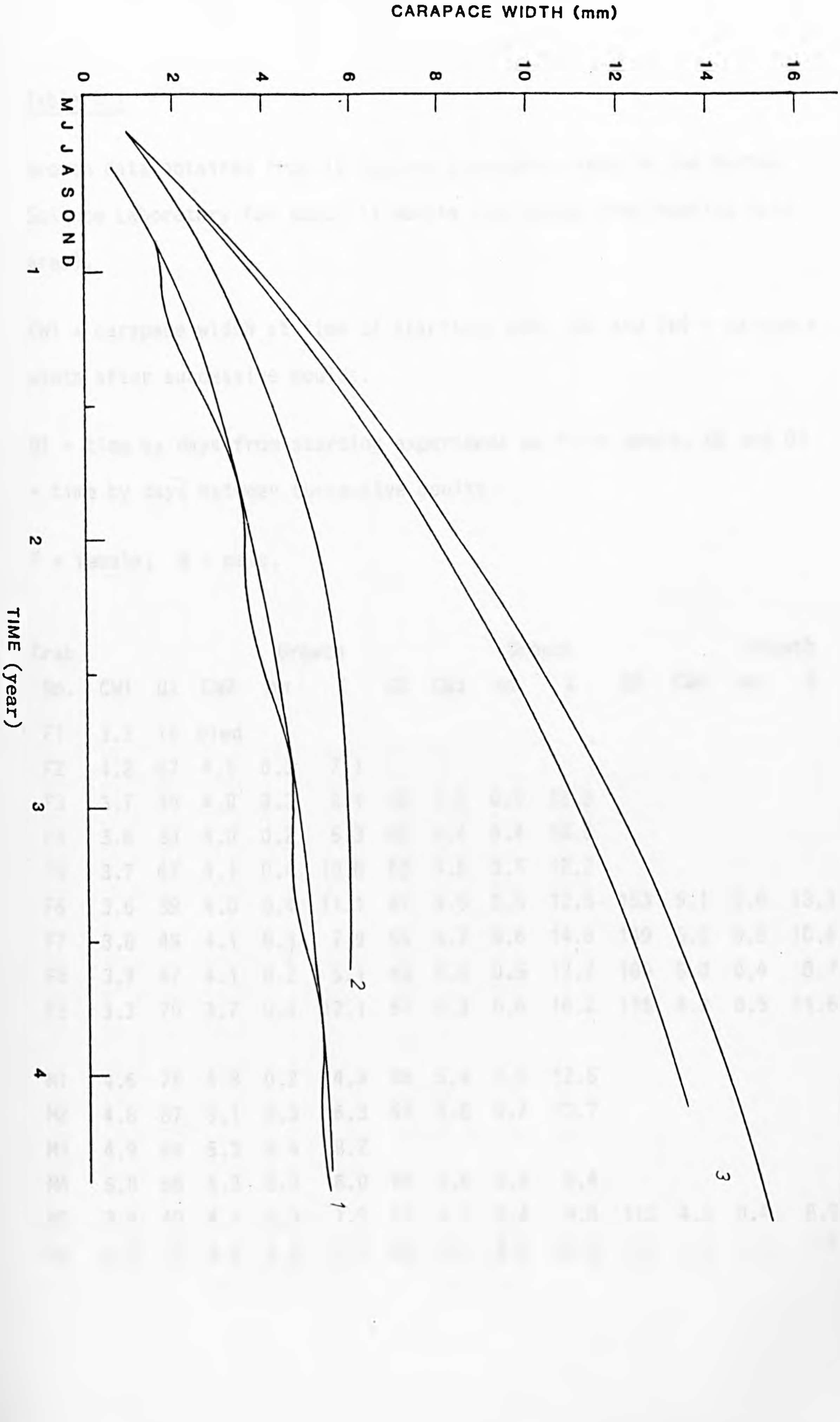

CARAPACE WIDTH (mm)
0
2
4
6
8
10
12
14
16
M J J A S O N D
1
2
3
4
TIME (year)
1
2
3

Figure 5.30

Reconstructed life time growth curves based on size of field recruits and results of laboratory growth studies.

1. *Diogenes pugilator*
2. *Pagurus bernhardus* intertidal
3. *P. bernhardus* sublittoral

Table 5.1

Growth data obtained from 15 *Pagurus bernhardus* kept in the Marine Science Laboratory for about 11 months (collected from Mumbles Head area).

CW1 = carapace width at time of starting; CW2, CW3 and CW4 = carapace width after successive moults.

D1 = time by days from starting experiment to first moult; D2 and D3 = time by days between successive moults.

F = female; M = male.

| Crab |  |  |  | Growth |  |  |  | Growth |  |  |  | Growth |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. | CW1 | D1 | CW2 | mm | % | D2 | CW3 | mm | % | D3 | CW4 | mm | % |
| F1 | 3.3 | 10 | Died |  |  |  |  |  |  |  |  |  |  |
| F2 | 4.2 | 67 | 4.5 | 0.3 | 7.1 |  |  |  |  |  |  |  |  |
| F3 | 3.7 | 35 | 4.0 | 0.3 | 8.1 | 52 | 4.5 | 0.5 | 12.3 |  |  |  |  |
| F4 | 3.8 | 33 | 4.0 | 0.2 | 5.3 | 60 | 4.4 | 0.4 | 10.0 |  |  |  |  |
| F5 | 3.7 | 67 | 4.1 | 0.4 | 10.8 | 53 | 4.5 | 0.5 | 12.2 |  |  |  |  |
| F6 | 3.6 | 39 | 4.0 | 0.4 | 11.1 | 47 | 4.5 | 0.5 | 12.5 | 153 | 5.1 | 0.6 | 13.3 |
| F7 | 3.8 | 49 | 4.1 | 0.3 | 7.9 | 55 | 4.7 | 0.6 | 14.6 | 149 | 5.2 | 0.5 | 10.6 |
| F8 | 3.9 | 47 | 4.1 | 0.2 | 5.1 | 40 | 4.6 | 0.5 | 12.2 | 106 | 5.0 | 0.4 | 8.7 |
| F9 | 3.3 | 70 | 3.7 | 0.4 | 12.1 | 57 | 4.3 | 0.6 | 16.2 | 115 | 4.8 | 0.5 | 11.6 |
| M1 | 4.6 | 76 | 4.8 | 0.2 | 4.3 | 86 | 5.4 | 0.6 | 12.5 |  |  |  |  |
| M2 | 4.8 | 87 | 5.1 | 0.3 | 6.3 | 69 | 5.8 | 0.7 | 13.7 |  |  |  |  |
| M3 | 4.9 | 64 | 5.3 | 0.4 | 8.2 |  |  |  |  |  |  |  |  |
| M4 | 5.0 | 68 | 5.3 | 0.3 | 6.0 | 84 | 5.8 | 0.5 | 9.4 |  |  |  |  |
| M5 | 3.8 | 49 | 4.1 | 0.3 | 7.9 | 56 | 4.5 | 0.4 | 9.8 | 113 | 4.9 | 0.4 | 8.9 |
| M6 | 4.2 | 72 | 4.6 | 0.4 | 9.5 | 89 | 5.1 | 0.5 | 10.9 | 143 | 5.5 | 0.4 | 7.8 |

## Table 5.2

Growth data obtained from 12 large specimens of hermit crab *Pagurus bernhardus*, collected by trawling at Oxwich Bay and kept at the Marine Science Laboratory for about 11 months.

CW1 = carapace width at time of starting; CW2, CW3 and CW4 = carapace width after successive moults.

D1 = time by days from starting experiment to first moult; D2 and D3 = time by days between successive moults.

F = female; M = male.

| Crab | | | | Growth | | | | Growth | | | | Growth | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. | CW1 | D1 | CW2 | mm | % | D2 | CW3 | mm | % | D3 | CW4 | mm | % |
| F1 | 13.1 | 31 | 13.6 | 0.5 | 3.8 | 130 | 14.6 | 1.0 | 7.4 | | | | |
| F2 | 10.7 | 40 | 11.3 | 0.6 | 5.6 | 70 | 12.1 | 0.8 | 7.1 | 97 | 12.6 | 0.5 | 4.1 |
| F3 | 12.0 | 53 | 12.6 | 0.6 | 5.0 | 94 | 13.4 | 0.8 | 6.3 | | | | |
| F4 | 11.4 | 23 | 11.6 | 0.2 | 1.8 | 67 | 12.2 | 0.6 | 5.2 | | | | |
| F5 | 8.8 | 25 | 9.2 | 0.4 | 4.6 | 53 | 10.2 | 1.0 | 10.9 | | | | |
| M1 | 11.8 | 42 | 12.2 | 0.4 | 3.4 | 90 | 13.1 | 0.9 | 7.4 | | | | |
| M2 | 11.2 | 48 | 11.9 | 0.7 | 6.3 | 97 | 12.8 | 0.9 | 7.6 | | | | |
| M3 | 9.4 | 65 | 10.1 | 0.7 | 7.5 | | | | | | | | |
| M4 | 13.1 | 36 | 13.4 | 0.3 | 2.3 | | | | | | | | |
| M5 | 11.4 | 47 | 11.8 | 0.4 | 3.5 | 90 | 12.5 | 0.7 | 5.9 | | | | |
| M6 | 13.5 | 53 | 14.1 | 0.6 | 4.4 | 92 | 15.0 | 0.9 | 6.4 | | | | |
| M7 | 17.8 | 55 | 18.4 | 0.6 | 3.4 | | | | | | | | |

Table 5.3. Growth data obtained from 10 *Pagurus bernhardus* males and females reared in the Marine Science Laboratory for about nine months and were offered larger gastropod shells.

CW1 = carapace width at time of starting; CW2, CW3, CW4 and CW5 = carapace width after successive moults.

D1 = time by days from starting experiment to first moult; D2, D3, D4, D5 and D6 = time by day between successive moults.

F = female; M = male.

| Crab | | | | | Growth | | | | Growth | | | | Growth | | | | Growth | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. | D1 | CW1 | D2 | CW2 | mm | % | D3 | CW3 | mm | % | D4 | CW4 | mm | % | D5 | CW5 | mm | % |
| M1 | 2 | 5.2 | 66 | 5.6 | 0.4 | 7.7 | 123 | 6.2 | 0.6 | 10.7 | 41 | 6.9 | 0.7 | 11.3 | | | | |
| M2 | 3 | 4.7 | 72 | 5.2 | 0.5 | 10.6 | 51 | 5.9 | 0.7 | 13.5 | 106 | 7.1 | 1.2 | 20.3 | | | | |
| M3 | 39 | 5.7 | 116 | 6.5 | 0.8 | 14.0 | | | | | | | | | | | | |
| M4 | 61 | 5.2 | 68 | 5.9 | 0.7 | 13.5 | | | | | | | | | | | | |
| M5 | 85 | 4.9 | 92 | 5.8 | 0.9 | 18.4 | | | | | | | | | | | | |
| F1 | 3 | 4.9 | 82 | 5.6 | 0.7 | 14.3 | | | | | | | | | | | | |
| F2 | 2 | 3.7 | 90 | 4.1 | 0.4 | 10.8 | 69 | 5.0 | 0.9 | 22.0 | 71 | 5.8 | 0.8 | 16.0 | | | | |
| F3 | 6 | 4.6 | 82 | 5.1 | 0.5 | 10.9 | 63 | 5.6 | 0.5 | 9.8 | 47 | 6.2 | 0.6 | 10.7 | 34 | 7.3 | 1.1 | 17.7 |
| F4 | 7 | 4.6 | 52 | 5.1 | 0.5 | 10.9 | 70 | 5.6 | 0.5 | 9.8 | 103 | 6.1 | 0.5 | 8.9 | | | | |

Table 5.4

*P. bernhardus*. Data showing the size and the weight of 3 glaucothöe and one first crab stage and the species of gastropod shell occupied, collected from Mumbles Head on 10th June 1987.

| | | Species of gastropod | Carapace width (mm) | Carapace length (mm) | Weight (gm) |
|---|---|---|---|---|---|
| 1. | glaucothöe | *L. saxatilis* | 1.25 | 1.46 | 0.02 |
| 2. | glaucothöe | *L. saxatilis* | 1.23 | 1.36 | 0.02 |
| 3. | glaucothöe | *L. saxatilis* | 1.25 | 1.43 | 0.02 |
| 4. | 1st crab ♂ | *L. saxatilis* | 1.55 | 1.73 | 0.03 |

Table 5.5

*P. bernhardus.* Data recorded during rearing from hatching to the 4th crab stage; with duration and age.

| Carapace width (mm) | | Duration (days) | Age (since hatching of egg) |
|---|---|---|---|
| | Larval life | 33 | |
| 0.9 | 1st crab stage | 11 | 33 |
| 1.1 | 2nd crab stage | 15 | 44 |
| 1.2 | 3rd crab stage | 48 | 54 |
| 1.3 | 4th crab stage | (discontinued) | 107 |

Table 5.6

Growth data obtained from 16 hermit crabs of *Diogenes pugilator*, collected intertidally from Rhossili Bay and kept for about 11 months at the Marine Science Laboratory.

CW1 = carapace width at time of starting; CW2, CW3 and CW4 = carapace width after successive moults.

D1 = time by days from starting experiment to the first moult;

D2 and D3 = time by days between successive moults.

F = female; M = male.

| Crab |  |  |  | Growth |  |  |  | Growth |  |  |  | Growth |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. | CW1 | D1 | CW2 | mm | % | D2 | CW3 | mm | % | D3 | CW4 | mm | % |
| F1 | 3.0 | 67 | 3.3 | 0.3 | 10.0 | 189 | 3.7 | 0.4 | 12.1 |  |  |  |  |
| F2 | 3.5 | 60 | 3.7 | 0.2 | 5.7 | 196 | 4.1 | 0.4 | 10.8 |  |  |  |  |
| F3 | 3.6 | 62 | 4.0 | 0.4 | 11.1 |  |  |  |  |  |  |  |  |
| F4 | 2.8 | 61 | 3.1 | 0.3 | 10.7 | 263 | 3.6 | 0.5 | 16.9 |  |  |  |  |
| F5 | 2.9 | 23 | 3.1 | 0.2 | 6.9 | 128 | 3.4 | 0.3 | 9.7 | 148 | 3.8 | 0.4 | 11.8 |
| F6 | 2.8 | 71 | 3.1 | 0.3 | 10.7 | 146 | 3.6 | 0.5 | 16.1 | 112 | 3.9 | 0.3 | 8.3 |
| F7 | 3.0 | 48 | 3.4 | 0.4 | 13.3 | 194 | 3.6 | 0.5 | 14.7 |  |  |  |  |
| M1 | 4.0 | 97 | 4.3 | 0.3 | 7.5 | 143 | 4.7 | 0.4 | 9.3 |  |  |  |  |
| M2 | 3.8 | 75 | 4.2 | 0.4 | 10.5 |  |  |  |  |  |  |  |  |
| M3 | 4.0 | 99 | 4.4 | 0.4 | 10.0 |  |  |  |  |  |  |  |  |
| M4 | 3.6 | 47 | 3.8 | 0.2 | 5.6 | 195 | 4.3 | 0.5 | 13.2 |  |  |  |  |
| M5 | 3.6 | 71 | 3.9 | 0.3 | 8.3 |  |  |  |  |  |  |  |  |
| M6 | 3.2 | 73 | 3.5 | 0.3 | 9.4 | 224 | 4.0 | 0.5 | 14.3 |  |  |  |  |
| M7 | 3.2 | 84 | 3.4 | 0.2 | 6.3 | 131 | 3.8 | 0.4 | 11.8 | 118 | 4.1 | 0.3 | 7.9 |
| M8 | 3.6 | 93 | 3.9 | 0.3 | 8.3 | 154 | 4.3 | 0.4 | 10.3 |  |  |  |  |
| M9 | 4.0 | 82 | 4.2 | 0.2 | 5.0 | 220 | 4.6 | 0.4 | 9.5 |  |  |  |  |

Table 5.7. Moulting season of hermits in laboratory rearing experiments.

Note that *Diogenes* stops moulting in winter.

| | Aug | Sept | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | June |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pagurus bernhardus* (intertidal and sublittoral) | | | | | | | | | | | |
| No. moulted | 2 | 15 | 14 | 4 | 8 | 3 | 2 | 3 | 1 | - | - |
| Total alive | 26 | 26 | 26 | 23 | 20 | 17 | 11 | 5 | 3 | 0 | - |
| % age moulted | 7.7 | 57.7 | 53.8 | 17.4 | 40 | 17.6 | 18.2 | 20 | 33.3 | - | - |
| *Diogenes pugilator* | | | | | | | | | | | |
| No. moulted | 1 | 3 | 9 | 3 | 1 | 0 | 0 | 5 | 3 | 3 | 2 |
| Total alive | 16 | 16 | 16 | 13 | 12 | 12 | 12 | 12 | 8 | 5 | 4 |
| % age moulted | 6.2 | 18.7 | 56.3 | 23.1 | 8.3 | 0 | 0 | 41.7 | 37.5 | 60 | 50 |

# CHAPTER 6

# Reproduction

## 6.1 INTRODUCTION

The most recent, though brief, review of the reproductive biology of decapod crustaceans is given in Adiyodi and Adiyodi (1983, 1984). Earlier but useful reviews of crustacean reproduction include those of Waterman (1960, 1961) especially on sex determination, Lockwood (1968) on physiology and Warner (1977) on reproduction of crabs. As recently as 1982, Anderson reviewed the whole topic of embryology of Crustacea.

The general breeding biology of hermit crabs can be summarised briefly as follows. All members of the Paguridae are thought to be gonochoristic, iteroparous, perennials with marked sexual dimorphism of the major chelae and pleopods. Breeding is usually (but not in all species) seasonal. The paired gonads are located in the abdomen; ovaries open by gonopores on the coxae of the 5th pereopods, testes open via seminal vesicles on the coxae of the 3rd pereopods. Ripe eggs are produced in a succession of batches; sperms are produced in small packets called spermatophores, in a continuous process.

Elaborate courtship and precopulatory behaviour is followed by brief vacating of their shells by both male and female for copulation. Spermatophores are deposited and stick to the female in the vicinity of her gonopores. Extrusion of a batch of eggs results in release of sperms from the spermatophores and fertilization takes place near the female gonopores. The fertilized eggs become attached to the relatively large setose pleopods of the female and are incubated there within the carcinoecium. Hatching occurs a few weeks later, releasing the small, planktotrophic zoea larvae into the plankton. Four successive zoeal stages in Paguridae (2-7 or eight in Diogenidae) are followed by a single megalopa (called a glaucothoe in this group) which performs the transition from planktonic to benthic environment where it seeks a suitable carcinoecium, usually a gastropod shell. In general terms, hermit crabs can be said to be "r-selected" producing large numbers of small eggs, resulting in wide dispersal over uncertain settlement areas. Very high larval mortality is followed by low adult mortality.

Some detailed examples of previous work on breeding biology of hermit crabs follows:-

General studies on the reproduction and breeding of pagurid crabs include: the work by Reese (1968) on the annual breeding seasons and the factors controlling breeding of three sympatric tropical species, *Calcinus laevimanus* (Randall), *C. latenus* (Randall) and *Clibanarius zebra* (Dana), and a study on the breeding biology of the two sympatric species of tropical hermit crabs. *Clibanarius chapini* Schmitt and *C. senegalensis* Chevreux and Bouvier by Ameyaw-Akumfi (1975). The reproductive strategies of four hermit crabs, *Clibanarius longitarsus*, *C. padavensis*, *C. olivaceus* and *Diogenes avarus* were described by Khan and Natarajan (1981); and the reproduction of the continuously breeding tropical species *Clibanarius clibanarius* Dana was described by Varadarajan and Subramonian in 1981.

### 6.1.1 The male system

Mouchet (1931), in a massive work, described the male organs and the shape of the sperm and the spermatophores of several species of hermit crabs including *Pagurus bernhardus* (L.) in considerable detail. The ultrastructure of sperm and spermatophores in *P. novaezealandiae* (Dana) was explained by Greenwood (1972). Matthews (1956) described the probable method of fertilization in terrestrial hermit crabs, *Coenobita* and *Birgus*, based on a comparative study of spermatophores.

### 6.1.2 The female system

Much less specialist attention has been given to the female system of pagurids. The best studies are those of Kamalaveni (1949) and Varadarajan and Subramonian (1980) who gave considerable details of the histology of the ovarian cycle of diogenid hermit crabs of the genus *Clibanarius*. Recently, Komm and Hinch (1985) have described the oogenesis in the terrestrial hermit crab, *Coenobita clypeatus*, in Tampa, Florida.

### 6.1.3 Courtship and mating behaviour

Courtship and mating behaviour of *Pagurus bernhardus* has been described in several publications (Jackson, 1913; Hazlett, 1968, 1970). Briefly, the male initially pulls the female about for some hours to days by grasping the rim of her shell aperture with his minor cheliped. He later shifts his grasp to one of her right ambulatory legs and executes sequences of jerking the female toward himself and tapping the female appendages with his major cheliped. Just before the pair ease out of their shells to copulate, the female palpates the male's mouth parts with her chelipeds and free ambulatory legs.

The sexual and mating behaviour for other species of pagurid crabs have also been studied. For example, the courtship and mating behaviour of *Pagurus* samuelis was described by Coffin (1958). The sexual behaviour patterns of nine species of hermit crabs in the family Paguridae were described by Hazlett (1968). Later Hazlett (1972) describes the behaviour patterns executed by hermit crabs during sexual behaviour for eight species in the genus *Calcinus* and ten species of the genus *Paguristes*. Snyder-Conn (1981) recorded the mating behaviour of the hermit crab, *Clibanarius digueti*. He noted that copulation in nature occurred between May and September and stated that under laboratory conditions, the typically larger male holds the female for twelve or more hours. Helfman (1977) reported on the copulatory behaviour of the coconut or robber crab, *Birgus latro* (L.). He found that after 250 hours of field observation, he had witnessed only one courtship-copulation sequence.

### 6.1.4 Breeding biology of *Pagurus bernhardus*

The earliest known detailed anatomical and histological studies of the reproductive system of *P. bernhardus* were given by Jackson (1913). Later, Selbie (1921) provided information on ovigerous females of *P. bernhardus* in Irish waters, but the study was based on small and infrequent samples. Pike and Williamson in 1959 produced a classic study on the breeding of the British species of hermit crabs including sublittoral *P. bernhardus*. Contrary to the assumption of Pandian and Schuman (1967), copulation does not follow closely after moulting as in most crabs (see Edwards, 1966; Crothers, 1967). Hazlett (1970) showed that copulation and spermatophore transfer can occur at various stages of the moult cycle.

### 6.1.5 Breeding biology of *Diogenes pugilator*

Very little published information is available on breeding of *D. pugilator*, except for that by Pike and Williamson (1959), suggesting that two broods are produced during the summer months in U.K. populations. They also reported that the number of eggs carried ranges from about 790 at 4 mm, to 1700 at 6 mm carapace length. Unlike the condition in *Pagurus bernhardus*, copulation in *Diogenes* does seem to follow moulting - females are carried about by males awaiting this event (Hazlett, 1966).

The objectives of this study were to determine the extent to which the small *P. bernhardus* found intertidally were sexually mature and whether they had the same pattern of reproduction as sublittoral populations. It was also hoped to shed some light on the number of broods produced by individual crabs in one season, and the onset of puberty in relation to the breeding season. *Diogenes pugilator* was to be studied similarly as an instructive comparison.

## 6.2 MATERIALS AND METHODS

Several different field sampling and laboratory analyses were used in the study of breeding. The great majority of these studies were based on the intertidal population at Mumbles Head, but a few (indicated in text) incorporated information from sublittoral samples.

### 6.2 1 Field sampling

The seasonal pattern of breeding was studied by using the monthly samples that were collected for the size frequency distribution and other population studies described in Chapter 2. In order to ensure that valid results were obtained, samples were examined fresh, as soon after collection as possible, which was usually the same day or the next day. All specimens were sexed and egg carrying by females was recorded. For routine purposes the embryos were merely classified as being "eyed" or "not eyed". This information was recorded along with details of the size of the crabs and their shells as mentioned in Chapter 2.

### 6.2.2 Egg counts

The total number of eggs carried by individual females was counted from about 100 specimens. These counts were made at various times through the breeding season. The method used was a modification of the method described by Choy (1985). After snipping off the eggs together with the pleopods, they were briefly treated (2-3 minutes) with 50% solution of household bleach (Sodium

Hypochlorite Solution with 4% available $Cl_2$). This freed the eggs allowing subsampling for counts in a Sedgewick Rafter counting chamber.

Eggs were measured on freshly collected material using an eyepiece graticule. Eggs at different embryonic stages were measured in this way.

### 6.2.3 Embyronic development

In a separate study eggs from each female in a March sample were also carefully studied and classified according to the state of development of the embryo following the method which had been used by Scheidegger (1976) on *Pagurus prideauxi* describing 13 stages from blastula to the newly hatched zoea larva. This procedure was found to be too difficult and time consuming for routine analysis.

### 6.2.4 Gonad examination

Regular analysis of the gonads to record their cyclical activity through the seasons was planned. After initial examination of both male and female systems, it was decided to concentrate on the ovarian sequence and studies of the male system abandoned.

To describe the development of ovaries of the hermit crab *P. bernhardus*, macroscopic examination was initially carried out by dissecting the abdomen under a low power stereoscope microscope.

For detailed microscopic examiantion, standard histological sections (Humason, 1979) of the ovaries, were made after fixing the gonads in sea-water Bouin's fluid for at least two days. Sections (7-10 μm) in DPX (BDH Chemicals Ltd., Poole, England). 0.5% Colloidin was used after partial dehydration to prevent sections from falling off the slide during staining and subsequent dehydration (Steedman, 1966).

## 6.3 RESULTS

### 6.3.1 Sex ratio

The results of sex ratio findings (Figs. 6.4, 6.8 and 6.11) are detailed in Chapter 2.

### 6.3.2 Male system of *Pagurus bernhardus* and *Diogenes pugilator*

Preliminary studies of the male reproductive system were not pursued. Photographs of various features examined are however given here in the plates as they provide a useful background to the other studies of reproduction.

### 6.3.3 Female system of *Pagurus bernhardus*

The ovaries in *Pagurus bernhardus* are paired, elongated organs (Plate 6.1) occupying most of the posterior part of the abdomen, and lie on the hepatopancreas (Plate 6.2). Although the ovaries lie side by side they are never interconnected at any stage. The right ovary is slightly **larger** than the left (Plate 6.1). Anteriorly, they are prolonged into two ovaries which open independently on either side at the base of the coxae of the third pereopods.

Oögenesis was divided into five arbitrary stages adapted from Laulier and Demeusy (1974) which corresponded to a series of changes in the size and colour of the ovaries (Table 6.4). At any one time, the ovaries of different females were often (histologically) in a series of stages. Ovaries of crabs that had recently spawned were either in the immature or recovering (developing) stages. Spent ovaries sometimes had a few mature ova that failed to be released. Ovaries of hermit crabs in the later stages of ovarian development sometimes showed a few large ova that looked as if they were degenerating. Histological sections of gravid females showed that their ovaries could be in either early recovery or active phase of development. Females which had just released larvae often had mature ovaries indicating that they could produce another brood (see Plate 6.4).

Histological sections reveal the arrangement of oöcytes in the ovary. Plate 6.5 shows the germinal zone and pre-vitellogenic stages. These oöcytes contained a very large nucleus with a small nucleolus and other inclusions visible. The ventral oogonial cells measured below 50 μm in diameter, the pre-vitellogenic oocytes measured between 50 μm - 150 μm. These oocytes contained granulated cytoplasm with no yolk globules. As soon as the oocytes grow to more than 150 μm and enlarge to reach around 375 μm, they are well surrounded by special cells called follicle-cells (Plate 6.5). As the oocytes increase in size, the follicle cells stretch to their maximum extent as a thin layer (see Plate 6.5).

The dark grey distended ovary contains almost exclusively, oocytes larger than 375 μm in diameter. Nuclei are no longer visible in all sections of these oocytes which have for the most part, completed vitellogenesis and are very large. The yolk-laden oocytes crowd the germinal area into a restricted ventral position. This band is thrown into folds by the pressure of yolky oocytes. Eventually the germinal zone becomes completely surrounded by overhanging vitellogenic oocytes giving it an apparent internal position.

Figures 6.22 and 6.23 show the results of oocyte measurements of ovaries of the hermit crabs *Pagurus bernhardus* studied histologically from June 1985 to February 1986, and *Diogenes pugilator* from April 1985 until October 1985. The graphs show that *P. bernhardus* oocytes increase in size starting in June, when the maximum size of the oocytes is 100 µm and this oocyte development continues gradually from one month to another until they reach breeding season. Some ovaries were sectioned during August, September, October and November (see figure 6.22). The size of the oocytes ranged between 140 µm in August to 400 µm during November.

During the breeding season in December the ovary of a non-gravid female was histologically studied. The oocytes were in two groups; in one, the size of the oocytes reached 100 µm and in the second group ranged between 200 µm to 420 µm. It appeared that the second group of oocytes were vitellogenic and ready to produce the first brood, and the first group (in the germinal zone) were starting to grow up for the second one. In January 1986 two females were selected for histological study. One of them was gravid, the other was not (Fig. 6.22). The results showed that the size of the oocytes of the non-gravid female had reached 120 µm for the first group of oocytes and ranged between 230 µm to 450 µm for the second group. In the gravid female, the oocytes still inside the ovary measured up to 200 µm. Similar results were reached again in February when female carrying external eggs was histologically studied, one group of oocytes (shown in the graph) reaching 120 µm.

### 6.3.4 Gonads of *Diogenes pugilator*

*Diogenes pugilator* was also studied histologically from April to October 1985. So the first study was just two months before the breeding season of this hermit crab.

The germinal zone in *D. pugilator* also appears to get restricted to a small area as oocytes steadily increase in diameter owing to yolk accumulation (see Plate 6.6). The growing oocytes engaged in vitellogenesis move away from the ventral germinal zone to a more dorsal position, distending the ovarian wall on that side. Simultaneously oocytes proliferated anew from the germinal zone take their place. Nucleoli as seen in *Pagurus bernhardus* oocyte nuclei were not seen in *D. pugilator*.

The follicle-cells surrounding the large oocytes are shown in Plate 6.6.

The results of the oocyte counts are shown in Fig. 6.23. The ovary of a female not carrying external eggs was histologically studied in April 1985. The size of the oocytes at this time reached a maximum of less than 130 μm in diameter. In May the ovary of a female without external eggs was studied. It was seen to contain two groups of oocytes, the first group measuring less than 100 μm in diameter, the second group measuring between 160 μm to 230 μm (Fig. 6.23). During the breeding season ovaries of different females, berried and non-berried, were histologically studied. In June, the ovary of an ovigerous female was sectioned, and results based on this histological study are plotted in figure 6.23. From the histogram it can be seen that this female (carrying the first batch of eggs externally) also had another group of oocytes measuring below 120 µm in diameter. During July another female was histologically studied, this time a female without external eggs was chosen. The results show that two groups of oocytes were present in the ovary. The first group measured less than 125 µm in diameter, and the second ranged between 155 µm to 240 µm. In August and September two females, one from each month, were histologically studied; these two females were not carrying any external eggs. They gave similar results to that female which was studied earlier in April.

During the final period of the breeding season, one more female without external eggs was examined. The histological study of this ovary is shown in figure 6.23. The size of the oocytes was very small (below 80 µm in diameter).

### 6.3.5 Breeding season

The annual reproductive cycle of the intertidal hermit crab *P. bernhardus* was studied for more than one year (Fig. 6.1). The breeding season intertidally extended from December to July, with peak number of gravid females in February (Fig. 6.3), when 90% were found to be berried. Numbers of gravid females in June and July were very low (Table 6.1). From August to November not a single ovigerous female could be collected. Eyed-embryos first appeared in the month of February with a high percentage (33.3%) in April.

Figure 6.2 shows that the principal size group of reproductive hermit crabs was those measuring between 3.0 to 5.0 mm carapace width. This result also shows that the larger crabs (4.0-6.0 mm) breed throughout the breeding season, while the smaller mature crabs,

< 2.0 - 4.0 mm carapace width, ceased breeding relatively early in the breeding season.

Four months of sampling from Oxwich Bay showed that the reproductive cycle of the sublittoral *P. bernhardus* started after October 1982 and before February 1983 (Table 6.2). The ovigerous females appeared first in February and continued to be present until the last sampling month (April) (Fig. 6.5). The percentage of gravid and non-gravid females is shown in figure 6.7. The highest number of berried females was again collected in February (86.4%). Eyed-embryos first appeared in February with a high percentage in the month of March (50%).

The annual reproductive cycle of the hermit crab *D. pugilator* is plotted in Figure 6.9. The breeding season in these two years (1983-1984) showed peak values in August 1983 and July 1984 when 83% of females were found to be berried (Fig. 6.10). Eyed-embryos first appeared in both years in the month of June, with a percentage of 28% in August 1983 and 30% in July 1984.

### 6.3.6 Fecundity

There is a direct correlation between body size and the number of eggs carried by female *P. bernhardus* (Fig. 6.13). About 100 intertidal hermit crabs of various carapace width, a range covering the smallest to the largest ovigerous females found in the samples collected during 1982-1983, were examined and the eggs were counted. The smallest number of eggs carried by a female was just over 300 (carapace width 1.7 mm) and the largest was less than 3000 (carapace width 5.4 mm).

Figure 6.14 shows the mean number of eggs plotted against the mean carapace width, with curve fitted by eye.

About 75 ovigerous females of the hermit crab, *P. bernhardus*, collected sublittorally by trawling from Oxwich Bay, were carefully extracted from their gastropod shells and their eggs were snipped from the pleopods and counted individually. Figure 6.15 shows the relation between the female carapace width and the number of eggs of these sublittoral specimens. The smallest female (2.8 mm carapace width) carried just over 400 eggs and the largest (15.6 mm carapace width) carried nearly 11,000 eggs. Figure 6.15 also shows that the number of eggs was directly related to the body size of the female *P. bernhardus*, the relationship being an exponential one.

Forty ovigerous females of the hermit crab *D. pugilator* were carefully extracted from their gastropod shells and their eggs counted individually and plotted against the carapace width of the same females (Figure 6.16). The smallest female (2.6 mm carapace width) was carrying more than 250 eggs and the largest female (4.3 mm carapace width) was carrying almost 1,500 eggs. Figure 6.16 also shows that the number was related to the size of the hermit crab.

Relation between the number of eggs and the size of carapace for both *P. bernhardus* (intertidally) and *D. pugilator* are shown in figure 6.17. These two curves were fitted by eye and show that small (less than 4.0 mm carapace width) females of *P. bernhardus* carry larger numbers of eggs than *D. pugilator* females of the same carapace size. The largest female *D. pugilator* on the other hand carry more eggs than the same size *P. bernhardus*.

Figures 6.18 & 6.19 show relation between weight of eggs and the carapace width of the two species of hermit crabs, *P. bernhardus* and *D. pugilator*. It can be seen that the weight of eggs of *P. bernhardus* is more than the weight of eggs of *D. pugilator* at the same carapace width. The heaviest quantity of eggs from an intertidal female *P. bernhardus* was 0.42 g, the heaviest for *D. pugilator* was 0.07%.

The eggs as a percentage of body weight were plotted against the size of the carapace for both species in figure 6.20. The highest (50%) was for *P. bernhardus* at carapace width of 2.4 mm and 25% for *D. pugilator* at 4.3 mm.

Figure 6.21 shows the relation between the number of eggs and body weight of both species, *P. bernhardus* and *D. pugilator*. It also compares these results from these two species to those of Pike and Williamson (1959) after converting the carapace length to carapace width.

### 6.3.7 Size of eggs

When the eggs are laid in December for both populations of *P. bernhardus*, they measured approximately 0.55 x 0.50 mm. Fifty eggs were taken at random from a range covering the smallest to the largest ovigerous females in the samples. These were examined and showed that there was no direct correlation between egg size and carapace width of the parent. If there was any difference in size, it was mainly due to the advanced stage of development in the egg.

During the first two months of incubation, the eggs showed no substantial increase in size, most of them exhibiting late gastrula and "early" eye-pigmentation at this stage. With the passage of time, size increased until the development of the egg reached the final stage. By late February and March the majority measured between 0.79 x 0.71 mm, all having "early" or "late" eye-pigmentation; the shape of egg is then almost spherical.

The egg size of the hermit crab, *D. pugilator*, during the early stage was small (0.23 mm x 0.19 mm) and it increased in size gradually toward maturity. The eyed-embryos egg measures 0.45 x 0.23 mm; the egg shape of this crab is more oval than that of *P. bernhardus*.

