

THE ROCK LOBSTERS (PALINURIDAE) OF SOUTH-EAST AFRICA
WITH PARTICULAR REFERENCE TO THE LIFE HISTORIES OF
PANULIRUS HOMARUS AND PALINURUS DELAGOAE.

by
Patrick F. Berry



A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Department of Animal Biology, University of Natal, Durban. December 1970.

PREFACE

"ECCE GUBERNATOR"

Vergil VI.

The legend of Palinurus, who was the helmsman of Aeneas' ship and pilot of the small fleet of Trojan ships which fled from from the sack of Troy, is to be found in Vergil's Aeneid, Books 3, 5 and 6.

While at the helm and ostensibly watching the stars, Palinurus was overcome by the god Sleep and hurled into the sea at the command of Neptune. After three days, he was washed ashore on the Lucanian coast of Italy near Sicily, only to be attacked and killed by barbarians. Not having received burial, his ghost could not cross the Styx into Hades. Aeneas, on his official visit to Hades, came across the shade of Palinurus, miserably haunting the banks of the river and being chased away by the ferryman, Charon. Palinurus begged permission to cross to the Underworld, protesting his innocence, but this was refused by the Sibyl. However, in reconciliation, the barbarians who killed him were prevailed upon by the gods to build a tomb to his memory and the Cape where he died was ordained evermore to bear his name.

The obscure Cape Punto Palinuro in Italy, where some ruins are popularly called the Tomb of Palinurus, still retains its ancient name.

More recently, the name of the luckless pilot was given to a genus of rock lobsters by Fabricius, in 1798 and from it the Family Palinuridae is derived.

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1.

INTRODUCTION

During the first half of this century, studies of rock lobsters occurring along the east coast of southern Africa were limited to taxonomy and distribution, the most notable contributions having been made by T.R.R. Stebbing and K.H. Barnard.

The possibility of commercial exploitation of Panulirus homarus off the Transkeian coast resulted in a preliminary study of the life history of this species by the South African Division of Sea Fisheries (Heydorn, 1969a). This was concentrated in Transkeian waters, but also extended into Natal and the Eastern Province.

Rapid expansion of a trawl fishery for the deep-water species Palinurus delagoae (= P. gilchristi var. natalensis and var. delagoae) during 1965 off the Natal coast and the urgent need for modification of conservatory measures for P. homarus off Natal, led to inception of the East Coast Rock Lobster Research Programme in 1967/68. The author and a technical assistant were appointed to undertake this programme, the object of which was to expand Heydorn's work on P. homarus and to initiate a study of the biology of P. delagoae. The project, which forms part of the South African National Programme for Oceanographic Research, was undertaken by the Oceanographic Research Institute, Durban, in collaboration with the Division of Sea Fisheries and the Natal Parks, Game and Fish Preservation Board.

This thesis is based on published and unpublished results of research conducted by the author from mid-1967 to 1970 and is presented in five sections. In Section 1, features of the marine environment of the south-east African region are outlined and an account is given of the species of rock lobsters occurring, with notes on the habitat preference and behaviour of each. Section 2 deals with variation in Panulirus homarus and a taxonomic study within the genus Puerulus. In Sections 3 and 4 respectively, the results of investigation of the life histories of Panulirus homarus and Palinurus delagoae are presented, while Section 5 comprises a comparative study of the spermatophoric masses and mechanisms of fertilization in southern African rock lobsters.

SECTION 1

FEATURES OF THE MARINE ENVIRONMENT OF THE SOUTH-EAST AFRICAN REGION, THE ROCK LOBSTERS OCCURRING AND NOTES ON HABITAT PREFERENCE AND BEHAVIOUR OF EACH

1.

INTRODUCTION

In the course of the East Coast Rock Lobster Project, an intensive diving programme was undertaken both in the surf zone and on offshore reefs. This was concentrated in Natal and Zululand waters, but diving in the surf zone was extended into southern Mozambique on five field trips. The programme has resulted in extension of records of distribution of several species of the shallow-water genus Panulirus and provided an excellent opportunity to make observations on habitat preference and behaviour in the five species recorded. Commercial trawlers operating down to depths of about 500m off Natal and Mozambique provided information on distribution and habitat of various deep-water rock lobsters and several new species have been recognised on the basis of material they obtained.

The region covered and referred to as the south-east African coast in the present investigation extends from Port Edward in the south, to Barra Falsa in the north, (see Fig.1). In this Section, the features of the marine environment of the region are outlined and an account is given of the rock lobsters recorded, their habitat preferences and behaviour.