### 6.3.8 Size at puberty

The samples obtained from the intertidal population of the hermit crab, *P. bernhardus*, consisted of specimens ranging from less than 2.0 to 6.0 mm in carapace width. The smallest mature females (carrying eggs) was 1.7 mm (Fig. 6.2).

The size of the smallest female carrying external eggs from the sublittoral population was 3.5 mm carapace width, and the largest was 15.5 mm (Fig. 6.6).

The smallest gravid female of *Diogenes pugilator* was less than 2.8 mm carapace width (Fig. 6.12). Table 6.3 shows details of the number of males, gravid and non-gravid females.

## 6.4 DISCUSSION

### 6.4.1 Breeding season

For present purposes, this was defined as the period during which gravid females were present in the population.

The almost exactly opposite seasons for the breeding of the two species, *Pagurus bernhardus* and *Diogenes pugilator* seems to be a reflection of their different geographical distributions, as seen in some other pairs of species where distributions overlap in the British Isles. For instance, the intertidal barnacles, *Semibalanus balanoides* and *Chthamalus montagui* (which breed respectively in winter and summer) have distributions centred to north and south of the British Isles respectively (see Lewis, 1964, as *Balanus balanoides* and *Chthamalus stellatus*). Here *Diogenes pugilator*, which is centred in low latitudes (see map, Fig. 1.1) like *C. montagui*, is near its northern limit and breeds only in the warmer months. *Pagurus bernhardus*, on the other hand like *Semibalanus*, has a distribution centred at much higher latitudes and its winter breeding is an adaptation to allow its larvae to exploit spring plankton conditions which are relatively brief further north. The comparison ends here however. *Semibalanus balanoides* is single brooded whereas *P. bernhardus* is multibrooded. Furthermore, rather than being later further north as in *Semibalanus*, the breeding season of *P. bernhardus* is longer further north. Pike and Williamson (1959) found gravid females as early as November and as late as August whereas in the present study the breeding season was always restricted to the period December to July. However, numbers involved in June and July were very low indeed so that May is effectively the last month of the breeding season for intertidal *P. bernhardus*. Sublittorally, it might be longer.

### 6.4.2 The ovarian cycle and number of broods

In common with other decapod Crustacea, the processes leading to production of ripe ova is divided into two tissue types in the ovary; firstly, the germinal zone consisting of all previtellogenic stages of gametogenesis including primary and secondary oocytes, and secondly a single batch of oocytes undergoing vitellogenesis (see Figs. 6.22 and 6.23). It is never possible to recognise two separate successive batches of oocytes within the ovary in the way that several successive batches (representing several future spawnings) may be recognised in ovaries of some animals, for instance the fish, *Blennius pholis* (Qasim, 1956).

Furthermore, ovarian development (especially vitellogenesis) and ecdysis are antagonistic processes in most Crustacea (Passans, 1960; Aiken and Waddy, 1976), enhancement of one, suppresses the other. Thus in crabs such as *Carcinus*, copulation precedes egg laying by several months, taking place immediately after ecdysis (Crothers, 1969). This is seen even in some anomura such as *Lithodes aeguispina* (Lewell *et al.*, 1985); such animals have sperm storage in spermathecae. Sperm will even survive ecdysis in *Portunus sanguinolentus* (Ryan, 1967). Hence the presence of mature ova in gravid females as seen in *Pagurus bernhardus* might be thought to indicate not only sequential breeding (more than one brood by season) but also successive spawnings in one intermoult. In view of the lack of sperm storage (no spermatheca) in hermit crabs, it follows that copulation and spermatophore transfer must also take place a second time in the same intermoult. In female *Diogenes* maturing ovaries are again present in gravid females (Pike and Williamson, 1959) which seems to conflict with the idea that moulting must precede mating in this species.

The approximate state of ovarian development is indicated by its colour - often visible through the integument (Pike and Williamson, 1959). Colour can be related to mean oocyte size in the developing batch (see Table 6.4).

It is quite clear that at least two broods may be produced by individual females of both species as suggested by previous workers (Pike and Williamson, 1959; Dawirs, 1979). Equally, since in both species, temperatures are in general rising throughout the season, successive broods probably take less time to develop.

### 6.4.3 Size of brood

As in other decapods, the number of eggs produced per brood is related to animals size. Gonzalez Gurriarán (1985) obtained a logarithmic relationship between carapace width and number of eggs produced per brood in *Liocarcinus puber*.

In general brood size of crabs is related to latitude. In temperate latitudes there are smaller broods with larger eggs than in warm water latitudes (Sastry, 1983). Choy (1986) showed that whereas at terminal size, *Carcinus* and *Liocarcinus* produce 0.5-1.0 million eggs, the lower latitude genera *Portunus*, *Scylla*, *Callinectes*, *Ovalipes* of same size produce 1-2 million. Strict comparisons are difficult but at the overlap of size (0.2-0.3 g) measured as wet weight, *Diogenes pugilator*, as expected from the argument, produces more eggs than *Pagurus bernhardus* (see Figure 6.21).

### 6.4.4 Puberty moult

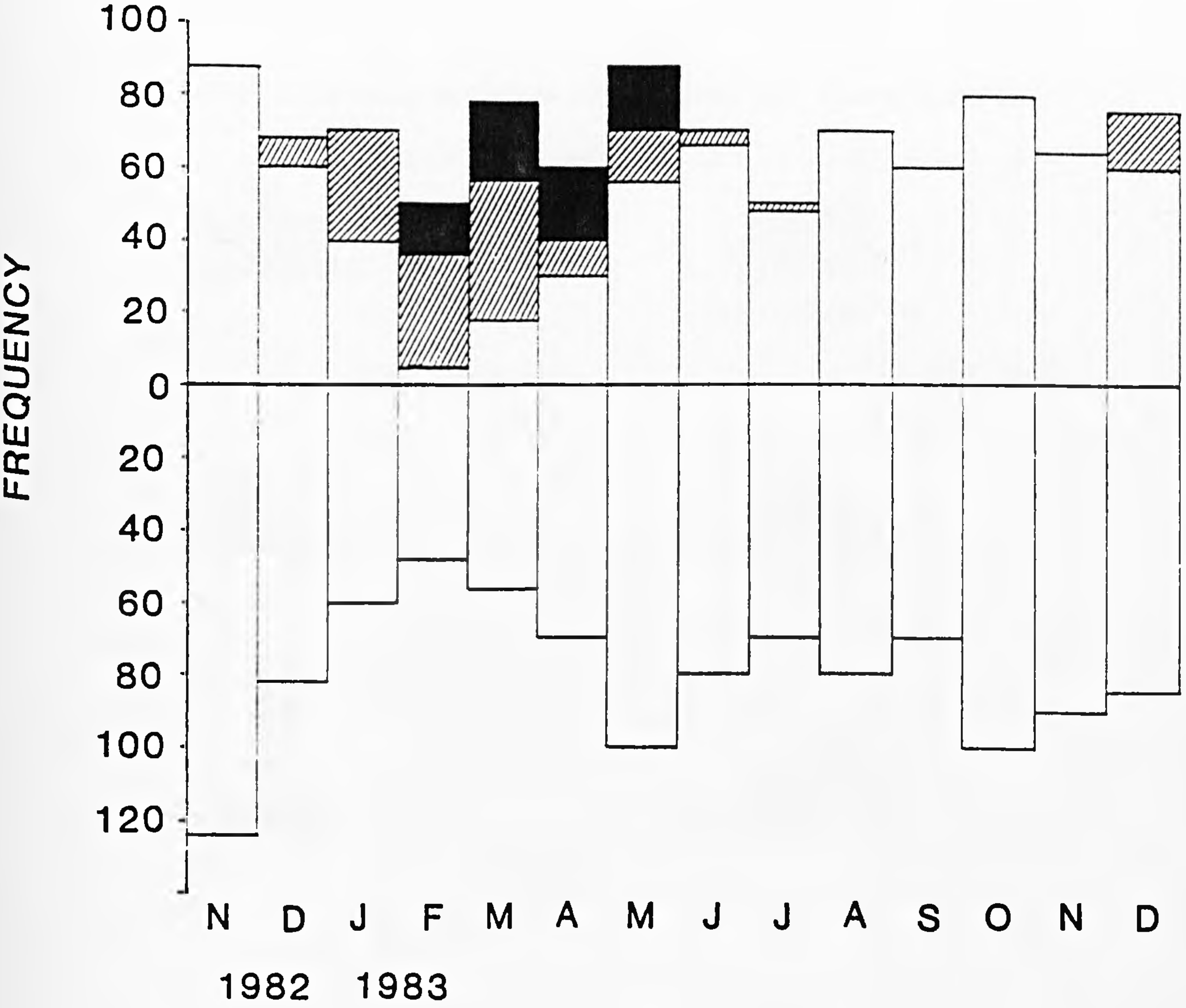
Various criteria have been used as an indication of the moult of puberty: 1) presence of ripe gametes in the gonad; 2) copulatory behaviour; 3) onset of allometric growth of certain appendages or the abdomen of the females; 4) presence of spermatophores on a female; 5) carrying of fertilized eggs. The onset of sexual maturity in Crustacea occurs at a moult, the pubertal moult, before which the animal is immature by any or all of these criteria. Full sexual maturity develops in the instar following the pubertal moult. Sexual dimorphism, manifest as secondary sexual characters usually appears before the pubertal moult. So far as these two species are concerned, carrying of fertilized eggs by females is simple and unambiguous indication. Examination of smallest gravid females of the two species indicate that they were hatched the previous season. It seems likely that as in the case of other seasonally breeding crabs at these latitudes such as *Carcinus maenas* (Crothers, 1967) and *Liocarcinus puber* (Choy, 1986), recruits first breed in the next breeding season, i.e. when less than a year old.

Careful comparison of the size of these youngest breeding females of *Pagurus bernhardus* with that of young hermits raised in the laboratory suggest that the moult of puberty may be as early as the second or third post larval moult and that therefore the 3rd or 4th hermits are the first to be mature. Males do not become mature until slightly larger, but this is probably at the same age and the same moult since males grow faster than females. However, it is equally obvious that early recruits to a population will have grown beyond this size by the time of onset of the new breeding season.

Size and therefore age at first sexual maturity will thus probably depend on the date of settlement of the individual glaucothoe. Those that settle very early in the season, say May, will have achieved a larger size by November, than those that settle later, say July. However, no settlement is likely to take place so late in the summer that individuals are still too small to breed in the first breeding season following the one in which they hatched. Males on the other hand, compete for mates, such that it is probable that very small males, even if mature, perform very few matings in this first available season.

The moult of puberty in *Diogenes pugilator* can be judged approximately from the data in Table 6.5. As in the case of *P. bernhardus* females will probably first breed in the summer of the year following that of their hatching. Recruitment of 1st hermits to the benthic population in August-October will be followed by little growth during the winter hence the very small size of the smallest gravid females in June.

It should perhaps be emphasised that for both these species, rates of development of embryos and larvae are too slow for individuals to breed in the season of their recruitment. The earliest recruits to a population were recorded only when the season was ending (see Table 6.5).


FREQUENCY
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80
60
40
20
0
20
40
60
80
100
120
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1982
1983

Figure 6.1

Number of males and females and reproductive state of females in samples of *P. bernhardus* collected from Mumbles Head. Females above X-axis and males below.

☐ No eggs

▨ Eggs without eye pigment

■ Eggs with eye pigment

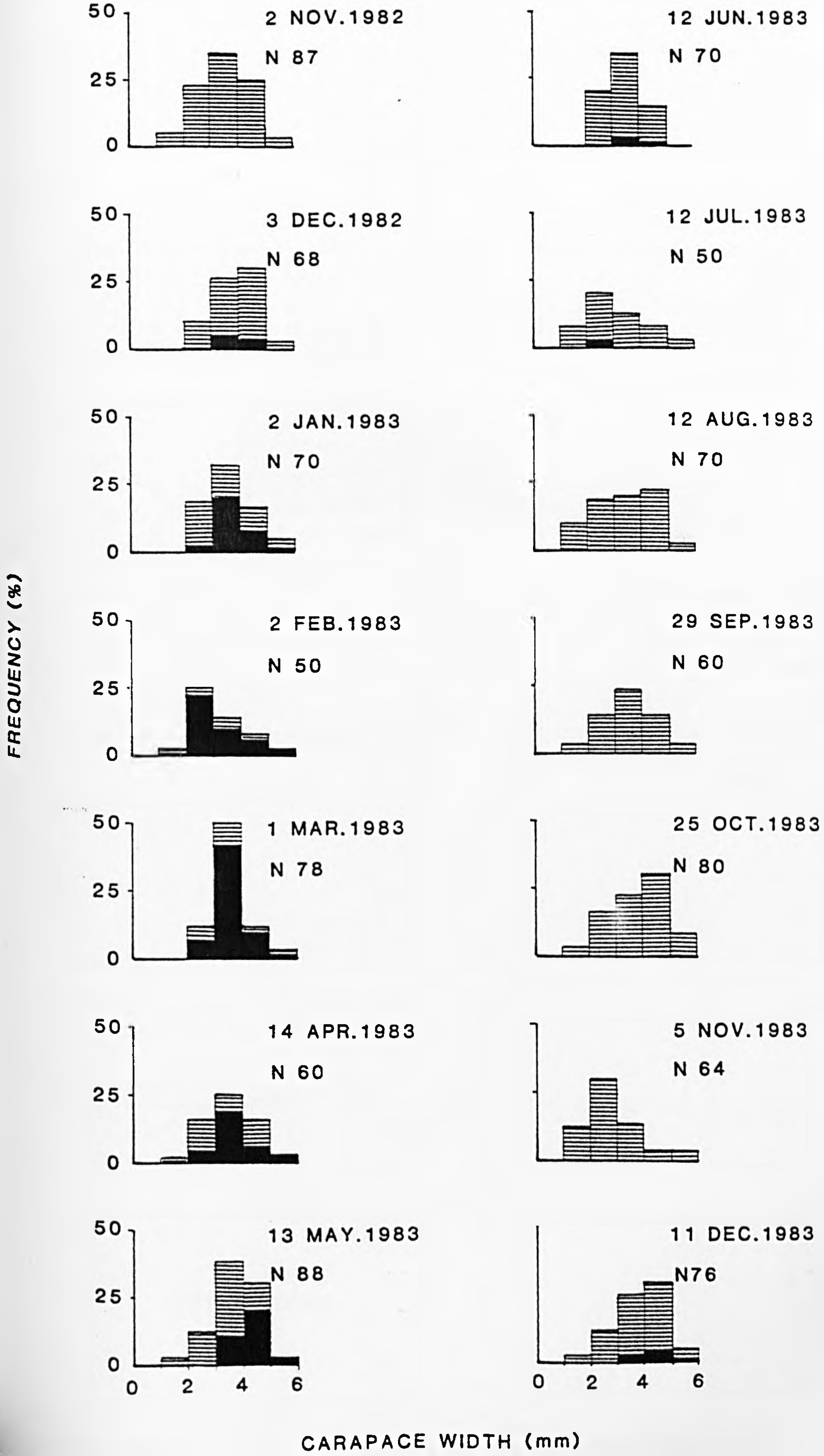
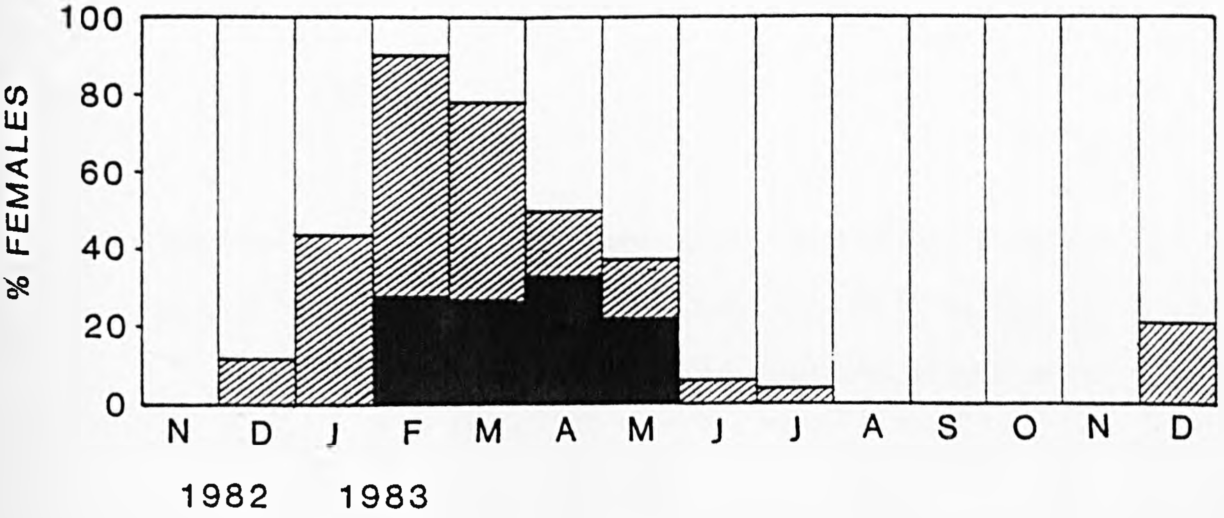

2 NOV.1982
N 87
12 JUN.1983
N 70
3 DEC.1982
N 68
12 JUL.1983
N 50
2 JAN.1983
N 70
12 AUG.1983
N 70
2 FEB.1983
N 50
29 SEP.1983
N 60
1 MAR.1983
N 78
25 OCT.1983
N 80
14 APR.1983
N 60
5 NOV.1983
N 64
13 MAY.1983
N 88
11 DEC.1983
N76
50
25
0
0
2
4
6
FREQUENCY (%)
CARAPACE WIDTH (mm)

Figure 6.2

Monthly values for berried and non-berried females of *P. bernhardus* collected from Mumbles Head.

■ Berried

▤ Non-berried


% FEMALES
100
80
60
40
20
0
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1982
1983

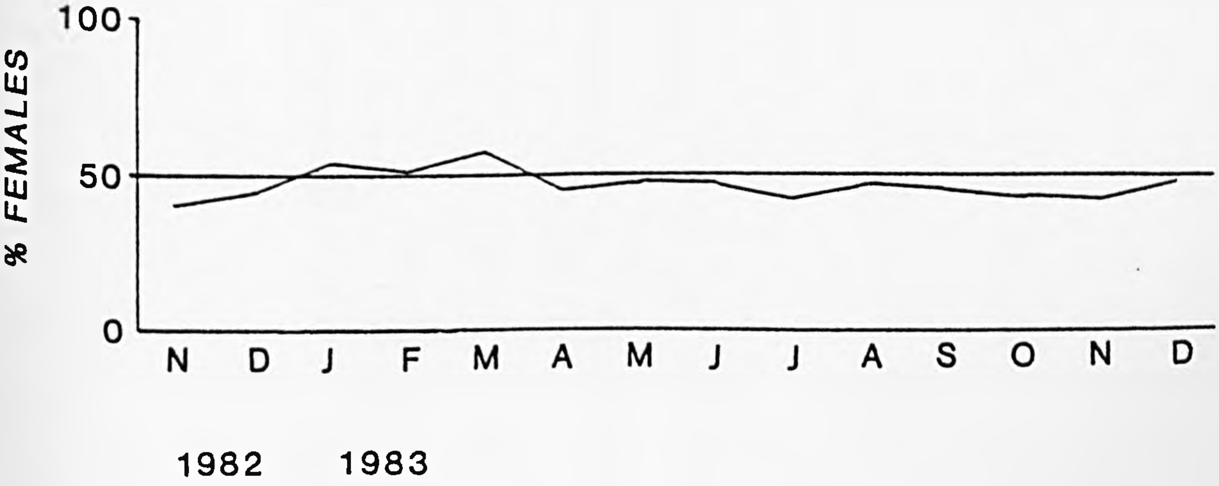

% FEMALES
100
50
0
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1982
1983

Figure 6.3

Percentage of gravid females of *P. bernhardus* collected on the standard transect (see text).

☐ ♀ without eggs

▨ ♀ with early stage eggs (non eyed-embryo)

■ ♀ with late stage eggs (eyed-embryo)

Figure 6.4

Sex-ratio (% females) of *P. bernhardus* from Mumbles Head during 1982/83.

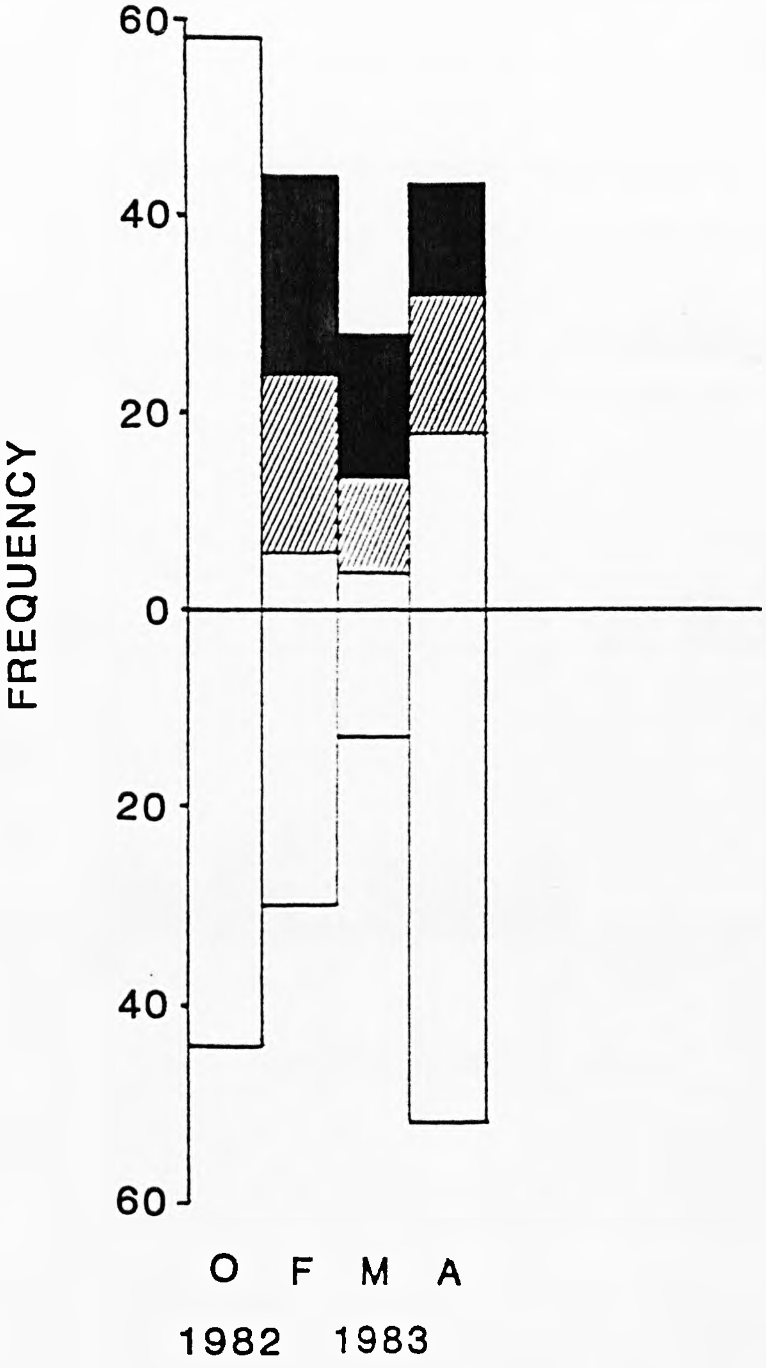

60
40
20
0
20
40
60
FREQUENCY
O
F
M
A
1982
1983

Figure 6.5

Number of males and females and reproductive state of females in samples of *P. bernhardus* from sublittoral zone. Females above X-axis and males below X-axis.

- ☐ No eggs
- ▨ Eggs without eye pigment
- ■ Eggs with eye pigment

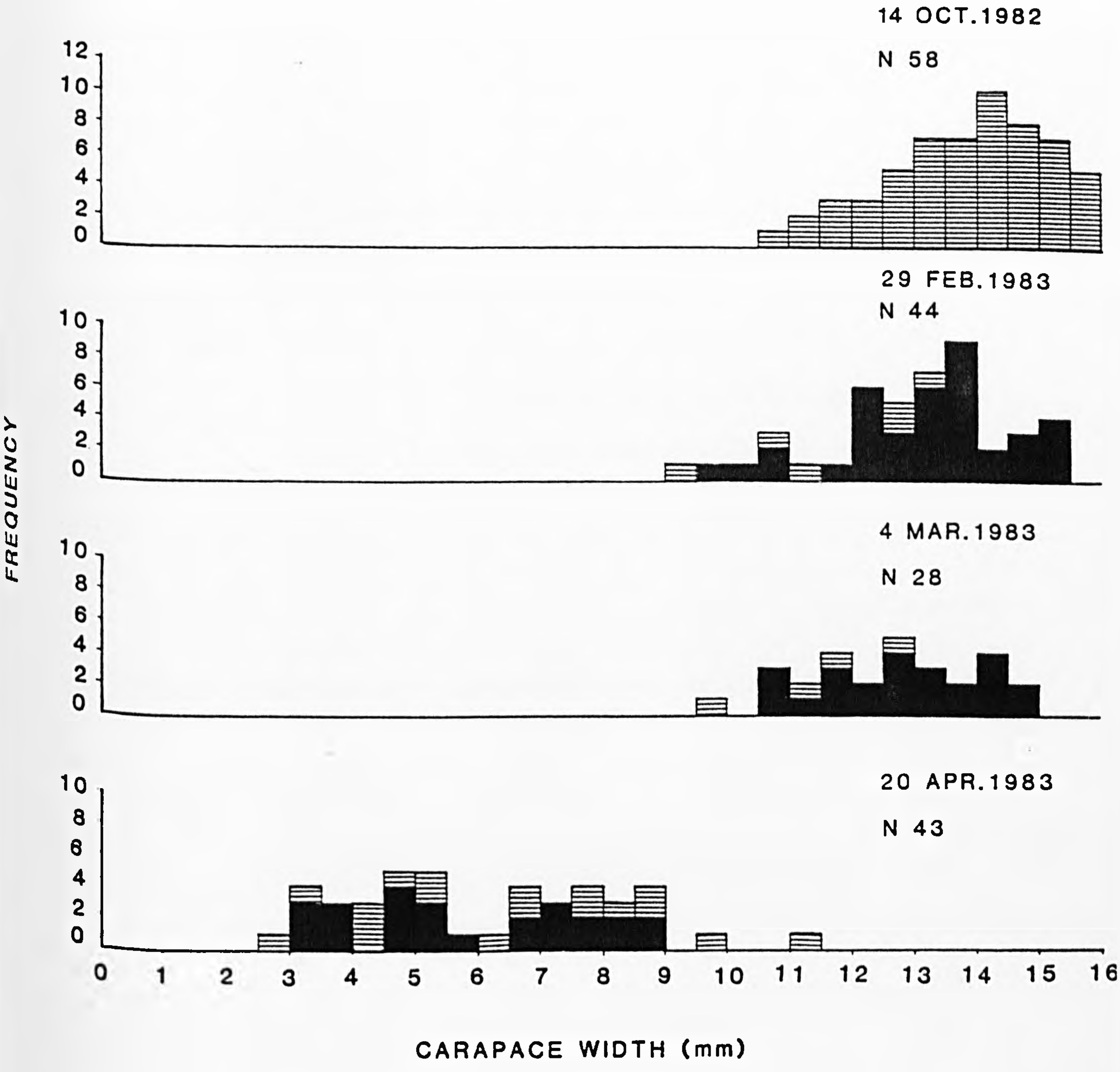
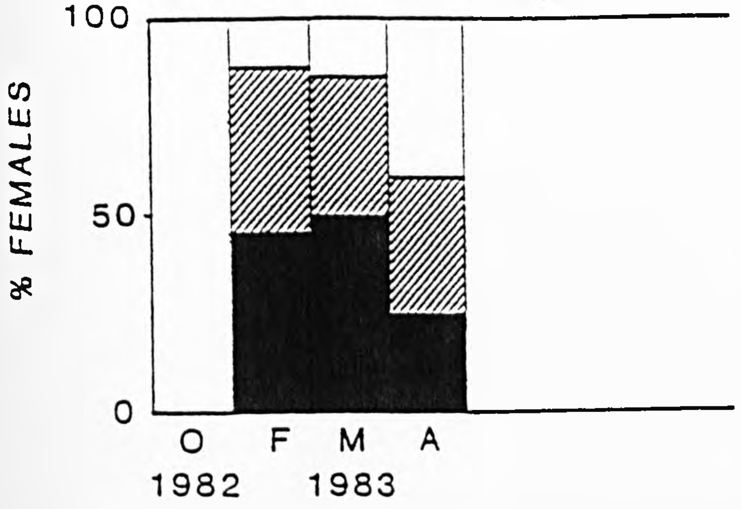

14 OCT.1982
N 58
29 FEB.1983
N 44
4 MAR.1983
N 28
20 APR.1983
N 43
FREQUENCY
12
10
8
6
4
2
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
CARAPACE WIDTH (mm)

Figure 6.6

Incidence of berried and non-berried females for each size group of *P. bernhardus* collected from sublittoral zone.

■ Berried

▤ Non-berried


% FEMALES
100
50
0
O
F
M
A
1982
1983

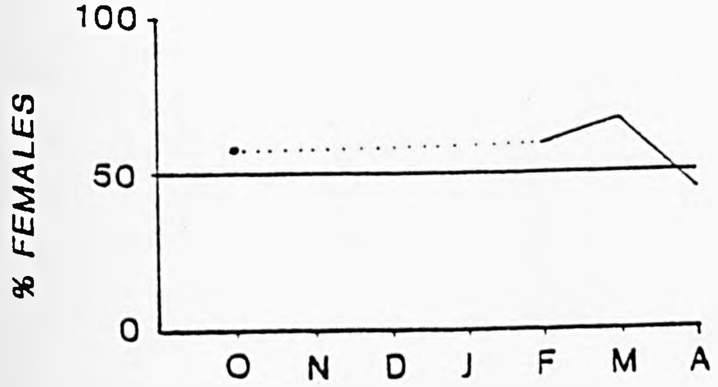

% FEMALES
100
50
0
O
N
D
J
F
M
A

Figure 6.7

Percentage of gravid and non-gravid females of *P. bernhardus* collected from sublittoral zone.

☐ ♀ without eggs

▨ ♀ with early state eggs

■ ♀ with late state eggs (embryo)

Figure 6.8

Sex-ratio (% females) of *P. bernhardus* from sublittoral zone.

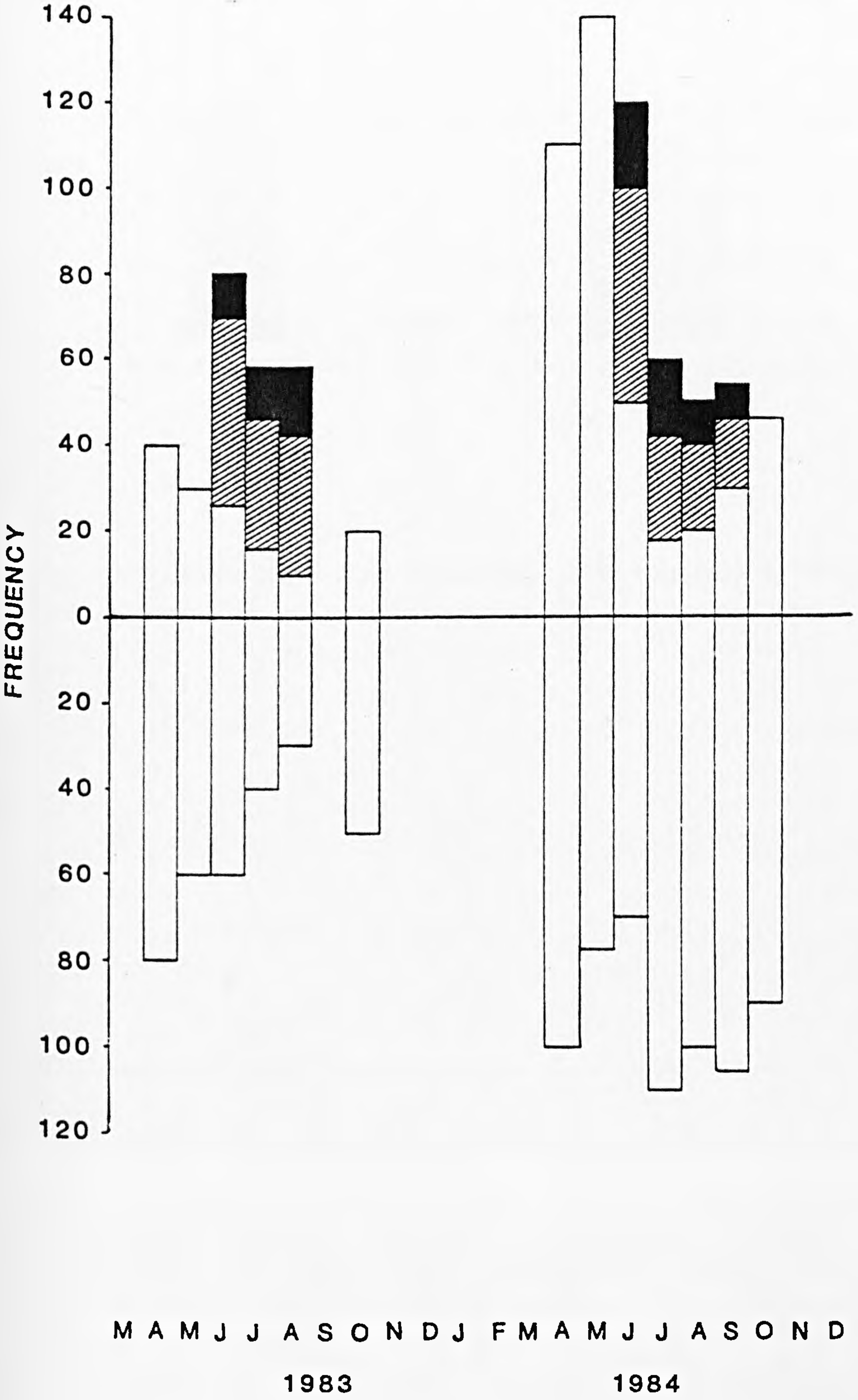

140
120
100
80
60
40
20
0
20
40
60
80
100
120
FREQUENCY
M A M J J A S O N D J F M A M J J A S O N D
1983
1984

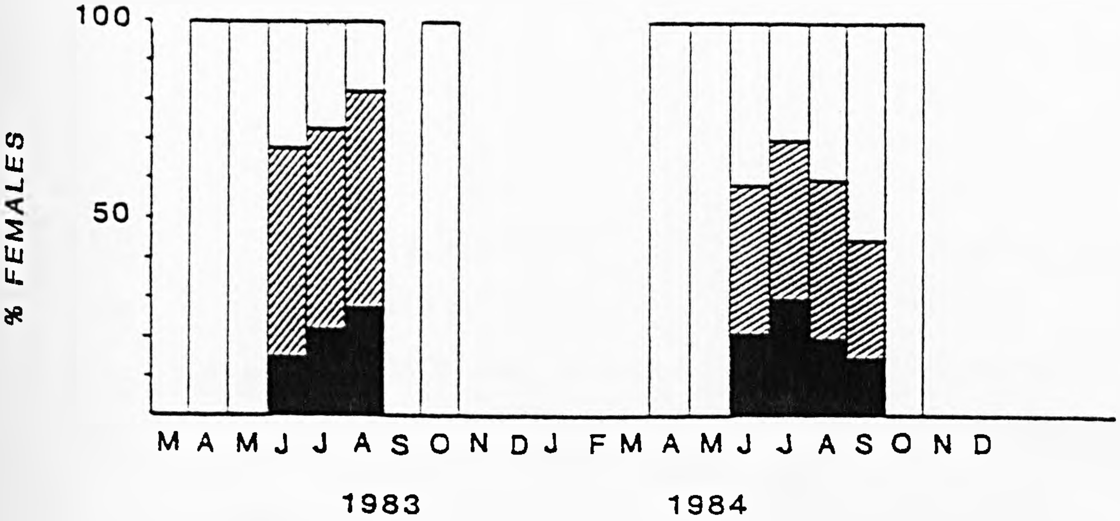
Figure 6.9

Number of males and females and reproductive state of females in samples of *D. pugilator* from Rhossili Bay. Females above X-axis and males below.

☐ No eggs

▨ Eggs without eye pigment

■ Eggs with eye pigment


100
50
% FEMALES
M A M J J A S O N D J F M A M J J A S O N D
1983
1984

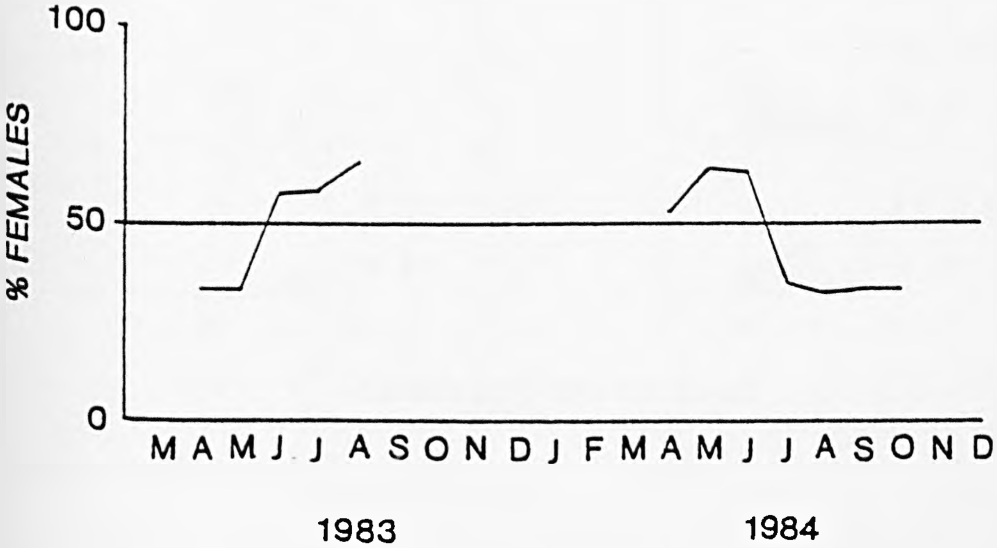

100
50
0
% FEMALES
M A M J J A S O N D J F M A M J J A S O N D
1983
1984

Figure 6.10

Percentage of gravid and non-gravid females of *D. pugilator*.

☐ ♀ without eggs

▨ ♀ with early state eggs

■ ♀ with late state eggs (embryo)

Figure 6.11

Sex-ratio (% females) of *D. pugilator* from Oxwich Bay.

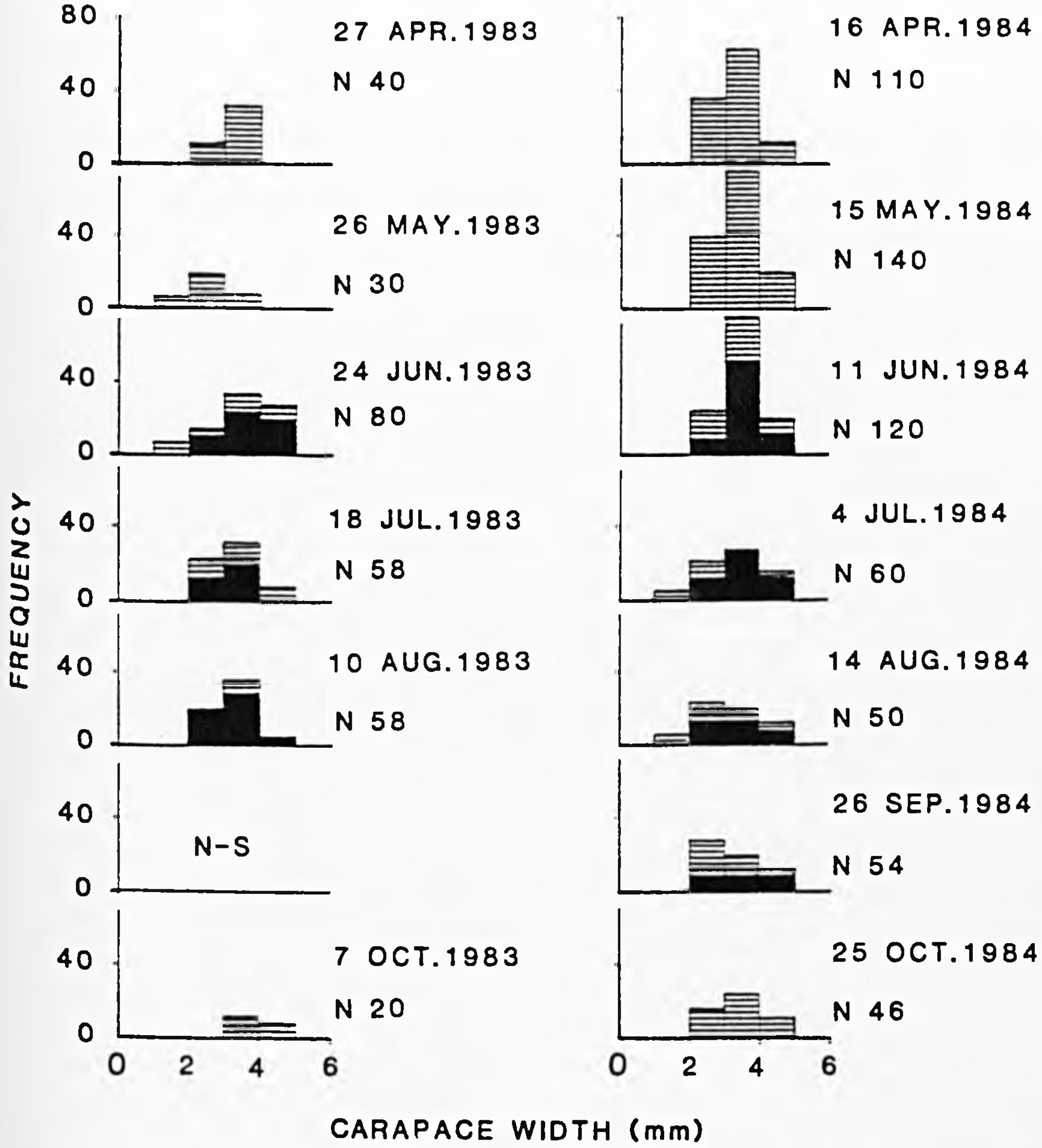

80
40
0
27 APR.1983
N 40
26 MAY.1983
N 30
24 JUN.1983
N 80
18 JUL.1983
N 58
10 AUG.1983
N 58
N-S
7 OCT.1983
N 20
16 APR.1984
N 110
15 MAY.1984
N 140
11 JUN.1984
N 120
4 JUL.1984
N 60
14 AUG.1984
N 50
26 SEP.1984
N 54
25 OCT.1984
N 46
FREQUENCY
0
2
4
6
CARAPACE WIDTH (mm)

Figure 6.12

Histograms of size groups of gravid females of *D. pugilator* from monthly samples.

■ gravid

▤ non-gravid

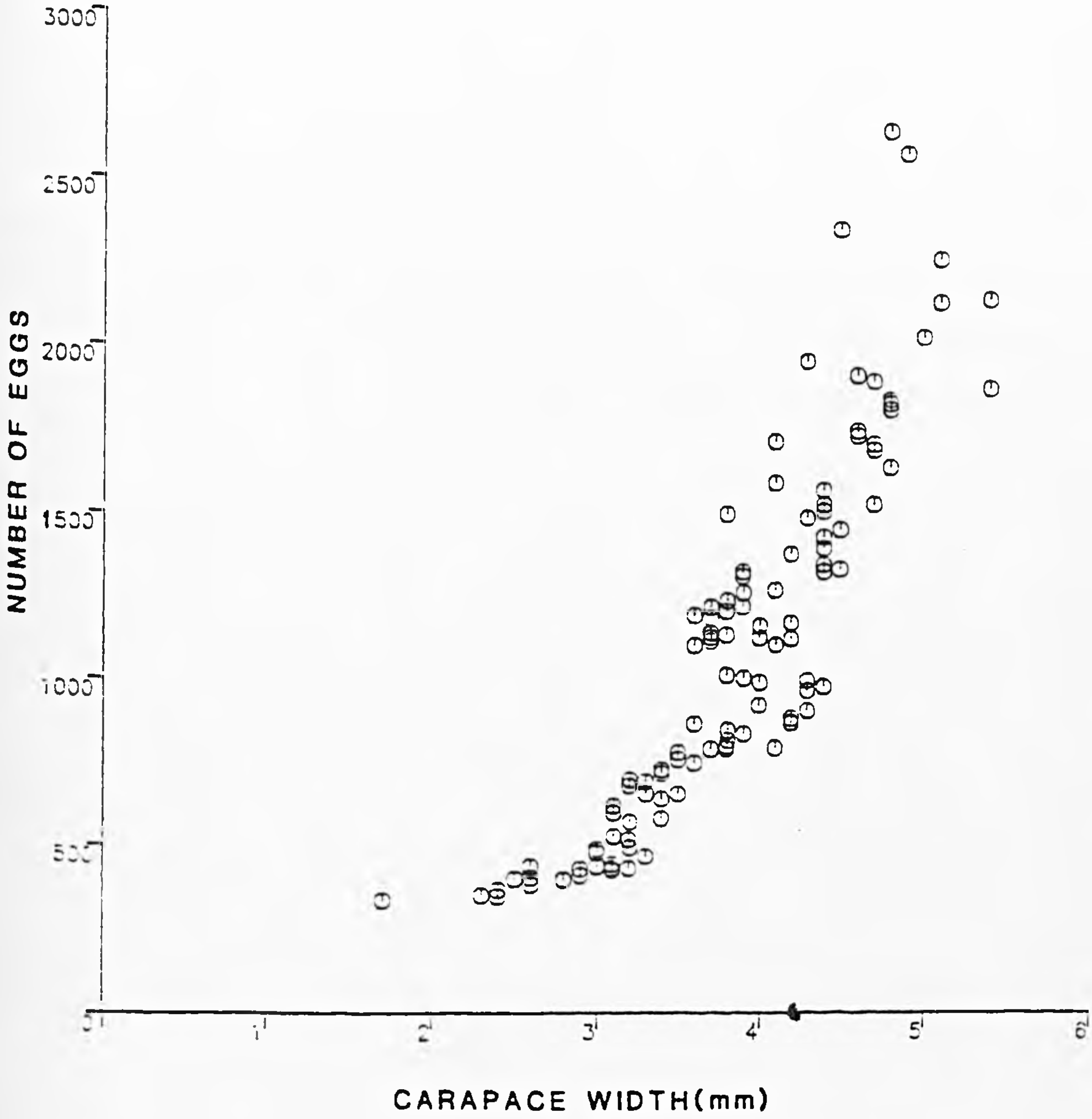

NUMBER OF EGGS
3000
2500
2000
1500
1000
500
0
1
2
3
4
5
6
CARAPACE WIDTH(mm)

Figure 6.13

Relation between number of eggs carried by intertidal ovigerous females, and the size of the hermit crab *P. bernhardus*, raw data, collected from Mumbles Head.

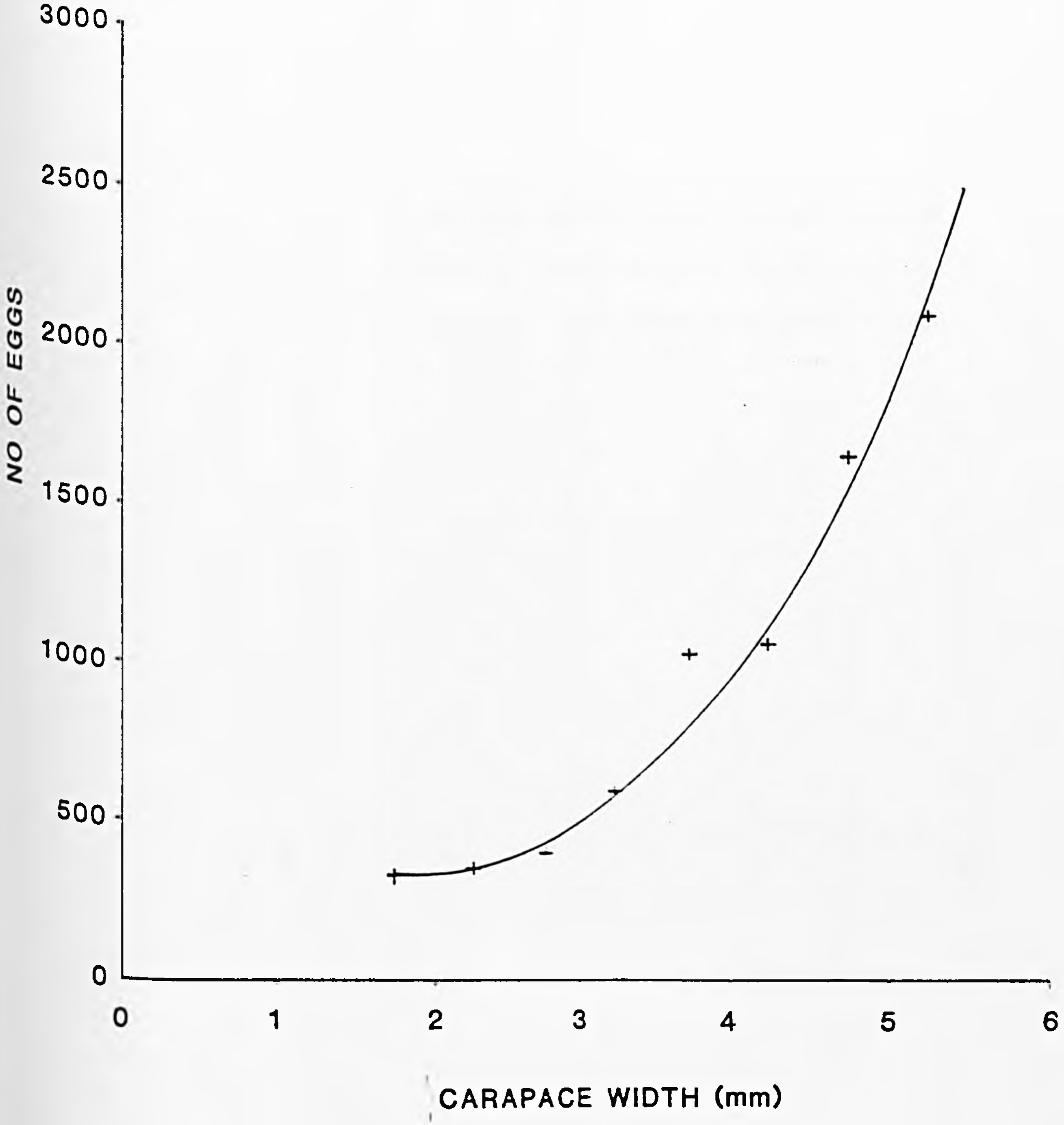

3000
2500
2000
1500
1000
500
0
NO OF EGGS
0
1
2
3
4
5
6
CARAPACE WIDTH (mm)

Figure 6.14

Relation between number of eggs and size of the carapace of *P. bernhardus*. Each point represents a mean of 10 measurements, with curve fitted by eye.

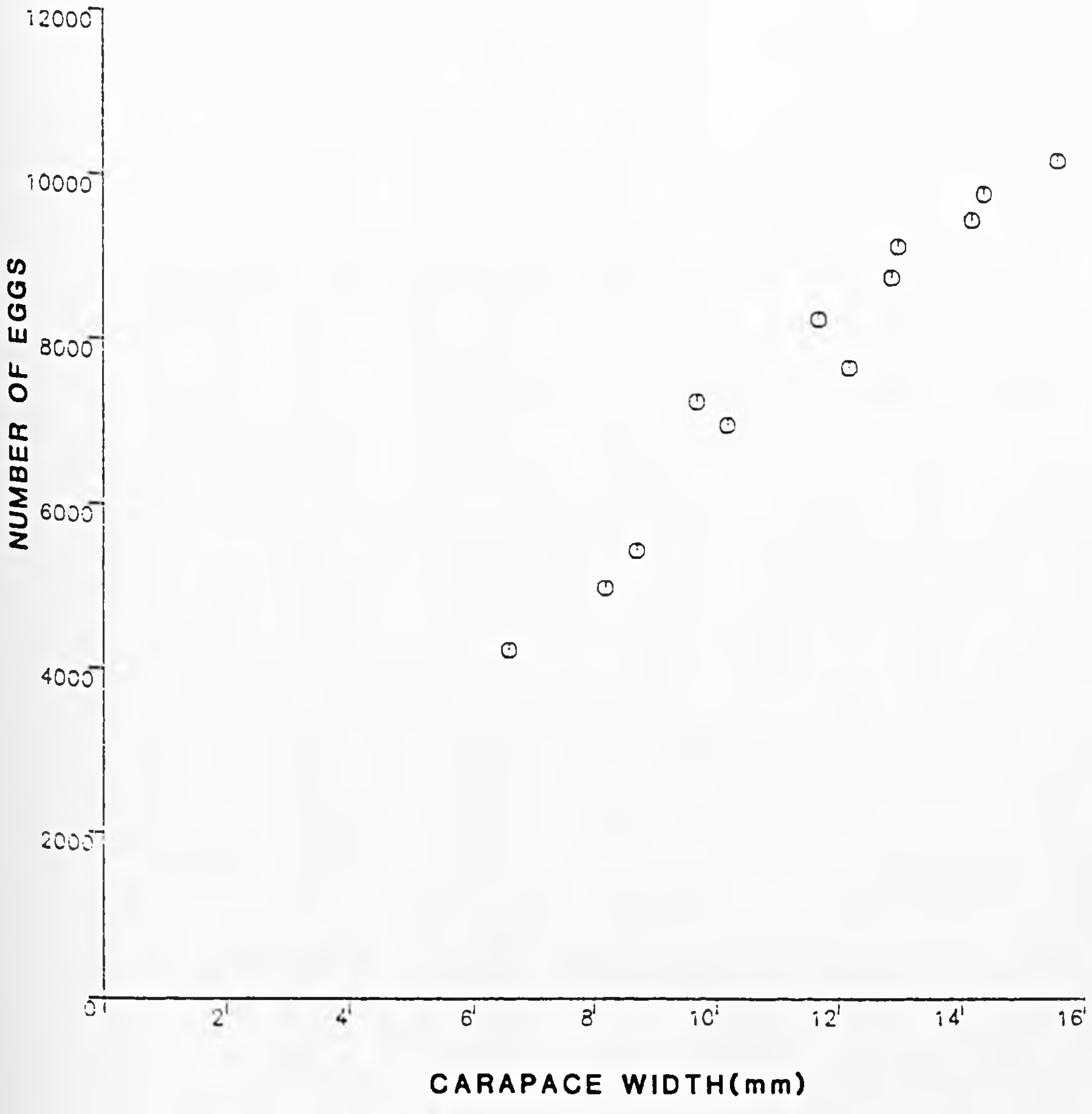

NUMBER OF EGGS
12000
10000
8000
6000
4000
2000
0
2
4
6
8
10
12
14
16
CARAPACE WIDTH(mm)

Figure 6.15

Relation between number of eggs carried by ovigerous females and the size of the hermit crab, *P. bernhardus*, collected sublittorally from Oxwich Bay, raw data.

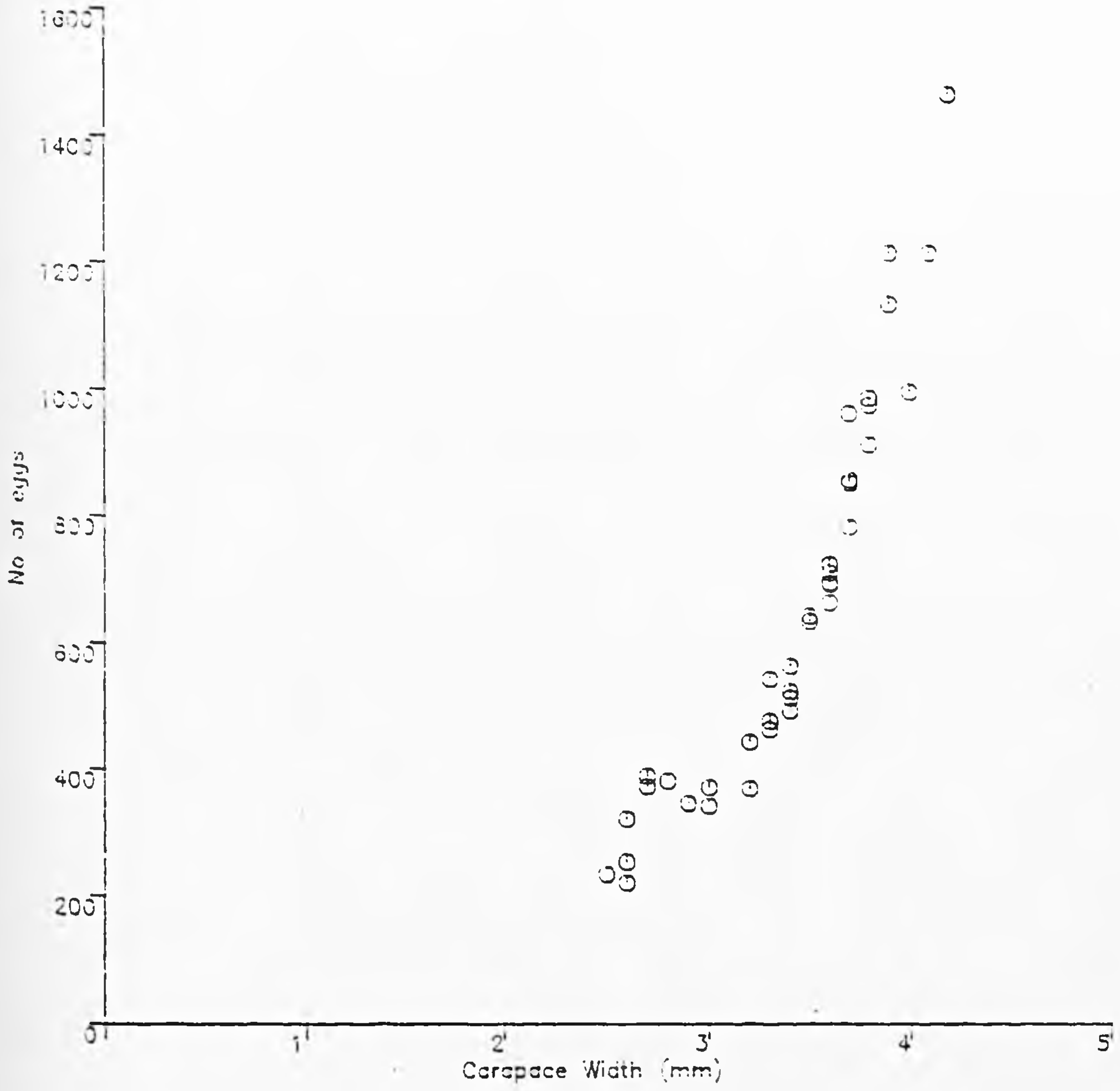

No of eggs
1600
1400
1200
1000
800
600
400
200
0
1
2
3
4
5
Carapace Width (mm)

Figure 6.16

Relation between number of eggs carried by ovigerous females and the size of the hermit crab, *D. pugilator*, collected from Rhossili Bay, raw data.

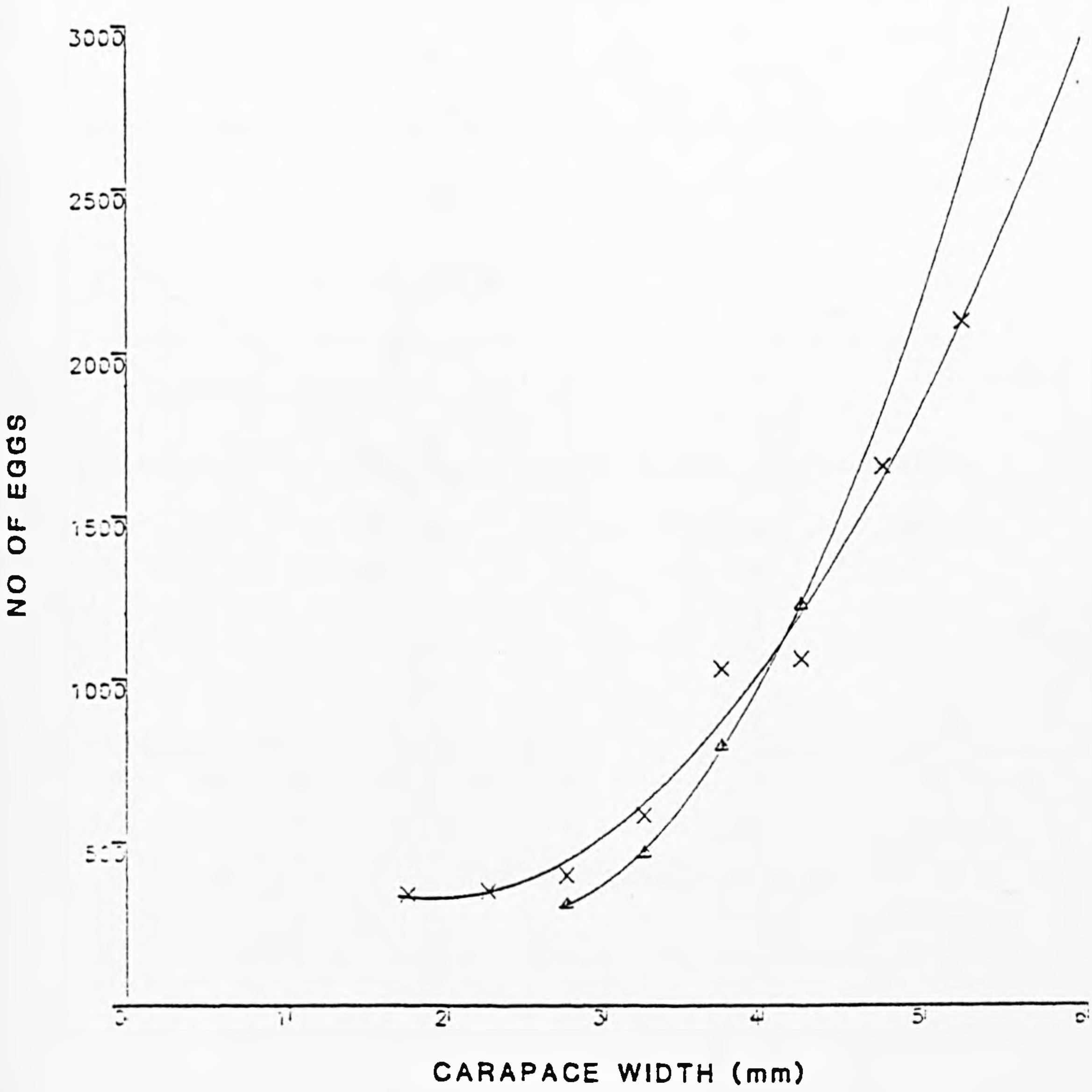

NO OF EGGS
3000
2500
2000
1500
1000
500
0
1
2
3
4
5
6
CARAPACE WIDTH (mm)

Figure 6.17

Relationship between number of eggs of *P. bernhardus* and *D. pugilator* and the size of the carapace width. Each point represents the mean of 10 measurements, with curve fitted by computer.

X = *P. bernhardus*

Δ = *D. pugilator*

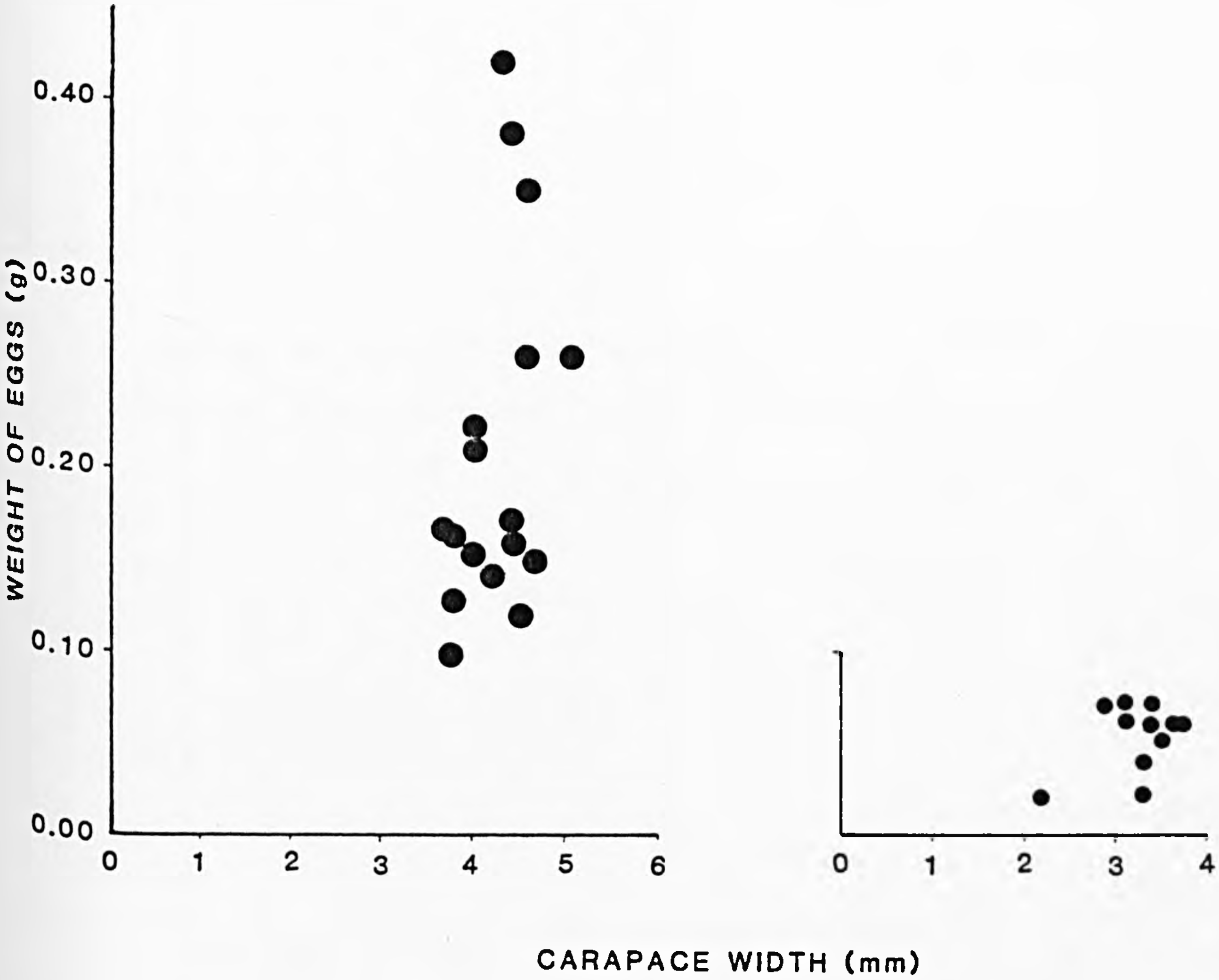

WEIGHT OF EGGS (g)
0.40
0.30
0.20
0.10
0.00
0
1
2
3
4
5
6
0
1
2
3
4
CARAPACE WIDTH (mm)

Figure 6.18

Relation between weight of eggs and the size of the carapace width for *P. bernhardus*, raw data. ●

Figure 6.19

Relation between weight of eggs and the size of the carapace for *Diogenes pugilator*. ●

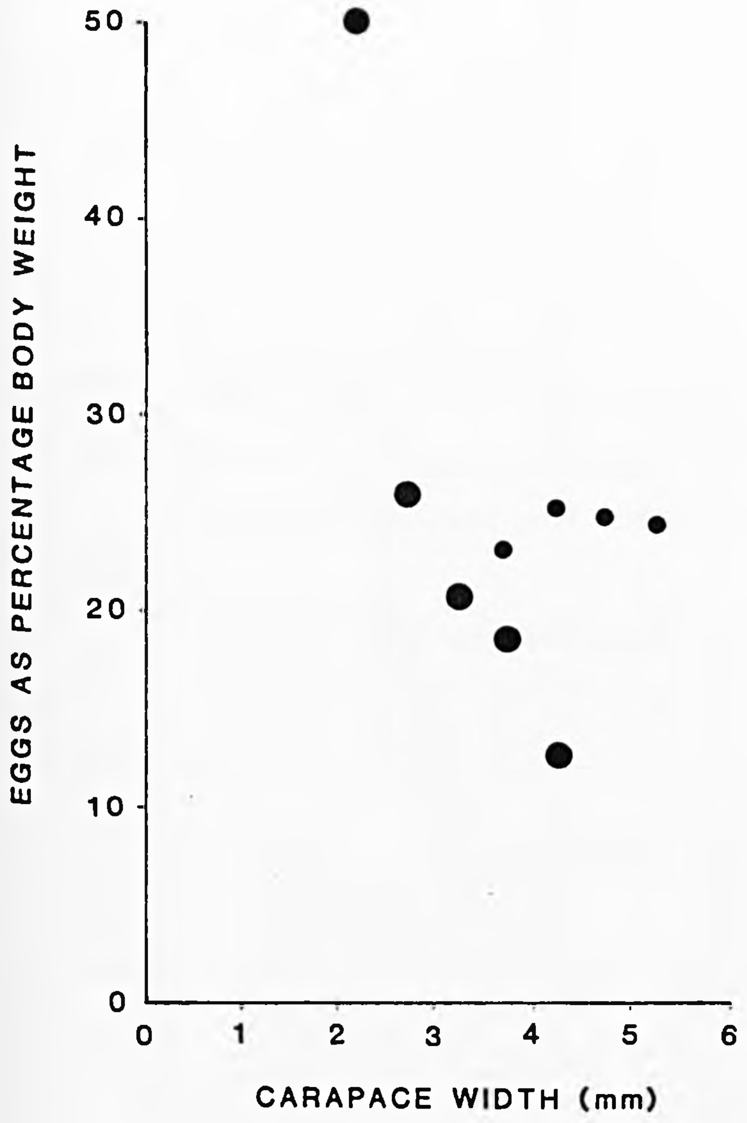

EGGS AS PERCENTAGE BODY WEIGHT
50
40
30
20
10
0
0
1
2
3
4
5
6
CARAPACE WIDTH (mm)

Figure 6.20

Relation between eggs as percentage body weight and the size of the carapace width for both *P. bermhardus* and *D. pugilator.*

● = *P. bermhardus*

● = *D. pugilator*

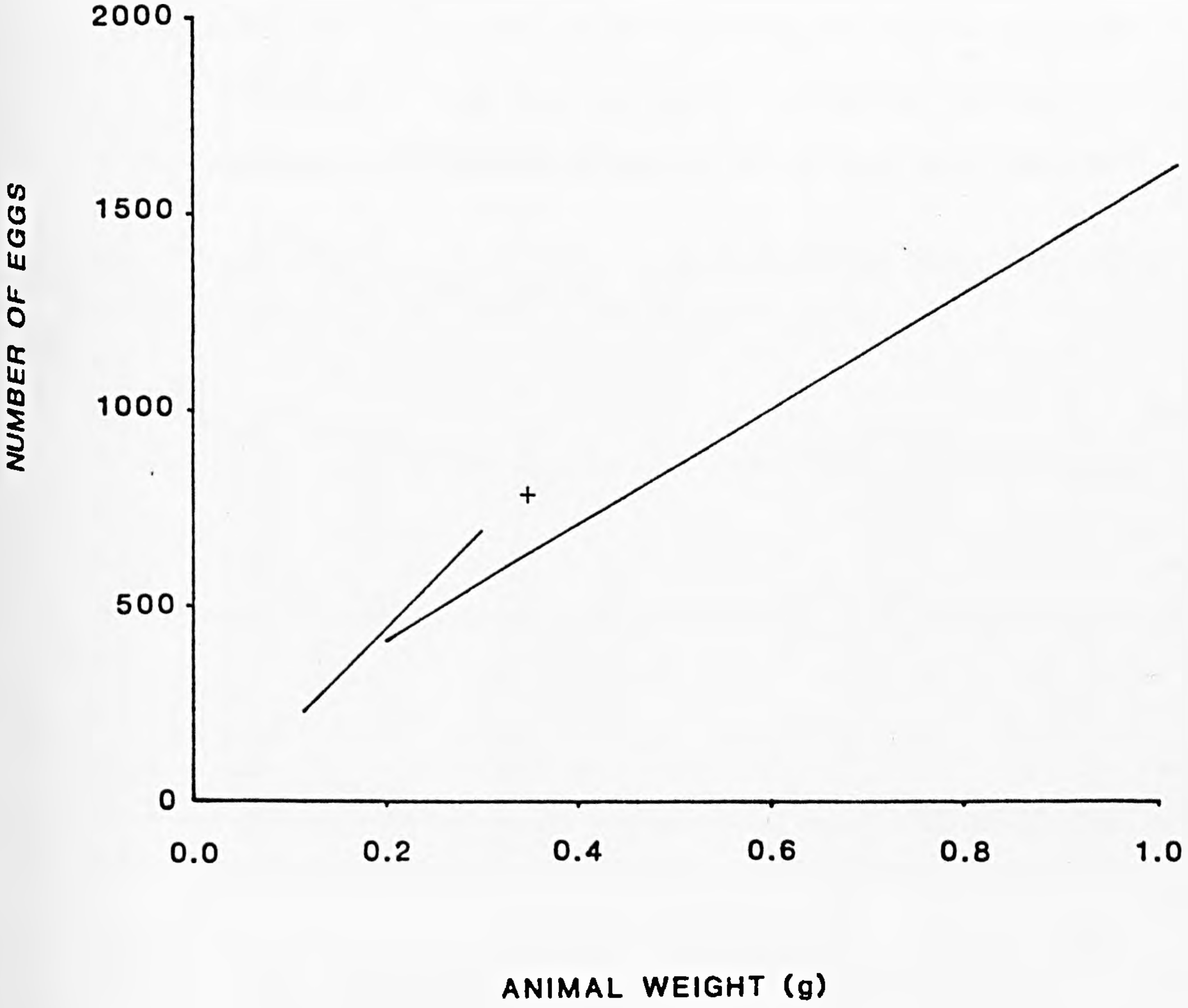

NUMBER OF EGGS
2000
1500
1000
500
0
0.0
0.2
0.4
0.6
0.8
1.0
+
ANIMAL WEIGHT (g)

Figure 6.21

Relationship between number of eggs and the body weight of the females of both species *P. bernhardus* and *D. pugilator*, with lines fitted by eye. The short line represents *D. pugilator*.

+ = published result (Pike & Williamson, 1959).

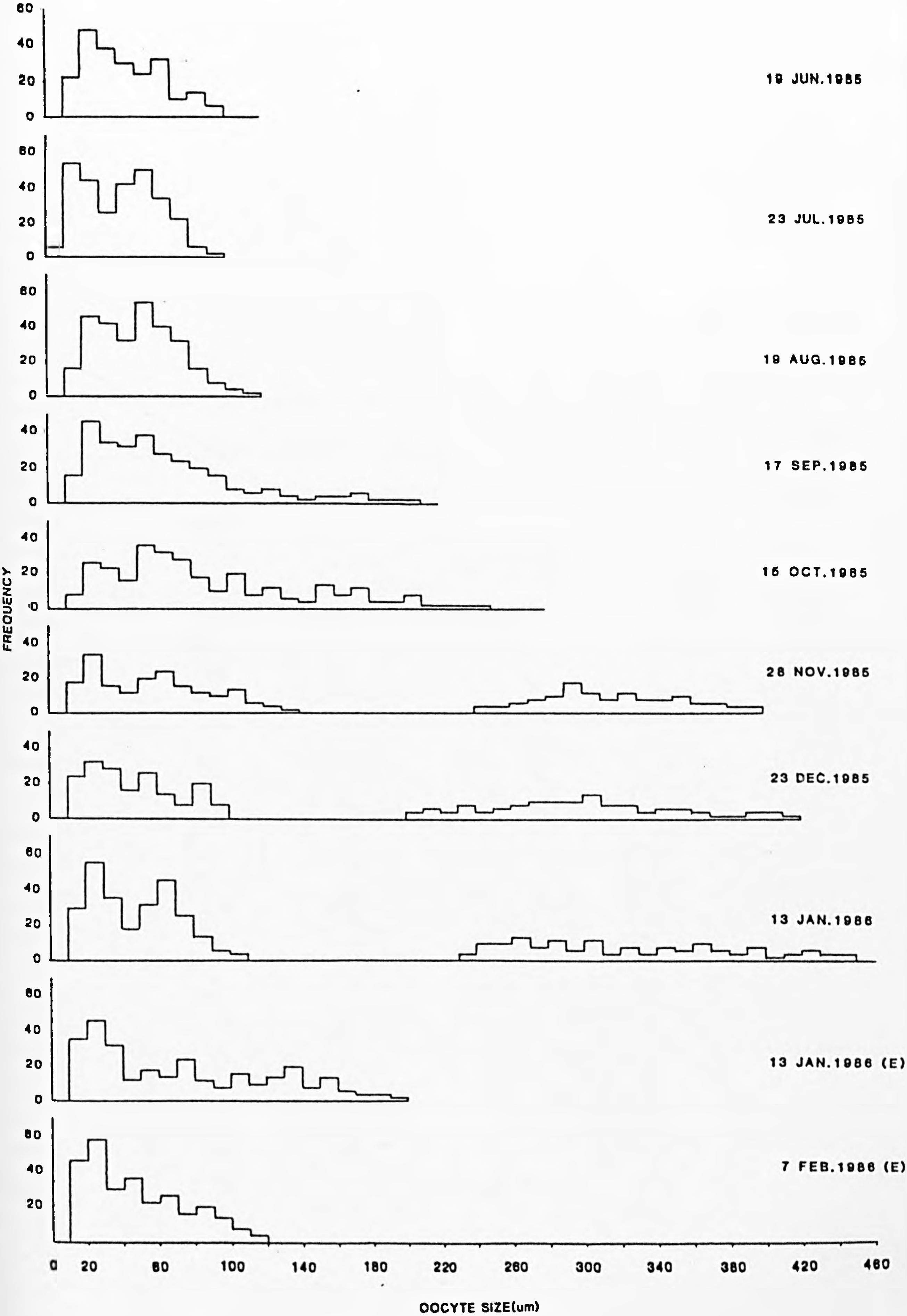

19 JUN.1985
23 JUL.1985
19 AUG.1985
17 SEP.1985
15 OCT.1985
28 NOV.1985
23 DEC.1985
13 JAN.1986
13 JAN.1986 (E)
7 FEB.1986 (E)
FREQUENCY
0
20
40
60
0
20
60
100
140
180
220
260
300
340
380
420
460
OOCYTE SIZE(um)

Figure 6.22

Relation between the diameter of the oocyte and their frequency for *Pagurus bernhardus*. Drawings were made from results obtained from each month during the histological studies.

(E) = carrying external eggs

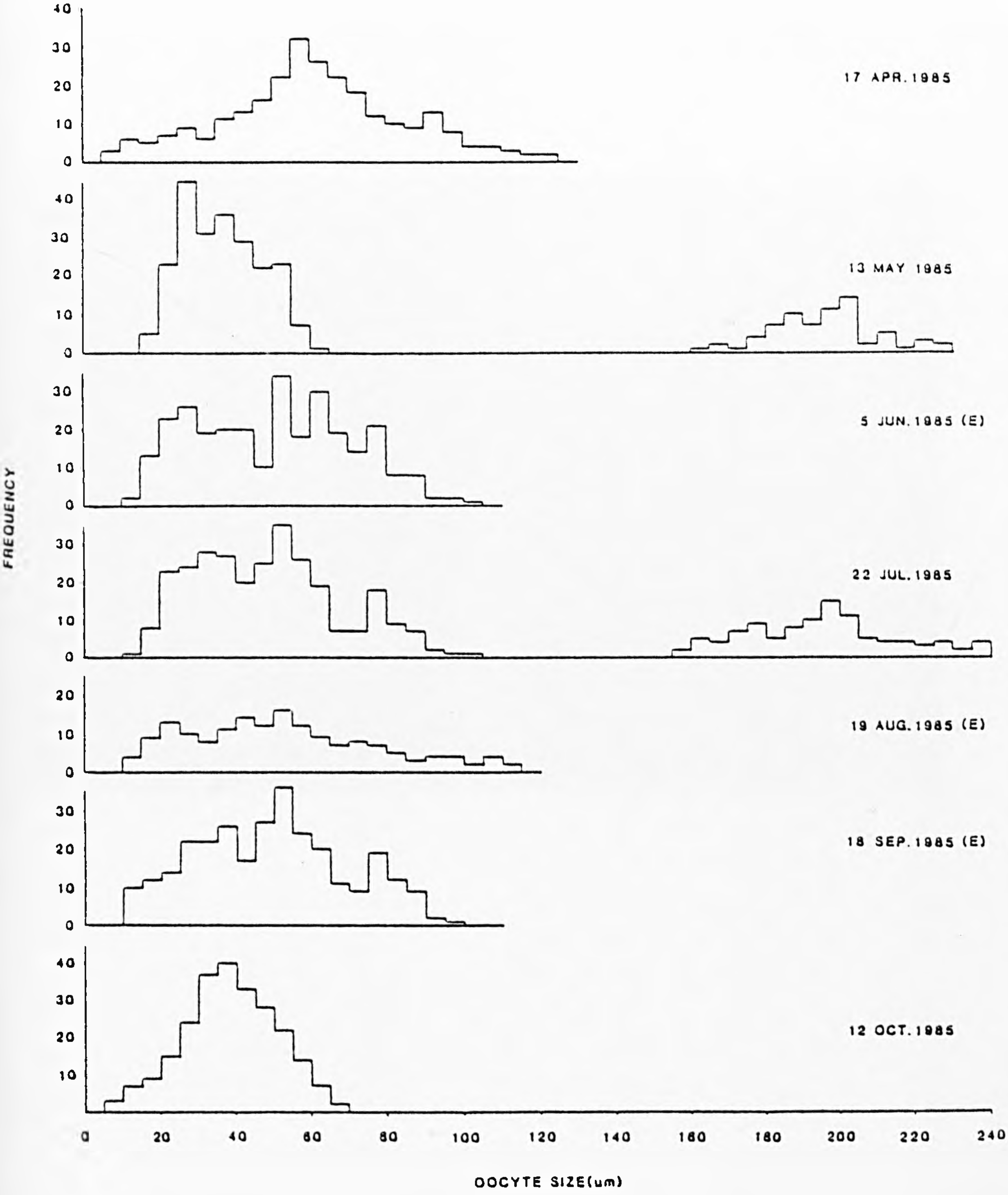

FREQUENCY
17 APR.1985
13 MAY 1985
5 JUN.1985 (E)
22 JUL.1985
19 AUG.1985 (E)
18 SEP.1985 (E)
12 OCT.1985
0
10
20
30
40
0
20
40
60
80
100
120
140
160
180
200
220
240
OOCYTE SIZE(um)

Figure 6.23

Relation between the diameter of the oocytes and their frequency, for *Diogenes pugilator*. Drawings were made for each month during the histological studies.

(E) = carrying external eggs

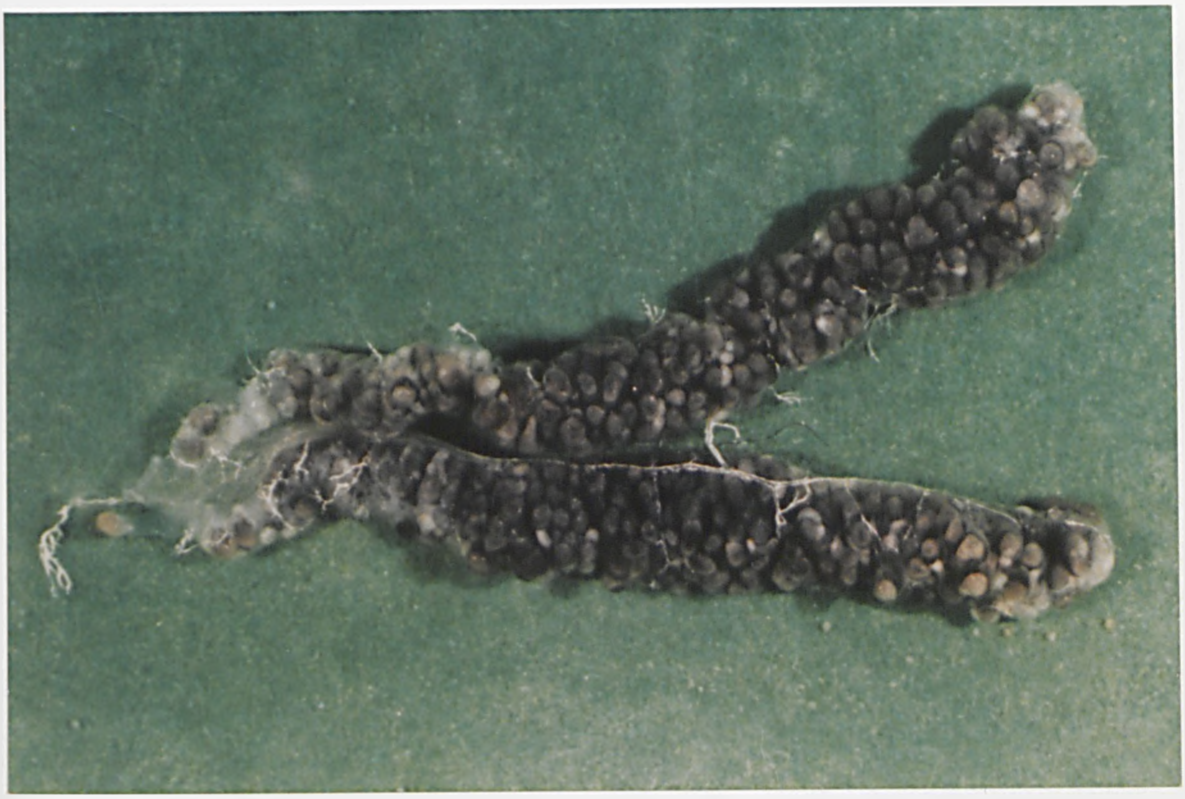


Plate 6.1

*Pagurus bernhardus*. Ripe ovaries (stage 4) of small female. Right ovary (above) slightly larger than left. Ovaries full with dark brown oocytes visible with the naked eye (x 20). Oviducts seen at left.

211

Plate 6.2

*Pagurus bernhardus*. Stage 3 ovary entwined with the hepatopancreas in a large intertidal specimen. They are irregularly disposed, the left organ lying above its fellow at the anterior end, and, more posteriorly, on the right side of it. (x 5).

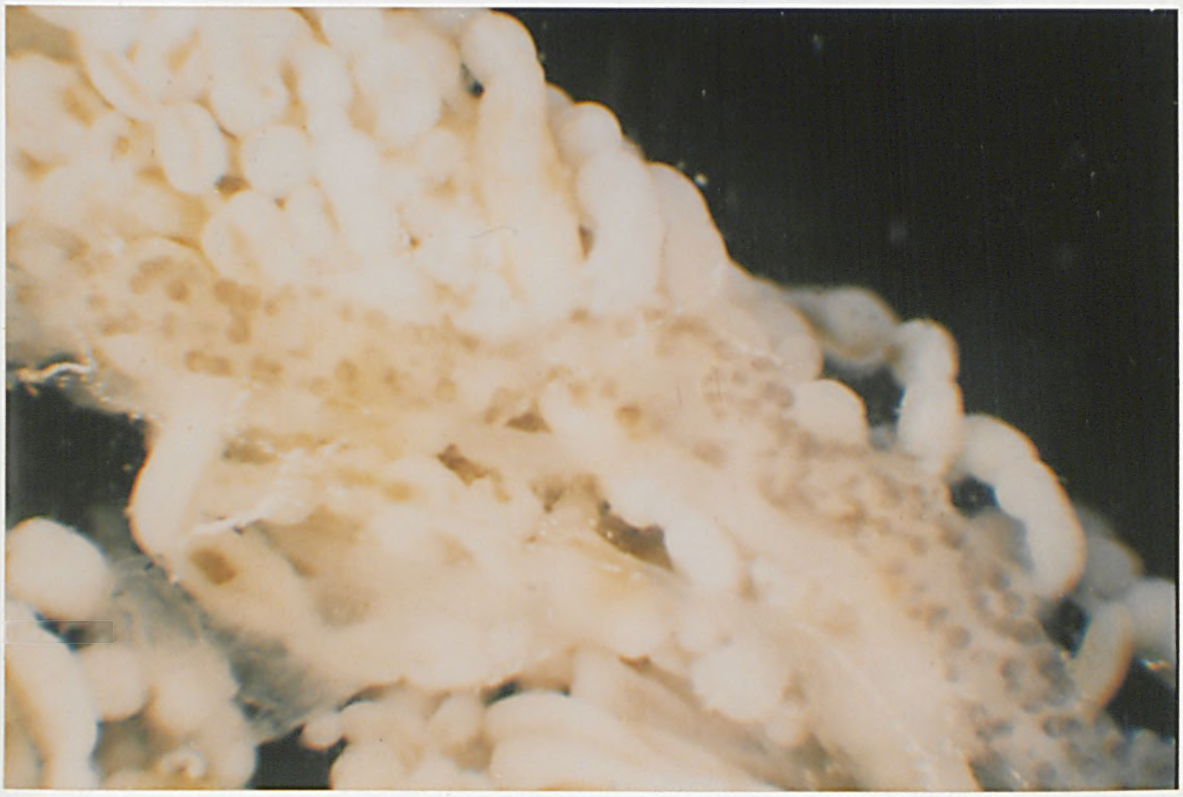


Plate 6.3

A. Ovary of *Pagurus bernhardus* of the breeding season. Stage 5 orange coloured shrunk to a thin strand sometimes indistinguishable from the colour of the digestive glands. (x 10)

B. *Pagurus bernhardus* showing the transparent ovary with strands of oocytes scattered along its length. (x 10)


1cm

Plate 6.4

Gravid female *Pagurus bernhardus* dissected to show brown-eyed embryos ready to hatch and at the same time full dark ovary (stage 4). This is a good example of a female carrying batch of external eggs as well as a group of ripe oocytes internally.

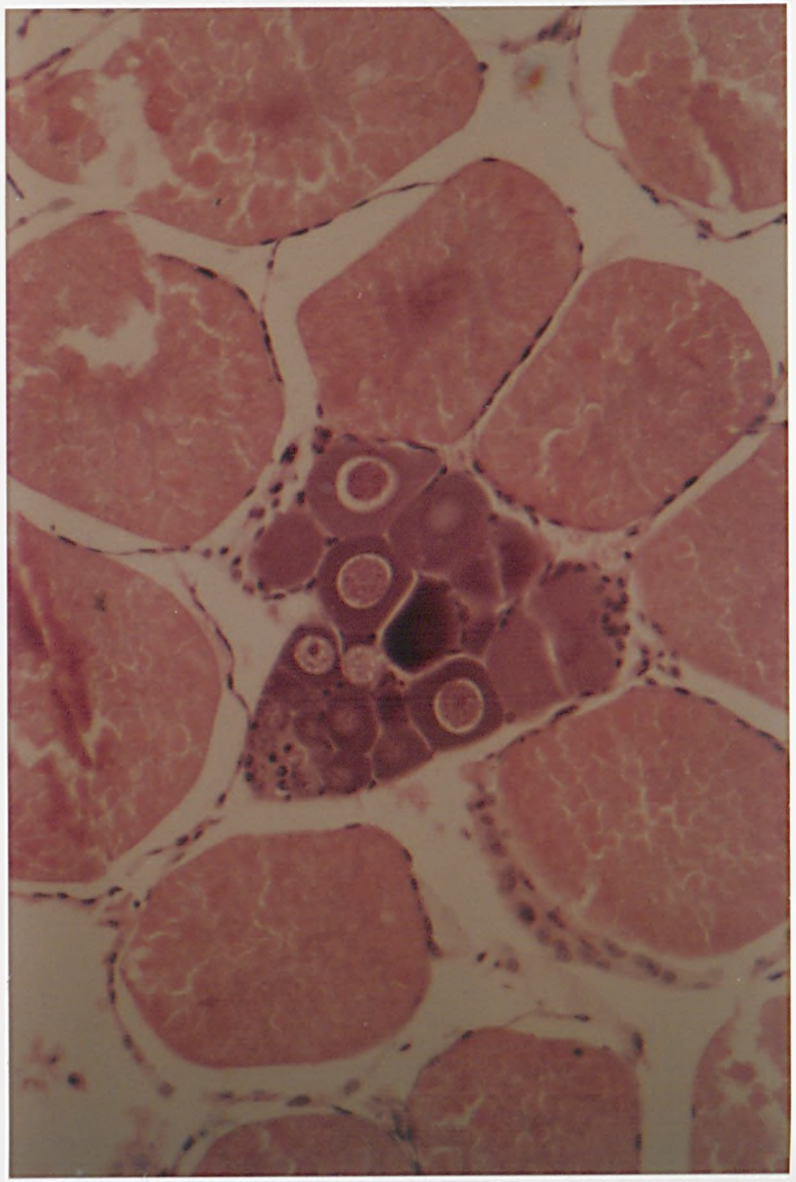


Plate 6.5

A section showing the germinal area of the ovary of the hermit crab, *Pagurus bernhardus*. The germ cells are centrally located and are themselves surrounded by previtellogenic (dark staining) and vitellogenic (pink) oocytes. The vitellogenic oocytes are surrounded by a membrane of dark staining accessory cells called follicle cells. (x 100)

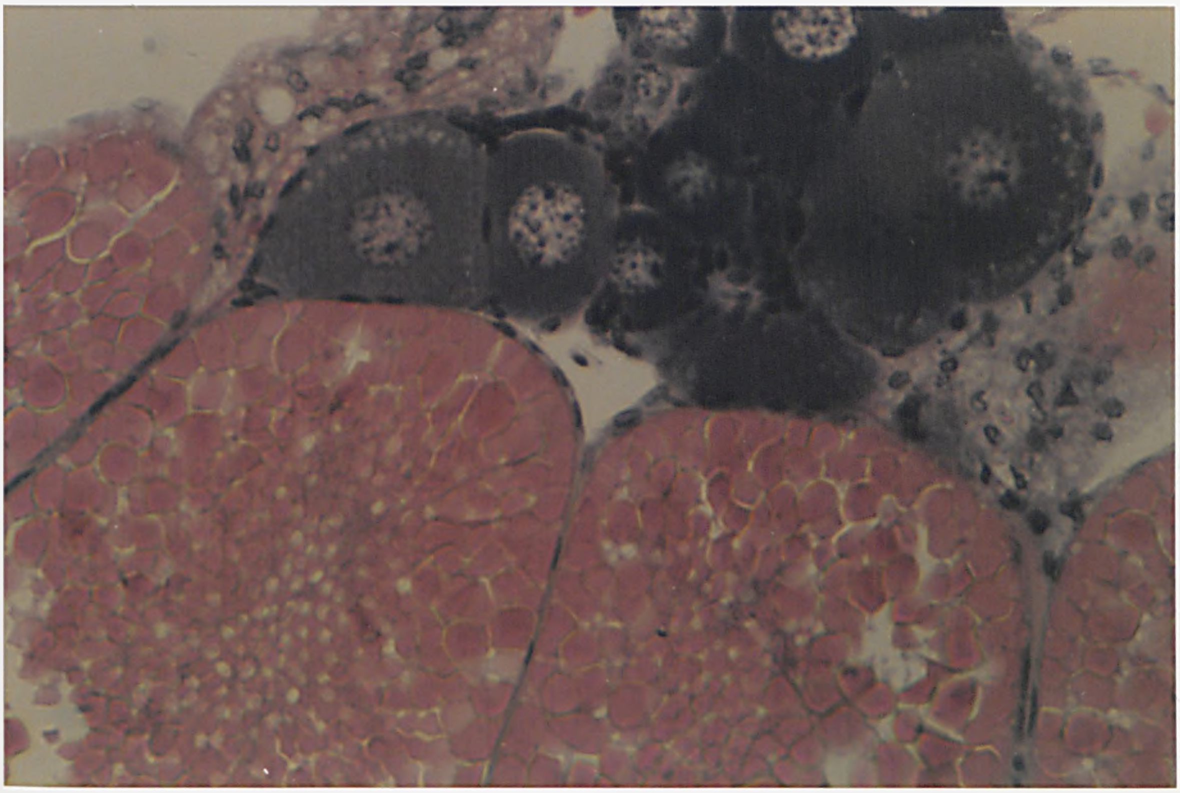


Plate 6.6

Transverse section of ripe ovary of *Diogenes pugilator* showing the fully grown oocytes surrounded by follicle cells and the dark staining germinal zone.

Plate 6.7

*Pagurus bernhardus* male organs. Left larger than right. Each testis is a long sacculated tubule folded upon itself and bound together by connective tissue to form a solid body (bottom of photo). Testis leads into long coiled vas deferens consisting of seven regions (see Greenwood, 1972). (x 6)

Plate 6.8

*Pagurus bernhardus*. A transverse section through part of the whorled area (region IV) of the vas deferens. This section shows the elongated capsule and pedestal formation. The capsule contains a mass of sperms. The vas deferens wall consists of vacuolated epithelial cells, with very large peripheral nuclei. (x 300)

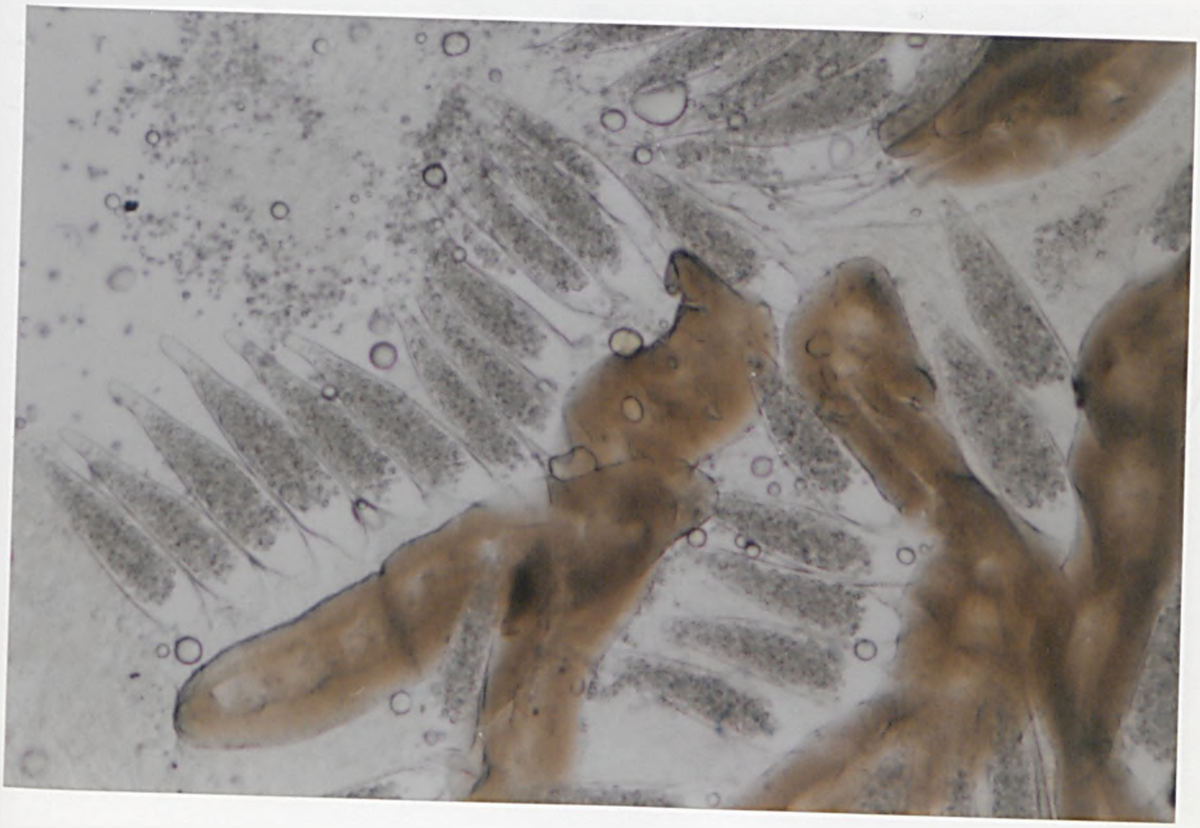


Plate 6.9

*Pagurus bernhardus*. Typical spermatophore group from whorled region of vas deferens squashed on slide. Each spermatophore has a short stalk connected at the bottom by pedestal. (x 300)

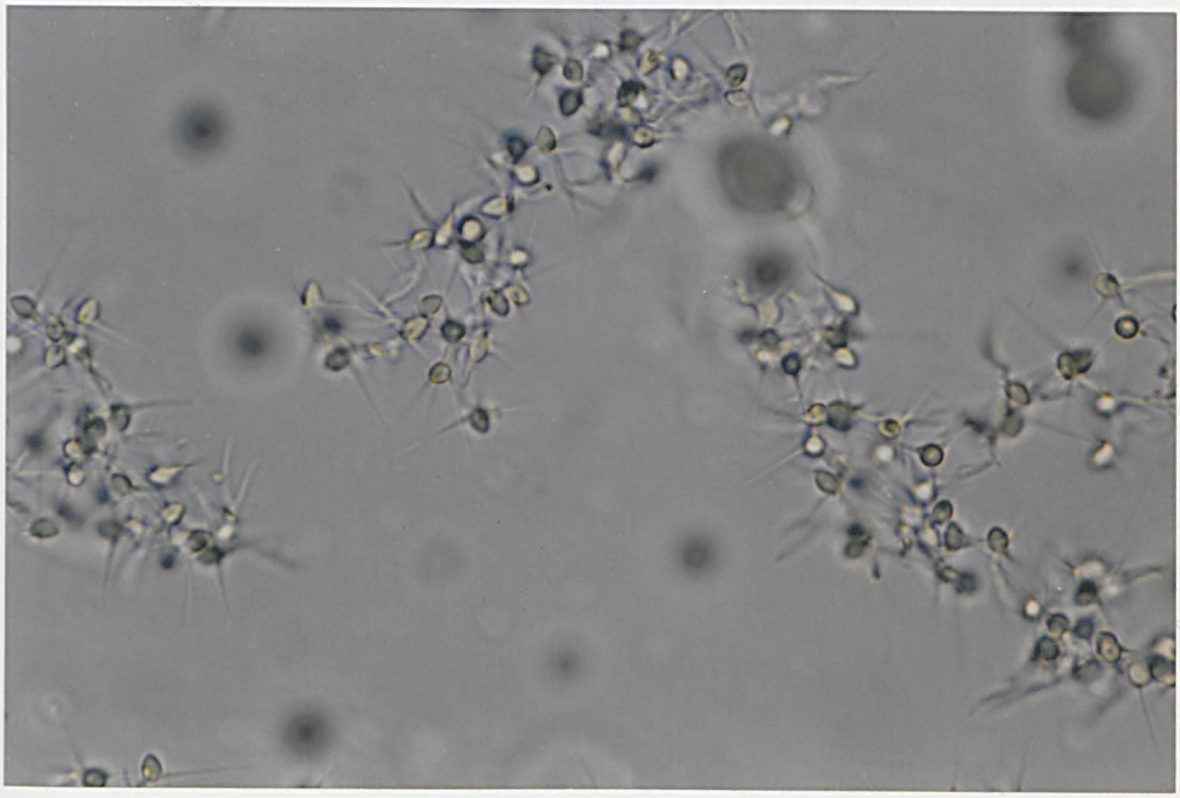


Plate 6.10

*Pagurus bernhardus* sperms after release from the surrounding sheath. (x 600)

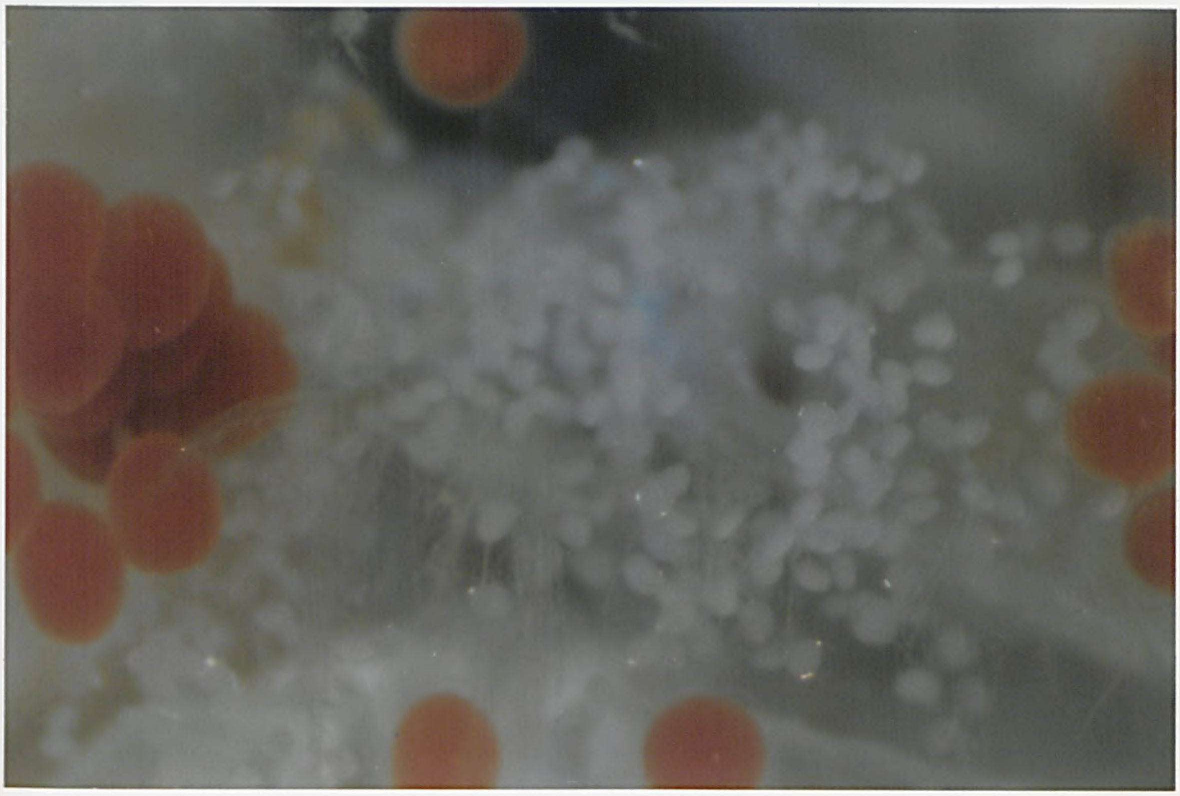
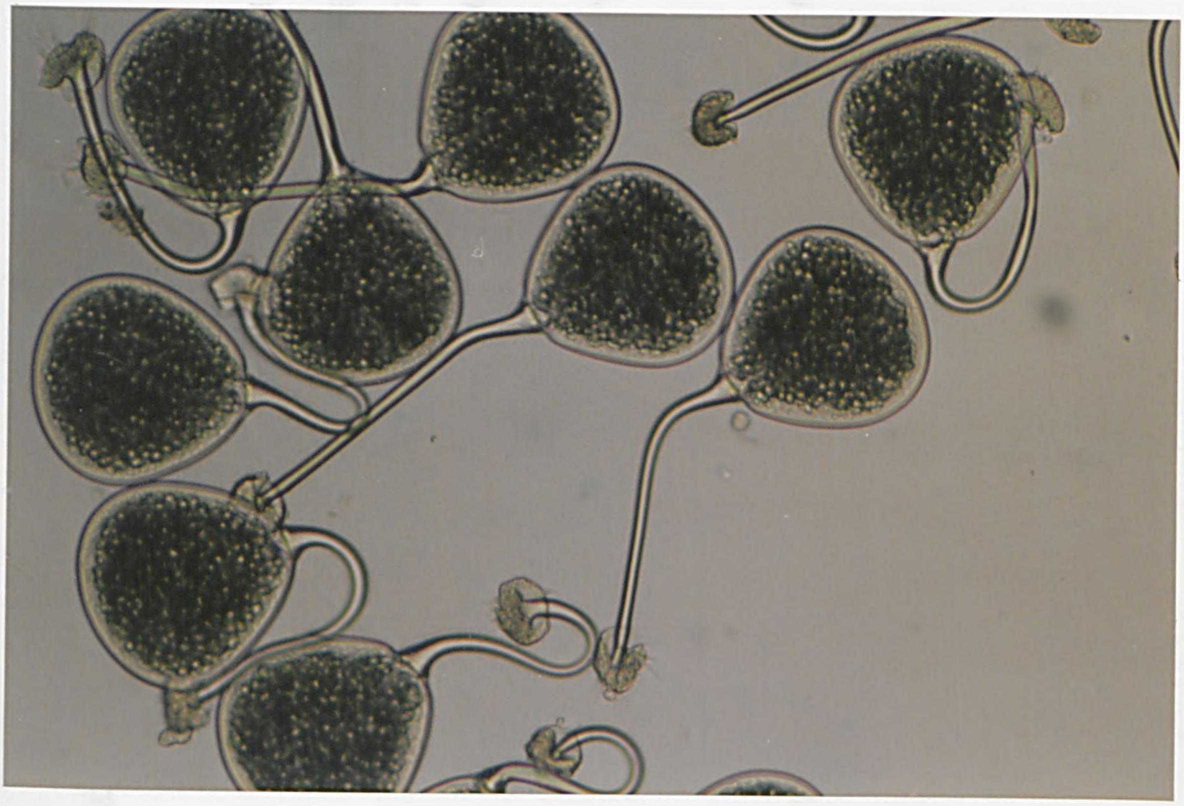


Plate 6.11

*Diogenes pugilator* spermatophores attached to setae around the female opening. A few recently extruded eggs (unnatural colour of eggs due to preservative). (x 20)



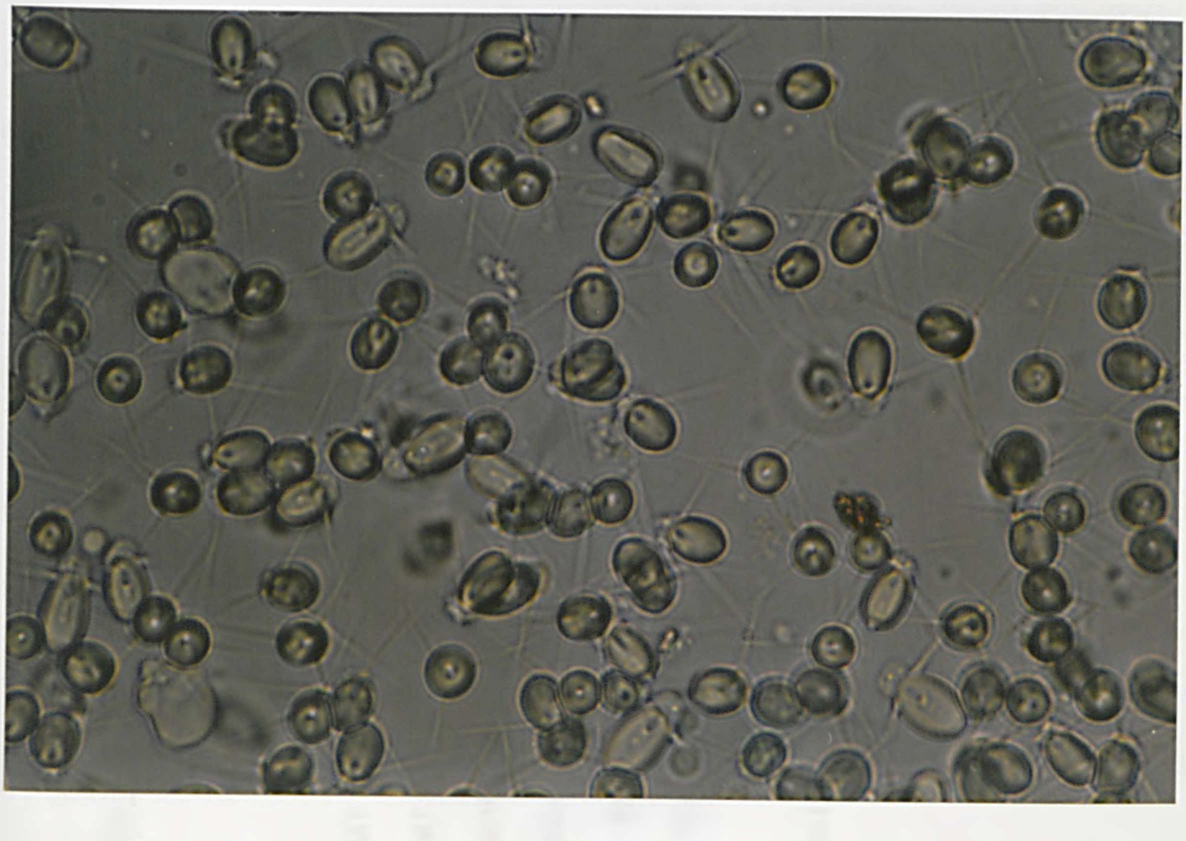


Plate 6.12

A. A number of *Diogenes pugilator* spermatophores. Each spermatophore consists of a long stalk carrying capsule full with sperms. (x 300)

B. Sperm of *Diogenes pugilator* showing three flagellae. ( x 600)

Table 6.1 Details of samples of *Pagurus bernhardus* in 1982-1983, collected from Mumbles Head, Swansea.

| | 1982 | | 1983 | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | D | J | F | M | A | M | J | J | A | S | O | N | D |
| Total males | 124 | 82 | 60 | 48 | 57 | 70 | 100 | 80 | 70 | 80 | 70 | 100 | 90 | 84 |
| Total females | 87 | 68 | 70 | 50 | 78 | 60 | 88 | 70 | 50 | 70 | 60 | 80 | 64 | 76 |
| Females without eggs | 87 | 60 | 39 | 5 | 17 | 30 | 56 | 66 | 48 | 70 | 60 | 80 | 64 | 60 |
| Gravid females: | | | | | | | | | | | | | | |
| A. Eggs without eye-pigment | 0 | 8 | 31 | 31 | 40 | 10 | 14 | 4 | 2 | 0 | 0 | 0 | 0 | 16 |
| B. Eggs with eye-pigment | 0 | 0 | 0 | 14 | 21 | 20 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total 2086 | 211 | 150 | 130 | 98 | 135 | 130 | 188 | 150 | 120 | 150 | 130 | 180 | 154 | 160 |

Table 6.2

Details of sublittoral samples of *Pagurus bernhardus* in 1982-1983, collected by trawling at Oxwich Bay.

| | 1982 | 1983 | | |
|---|---|---|---|---|
| | Oct | Feb | March | April |
| Total males | 44 | 30 | 13 | 52 |
| Total females | 58 | 44 | 28 | 43 |
| Females without eggs | 58 | 6 | 4 | 18 |
| Gravid females: | | | | |
| A. Eggs without eye-pigment | 0 | 18 | 10 | 4 |
| B. Eggs with eye-pigment | 0 | 20 | 14 | 11 |

Table 6.3 Details of samples of *Diogenes pugilator* in 1983-1984, collected from Rhossili Bay, Gower, South Wales.

| | 1983 | | | | | | | 1984 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | M | J | J | A | S | 0 | A | M | J | J | A | S | 0 |
| Total males | 80 | 60 | 60 | 40 | 30 | - | 50 | 100 | 78 | 70 | 110 | 100 | 106 | 90 |
| Total females | 40 | 30 | 80 | 58 | 58 | - | 20 | 110 | 140 | 120 | 60 | 50 | 54 | 46 |
| Females without eggs | 40 | 30 | 26 | 16 | 10 | - | 20 | 110 | 140 | 50 | 18 | 20 | 30 | 46 |
| Gravid females: | | | | | | | | | | | | | | |
| A. Eggs without eye-pigment | 0 | 0 | 44 | 30 | 32 | - | 0 | 0 | 0 | 50 | 24 | 20 | 16 | 0 |
| B. Eggs with eye-pigment | 0 | 0 | 10 | 12 | 16 | - | 0 | 0 | 0 | 20 | 18 | 10 | 8 | 0 |
| Total 1840 | 120 | 90 | 140 | 98 | 88 | N-S | 70 | 210 | 218 | 190 | 170 | 150 | 160 | 136 |

N-S = no sampling

Table 6.4

Corresponding stages of ovarian development based on the histological and morphological studies, with diameter of oocytes for each stage.

| Histological | Morphological |
|---|---|
| Stage 1 (immature) | Stage 1 |
| Oogonia with easily seen nucleus, cells basophilic measuring below 50 µm in both species *P. bernhardus* (see Plate 6.3B) and *D. pugilator* | The ovary is thin, pale yellow, transparent in both species |
| Stage 2 (developing) | Stage 2 |
| Primary and secondary oocytes numerous, nucleus with larger nucleolus in *P. bermhardus*. (No nucleolus seen at any stage in *D. pugilator*). Diameter of most cells between 50-125 µm in *P. bermhardus*, and 50-100 µm for *D. pugilator*. | The ovaries are yellow-orange and slightly larger. |
| Stage 3 (early maturity) | Stage 3 |
| Numerous post-vitellogenic oocytes, cytoplasm large and acidophilic. Some small basophilic oogonia and primary oocytes present. Diameter of post-vitellogenic oocytes between 125-225 µm in *P. bermhardus* and 100-150 µm in *D. pugilator*. | The ovary is olive-brown. |

Table 6.4 (cont.)

| Histological | Morphological |
|---|---|
| Stage 4 (ripe) | Stage 4 |
| Ova large, granules large and acidophilic, nucleus small. Some oogonia and primary oocytes present. Diameter of ripe ova 225-450 µm in *P. bernhardus* and 150-250 µm in *D. pugilator*. | Dark-brown ovary with large oocytes. |
| Stage 5 (spent) | Stage 5 |
| The ovary representing the spent stage has strands of follicle-cells with a few unspawned oocytes. | Thin, transparent and flaccid, and are a pale reddish hue (see Plate 6.3A). |

## Table 6.5

Sizes of larvae, post larvae and small hermits; carapace width (mm)

1) *Pagurus bernhardus*

| | | |
|---|---|---|
| a) glaucothöe (wild Mumbles) | | 1.25, 1.25, 1.25 |
| (wild, MacDonald *et al.*, 1957) | | 1.25 |
| b) reared hermit stages | 1st hermit | 0.9 |
| | 2nd hermit | 1.1 |
| | 3rd hermit | 1.2 |
| | 4th hermit | 1.3 |

| c) small, non gravid females | Date | Size |
|---|---|---|
| | 2/1/83 | 2.1, 2.3, 2.4 |
| | 1/3/83 | 2.0, 2.1, 2.3 |
| | 14/4/83 | 1.8, 2.1, 2.2, 2.3 |
| | 13/5/83 | 1.8, 2.1, 2.2, 2.4 |
| males | 12/6/83 | 1.2, 1.3 both ♂ |
| | 12/7/83 | 1.2, 1.3, 1.4 all ♂ |

| d) small, gravid females | Date | Size |
|---|---|---|
| | 2/2/83 | 1.2, 2.2, 2.4 |
| | 1/3/83 | 2.0 |
| | 14/4/83 | 1.8 |

Table 6.5 (cont.)

2) *Diogenes pugilator*

a) glaucothöe (wild, MacDonald *et al.*, 1957) 0.60, 0.67

b) small, non-gravid females (wild Rhossili)

June 1983 1.6, 1.7, 1.8, 1.8, 1.8, 1.9, 2.1

c) small gravid females (wild Rhossili)

June 1983 1.7, 1.9, 2.0, 2.2, 2.3, 2.4

d) small hermits 14/8/84 0.6, 0.7 both ♂

# CHAPTER 7

# Rearing Studies on Larvae of *Pagurus bernhardus*

## 7.1 INTRODUCTION

Previous laboratory studies on reared larvae of Paguridea have served various purposes. Most frequent has been the careful description of larval instars. Other experiments have aimed to determine survival and growth rate at different temperatures and salinities. Studies of early post larvae have also used reared stages.

### 7.1.1 Descriptions of larvae

Taxonomic determinations of pagurid larvae are often difficult and many descriptions are based only on planktonic catches. Moreover, in most areas more than one species of a given genus is present, for instance in Helgoland waters, where both *Pagurus bernhardus* and *P. pubescens* occur, giving rise to the possibility of confusion of identification of later zoeal, megalopa and crab stages (Bookhout, 1964). There can be no such confusion when descriptions are based on reared larvae.

The present species, *P. bernhardus*, was one of the earliest (probably the earliest) pagurid to have its larvae described. Rathke (1840, 1842) was the first to describe the zoea and the glaucothoe larvae of this species. Sars (1890) gave a fuller account of the first and second zoeal stages and the glaucothoe. Another early description was by Willamson (1910). Jackson (1913) gave a brief description but gave no drawing. Hart (1937) studied *Pagurus beringanus* from British Columbia. However, the first complete description of all the larval stages of *Pagurus bernhardus*, *Diogenes pugilator* and eight other British hermit crabs was by MacDonald, Pike and Williamson (1957). These authors reconstructed the larval sequences using a combination of wild larvae obtained from plankton hauls and early stage zoea larvae hatched in the laboratory from eggs of identified adults. Attempts were made to rear the early stage larvae with limited success. This was at a time when the use of freshly hatched *Artemia* larvae and cultures of the rotifer *Brachionus* were not routinely available as standard laboratory cultures for feeding to carnivorous larvae. MacDonald *et al.*(1957) were able to match successive larval stages, partly by using the patterns of the chromatophores.

Much more recently Dr. Ingle (Zoology Department, British Museum (Natural History), London) has prepared, as yet unpublished new detailed descriptions in conformity with present day standards (Ingle, personal communication).

Since the classic paper by MacDonald *et al.* (1957) descriptions of larval stages of further species of pagurids have been appearing at an increasing rate. Pike and Williamson (1960a, 1960b) using the same methods as MacDonald *et al.* (1957) have described larvae of various Mediterranean pagurids. Coffin (1958, 1960) studied *P. samnelis* and *P. hirsutiusculus* respectively from the coast of California.

Most recent studies have been based partly or entirely on larvae hatched and reared from eggs of identified gravid females. The standard food used is newly hatched *Artemia* nauplii with no supplements. Species to be studied in this way include *P. longicarpus* (Roberts, 1971) and *P. alatus* (Bookhout, 1972). Some other recent examples include *Pagurus prideauxi* (Goldstein and Bookhout, 1972), *P. criniticornis* (Dana) (Hebling and Brossi-Garcia, 1981) and *Phimochirus holthuisi* (Provenzano) (Gore and Scotto, 1983).

### 7.1.2 Temperature and salinity regimes

General methods for cultivation of decapod crustacean larvae are reviewed by Rice and Williamson (1970), Roberts (1975), Provenzano (1967) and Kinné (1977). Following the introduction of newly hatched *Artemia* as a complete food, studies on the abiotic requirements for reared pagurid larvae became possible. The justification given for such studies has often been the importance of pagurid larvae in the coastal plankton. Jackson (1913) and Bookhout (1964) point to the wide geographic range of *P. bernhardus* and the fact that a single large female may produce 15,000 eggs in a season. Anger and Nair (1979) reported that the larval stages of *P. bernhardus* (and the brachyuran *Hyas araneus*) are common components of the pelagic ecosystem of the German Bight. It is necessary to know the requirements of such larvae.

The earliest study of pagurid larval temperature and salinity requirements again featured experiments on *Pagurus bernhardus*. Larvae were reared by Bookhout (1964) at the Marine Biological Laboratory at Helsinger, Denmark in two series of experiments at a constant temperature of 10°C and five levels of salinity. Larvae were followed through to first crab stage (or earlier death).

More recently, a sophisticated study by Dawirs (1979) on *P. bernhardus* used three different temperatures (6°C, 12°C, 18°C) and 3 salinities (10, 20, 30‰).

Studies of the combined effect of temperature and salinity on pagurid larval survival and duration of larval life were conducted on the Brazilian hermit crab, *Pagurus criniticornis* (Dana) by Blaszkowski and Moreira (1986). The only related works on the combined effects of these two environmental parameters were on larval diogenids, *Clibanarius vittatus* (Young and Hazlett, 1978).

Coffin (1958) and later Dawirs (1979) drew attention to problems of cannabalism occurring amongst crowded late stage larvae.

### 7.1.3 Post larval studies

In a pioneering study of early crab stages of pagurids, Provenzano and Rice (1964) examined reared and museum specimens of *Paguristes sericeus*. They were able to shed some light on the size, but not the precise moult, at which puberty occurs.

The original objectives of the present study were to rear early crab stages of *P. bernhardus* in order to determine the moult of puberty. This objective achieved only limited success but results obtained on rearing requirements provide a useful corroboration of Dawirs (1979) findings.

## 7.2 MATERIALS AND METHODS

Ovigerous females of *Pagurus bernhardus* were obtained from the intertidal sampling area at Mumbles Head and maintained in aquaria with either closed or recirculating seawater. Healthy (strongly swimming) newly hatched larvae were transferred to culture vessels, and these larvae were reared at various combinations of temperature and salinity.

For rearing purposes the seawater used was collected from Mumbles Pier during high water spring tides and maintained in a large polythene tank until needed. Water was then filtered (2 µm "Millipore" membrane filter) and sterilized by passing it through a "Coastair" ultra-violet light unit.

Every other day the *P. bernhardus* larvae were transferred to fresh beakers with clean seawater. The contents of rearing beakers were carefully checked under the dissecting microscope and all dead individuals, exuviae and food organisms were removed. At the same time freshly hatched *Artemia salina* nauplii were added as food for all larval stages (ca. 10 nauplii $ml^{-1}$).

The *Artemia* nauplii used were hatched from eggs of a special strain supplied by the specialist *Artemia* centre in Belgium. This strain has particularly small eggs. The eggs were hatched by standard method. About 2 ml of eggs were placed in 500 ml of 20‰ seawater in a funnel-shaped polythene bag and vigorously aerated to keep the eggs in suspension. They were maintained at room temperature (20±2°C).

The cyst diameter of these *Artemia* was approximately 225 µm which is among the smallest of all known *Artemia*. Naupliar length (μm) is positively correlated with the cyst diameter (μm): $Y = 101.3 + 1.4698X$ ($r = 0.91$). Source: *Artemia* Reference Centre, State University of Ghent, Belgium.

1 litre tall-form glass beakers containing 800 ml of seawater were initially used for mass culture vessels. For short-term salinity, temperature tolerance experiments, 50 ml glass beakers containing 40 ml seawater were used. Twenty such vessels could be placed in a small tray to facilitate handling.

In the culture vessels the initial larval density was never more than about 200 individuals per litre (i.e. one individual per 5 ml). In the initial mass culture vessels 50 individuals per vessel were used. In the later experiments in small beakers 5 or 10 first zoea were used in each beaker.

In some preliminary experiments a variety of different algal cultures were added to the rearing vessels in addition to the *Artemia* nauplii. This did not appear to improve the survival or rate of development so was discontinued.

### 7.2.1 Experimental procedure

All experiments were carried out in temperature controlled rooms. These have sophisticated heating and cooling equipment ensuring accuracy to within 0.5°C. Five levels of temperature, 5°C, 10°C, 15°C, 20°C and 25°C, and four levels of salinity, 25, 28, 30 and 33‰ were compared as to their influence on the larval development. The different salinities were obtained by adding distilled water to natural sea water. Salinity was measured with a refractometer.

After hatching, the larvae were immediately exposed to experimental salinities, i.e. without prior adaptation. Most experiments were conducted in duplicate.

The term "stage" refers to the period between moults, while the term "duration" refers to the length of time of this period.

## 7.3 RESULTS

The larvae of *Pagurus bernhardus* were successfully reared to young hermit crabs at a range of different temperatures and salinities.

### 7.3.1 Temperature experiments

*P. bernhardus* was reared to the first crab stage at all the three temperatures, 5°, 10° and 15°, but 20° and 25°C rearing was not possible; the larvae died at the first zoeal stage (see Figs. 7.1-7.3). Differences were found in the duration of development and mortality rate at the successful temperature.

The duration of development was shortened by increasing temperature (Fig. 7.4). At 5°C, the first crab stages occurred after a minimum of 112 days; at 10°C, after 75 days and at 15°C, first metamorphosis to crab stage was completed after 45 days (see Figs. 7.1 and 7.2). Duration of particular stages during total larval development is shown in Fig. 7.4.

Total survival remained in the same order of magnitude at each temperature (Fig. 7.5).

Mortality rate increased from 5° to 15°C (see Fig. 7.6). Survival, 30 days after hatching was 50% at 5°C, 20% at 10°C and 15% at 15°C.

Mortality of stage I zoea was uniformly high (50-60%). There was no consistent pattern in the mortality of stage II, III and IV. Glaucothoe and first crab stages survived with very low mortality.

### 7.3.2 Salinity experiments

Figs. 7.7-7.14 illustrate duration of larval moulting periods as a function of salinity. In 25 and 30‰ salinities all larval development to the first crab stage was completed between 36 and 38 days at 15°C (Figs. 7.7). First metamorphosis took place between 33 and 34 days after hatching (Figs. 7.7 and 7.9). At 10°C, three different levels of salinity were used (25, 30 and 35‰), all larvae were moulted successfully for first crab in duration range between 74 to 80 days (Fig. 7.8). At 20°C, the success rate was lower and varied with salinity. At 25‰ glaucothoe stage was reached; at 30‰ 4th zoea were produced but at 35‰ all larvae died at stage I zoea (Fig. 7.10). At all different salinities at temperature 25°C all larvae died at first zoea stage (Fig. 7.11).

There was no significant differences in the influence of these four levels of salinity on survival rate, moulting periods and occurrence of particular larval stages at 15°C (Fig. 7.7).

In 25‰ S, 15% of the larvae completed their development whereas only 10% did so at a salinity of 33‰. Development from zoea I to first crab was very similar at both 28 and 30‰. The survival remained in the same order of magnitude at each salinity (Fig. 7.12). The total duration of larval development is shown in Fig. 7.13.

The cumulative mortality of larvae of *P. bernhardus* reared at different salinities is shown in Fig. 7.14.

## 7.4 DISCUSSION

The detailed results of rearing experiments such as those reported here can be examined from several viewpoints namely:- 1) validity of rearing procedure; 2) thermal and salinity tolerance and their ecological and geographical implications; 3) elucidation of the larval life history.

### 7.4.1 Validity of the rearing procedures

It has previously been demonstrated that *Pagurus bernhardus* can be reared to first crab stage on a diet consisting solely of *Artemia* nauplii (Bookhout, 1964). Subsequently, the problem of mortality has been examined by Dawirs (1982) who demonstrated that it can be drastically reduced by single, as opposed to group rearing, which eliminates cannibalism and other sorts of larval interaction. Nevertheless, Dawirs, in addition to earlier works, had accepted that even in isolation, larvae mortality rates are normally quite high in the early zoeal stages, often as high as 60% at stage I. The significance of such mortality has not been seriously examined but it seems likely that rather than being an innate feature it is a measure of the inadequacy of the diet or other aspects of rearing conditions. It is notable that in the present experiments, mortality rates even in mass culture were sometimes as low as 30% at stage I - equalled only by individual rearings by Dawirs. This low mortality of stage I zoea in the present experiments may be attributable to the specially small size *Artemia salina* nauplii food provided. Later, on the other hand, many of the present "mass" rearing experiments were reduced to only one survivor by the IVth zoeal stage. From that point on, however, development frequently went on to the second or 3rd crab stage before the experiment was terminated, demonstrating both the efficacy of the diet and the ability of the young crabs to continue to develop satisfactorily without a carcinoecium when the danger of cannabalism was removed.

### 7.4.2 Thermal and salinity tolerance ranges

The rate of development increases with increasing temperature in *P. bernhardus* in common with many other animals - a reflection of the effect of temperature on metabolic rate. The range over which this occurs had been examined previously by Bookhout (1964) and Dawirs (1979 and 1982). *P. bernhardus* is a high latitude (Arctic boreal) species and not surprisingly, successful rearing to crab stage has not been achieved at temperatures above 18°C. At this temperature, Dawirs achieved crab stages but at only 3°C higher in the present experiments only one successful moult occurred and at 25°C all larvae died quickly as first zoea.

The lowest temperature employed by Dawirs was 6°C at which the first crab stage was eventually produced after 109 days. Although this was improved on in the present study by rearing to first crab in 118 days at 5°C, it seems likely that this species could be reared at even lower temperatures which are certain to be expected in the field during its breeding season.

The varied rearing studies indicate *P. bernhardus* to be moderately euryhaline in addition to being eurythermal. Hypersaline values have not been tested but successful completion of larval life at 35‰ were achieved both by Dawirs and by the present experiments. The lowest salinity at which success has been recorded was 20‰ by Dawirs (1979) (at 18°C). It is perhaps surprising that Bookhout (1964) failed to rear larvae as far as the crab stage at either 20‰ or even 25‰ although he did obtain survival to mid zoeal stages.

Finally, on the thermo/haline theme it needs to be stressed that combinations of successful extreme temperature and salinity are together less likely to be successful than either in some other combination. Thus 35‰ and 20°C produced no successful moult and 35‰ and 5°C produced only early zoeae.

Overall, it is evident, as expected from its often estuarine extensions and its presence in the Baltic Sea that *P. bernhardus* larvae are well capable of survival and growth in low salinity.

### 7.4.3 Elucidation of larval life history

Laboratory rearing has frequently been used in order to obtain larvae of undoubted identity when describing ontogenetic stages. It eliminates possibility of confusion between species involved when plankton samples are used to piece together the instar sequence. Nevertheless, it has frequently been shown that reared larvae may diverge significantly from wild caught examples particularly in overall size. The suboptimal nature of laboratory diets are no doubt of blame and it must be assumed that less apparent features such as exact duration of individual instars may also be different in the field.

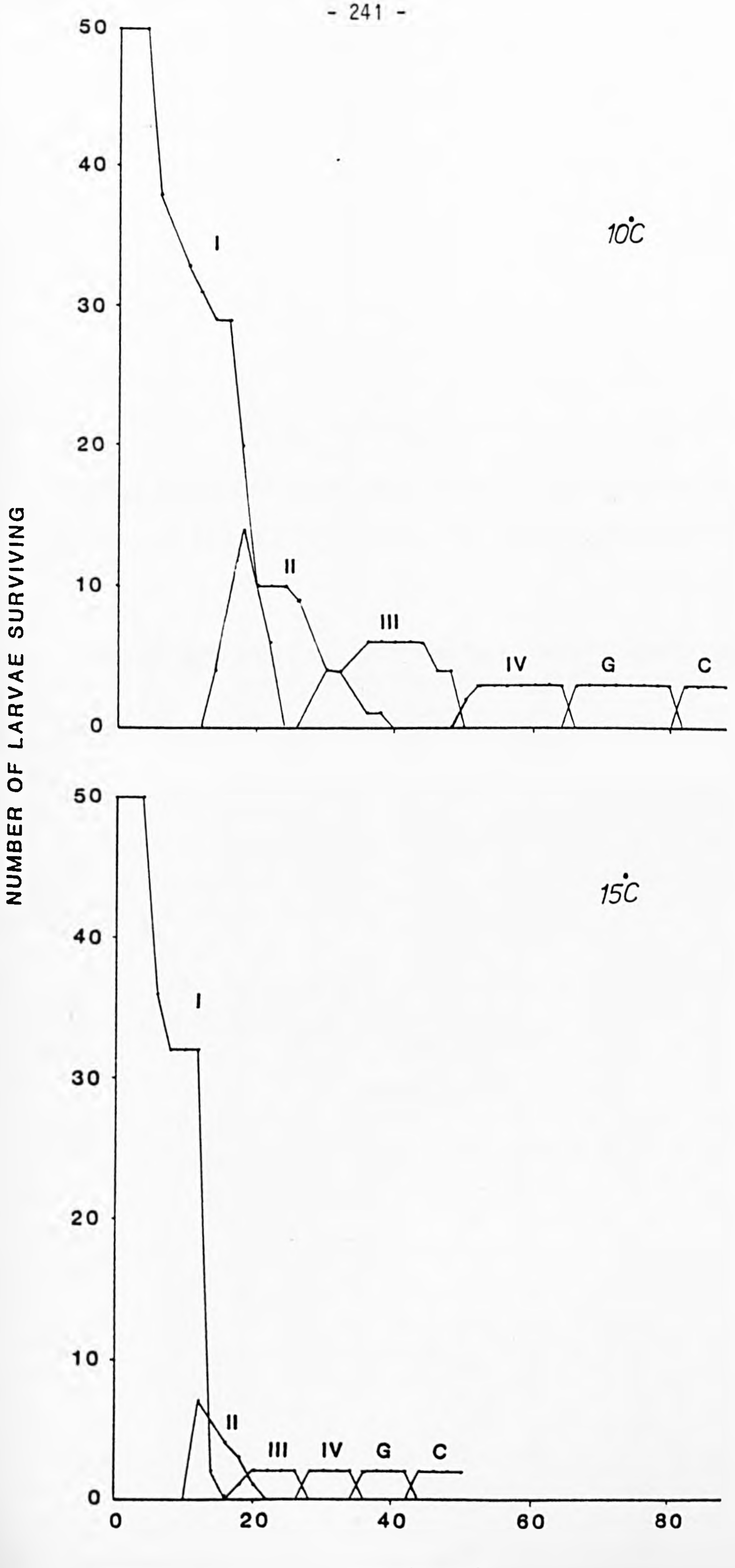

10°C
15°C
NUMBER OF LARVAE SURVIVING
0
10
20
30
40
50
I
II
III
IV
G
C
0
20
40
60
80
TIME (days)

Figure 7.1

*Pagurus bernhardus*. Larval development in culture at two different temperatures and one salinity.

I-IV: zoeal stages; G: glaucothoe; C: first crab stage

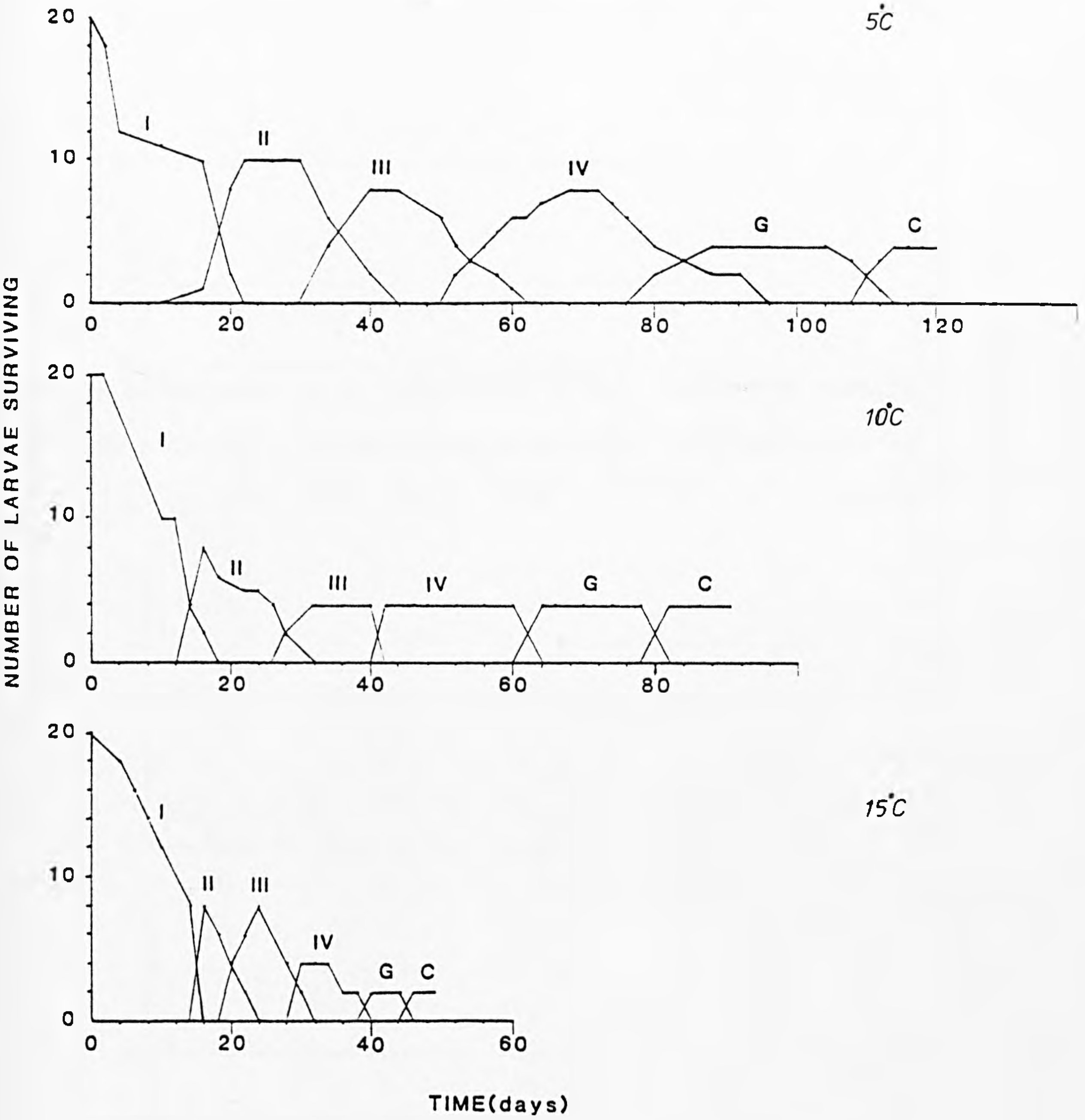

NUMBER OF LARVAE SURVIVING
5°C
20
10
0
I
II
III
IV
G
C
0
20
40
60
80
100
120
10°C
20
10
0
I
II
III
IV
G
C
0
20
40
60
80
15°C
20
10
0
I
II
III
IV
G
C
0
20
40
60
TIME(days)

Figure 7.2

*Pagurus bernhardus*. Larval development in culture at three different temperatures (5°, 10° and 15°C) and in one salinity (30‰).

I-IV: zoeal stages; G:glaucothoe; C: first crab stage.

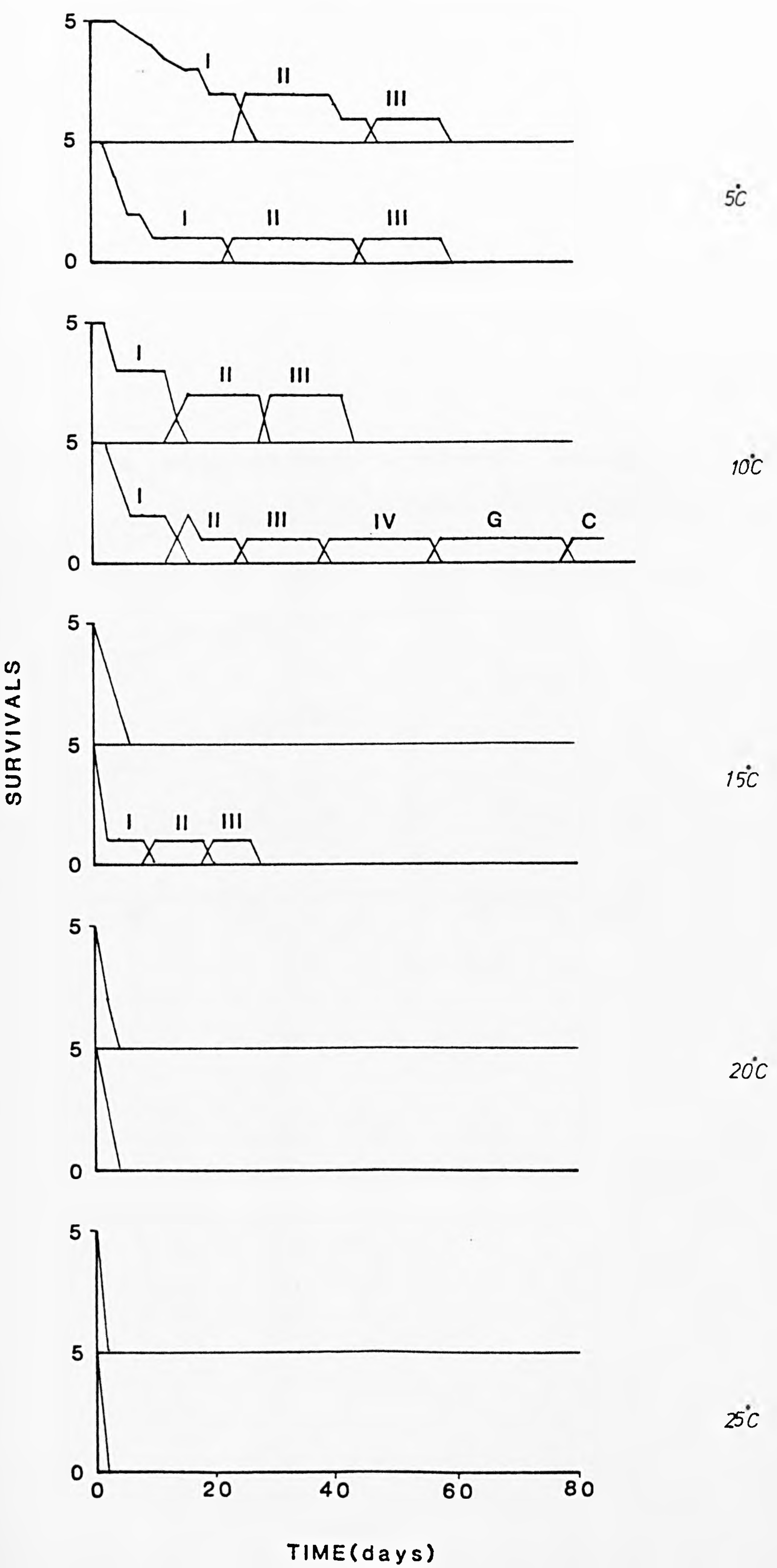

SURVIVALS
TIME(days)
5
5
0
I
II
III
I
II
III
5C
5
5
0
I
II
III
I
II
III
IV
G
C
10C
5
5
0
I
II
III
15C
5
5
0
20C
5
5
0
25C
0
20
40
60
80

Figure 7.3

*Pagurus bernhardus*. Larval development in culture reared at 25‰ salinity, and five different temperatures (5°, 10°, 15°, 20° and 25°C).

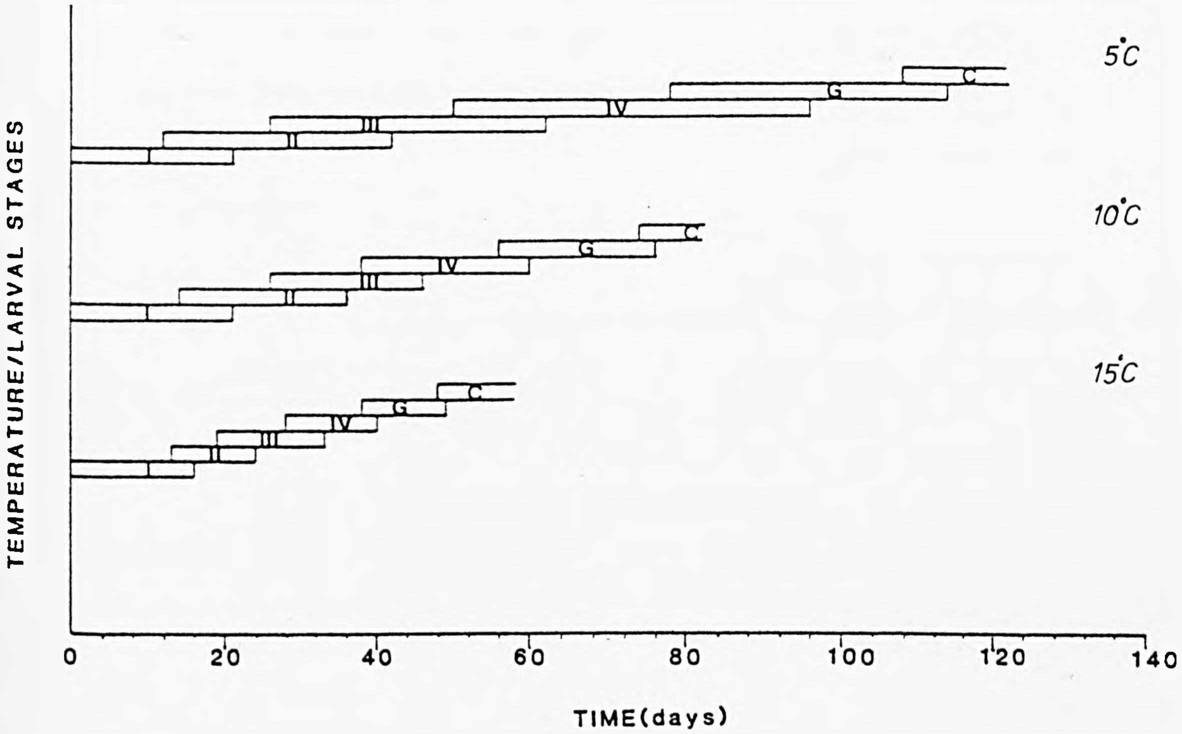

TEMPERATURE/LARVAL STAGES
5°C
10°C
15°C
II
III
IV
G
C
0
20
40
60
80
100
120
140
TIME(days)

Figure 7.4

*Pagurus bernhardus*. Duration of larval development in relation to temperature.

I-IV: zoeal stages; G: glaucothoe stage; C: first crab stage

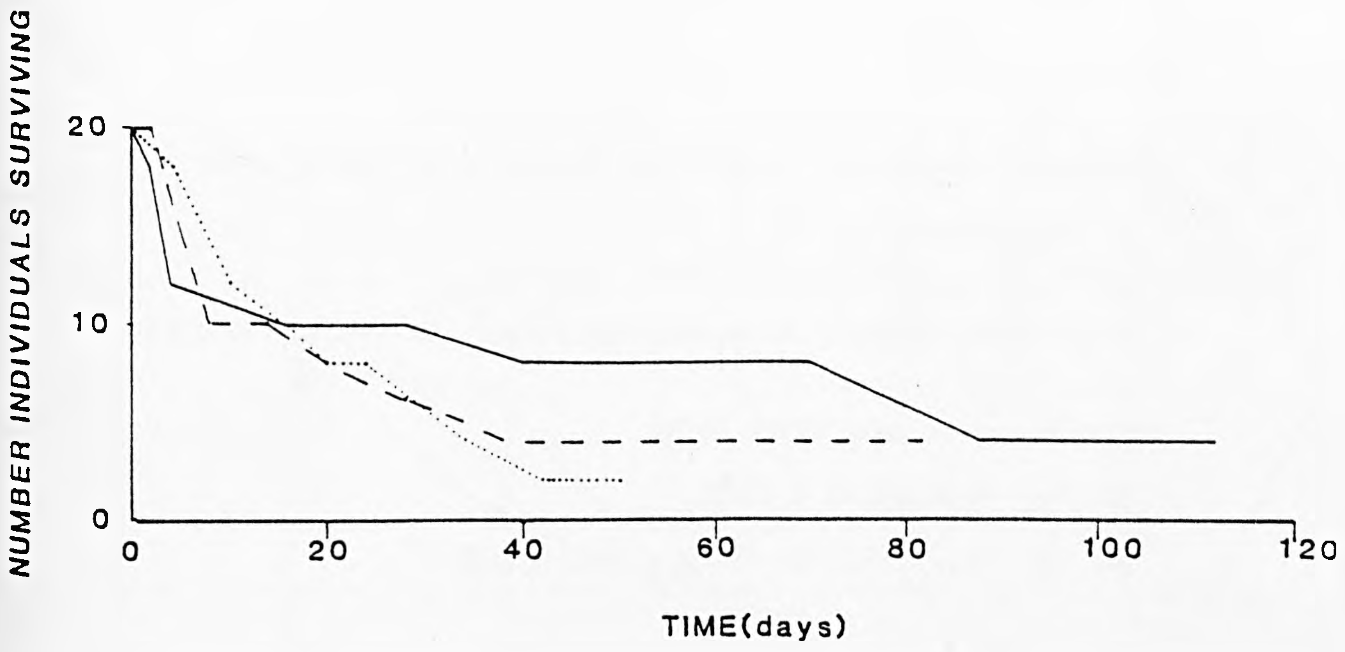

NUMBER INDIVIDUALS SURVIVING
20
10
0
0
20
40
60
80
100
120
TIME(days)

Figure 7.5

*Pagurus bernhardus.* Cumulative survival rates and moulting periods of larvae reared at different temperatures and one salinity (30‰).

———— 5°C

- - - - - 10°C Temperature

. . . . . 15°C

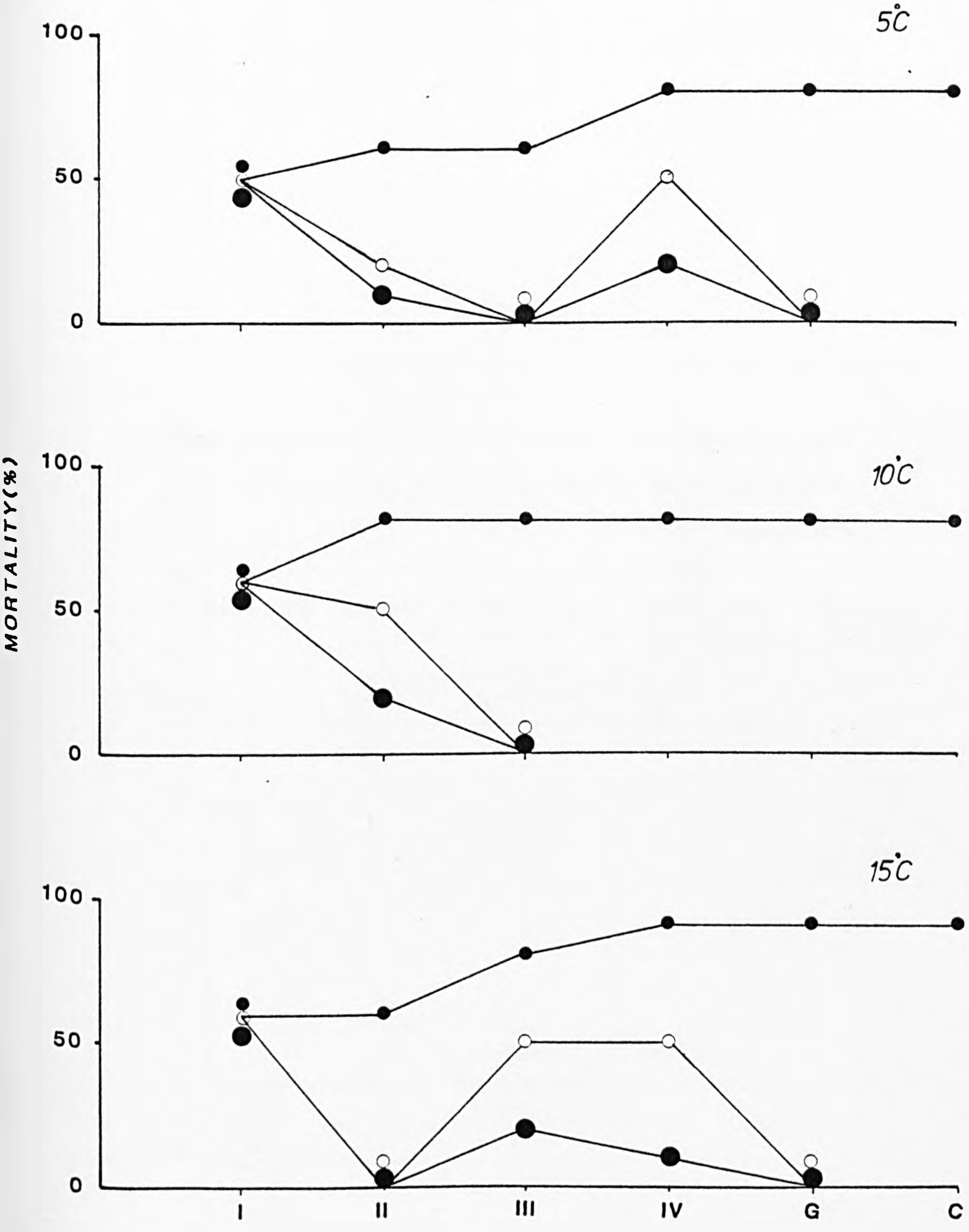

5°C
10°C
15°C
MORTALITY(%)
100
50
0
I
II
III
IV
G
C

Figure 7.6

*Pagurus bernhardus*. Cumulative larval mortality in relation to temperature.

I-IV: zoeal stages; G: glaucothoe stage; C: first crab stage.

○——○ % of each stage dying
•——• cumulative % death
●——● % of original dying at each stage

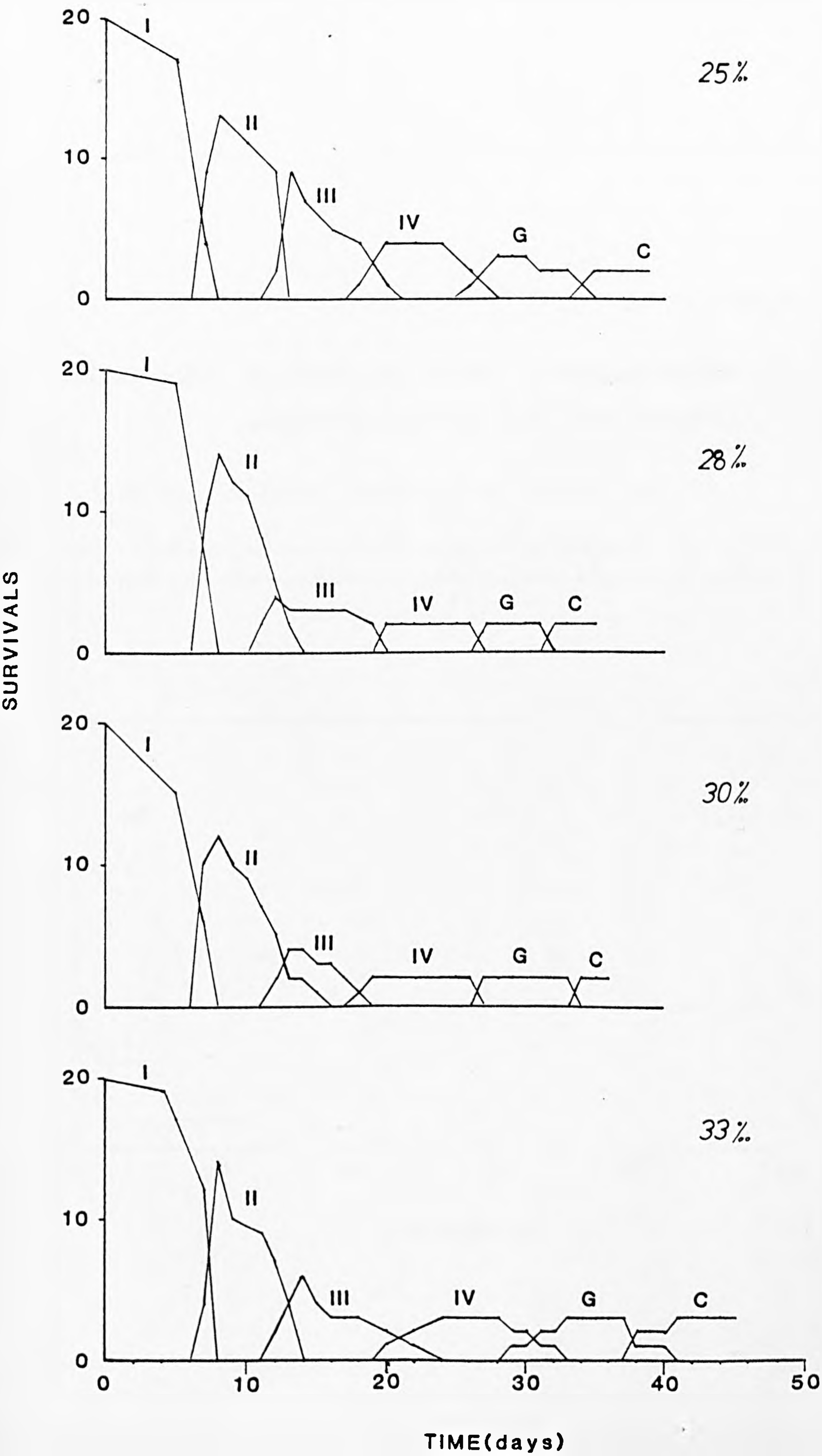

SURVIVALS
20
10
0
I
II
III
IV
G
C
25‰
28‰
30‰
33‰
0
10
20
30
40
50
TIME(days)

Figure 7.7

*Pagurus bernhardus*. Larval development in culture reared at four different salinities (25, 28, 30 and 33‰), and one temperature (15°C).

I-IV: zoeal stage; G: glaucothoe; C: first crab stage.

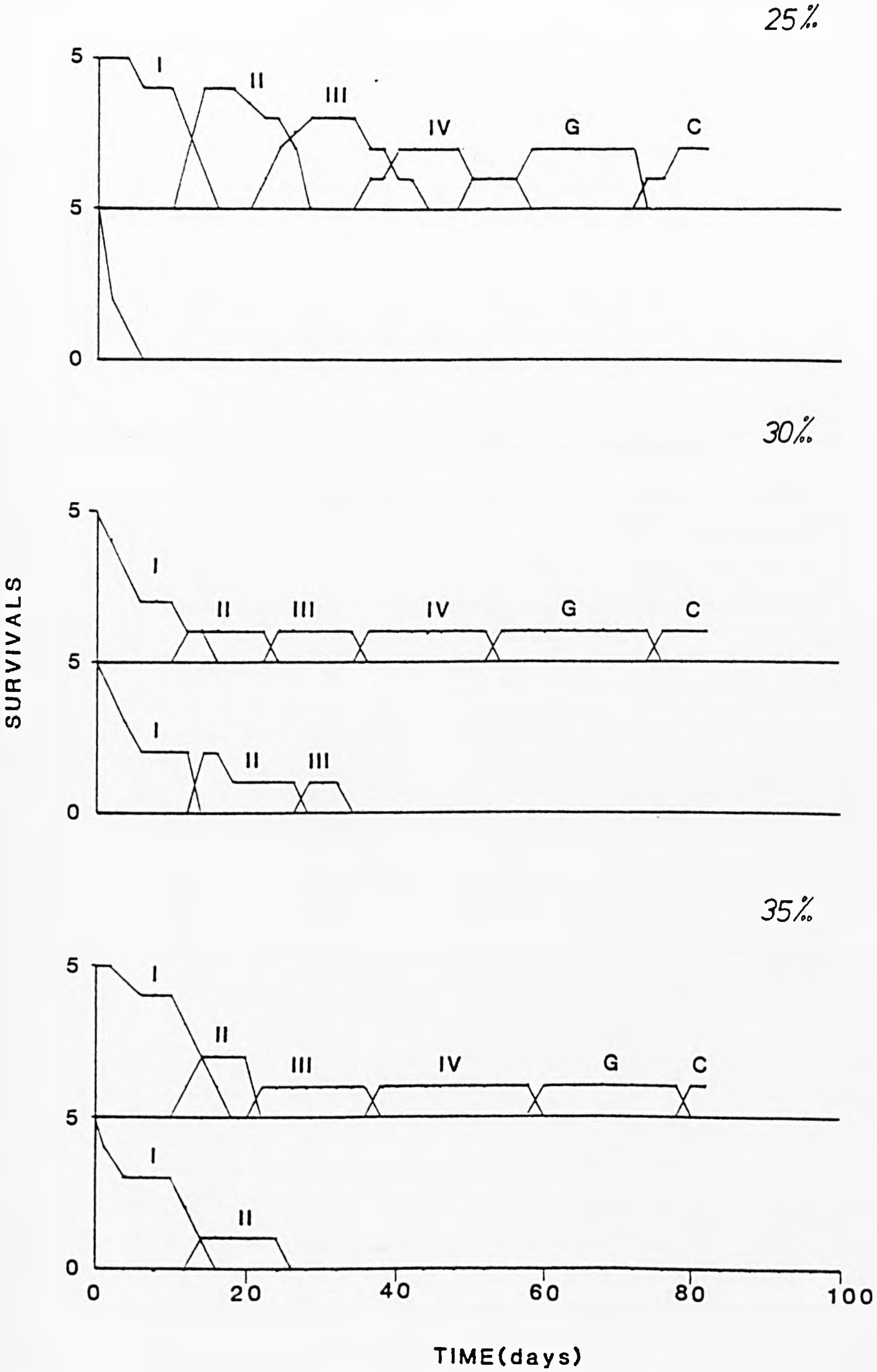

25‰
5
I
II
III
IV
G
C
5
0
30‰
5
I
II
III
IV
G
C
5
I
II
III
0
35‰
5
I
II
III
IV
G
C
5
I
II
0
0
20
40
60
80
100
SURVIVALS
TIME(days)

Figure 7.8

*Pagurus bernhardus*. Larval development in culture at three different salinities, and 10°C temperature.

I-IV: zoeal stages; G:glaucothoe; C: first crab stage.

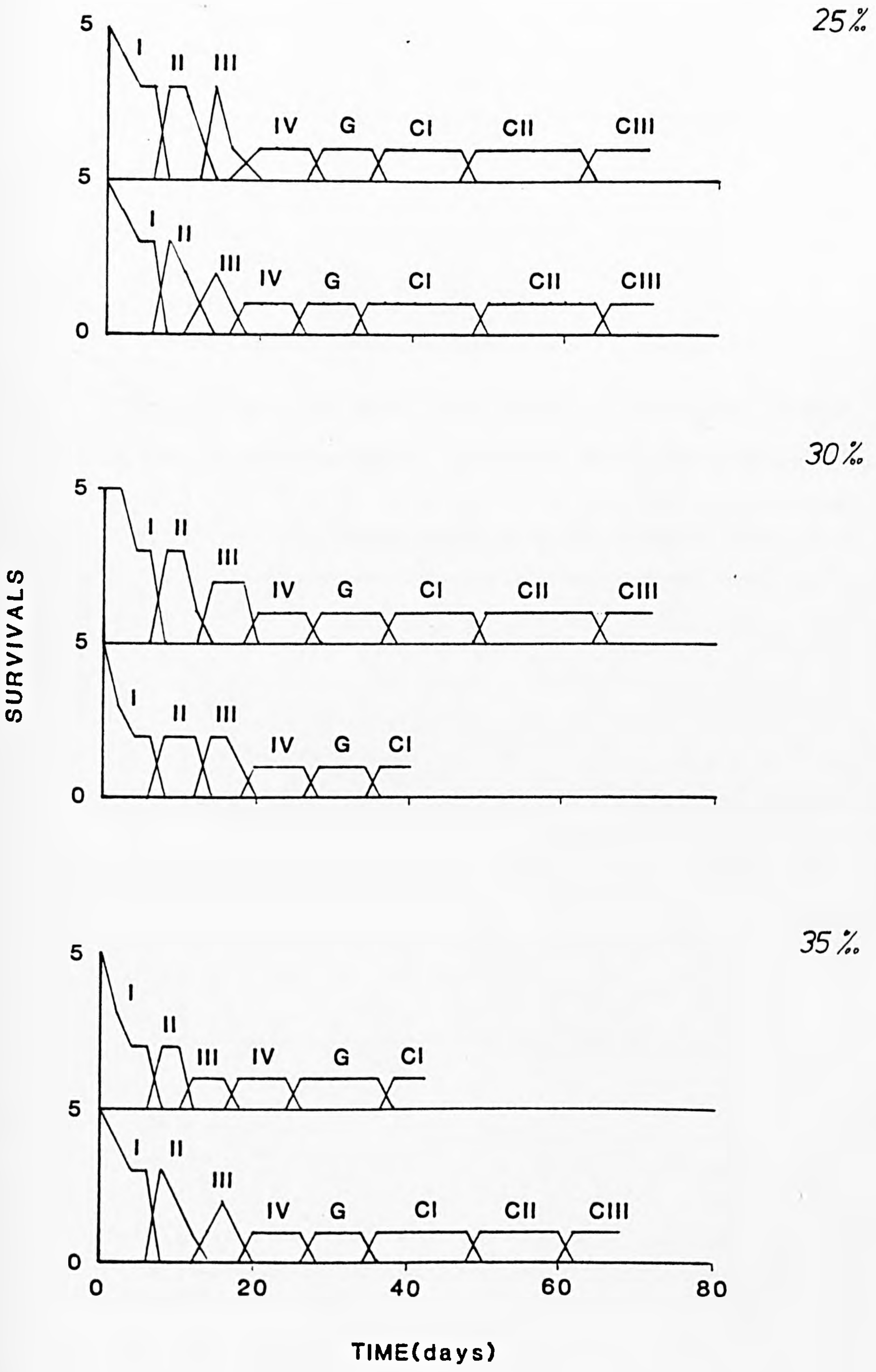

25‰
30‰
35‰
SURVIVALS
TIME(days)
0
20
40
60
80
5
0
I
II
III
IV
G
CI
CII
CIII

Figure 7.9

*Pagurus bernhardus.* Larval development of larvae reared at three different salinities (25, 30 and 35‰) and one temperature (15°C).

I-IV: zoeal stages; G: glaucothoe; Ci: first crab; Cii: second crab; Ciii: third crab stage.

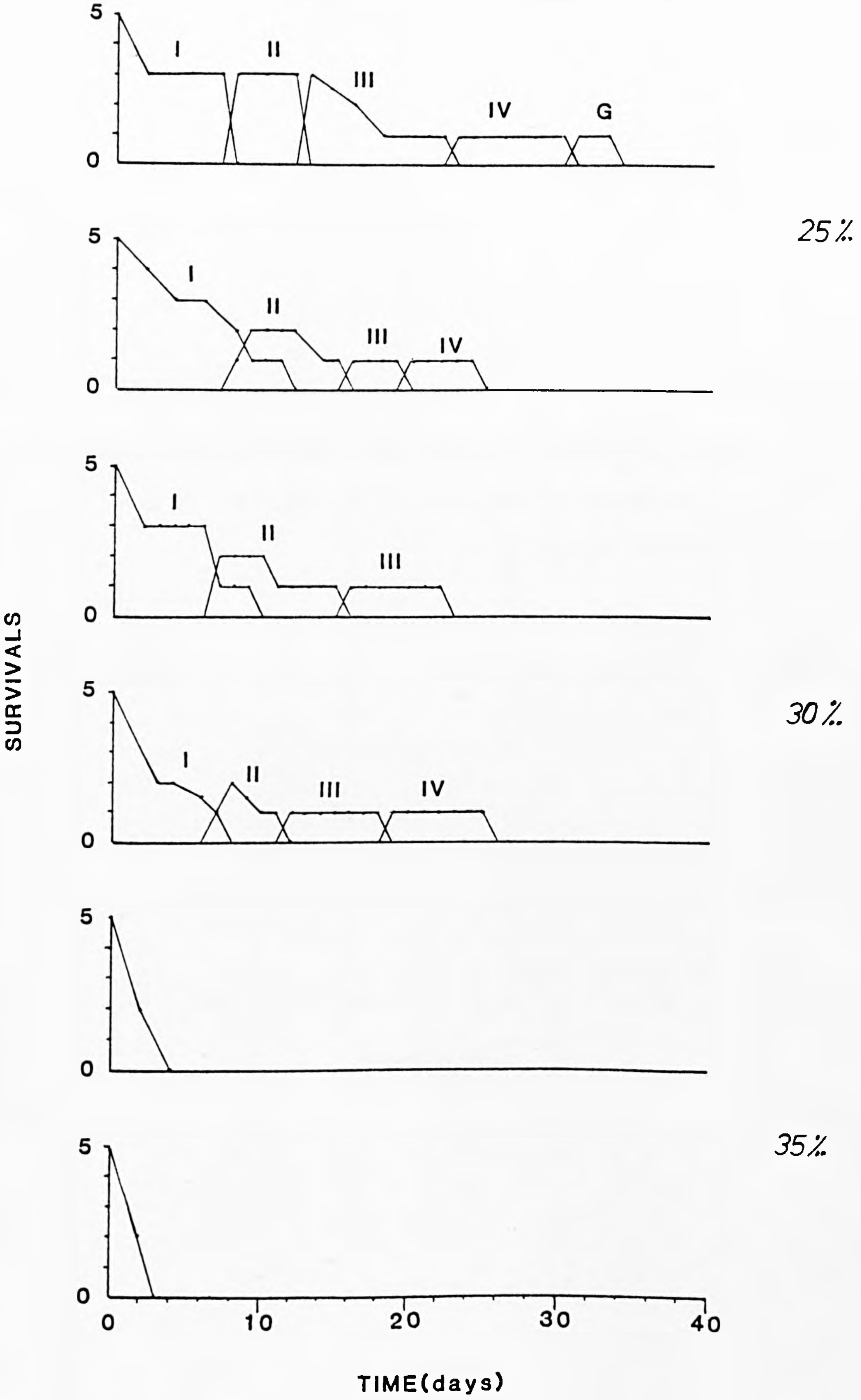

5
0
I
II
III
IV
G
25%
I
II
III
IV
I
II
III
SURVIVALS
30%
I
II
III
IV
35%
0
10
20
30
40
TIME(days)

Figure 7.10

*Pagurus bernhardus*. Larval development in culture at 20°C temperature, and three different salinities (25, 30, 35‰).

I-IV: zoeal stages; G: glaucothoe stage.

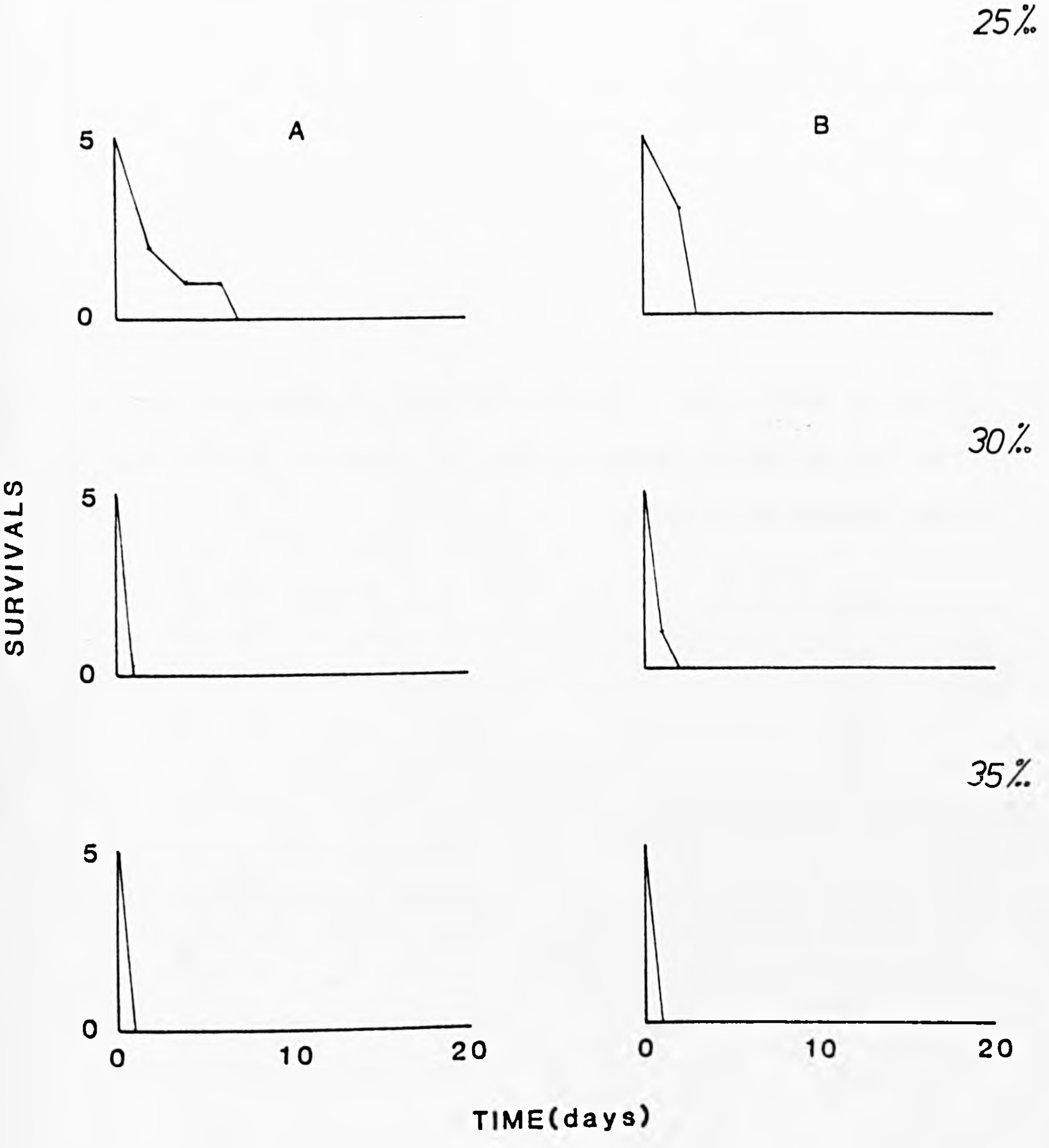

25‰
A
B
5
0
30‰
SURVIVALS
5
0
35‰
5
0
0
10
20
0
10
20
TIME(days)

Figure 7.11

*Pagurus bernhardus*. Larval development in culture reared at three different salinities (25, 30, 35‰) and in one temperature (25°C).

I: first zoea.

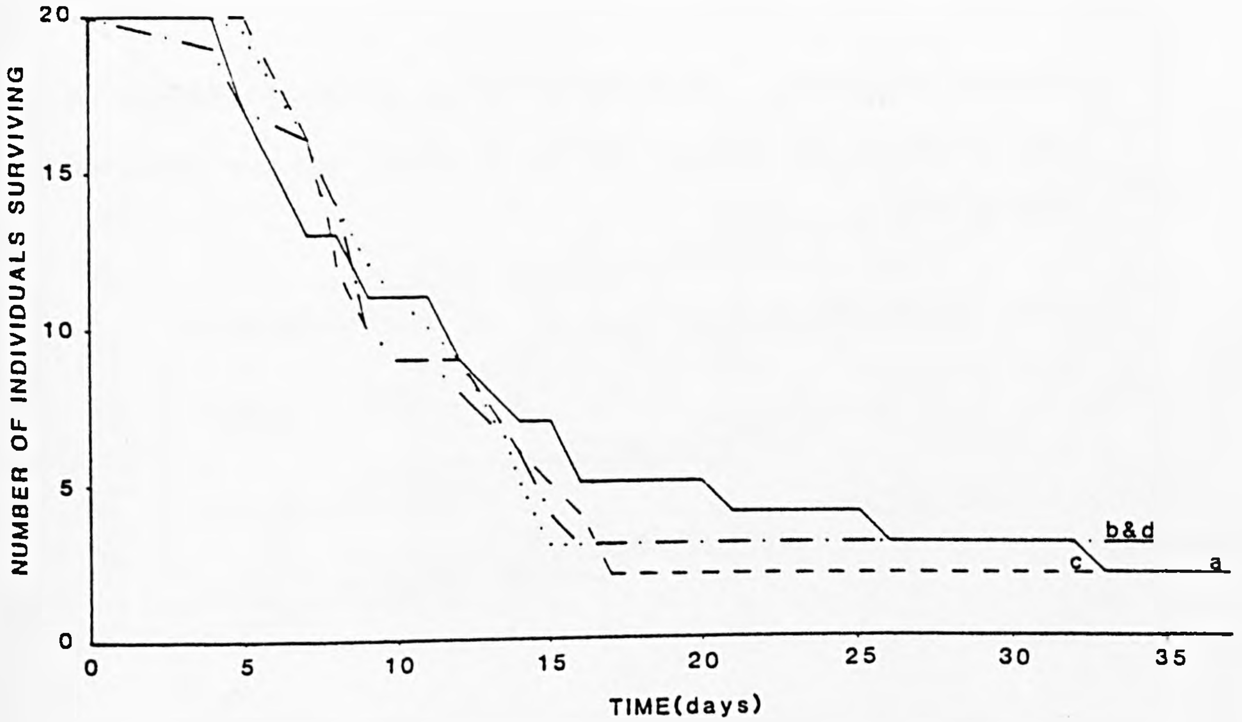

NUMBER OF INDIVIDUALS SURVIVING
20
15
10
5
0
0
5
10
15
20
25
30
35
TIME(days)
b&d
c
a

Figure 7.12

*Pagurus bernhardus*. Cumulative survival rates and moulting periods of larvae reared at four different salinities and in one temperature (15°C).

a = 33‰.

b = 30‰.

c = 28‰.

d = 25‰.

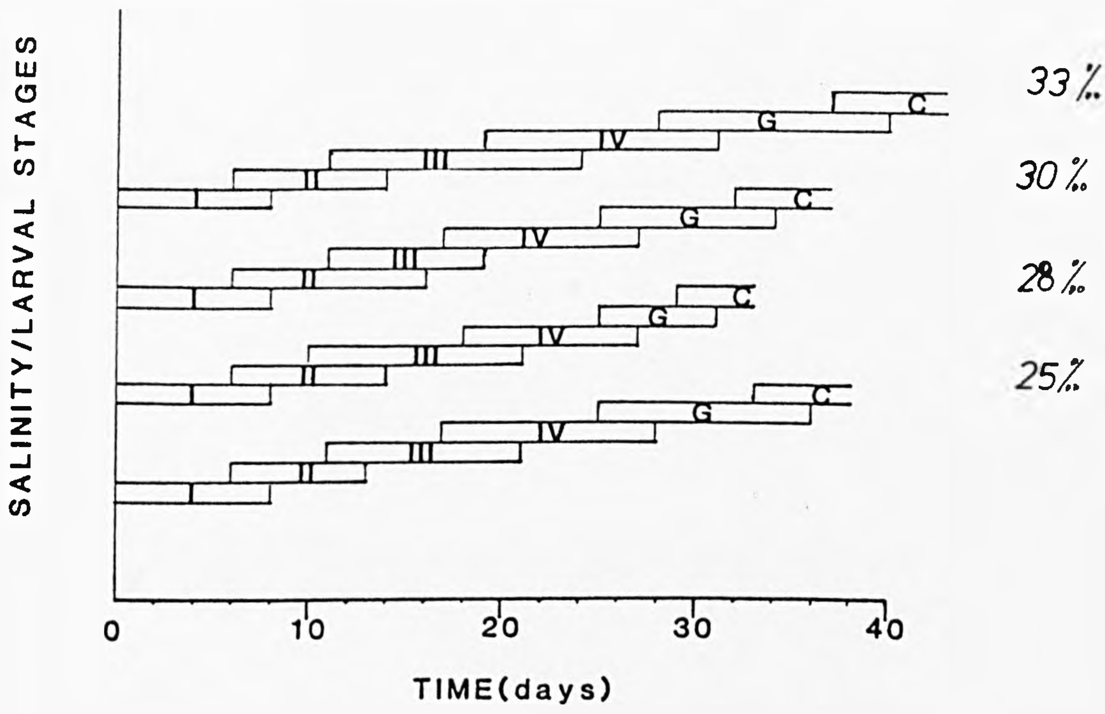

SALINITY/LARVAL STAGES
II
III
IV
G
C
33‰
30‰
28‰
25‰
0
10
20
30
40
TIME(days)

Figure 7.13

*Pagurus bernhardus*. Duration of larval development reared at four different salinities (33, 30, 28, 25‰) and one temperature (15°C).

I-IV: zoeal stages; G: glaucothoe; C: first crab stage.

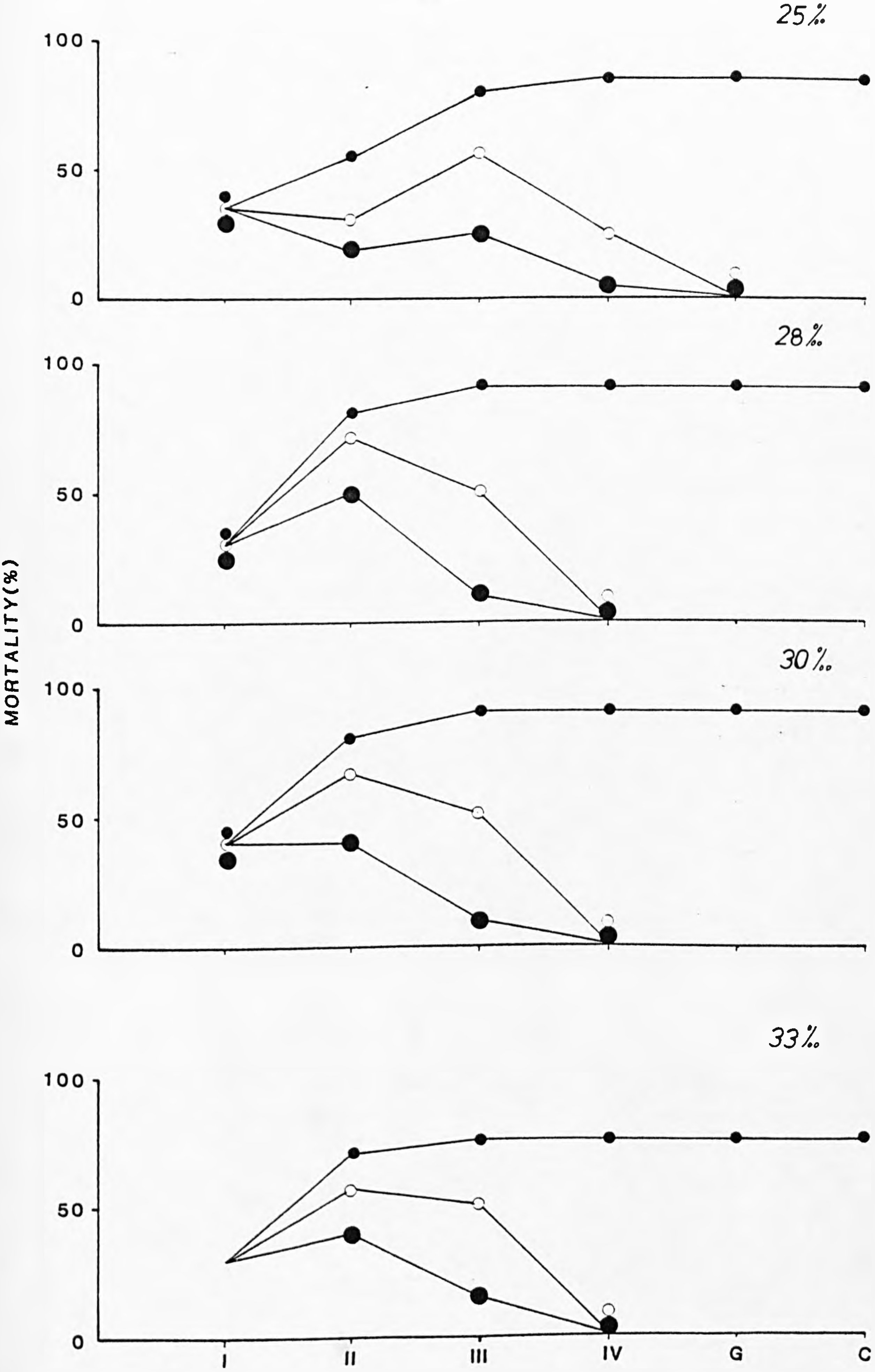

25‰
100
50
0
28‰
100
50
0
MORTALITY(%)
30‰
100
50
0
33‰
100
50
0
I
II
III
IV
G
C

Figure 7.14

*Pagurus bernhardus*. Cumulative mortality of larvae reared at four different salinities (25, 28, 30, 33‰) and in one temperature (15°C).

I-IV: zoeal stages; G: glaucothoe; C: first crab stages.

○——○ %age of each stage dying

•——• cumulative %age death

●——● %age of original number dying at each stage

# Chapter 8

# General Conclusions

## GENERAL CONCLUSIONS

There do not appear to be any published accounts of comprehensive studies made of intertidal populations of *Pagurus bernhardus* in the British Isles. Such accounts as do occur are brief or largely anecdotal, including for instance those of Pike and Williamson (1959), Southward and Southward (1977) and Elwood and Stewart (1985).

The present study includes an account of an extensive intertidal population in South Wales in which densities of up to 25.4 per square metre occur over a wide area and locally much higher densities are reached. Contrary to the findings of Southward and Southward (1977) the hermits do appear at times in winter to group into tight clusters, resulting in densities equivalent to 500 per square metre (measured in numbers per 0.25 metre square) of the sort reported by Synder-Conn (1980, 1981).

All the intertidally available species of gastropod shell were observed in use as carcinoecia. The overwhelming majority of these were *Littorina littorea*. In general extremely few shells of *Buccinum undatum* were to be found intertidally; probably less than one per 100 square metres. Most of these were badly damaged although whether by mechanical action or by predators could not be determined. Occasionally, near low tide level, more numerous undamaged *Buccinum undatum*, occupied by male hermits were to be found near low water mark. These appeared to have entered the intertidal temporarily from the sublittoral for mate seeking purposes.

The relative scarcity of unoccupied gastropod shells including those of a suitable small size for recruits, as well as of the larger sizes of *L. littorea*, suggested that the population was shell-limited rather than food-limited in much the same way as has been reported for other intertidal hermit crab populations by for instance, Kellogg (1976).

The size of the intertidal hermits was clearly related to the size of the available gastropod shell houses. The biggest specimens were to be found in the few *Buccinum undatum* shells available.

There was a striking difference between the relationship between shell size and hermit size seen intertidally and that recorded from sublittoral specimens. Amongst the latter, the largest of the crabs occupying large *Buccinum undatum* shells, amply filled their shells such that even when contracted their chelae bulged from the shell. The intertidal hermits on the other hand could in the majority of cases withdraw deeply inside their shells such that the chelae were out of sight. The difference applied even when intertidal and sublittoral specimens of the same size shell (*Littorina littorea*) were compared. This probably results from different predator pressure intertidally. Vance (1972) working on *Pagurus granosimanus* observed that predators preyed on hermits occupying smaller shells for a given size of crab in 15 out of 16 trials. It is postulated that wading birds common in the present study area at low tide may selectively predate hermits protruding from their shells.

Previously reported differences in the colour of intertidal *P. bernhardus* from sublittoral ones (Marine Biological Association 1957) were also observed in the present study. The pattern of commensal fauna also differed between intertidal and sublittoral stocks (see Chapter 2). Because of the wide range of differences it became important to know whether these were genotypic or phenotypic. An electrophoretic examination of the alloenzymes of representative specimens indicated no genetic differences and it was concluded that the differences must be ecophenotypic (Chapter 2).

A mark-recapture experiment on intertidal *P. bernhardus* at Mumbles revealed that the same specimens are to be found in an area after the passage of the tide, suggesting there is no large scale tidal migration as occurs in *Diogenes pugilator*. Furthermore, monthly sampling suggested that seasonal changes in the population are not marked. Recruitment was recorded but no seasonal emigration from the area of study was evident of the sort suggested by Pike and Williamson (1959).

Studies on the breeding of the intertidal population indicated that individuals become sexually mature in the breeding season following their recruitment so that virtually the whole population is reproductively active. Gravid females occurred from December to May (with insignificant numbers in November, June and July). This represents a slightly shorter breeding season than reported by Pike and Williamson (1959) for sublittoral populations in the Isle of Man and by Dawirs (1979) in the German Bight. There was some evidence that this was reflected in the local sublittoral population in South Wales.

The influence of shell-type on clutch size of the type reported by Bertness (1981) was not recorded apart from obvious differences associated with different shell size.

Morphometric studies related to major chela growth revealed some pronounced differences between intertidal and sublittoral populations. Results for sublittoral specimens indicated a pattern similar to that established by Bush (1930) for *Pagurus prideauxi*. Major chela growth for both male and female individuals up to a size of about 12 mm carapace width was close to isometric. At that size male specimens exhibited pronounced positive allometry of chela growth. In the intertidal population all specimens were of course well below the size at which the change in growth rate takes place sublittorally. However, it was found that growth rate of major chelae of males and females was not similar and isometric but much steeper in males. The net result was that, as in the sublittoral population, the largest males in the intertidal population (occupying the majority type shells) had larger major chelae than similar sized females. This did not seem to result from a sudden change in allometry. However, it did represent another important difference between intertidal and sublittoral populations and represented a growth pattern difference not previously reported.

Larval rearing studies amply confirmed the major findings of Dawirs (1982) on rate of development at a range of temperatures and salinity and confirmed the problems of cannibalism as a cause of mortality in mass rearing experiments. The long duration of larval life at the winter temperatures likely to occur in the Bristol Channel (30+ days at 10°C and up to four months at 5°C) confirm the suspicion that not even the smallest gravid females could have been recruited in the current breeding season.

Laboratory growth rate studies (Chapter 5) tended to corroborate the earlier findings of Markham (1968) that the growth rate of this species is considerably slowed down in the absence of suitably sized larger shells for the hermits to move into. Such a relationship between hermit growth and size of available shells is also reported by Bertness (1981) and Fotheringham (1976). Hazlett (1981) reports that for at least seven species of hermit crabs growth is slowed by occupation of a shell that is too small, even when excess food is present.

Hypothetical growth curves (Figure 5.9) reconstructed from field data on recruits and smallest breeders, and laboratory growth rate studies, give an indication of age related to size but cannot unfortunately give any accurate information about maximum age, for two reasons; firstly, the observed variability of growth rate and secondly, the general acceptance that laboratory growth results may not always be totally reliable (Hartnoll, 1982).

Most previous workers have assumed that the small intertidal *Pagurus bernhardus* are juveniles, although Southward and Southward (1977) (in the context of a paper on *Clibanarius erythropus*) appeared to have some doubt, when they wrote "The hermit crabs commonly found in tide-pools on British shores have always been assumed to be juveniles *or small specimens* (my italics) of *Pagurus bernhardus*". The present study interprets the intertidal specimens as small, but fully mature adult specimens and finds no reason to believe they normally proceed to a sublittoral stage. Existence of small specimens sublittorally makes it unnecessary anyway. Surprisingly and unexpectedly, evidence was found of temporary migration in the reverse direction, that is of large sublittoral males intent on mate seeking. Other evidence suggested that generally speaking the comparatively thin shells of *Buccinum undatum* are prone to damage intertidally, carrying therefore an increased risk of predation for the occupant.

The high nunbers of small individuals found intertidally probably have a similar reproductive output per unit area of habitat as could be expected from the equivalent small number of large individuals the same habitat could support. The reproductive strategy that obviates this arrangement is the extremely small size at which puberty occurs. This has been pointed out previously for hermit crabs (Bertness, 1981). What is different in the case of *Pagurus bernhardus* is the coexistence in neighbouring habitats of populations having such different life styles and different maximum size expectations in order to exploit the potentials of the habitat.

Overall, *Pagurus bernhardus* is seen to be eurytopic in the ecological requirements. In comparison, *Diogenes pugilator* is extremely stenotopic being confined to a narrow vertical zone on continuously surf pounded sandy beaches. On such shores *P. bernhardus* is precluded by the harsh physical conditions. In its absence *D. pugilator* is free to flourish. There are many examples in the marine environment of this type of division of the available habitat in which one species is confined to a harsh habitat and fails to compete with other species in the neighbouring habitats where conditions are physically less demanding. One such example is that of the Chthamalidae barnacles which thrive on the upper levels of intertidal rocky shores but fail in competition with later evolved species lower down. Such species are said to occupy refugial habitats, and themselves to be refugial species. *Diogenes pugilator* appears to fit into this category. Not surprisingly the refugial species develop special adaptations to the harsh habitat and some such are evident in the behaviour patterns of *D. pugilator*. It is noteworthy though that the diogenid hermit crabs are accepted as being comparatively primitive and the pagurids as a later evolved and highly successful group. It is tempting to speculate that before the advent of the pagurids the diogenids may have occupied much wider niche widths from which they later retreated to their present refugial habitats. Finally it must be recognised that the pagurid *Pagurus bernhardus* is a good example of the great success of the pagurid life style.

# REFERENCES

ABBAS, S.A.M., 1985. Predation of infaunal bivalves by *Carcinus maenas* (L.) in the Burry Inlet, S. Wales. Ph.D. thesis, Univ. Wales, 232pp.

ADIYODI, K.G. and ADIYODI, R.G., 1983. Reproductive biology of invertebrates. Vol. 1. Oogenesis, oviposition and oosorption. John Wiley and Sons, New York, 770 pp.

ADIYODI, K.G. and ADIYODI, R.G., 1984. Reproductive biology of invertebrates. Vol. 2. Spermatogenesis and sperm function. John Wiley and Sons, New York, 720 pp.

AHMED, M., SKIBINSKI, D.O.F. and BEARDMORE, J.A., 1977. An estimate of the amount of genetic variation in the common mussel *Mytilus edulis*. Biochem. Genet., 15: 833-846.

AIKEN, D.E. and WADDY, S.L., 1976. Controlling growth and reproduction in the American lobster *Homarus americanus*. J. Fish. Res. Bd. Can., 30: 1327-1334.

AJMAL, KHAN, S. and NATARAJAN, R., 19 . Laboratory rearing of larval stages of the estuarine hermit crab *Clibanarius longitarsus* (De Haan) (Decapoda : Anomura). Indian Journal of Marine Science, 10: 74-81.

ALCOCK, A., 1905. Catalogue of the Indian Decapoda Crustacea in the collection of the Indian Museum. Part II, Anomura; Fasc. 1, Pagurides.

ALLEN, E.J. and TODD, R.A., 1900. The fauna of the Salcombe Estuary. J. Mar. Biol. Ass. U.K. 6: 150-217.

ALLEN, J.A., 1967. The fauna of the Clyde Sea area. Crustacea: Euphausiacea and Decapoda. Scottish Marine Biological Association. Millport, 116 pp.

BALLANTINE, W.J., 1961. A biologically defined exposure scale for the comparative descriptions of rocky shores. Fld. Stud., 1 (3): 1-19.

AMEYAW-AKUMFI, C., 1975. The breeding biology of two sympatric species of tropical intertidal hermit crabs: *Clibanarius chapini* and *C. senegalensis*. Marine biology 29: 15-28.

ANDERSON, D.T., 1982. Embryology. In: The Biology of Crustacea. Vol. 2. Embryology, morphology and genetics (L.G. Abele, ed.). Academic Press, New York, pp. 1-14.

ANGER, K. and NAIR, K.C., 1979. Laboratory experiments on the larval development of *Hyas araneus* (Decapoda, Majidae). Helgoländer wiss. Meeresunters, 32: 36-54.

AVISE, J.C., 1974. Systematic value of electrophoretic data. Syst. Zool. 23: 465-481.

BAGENAL, T.B. (ed.), 1974. Ageing of fish. Proc. Internat. Symp. Uniwin Bros., Old Woking, Surrey, 243 pp.

BALSS, H., 1955. Ökologie, Decapod. In Bronn's Tierreichs Bd. 5 Abt. 1 Bch. 7 Lfg. 10: 1285-1476.

BATE, C.S. and WESTWOOD, J.O., 1868. A history of British sessile-eyed Crustacea. 2, 536 pp. London, J. van Voorst.

BELL, T., 1853. "A history of the British stalk-eyed Crustacea". Van Voorst, London, 386 pp.

BENEDICT, , 1901. Proc. U.S. Nat. Mus., vol. XXIII.

BENNETT, D.B., 1979. Population assessment of the edible crab (*Cancer pagurus* L.) fishery off southwest England. Rapp. P.-v. Rèun. Cons. int. Explor. Mer., 175: 229-235.

BERTNESS, M.D., 1981. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). Crustaceana 40(2), 197-205.

BERTNESS, M.D., 1981. Pattern and plasticity in tropical hermit crab growth and reproduction. The American Naturalist, 117(5): 754-773.

BLASZKOWSKI, C. and MOREIRA, S.G., 1986. Combined effects of temperature and salinity on the survival and duration of larval stages of *Pagurus criniticornis* (Dana) (Crustacea, Paguridae). J. Exp. Mar. Biol. Ecol., Vol. 103, pp. 77-86.

BOLTT, R.E., 1961. Antennary feeding of the hermit crab *Diogenes brevirostris* Stimpson. Nature, 192: 1099 - 1100.

BONNIER, J., 1900. Contribution à l'étude des Épicaridae: Les Bopyridae. 396 pp. Lille.

BOOKHOUT, C.G., 1964. Salinity effects on larval development of *Pagurus bernhardus* (L.) reared in the laboratory. Ophelia, 1, 275-294.

BOOKHOUT, C.G., 1972. The effect of salinity on moulting and larval development of *Pagurus alatus* Fabricius, reared in the laboratory. In, Fifth European Marine Ecology Symposium, edited by B. Battaglia, Piccin Editore, London, pp. 173-187.

BOSCHMA, H., 1928. Rhizocephala of the North Atlantic Region. Dan. Ingolf-Exped., Vol. 3, No. 10, pp. 1-49.

CASSIE, R.M., 1954. Some uses of probability paper in the analysis of size frequency distributions. Aust. J. mar. Freshwater Res., 5: 513-522.

CHOY, S.C., 1985. A rapid method for removing and counting eggs from fresh and preserved decapod Crustaceans. Aquaculture, 48: 369-372.

BOURDON, R., 1963. Épicarides et Rhizocéphales de Roscoff. Cah. Biol. mar., 4: 415-434.

BOUVIER, E.L., 1891. Études de quelques Paguriens recueillis par M.J. de Guerne. Sur les côtes de France et da Norvège. Mém. Soc. Zool. Fr. 4: 393-407.

BOUVIER, E.L., 1940. Decapodes marcheurs. Faune de France., No. 37. Lechevalier, Paris, 404 pp.

BRATTSTRÖM, H., 1958. Cirripedia and Ascothoracica from the Sound and southeastern Kattegat. Acta Univ. Lund. N.F. (Avd. 2), 54(6): 1-26.

BRUCE, J.R., COLMAN, J.S. and JONES, N.S., 1963. Marine Fauna of the Isle of Man. 370 pp. Liverpool Univ. Press.

BUSH, S.F., 1930. Asymmetry and relative growth of parts in the two sexes of the hermit crab, *Pagurus prideauxi*. Archiv. Für Mikroskopische Anatomie und Entwicklungsmechanik., vol. 123, pp. 39-79.

BUSH, S.F. and HUXLEY, J.S., 1930. Distribution of growth activity in *Pagurus*. Nature, 126, pp. 240-241.

CHITTLEBOROUGH, R.G., 1976. Growth of juvenile *Panulirus longipes cygnus* George on coastal reefs compared with those reared under optimal environmental conditions. Aust. J. mar. Freshw. Res., 27: 279-295.

CHOY, S.C., 1986. Ecological studies on *Liocarcinus puber* (L.) and *L. holsatus* (Fabricius) (Crustacea, Brachyura, Portunidae) around the Gower Peninsula, South Wales. Ph.D. thesis, Univ. Wales, 341 pp.

COBB, J.S. and PHILLIPS, B.F. (eds.), 1980. The biology and management of lobsters. Vol. I. Physiology and behaviour. Academic Press, New York, 463 pp.

COFFIN, H.G., 1958. The laboratory culture of *Pagurus samuelis* (Stimpson) (Crustacea, Decapoda). Walla Coll. Publs. Dept. Biol. Sci., Vol. 22: 1-5.

COFFIN, H.G., 1960. The ovulation, embryology and developmental stages of the hermit crab, *Pagurus samuelis* (Stimpson). Walla Walla College Publ. 25: 1-30.

COLE, H.A. (ed.), 1965. Special meeting 1962, to consider problems in the exploitation and regulations of fisheries for Crustacea. Rapp. P.-v. Rèun. int. Explot. Mer., 156: 1-217.

CRAMP, S., 1983. Handbook of the Birds of Europe, the Middle East and North Africa. Vol. III, Oxford, 913 pp.

CROTHERS, J.H., 1967. The biology of the shore crab *Carcinus maenas* (L.); 1. The background - anatomy, growth and life history. Fld. Stud., 2: 407-434.

CROTHERS, J.H., 1969. The distribution of crabs in Dale Road (Milford Haven Pembrokeshire) during summer. Fld. Stud., 3: 109-124.

DAHL, E., 1946. Epicaridea and Rhizocephala from the northern Norway with a discussion on the bathymetrical distribution of Rhizocephala. Tromso Mus. Arsh., vol. 69(1), pp. 1-44.

DAWIRS, R.R., 1979. Effects of temperature and salinity on larval development of *Pagurus bernhardus* (Decapoda, Paguridae). Mar. Ecol. Prog. Ser., 1: 323-329.

FOREST, J., 1955. Crustaces Decapodes, Pagurides. Res. Sci. Exped. Oceanogr. Belg. Eaux. Côt. Afr. 3: 21-147.

DAWIRS, R.R., 1982. Methodical aspects in rearing decapod larvae, *Pagurus bernhardus* (Decapoda, Paguridae) and *Carcinus maenas* (Decapoda, Portunidae). Helgolander wiss. Meeresunters, 35: 439-464.

DRAPKIN, E.I., 1963. Effect of *Rapana bezear* Linne (Mollusca, Muricidae) on the Black Sea fauna. Dokl. Akad. Nauk. SSR 151: 700-703.

EDWARDS, E., 1966. Mating behaviour in the European edible crab (*Cancer pagurus* L.). Crustaceana 10, 23-30.

EDWARDS, E., 1979. The edible crab and its fishery in British Waters. Fishing News Books Ltd., Surrey, 142 pp.

ELWOOD, R.W. and STEWART, A., 1985. The timing of decisions during shell investigation by the hermit crab, *Pagurus bernhardus*. Anim. Behav., Vol. 33: 620-627.

EMMERSON, W.D. and ALEXANDER, M.D., 1986. Shell utilization and morphometrics of the hermit crab, *Diogenes brevirostris* Stimpson. South Africa Tydskr. Dierk., 21: 211-216.

FORSTER, J.R.M., 1970. Further studies on the culture of *Palaemon serratus* Pennant, with emphasis on the post-larval stages. Fishery Invest. Ser. 2, Lond., 26(6): 1-40.

FOTHERINGHAM, N., 1976. Effects of shell stress on the growth of hermit crabs. J. Exp. Mar. Biol. Ecol., 23, 299-305.

GERLACH, S.A., EKSTRØM, D.K. and EKHARDT, P.B., 1976. Filter feeding in the hermit crab, *Pagurus bernhardus*. Oecologia 24: 257-264.

GRASSE, P.P., 1961. Traite de Zoologie. Vol. 4 Plathelminthes, Mesozoaires Acanthocephales, Nemertiens, 944 pp. Masson et Cie, Paris.

GOLDSTEIN, B. and BOOKHOUT, G.C., 1972. The larval development of *Pagurus prideauxi* (Leach) under laboratory conditions (Decapoda, Paguridae). Crustaceana. 23: 263-281.

GONZÀLEZ, GURRIARÀN, E., 1985. Reproduccion de la nécora *Macropipus puber* (L.) (Decapoda, Brachyura), y ciclo reproductive en la Ría de Arousa (Galicia, N.W. España). Boln. Inst. Españ. Oceanogr., 2(1): 10-32.

GORE, R.H. and SCOTTO, E.L., 1983. Early larval stages of the Indo-Pacific coral gall-forming crab *Hapalocarcinus marsupialis* Stimpson, 1859 (Brachyura, Hapalocarcinidae) cultured in the laboratory. Crustaceana 44(2): 141-150.

GOTTO, R.V., 1969. Marine animals, partnerships and other associations. The English University Press, London. 88 pp.

GREENWOOD, J.G., 1972. The male reproductive system and spermatophore formation in *Pagurus novaezealandiae* (Dana) (Anomura: Paguridae). J. Nat. Hist., 6: 561-574.

GULLAND, J.A. and ROTHSCHILD, B.J. (eds.), 1984. Penaeid shrimps: their biology and management. Fishing News Books Ltd., Surrey, England, 308 pp.

GURNEY, R., 1927. Appendix 1 to the report on the Crustacea Decapoda (Natantia and Anomura). Trans. Zool. Soc. London, 22: 228-229.

HANSEN, H.J., 1908 . "Crustacea Malacostraca, 1". The Danish Ingolf Expedition, Vol. III, part 2.

HANSEN, H.J., 1916. Crustacea Malacostraca, III, The Danish Ingolf Expedition, 3(5), 1-262.

HART, Josephine F.L., 1937. Larval and adult stages of British Columbia Anomura. Canad. J. Res., 15D: 179-220.

HARTNOLL, R.G., 1978. The effect of salinity and temperature on the post-larval growth of the crab *Rithropanopeus harrisii*. In: Physiology and behaviour of marine organisms (D.S. McLusky and A.J. Berry, eds.). Pergamon Press, Oxford, pp. 349-358.

HARTNOLL, R.G., 1982. Growth. In: The Biology of Crustacea, Vol. 2. Embryology, morphology and genetics (L.G. Abele, ed.). Academic Press, New York, pp. 111-196.

HAZLETT, B.A., 1966. Social behaviour of the Paguridae and Diogenidae of Curacao. Studies fauna Curacao and other Car. Islands. 23: 1-143.

HAZLETT, B.A., 1968. The sexual behaviour of some European hermit crabs (Anomura : Paguridae). Publ. Staz. Zool. Napoli, 36(2): 238-252.

HAZLETT, B.A., 1970. The effect of shell size and weight on the agonistic behaviour of a hermit crab. Zeit of Terpsychol., 27: 369-374.

HAZLETT, B.A., 1972. Shell fighting and sexual behaviour in the hermit crab genera *Paguristes* and *Calcinus*, with comments on *Pagurus*. Bull. Mar. Sci. 22(4): 806-823.

HAZLETT, B.A., 1981. The behavioral ecology of hermit crabs. Ann. Rev. Ecol. Syst., 12: 1-22.

HEBLING, N.J. and BROSSI-GARCIA, A.L., 1981. Desenvolvimento pós-embrionário de *Pagurus criniticornis* (Dona) (Crustacea: Paguridae), em laboratório. Revta. Bras. Biol., 41: 765-779.

HELFMAN, G.S., 1977. Copulatory behavior of the coconut or robber crab *Birgus lata* (L.) (Decapoda, Anomura, Paguridae, Coenobitidae). Crustaceana, 33: 198-202.

HENDERSON, J.R., 1885. The Decapod and Schizopod Crustacea of the Firth of Clyde. Trans. Nat. Hist. Soc. Glasgow, 1: 315-353.

HØEG, J., 1982. The anatomy and development of the rhizocephalan barnacle *Clistosaccus paguri* Lilljeborg and relation to its host *Pagurus bernhardus* (L.). J. exp. mar. Biol. Ecol. 58: 87-125.

HØEG, J. and LÜTZEN, J., 1985. Crustacea rhizocephala. Mar. Invs. Scan. No. 6, pp. 92.

HORNELL, J., 1892. Report on the polychaetous annelids of the L.M.B.C. district. Fauna Liverpool Bay, Rep. 111, p. 126. London.

HUMASON, G.L., 1979. Animal tissue techniques. W.H. Freeman & Co., San Francisco, 661 pp.

HUXLEY, J.S., 1924. Constant differential growth ratios and their significance. Nature (Lond.) 114: 895-896.

HUXLEY, J.S., 1927. Further work on heterogonic growth. Biol. Zbl. 47(3): 151-163.

HUXLEY, J.S., 1932. Problems of relative growth. London, Methuen. 276pp.

HUXLEY, J.S. and RICHARDS, O.W., 1931. Studies in heterogonic growth. (8). Changes in proportions in the abdomen of the shore-crab, *Carcinus maenas*. J. mar. biol. Ass. U.K., 17: 1001.

ICHIKAWA, A. and YANAGIMACHI, R., 1958. Studies on the sexual organization of the Rhizocephala. I. The nature of the "testes" of *Peltogasterella socialis* Krüger. Annot. Zool. Jpn., 31: 82-96.

ICHIKAWA, A. and YANAGIMACHI, R., 1960. Studies on the sexual organization of the Rhizocephala. II. The reproductive function of the larval (cypris) males of *Peltogaster* and *Sacculina*. Annot. Zool. Jpn., 33: 42-56.

JACKSON, H.G., 1913. *Eupagurus*. L.M.B.C. memoir No. XXI of the Liverpool marine biological committee. pp. 1-79.

KAMALVENI, S., 1949. On the ovaries copulation and egg formation in the hermit crab *Clibanarius olivacious* (Henderson) (Crustacea, Decapoda). J. Zool. Soc. India, 1: 120-128.

KELLOGG, C.W., 1976. Gastropod shells: A potentially limiting resource for hermit crabs. J. exp. mar. Biol. Ecol., 22: 101-111.

KINNE, I., 1977. Research cultivation. In: O. Kinne (Ed.), Marine Ecology, Vol. III, Cultivation, Part 2. Wiley, Chichester, pp. 579-1293.

KOMM, B.S. and HINSCH, G.W., 1985. Oogenesis in the terrestrial hermit crab *Coenobita clypeatus* (Decapoda, Anomura). 1.

LAULIER, M. and N. DEMEUSY., 1974. Etude histologique du functionement ovarien au cours d'une maturation de ponte chez le crabe *Carcinus maenas* L. (Crustace Decapode). Cah. Biol. mar., 15: 343-350.

LEWIS, J.R., 1964. The ecology of rocky shores. The English Univ. Press, 323 pp.

Previtellogenic Oocytes. J. Morph., 183(2): 219-224.

LAGERBERG, 1908. "Sveriges Decapoder", - Goteborgs Kungl, Vetenskapsoeh Vitterhets samhallet Handlingar. Tjarde Foliden, XI, 2.

LILLJEBORG, W., 1860. Supplément au mémoire dur les genres *Liriope* et *Peltogaster* H. Rathke. Nova Acta R. Soc. scient. Upsal. (Ser. 3) 3: 73-102.

LILLJEBORG, W., 1861. Supplementary memoir on the genera *Liriope* and *Peltogaster*, Rathke. Ann. Mag. Nat. Hist., Ser. 3, 7: 47-63.

LILLJEBORG, W., 1864. Supplément au mémoire sur les genres *Liriope* et *Peltogaster*. Ann. Sci. Nat. Hi-t. (Zool.), Ser. 5, 2: 325-355.

LINDNER, M.J. and ANDERSON, W.W., 1956. Growth, migrations, spawning and size distribution of shrimp *Penaeus setiferus* (Linnaeus, 1767). In: Proceedings of the World Scientific Conference on the biology and culture of shrimps and prawns (M.N. Mistakidis, ed.). FAO Fish. Rep., 59(4): 1439-1469.

LOCKWOOD, A.P.M., 1968. Aspects of the Physiology of Crustacea. Freeman, London, 328 pp.

MACDONALD, J.D., PIKE R.B. and WILLIAMSON, D.I., 1957. Larvae of the British species of *Diogenes*, *Pagurus*, *Anapagurus* and *Lithodes* (Crustacea, Decapoda). Proceedings of the Zoological Society of London, 128: 209-257.

MAINARDI, D. and ROSSI, A.C., 1972. Social status and its effects in some hermit crabs (Decapoda, Anomura). Fifth European marine biology symposium, 317-326.

MARINE BIOLOGICAL ASSOCIATION, 1957. Plymouth marine fauna. 457 pp.

MARKHAM, J.C., 1968. Notes on growth patterns and shell utilization of the hermit crab *Pagurus bernhardus*. Ophelia 5, 189-205.

MATHEWS, D.C., 1956. The probable method of fertilization in terrestrial hermit crabs based on a comparative study of spermatophores. Pacific Science, vol. 10, pp. 303-309.

MCLAY, C.L., 1985. Moulting and growth in *Pagurus traversi* and *P. novizealandiae* (Decapoda, Anomura, Paguridae): the effects of neighbours. New Zealand Journal of Marine and Freshwater Research, vol. 19: 327-337.

MENON, M.D., 1950. The use of bones other than otoliths in determining the age and growth rate of fishes. J. Cons. perm. int. Explor. Mer., 16(3): 311-340.

MILNE-EDWARDS, A. and BOUVIER, E.L., 1893. "Reports on the results of dredging in the Gulf of Mexico, and in the Caribbean Sea and along the Atlantic coast of the United States, by the Blake. Description des Crustacés de la famille de Paguriens recueillis pendant l'expédition." Mém. Mus. Comp. Zool. Harvard. Vol. XIV, No. 3.

MILNE-EDWARDS, A., and BOUVIER, E.L., 1897. "Sur les resemblances le dimorphisme parallêles de l'*Eupagurus excavatus* Herbst., et de l'*Eupagurus variabilis* Edw. and Bouv." Bull. Soc. Zool. France. XXII.

MOORE, H.B., 1937. The biology of *Littorina littorea*. J. mar. biol. Ass. U.K., 21: 721-742.

NORMAN, A.M., 1907. Notes of the Crustacea of the Channel Islands. Ann. Mag. nat. Hist., 20 (7), 356-371.

MOUCHET, S., 1931. Spermatophores des Crustacés Décapodes Anomoures et Brachyoures et castration parasitaire chez quelques Pagures. Station Océanographique de Salammbô Annales, No. VI, 1-203.

MOYSE, J., THORPE, J.P. and AL-HAMADANI, E., 1982. The status of *Littorina aestuarii* Jeffreys and approach using morphology and biochemical genetics. J. Conch., 31: 7-15.

NAYLOR, E., 1958. Tidal and diurnal rhythms of locomotor activity in *Carcinus maenas* (L.). J. exp. Biol., 35: 602-610.

NAYLOR, E., 1962. Seasonal changes in a population of *Carcinus maenas* (L.) in the littoral zone. J. Anim. Ecol., 31: 601-609.

NELSON-SMITH, A. and BRIDGES, E.M. (eds.), 1977. Problems of a small estuary. Proc. Symp. Burry Inlet (S. Wales), 13-15 Sept., 1976. Inst. Mar. Stud., Univ. Coll. Swansea, Wales.

NEWMAN, W.A., ZULLO, V.A. and WITHERS, T.H., 1969. Cirripedia. pp. 206-295 in R.C. Moore (ed.): Treatise on Invertebrate Palaeontology, part R, Arthropoda 4. Geol. Soc. Am. Univ. Kansas Press.

NIELSON, S.O., 1970. The effects of the rhizocephalan parasites *Peltogaster paguri* Rathke and *Gemmosaccus sulcatus* (Lilljeborg) on five species of paguridan hosts (Crustacea, Decapoda). Sarsia 42: 17-32.

NOBILI, G., 1906. Faune carcinologique de la Mer Rouge: Decapodes et Stomatopodes. Ann. Sci. Nat. Zool. Ser. 9, vol. IV. Masson, Paris.

NORMAN, A.M., 1861. "Contribution to British Carcinology". Ann. Mag. Nat. Hist. Ser. 8, VIII.

NORMAN, A.M. and SCOTT, T., 1906. The Crustacea of Devon and Cornwall. Wesley, London, 280 pp.

O'SULLIVAN, G., 1977. The influence of wave exposure on shallow water macrobenthos communities. Unpublished M.Sc. thesis. Univ. College of North Wales, Bangor.

PANDIAN, T.J. and SCHUMAN, K.H., 1967. Chemical composition and caloric content of egg and zoea of the hermit crab *Eupagurus bernhardus*. Helgolander wiss. Meerensunters. 16: 225-230.

PASSANO, L.M., 1960. Moulting and its control. In: The Physiology of Crustacea. Vol. I (T.W. Waterman, ed.). Academic Press, London, pp. 473-536.

PAULY, D., INGLES, J. and NEAL, R., 1984. Application to shrimp stocks of objective methods for the estimation of growth, mortality and recruitment related parameters from length-frequency data. (ELEFAN I and II). In: Penaeid shrimp: their biology and management (J.A. Gulland and B.J. Rothschild, eds.). Fishing News Books, Farnham, Surrey, England, pp. 220-234.

PENN, J.W., 1975. Tagging experiments with the western king prawn *Penaeus latisulcatus* Kishinouye. 1. Survival, growth and reproduction of tagged prawns. Aust. J. mar. Freshwater Res., 26: 197-211.

PENN, J.W., 1976. Tagging experiments with the western king prawn, *Penaeus latisulcatus* Kishinouye. II. Estimation of population parameters. Aust. J. mar. Freshwater Res., 27: 239-250.

PERÈZ, C., 1929. Notes sur les Épicarides et les Rhizocéphales des côtes de France. Bull. Soc. Zool. Fr. 54: 607-609.

PERÈZ, C., 1934. Notes sur les Épicarides et les Rhizocéphales des côtes de France. VIII. Arch. Zool. Exp. Gen., 75: 541-565.

PIKE, R.B., 1953. The bopyrid parasites of the Anomura from British and Irish waters. J. Linn. Soc., 42(285), 219-238.

PIKE, R.B., 1961. Observations on Epicaridea obtained from hermit crabs in British Waters, with notes on the longevity of the host species. Ann. Mag. nat. Hist., 13(4), 225-240.

PIKE, R.B. and WILLIAMSON, D.I., 1959. Observation on the distribution and breeding of British hermit crabs and the stone crab (Crustacea, Diogenidae, Paguridae and Lithodidae). Proc. Zool. Soc. London, 132, 551-573.

PIKE, R.B. and WILLIAMSON, D.I., 1960a. Larvae of decapod Crustacea of the families Diogenidae and Paguridae from the Bay of Naples. Pubbl. Stn. Zool. Napoli 31, 493-552.

PIKE, R.B. and WILLIAMSON, D.I., 1960b. Larvae of decapod Crustacea of the families Dromiidae and Homolidae from the Bay of Naples. Pubbl. Stn. Zool. Napoli 31, 553-563.

POOLE, R.L., 1967. Preliminary results of the age and growth of the marked crab (*Cancer magister*) in California. The age and growth of *Cancer magister* in Bodega Bay. Proc. Symp. Crustacea, Part II. Mar. biol. Ass. India, pp. 553-567.

PROVENZANO, A.J. Jr., 1967. Recent advances in the laboratory culture of decapod larvae. Proc. Symp. Crustacea, Part II. Mar. biol. Ass. India, pp. 940-945.

PROVENZANO, A.J. Jr. and RICE, A.L., 1964. The larval stages of *Pagurus marshi* (Benedict) (Decapoda, Anomura) reared in the laboratory. Crustaceana, 7: 217-235.

QASIM, S.Z., 1956. The spawning habits and embryonic development of the shanny (*B. pholis* L.). Proc. Zool. Soc. London 127: 79-93.

RATHKE, H., 1840. Zur Entwicklungsgeschichte der Dekapoden. Arch. Naturgesch., 6: 241-249.

RATHKE, H., 1842. Beitrage zur Vergleichenden Anatomie und Physiologie. II. Zur Entwicklyngsgeschichte der Dekapoden. Neust. Schr. d. Naturforch. Gesellesch., Danzig, 3: 23-55.

REBACH, S., 1974. Burying behaviour in relation to substrate and temperature in the hermit crab, *Pagurus longicarpus*. Ecology, 55: 195-198.

REESE, E.S., 1968. Annual breeding seasonal of three sympatric species of tropical intertidal hermit crabs, with a discussion of factors controlling breeding. J. exp. Mar. Biol. Ecol. 2: 308-318.

REINHARD, E.G., 1942. Studies on the life history and host-parasite relationship of *Peltogaster paguri*. Biol. Bull. mar. biol. Lab. Woods Hole, 83: 401-415.

REINHARD, E.C., 1946. Rhizocephala from New England and the Grand Banks. J. Wash. Acad. Sci. 36: 127-131.

RICE, A.L. and WILLIAMSON, D.I., 1970. Methods of rearing larval decapod Crustacea. Helgoländer wiss. Meeresunters, 20, 417-434.

RITCHIE, L.E. and HØEG, J.T., 1981. The life history of *Lernaeodiscus porcellanae* (Cirripedia : Rhizocephala) and co-evolution with its porcellanid host. J. Crustacean Biol. (Woods Hole, Mass.) Vol. 1(2), 14 pp.

ROBERTS, M.J. Jr., 1971. Larval development of *Pagurus longicarpus* Say reared in the laboratory. II. Effects of reduced salinity on larval development. Biol. Bull. 140: 104-116.

ROBERTS, M.H. Jr., 1975. Culture techniques for decapod crustacean larvae. In: W.L. Smith and M.H. Chanley (Eds.), Culture of Marine Invertebrate Animals. Plenum Press. New York. pp. 209-220.

ROSS, D.M., 1960. The association between the hermit crab *Eupagurus bernhardus* (L.) and the sea anemone *Calliactis parasitica* (Couch). Proc. Zool. Soc. London, 134: 43-57.

SABAR, F., 1980. Ecological separation in two species of hermit crabs: *Diogenes pugilator* (Roux) and *Pagurus bernhardus* (L.) on Anglesey. Unpublished M.Sc. thesis, Univ. College of North Wales, Bangor.

SAMUELSEN, T.J., 1970a. *Peltogaster curvatus* Kossmann, a rhizocephalan parasite new to the Norwegian fauna with notes on the synonymy of one of the hosts, *Pagurus prideauxi* Leach. Sarsia, 43: 81-86.

SAMUELSEN, T.J., 1970b. The biology of six species of Anomura (Crustacea, Decapod) from Raunefjorden, Western Norway. Sarsia 45: 25-52.

SARS, G.O., 1882. The Norwegian North Atlantic Expedition, 1876-1878. Crustacea. Christiania. Vol. VI, pp. 1-161.

SARS, G.O., 1890. Bidrag til Kundskaben om Decapodem es Forvandlinger. II. *Lithodes*, *Eupagurus*, *Spiropagurus*, *Galathodes*, *Galathea*, *Munida*, *Porcellana*, *Nephrops*. Arch. Math. Naturv., 14: 132-195.

SARS, G.O., 1899. An account of the Crustacea of Norway, 2. Isopoda, 270 pp.

SASTRY, A.N., 1983. Ecological aspects of reproduction. In: The Biology of Crustacea. Vol. 8. Environmental adaptations. (F.J. Vernberg and W.B. Vernberg, eds.). Academic Press, New York, pp. 179-270.

SCHEIDEGGER, G., 1976. Stadien der Embryonalentwicklung von *Pagurus prideauxi* Leach. (Crustacea, Decapoda, Anomura) unter besonder Berücksichtigung der Darmentwicklung. Zool. Jb. Anat. Bd., 95: 297-353.

SCHEMBRI, P.J., 1982. Locomotion, feeding, grooming and the behavioural responses to gravity, light and hydrostatic pressure in the stage I zoea larvae of *Ebalia tuberosa* (Crustacea, Decapoda, Leucosiidae). Marine Biology, 72(2), 125-146.

SCHRAM, F.R., 1986. Crustacea. Oxford University Press, New York. 606 pp.

SCOTT, T., 1897. Marine Fishes and Invertebrates of Loch Fyne. 15th Rept. Fish. Bd. Scot. 107-174.

SELBIE, C.M., 1921. The Decapoda Reptantia of the coasts of Ireland. Part II. Paguridae. Scient. Invest. Fish. Brch. Ire., No. 1, 68 pp.

SHAW, C.R. and PRASAD, R., 1970. Starch gel electrophoresis of enzymes - a compilation of recipes. Biochem. Genet. 4: 297.

SNYDER-CONN, E., 1980. Tidal clustering and dispersal of the hermit crab *Clibanarius digueti*. Mar. Behav. physiol. 7: 135-154.

SNYDER-CONN, E.K., 1981. The adaptive significance of clustering in the hermit crab *Clibanarius digueti*. Mar. Behav. Physiol., 8: 43-53.

SOUTHWARD, A.J. and SOUTHWARD, Eve C., 1977. Distribution and ecology of the hermit crab *Clibanarius erythropus* in the Western Channel. J. mar. Biol. Ass. U.K., 57: 441-452.

SPIVEY, H.R., 1982. Rhizocephala, pp. 229 in S.P. Parker (ed.). Synopsis and Classification of living Organisms. McGraw-Hill Co.

STEBBING, T.R.R., 1900. Marine investigations in South Africa: S. African Crustacea. Part IV. Richards & Sons, Capetown.

STEEDMAN, H.F., 1966. Section cutting in microscopy. Blackwell, Oxford, 172 pp.

TESCH, J.J., 1908. "Bijdragen tot de fauna der zuidelijke Noordzee, IV, Decapode Crustaceen ten deele versameld met de Wodan". Jaarb, Rijksint. Onderz. Zee, Helder.

WALTON, B.C. and STEVENS, B.A., 1955. Notes of the use of the generic names *Pagurus*, *Eupagurus* and *Dardanus* (Crustacea, Anomura). Bull. 5th Calif Acad. Sci. 54 (1): 40-42.

THOMAS, H.J. (ed.), 1979. Population assessments of shellfish stocks. Rapp. P.-v. Rèun. int. Explor. Mer., 175: 1-288

THORPE, J.P., 1979. Enzyme variation and taxonomy: the estimation of sampling errors in measures of interspecific genetic similarity. J. Linn. Soc. (Biol.), 11: 369-386.

TOMLINSON, J.T., 1960. Low hermit crab migration rates. Notes and News. The veliger. 2(3): 61.

VANCE, R.R., 1972a. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. Ecology, 53: 1062-1074.

VANCE, R.R., 1972b. The role of shell adequacy in behavioural interactions involving hermit crabs. Ecology, 53: 1075-1083.

VARADARAJAN, S. and SUBRAMONIAM, T., 1981. Reproduction of the continuously breeding tropical hermit crab, *Clibanarius clibanarius*. Mar. Ecol. Prog. Ser. Vol. 8, 197-201.

WARNER, G.F., 1977. The biology of crabs. Elek Science, London. 202 pp.

WATERMAN, T.H. (ed.), 1960. The Physiology of Crustacea. Vol. 1. Metabolism and growth. Academic Press, New York, 670 pp.

WATERMAN, T.H. (ed.), 1961. The Physiology of Crustacea. Vol. II. Sense organs, integration, and behaviour. Academic Press, New York, 681 pp.

WIDDOP, T.H., 1979. The ecology of the hermit crab, *Diogenes pugilator* (Roux) (Anomura, Paguridae) on Anglesey. Unpublish. M.Sc. thesis, Univ. College of North Wales, Bangor.

WILLIAMSON, H.C., 1910. On the larval and later stages of certain decapod Crustacea. Rep. Fish. Bd. Scot., 1: 1-20.

WILSON, D.P., 1935. Life of the shore and shallow sea. Ivon Nicholson and Watson Ltd., London, pp. 111-200.

YONGE, C.M., 1954. The sea shore. Collins, St. James Palace, London, 311 pp.

YOUNG, A.M. and HAZLETT, T.L. III, 1978. The effect of salinity and temperature on the larval development of *Clibanarius vittatus* (Bose) (Crustacea, Decapoda, Diogenidae). J. exp. mar. Biol. Ecol., 34: 131-141.

# APPENDIX

## INTRODUCTION

Apart from epizoites and other animsla "associated" with hermit crabs and their shells, the present species were seen to be infected by a number of parasites. Some of these were ectoparasites - particularly Rhizocephala and Isopoda. Internally, a cestode parasite was observed.

There is an extensive literature on parasites of pagurids and it is worth reviewing this by way of introduction.

### Rhizocephala

The Rhizocephala are highly modified representatives of the Crustacea , class Cirripedia and all are parasites of other crustaceans, principally Decapoda. Among the six rhizocephalan families, the *Clistosaccidae* and *Peltogastridae* are known to parasitize hermit crabs.

The majority of Rhizocephala belong to the families Peltogastridae, Sacculinidae and Lernaeodiscidae. These three families have, in recent years, been proved to be dioecious (Ichikawa and Yanahirmachi, 1958, 1960; Ritchie and Høeg, 1981). Also, there are indications that these three families are more closely related mutually than they are to the other families (Høeg and Lützen, 1985). Lilljeborg (1860, 1861, 1864) described two rhizocephalan species, *Clistosaccus paguri* and *Apeltes paguri*, parasitizing hermit crabs, with a brief account of their anatomy. Boschma (1928) worked with larger material and proved the *C. paguri* and *A. paguri* belong to the same species; the name *C. paguri* has priority and it is the only member of the Clistosaccidae. The "*A. paguri*" of Lilljeborg represents the mature external stage of the species with a mantle aperture (Høeg, 1982).

Family - Clistosaccidae Lilljeborg, 1860

Genus - Clistosaccus Lilljeborg, 1860

*Clistosaccus paguri*

Internal stages common and easily recognized as circular whitish discs, 1-2 mm across, and covered by host tissue, or just prior to emergence situated directly beneath the host cuticle. Externa emerge as circular, slightly convex discs, and grow through subcylindrical into cylindrical-elongate shape. Immature externae measure 2.5-13.0 mm in length, and 1.5-4.5 mm in width. Mature externae measure 2.5-26.0 mm. Size at first oviposition and acquisition of mantle aperture extremely variable. Externa size rather independent of host size and number of parasites per host.

Separation from *Peltogaster paguri*. Within most of its distribution area *Clistosaccus paguri* is sympatic with *P. paguri*; in the Atlantic, both species occur on *P. bernhardus* and *P. pubescens*. These two parasites have rather often been confused in the literature and in collections. Live specimens and preserved mature externae with poorly defined colour are separated by the narrow stalk (max. 1/10th of externae length) associated with a conspicuous shield in *P. paguri*. A shield is absent in *C. paguri* and the stalk is much broader (Høeg and Lutzen, 1985). Outside the area they say it occurs on: *P. capillatus*(Benedict), *P. dalli* (Benedict), *P. sphendescens* Owen, and *P. trigonucheirus* (Stimpson).

Along the west coast of Sweden, 2-3% of the *P. bernhardus* population is visibly infected. It occurs in the Kattegat; the entire west and north coasts of Norway; Spitzbergen, the Faroes and Iceland. It has been recorded also in the North Atlantic, off Nova Scotia, Newfoundland, and East Greenland (Boschma, 1928; Dahl, 1946; Reinhard, 1946; Brattström, 1958). It occurs from rather shallow water to a depth of 970 metres (Høeg, 1982).

Høeg (1982) made an interesting detailed study sampling *C. paguri* near the Kristineberg Marine Biological Station on the west coast of Sweden at approximately six month intervals (10-24 July 1978, 1 December 1978, 13-21 August 1979, 29 November 1979 and 5-7 May 1980) at 20-40 metres depth. On examination, he found 211 *C. paguri* Lilljeborg on a total of 99 infected *P. bernhardus*. The total number of *P. bernhardus* caught in the last four samples was 2039, that in the first (July 1978) was not recorded.

The overall infection percentage was 4.2% when 310 apparently uninfected crabs from the November 1979 sample were dissected. It remains at 3.0-3.3% throughout the study period except for the May 1980 sample.

The infection of the two sexes was particularly studied in the November 1979 sample: 17 among 575 male crabs (3.2%) and 15 among 498 female crabs (3.0%) were externally visibly parasitized. Of the total number of parasitized crabs, 55 were males and 44 females. This ratio is very similar to the ratio between the two sexes in the November 1979 sample, which indicates that the two sexes are equally infected.

Høeg in 1982 also recorded that 53 out of 99 infected crabs were carrying only one *C. paguri* and the rest (46) were carrying two or more. Also recorded that the highest number of parasites on one crab was 37, when caught, it carried nine parasites, and five more appeared during 3 months observation. In addition, 23 primordia were found when its abdomen was sectioned.

Høeg and Lützen (1985) state that half of the infected crabs carry more than a single parasite; up to 10 externae on a single host. On multiple infected hosts the parasites are usually at different stages of development, not internally connected, and each probably represents its own individual infection.

Family - Peltogastridae Lilljeborg, 1859

Genus - Peltogaster Rathke, 1842

Two species of the family Peltogastridae appear to parasitize hermit crabs, namely *Peltogaster curvatus* and *Peltogaster paguri*, the latter parasitizing the hermit crab *P. bernhardus*, but the former infesting other species.

*Peltogaster paguri*

Recently emerged externae 1-2 mm long, of elongate shape reminiscent of mature ones, but without mantle aperture, and with no, or a poorly defined, shield. Mantle aperture usually appears when the externae is 3-4 mm long. The mature externae: 2-26 mm, rarely > 15 mm. Size of mature parasite is positively correlated with host size in some (Reinhard, 1942c) but not all populations (Nielson, 1970).

In N.W. Europe the following species are parasitized: *P. bernhardus*, *P. cuanensis*, *A. chiroacanthus* and *A. laevis*. It is claimed to infect *P. prideauxi* in Norwegian waters (Nielson, 1970), but Samuelson (1970a, b) found all infected *P. prideauxi* from the same locality to carry *P. curvatus* only. Outside the area it occurs on: *P. capillatus*, *P. hirsutiusculus*, *P. lanuginosus* and *P. trigonocheirus*. Infection percentage varies much with host and locality: along the west coast of Sweden it ranges from 1% on *P. bernhardus* to 5% on *P. cuanensis* and *A. chiroacanthus*. At Espergrand, West Norway, it is c. 2% on *P. bernhardus* and *P. cuanensis*, but only 0.7% on *A. chiroacanthus* (Høeg and Lützen, 1985). Perez (1934) reported many more female than male *P. bernhardus* to be infected by *P. paguri*. At places in the Channel coast of France *P. paguri* infects only females of *P. bernhardus*, but in Scandinavian waters there appears to be no such discrimination between host sexes (Høeg and Lützen, 1985).

The geographical distribution of this parasite extends from the Sound, Kattegat; Skagerrak; Oslofjorden; entire Atlantic coast of Norway north on about 70°N; Spitzbergen; the North Sea. Also recorded from the Barents Sea, the White Sea, the Irish Sea, the Channel, the Atlantic coast of France. Off Newfoundland and Nova Scotia to Cape Cod in the south (Høeg and Lützen, 1985).

Depth amplitude from shallow water to 190 metres.

## Isopoda

Naylor (1977) in his review of the British Marine Isopods, listed three different species of parasites of family Bopyridae as parasitizing *Pagurus bernhardus*, namely *Athelges paguri*, *Pseudione* *hyndmani* and *Pseudione proxima*. A further species is a hyperparasite *Liriopsis pygmaea*.

i. *Athelges paguri* (Rathke) (Sars, 1899) is the only species of *Athelges* recorded intertidally. The size of the females is up to 11 mm in length, but males are smaller 4 mm.

This species appears to be distributed round all the coasts of the British Isles and Ireland.

It was recorded by Bate and Westwood (1868) as *Phryxus paguri* from Strangford Loch, Ireland; Polperro, Cornwall; St. Andrews, east coast of Scotland.

An immature specimen was recorded by the same authors from Banff, N.E. Scotland, under the name of *Ph. fusticaudatus*. Norman (1907, p. 363) recorded it from both Jersey and Guernsey, Channel Islands, *Pagurus bernhardus*, and Cattley (1938, p. 289) recorded it from Plymouth, Devon, as having occurred in the branchial cavity of a single specimen of *P. bernhardus*. It occurs also parasitizing *P. bernhardus*, with an offshore "variety" (Pike, 1953) on *Anapagurus laevis*.

ii. *Pseudione hyndmanni* (Bate and Westwood, 1868; as *Phryxus*) (Bannier, 1900, nec Sars, 1899).

This species is distributed round all the coasts of the British Isles; records are more numerous for the south, west and north coasts than for the east coast. British records extend as far north as the Orkneys and Hansen (1916) has taken it from north and south Iceland. The first specimen, recorded by Bate and Westwood (1868) as *Phryxus hyndmanni* was taken at Groomsport, Ireland, by Mr. G.C.

Hyndman in 1851, and Bate and Westwood (1868) also recorded an immature specimen taken off the Durham coast. This latter record is the only one seen for the east coast. Records for the Firth of Clyde have been made by Henderson (1885) and Scott (1897). Also, this parasite has been recorded by Pike (1953) from northern and western Scotland and Ireland parasitizing the hermit crabs *P. bernhardus* and other species there. It has not been recorded from English or Welsh waters so far.

iii. *Pseudione proxima* Bonnier (1900)

Bonnier (1900) distinguished the Bate and Westwood species (*P. hyndmanni*) from the parasite *P. hyndmanni* described by Sars (1899) and referred the Sars species to *P. proxima* Bonnier. Pike (1953) considered that British material belonged to *P. hyndmanni* but pointed out that the material in some ways resembled *P. proxima*. One Plymouth record of *Pseudione* from intertidal *P. bernhardus* has been ascribed to *P. proxima* Bonnier (i.e. the Sars "*hyndmanni*") (see Pike, 1953).

Family Cryptoniscidae
Genus Cryptoniscus
*Liriopsis pygmaea* (Rathke)

Pike (1964) made observations on the hyperparasite *L. pygmaea* (Cryptoniscidae) found on *Peltogaster paguri* parasitizing both *Pagurus bernhardus* and *Anapagurus laevis* (Pike, 1961).

*L. pygmaea* is recorded particularly from barnacles, isopods and ostracods. Female stage sac-like, with few distinct somites and lacking pereopods. Male (cryptoniscus) antennule with basal article lamellar and often serrated; pereopods 3-7 usually slender with setiform dactyls; pleopods and uropods biramous.

Bourdon (1963) states that several species of Cryptoniscidae occur on French coasts, but only three of these have so far been recorded in Britain; one is *Liriopsis pygmaea* which parasitizes *P. paguri*, a parasite barnacle itself attached to the abdomen of the hermit crabs *A. laevis* and *P. cuanensis* (Marine Biological Association, 1957; Bruce, Colman and Jones, 1963). The other species are *Hemioniscus balani* from shore barnacles and *Ancyroniscus bonnieri* from the shore isopod *Dynamene bidentata*.

Pike (1961) recorded that of hermit crabs *P. bernhardus* collected from Clyde Sea 1% were parasitized by *Peltogaster paguri* and these in turn had a 9% parasitization by *Liriopsis*.

# RESULTS

## Parasites

During the field survey of the hermit crabs they were examined for the occurrence of external and internal parasites. It is worthwhile to record here that around 2086 hermit crabs, *Pagurus bernhardus*, collected intertidally from Mumbles Head, Swansea during 1982-1983, were examined in this way.

From these hermits the following species of parasites were recorded:-

1) *Clistosaccus paguri* (Lilljeborg)
2) *Peltogaster paguri* (Rathke)
3) *Athelges paguri* (Rathke)
4) *Liriopsis pygmaea* Rathke
5) *Eutetrarhynchus ruficollis* (Eysenhardt, 1829)

These will now be dealt with individually.

## Rhizocephala

Family - Clistosaccidae

Genus - Clistosaccus

1. *Clistosaccus paguri* Lilljeborg, 1860

Two hermit crabs were externally infected by *C. paguri* (Plate 1.1) from a total of 2086 crabs examined (Table 1.2). The percentage of infection was 0.1%. Also from the table it can be seen that no males of *P. bernhardus* were infected, but this is probably of no special significance, given the small sample size.

Table 1.2

*Clistosaccus paguri* parasitizing *Pagurus bernhardus*.

| No. of hermit crabs examined | | No. infected | | % of infection | |
|---|---|---|---|---|---|
| ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| 1115 | 971 | 0 | 2 | 0 | 0.21 |

Family - Peltogastridae

Genus - Peltogaster

2. *Peltogaster paguri* Rathke

About 11 hermit crabs, *P. bernhardus*, were found parasitized by another species of Rhizocephala, namely *P. paguri*. The percentage of infection was around 0.53%. Table 1.3 shows that more females were infected than males by the external parasite. Each hermit crab infected was carrying only one external parasite (Plate 1.2).

Comparing the percentage of infection by *P. paguri* and *C. paguri*, more hermit crabs were infected by *P. paguri* than *C. paguri*.

One hermit crab, *P. bernhardus*, from an intertidal population was parasitized by *P. paguri* and at the same time there was an Isopod hyper-parasite infecting the *P. paguri* (see under Isopoda).

Table 1.3

*Peltogaster paguri* parasitizing *Pagurus bernhardus*.

| No. of hermit crabs examined | | No. infected | | % of infection | |
|---|---|---|---|---|---|
| ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| 1115 | 971 | 4 | 7 | 0.36 | 0.72 |

Isopoda

Family - Bopyridae

Genus - *Athelges* Hesse

3. *Athelges paguri* (Rathke) (Sars, 1899)

Table 1.1 shows that 14 hermit crabs were parasitized by *A. paguri* (Plate 1.3). The percentage of infection was 0.7%. The infection of the two sexes as seen from the table: 5 among 1,115 male hermit crabs (0.45%) and 9 among 971 female crabs (0.93%). These were all visibly parasitized externally; very small parasites may have been overlooked. These results indicated that more female than male *P. bernhardus* were infected by *A. paguri* but this is probably no more than a statistical anomaly associated with the small sample size.

Table 1.1

*Athelges paguri* parasitizing *Pagurus bernhardus*.

| No. of hermit crabs examined | | No. infected | | % of infection | |
|---|---|---|---|---|---|
| ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| 1115 | 971 | 5 | 9 | 0.45 | 0.93 |

Family - Cryptoniscidae

Genus - Liriopsis

4. *Liriopsis pygmaea* Rathke

A single specimen of this hyperparasitic isopod was discovered attached to one of the specimens of *Peltogaster paguri* attached to a specimen of *P. bernhardus* from Mumbles Head, Swansea. Although of little value as a statistic, this represents an infection rate of 9.1% of the *Peltogaster paguri* by *Liriopsis pygmaea*.(Plate 1.4).

Class - Cestoda

Order - Tetrarhynchidae Claus

Superfamily - Heteracanthides Dollfus

Family - Eutetrarhynchidae Guiart

Genus - Eutetrarhynchus Pintner

5. *Eutetrarhynchus ruficollis* (Eysenhardt, 1829)

A total of 312 hermit crabs, *Pagurus bernhardus*, were collected subtidally by trawling from Oxwich Bay on four occasions. None of these crabs were externally parasitized, but when the abdomen of these hermit crabs was dissected, internal parasites were found.

Plate 1.5 illustrates one of the internal parasites. This parasite was identified for me by the parasitologist, Dr. B.L. James of this institution (Marine Research Group, School of Biological Sciences, University College, Swansea) to whom I am most grateful.

About 48 out of the 312 hermit crabs were found to be infected internally by this parasite (Table 1.4). The infection percentage was 15.4%. When the abdomen of infected hermit crabs was dissected it was found that many of these 48 crabs were carrying more than one parasite. More females were infected than males (Table 1.4). The highest number of parasites found in any one (female) host was twelve. The photograph (Plate 1.6) of part of the dissection of this hermit shows 4 of the parasites lying amongst the diverticula of the gut. The biology of this parasite has been studied by Pierre P. Grassé (1961).

Table 1.4

*Eutetrarhynchus ruficollis* parasitizing *Pagurus bernhardus*.

| No. of hermit crabs examined | | No. infected | | % of infection | |
|---|---|---|---|---|---|
| ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| 139 | 173 | 19 | 29 | 13.7 | 16.8 |

# DISCUSSION

The findings on parasite infection of the *P. bernhardus* in this study are broadly similar to results from elsewhere.

For two of the species, this appears to be the first record for Wales, namely, *Liriopsis pygmaea* and *Eutetrarhynchus ruficollis*.

Otherwise, observed infection rates were low compared with previous records. This may be attributed to the polluted nature of the Bristol Channel.

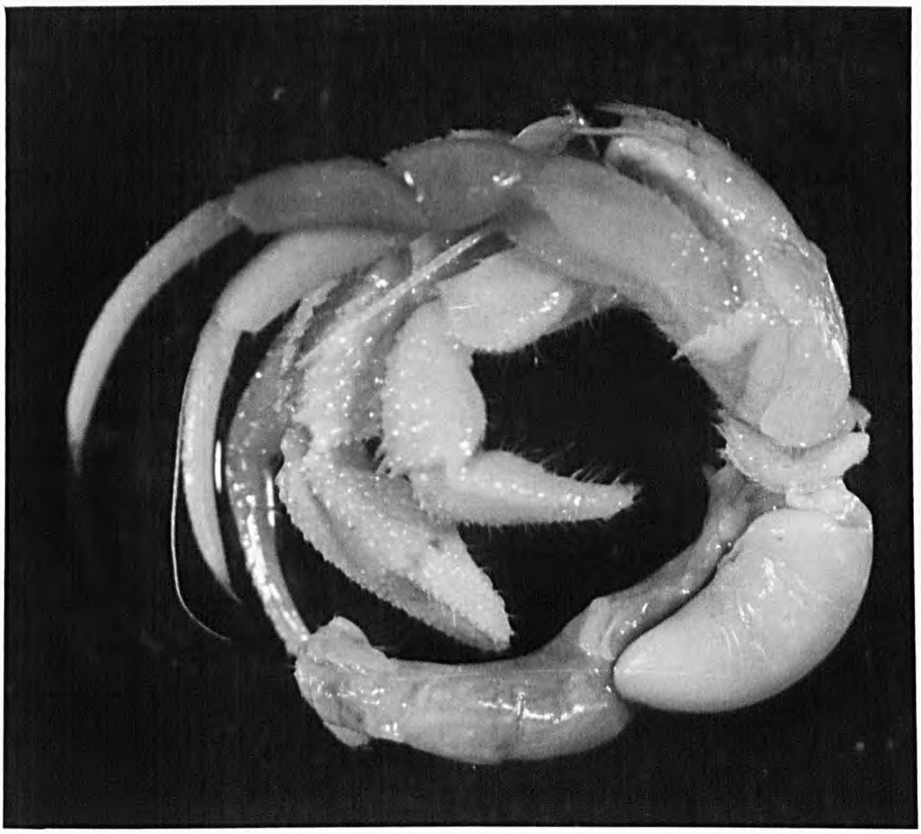


Plate 1.1

*Pagurus bernhardus* infected by one specimen of *Clistosaccus paguri*.

Plate 1.2

*Pagurus bernhardus* parasitized by one specimen of *Peltogaster paguri*.

Plate 1.3

Dorsal view of *Athelges paguri*, after removal from the abdomen of the hermit crab *Pagurus bernhardus*.

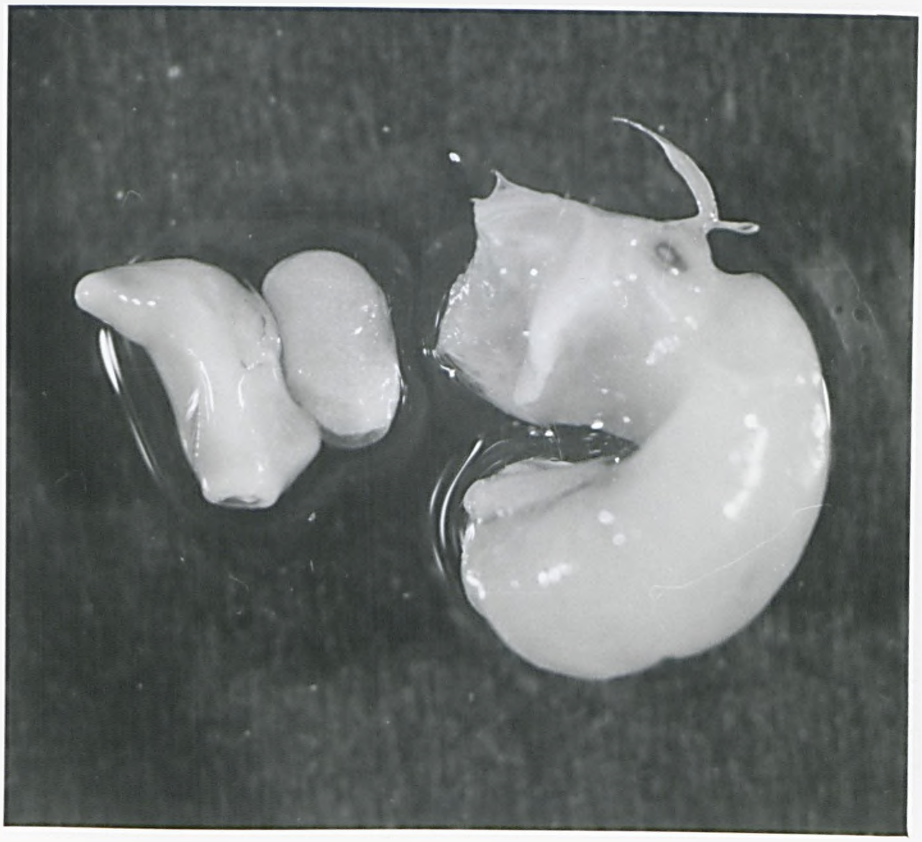


Plate 1.4

*Liriopsis pygmaea* Rathke (centre) parasitize *Peltogaster paguri* (left) a parasitic barnacle itself attached to the abdomen of the hermit crab *Pagurus bernhardus* (right). The plate also shows the fusiform shield and narrow stalk entrance into *Pagurus bernhardus* (dark orifice, top right).

Plate 1.5

*Eutetrarhynchus ruficollis* (Eysenhardt) dissected from the abdomen of the hermit crab *Pagurus bernhardus*. Removal of the membrane surrounding the parasite reveals its red neck.

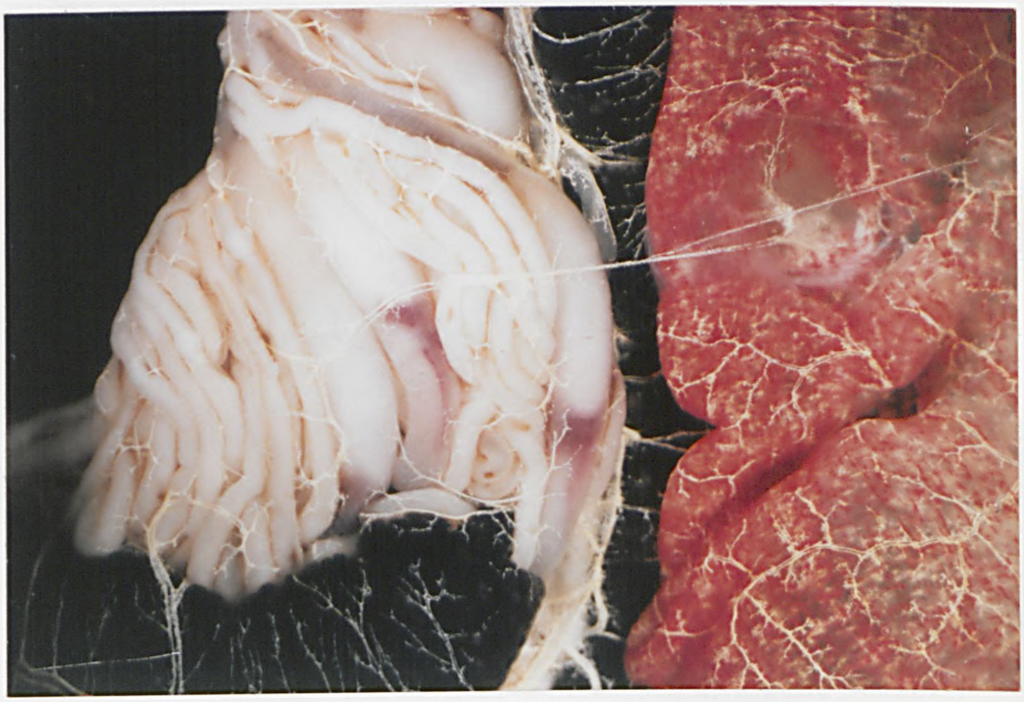


Plate 1.6

The gut of a female *Pagurus bernhardus* dissected to show 4 specimens of *Eutetrarhynchus ruficollis* lying amongst the gut diverticula.