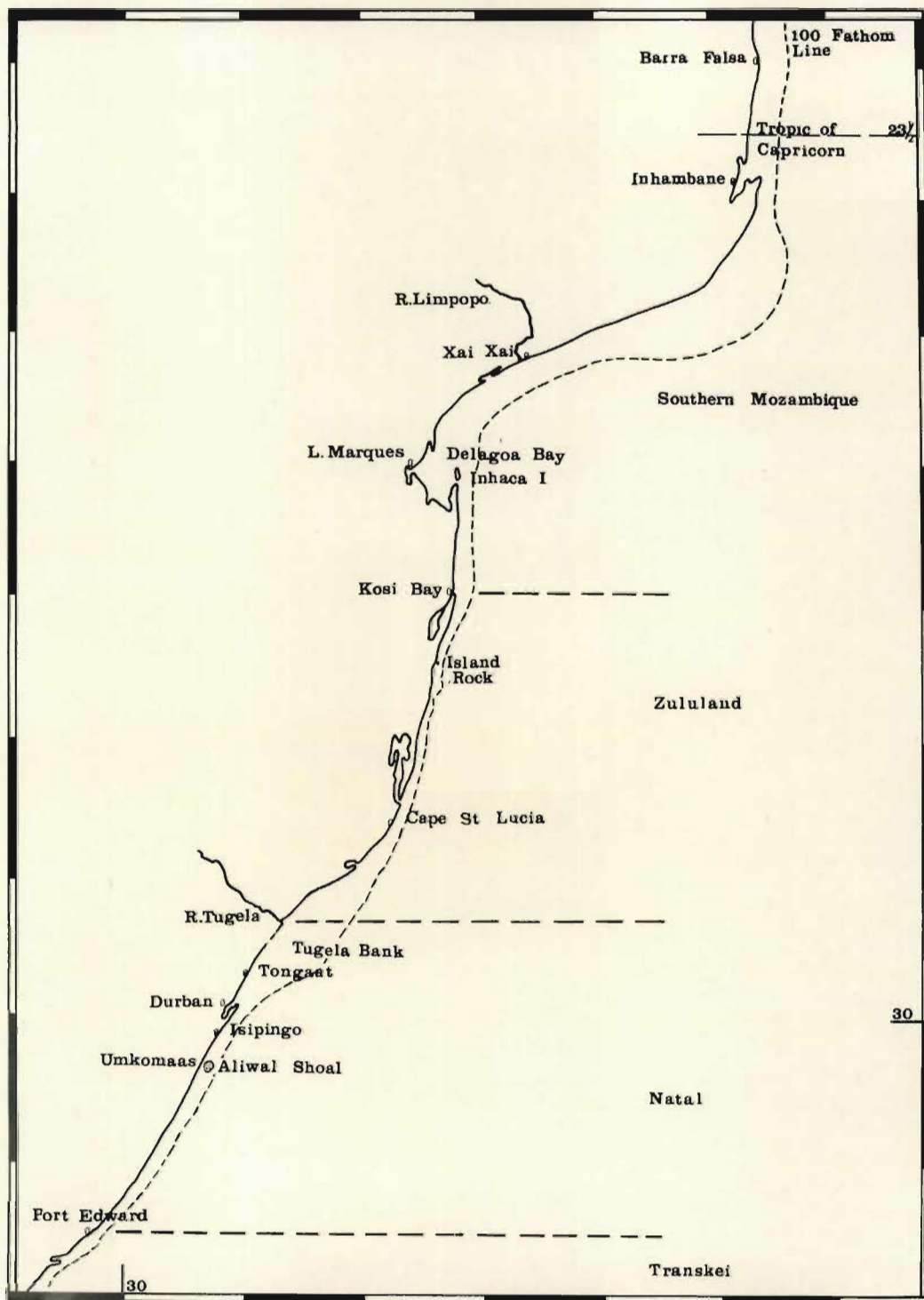


Fig. 1. Map of the south-east African region covered in the present investigation.

2. ENVIRONMENTAL FEATURES OF THE SOUTH-EAST AFRICAN REGION

Currents

The National Physical Research Laboratory and the National Institute for Water Research of the C.S.I.R. have been investigating the currents off the Natal coast for several years and the description given below of currents in the area, as well as the simplified account of water circulation in the western Indian Ocean, is based on a publication summarizing the work of these departments (Oliff, 1969). Additional information was supplied by Anderson and Oliff (pers. comm.).

Circulation of water in the western Indian Ocean is largely determined by two wind systems. The south-east trades drive surface water from the central Indian Ocean towards the African coast forming the Equatorial current, while the monsoons of the north-west Indian Ocean determine the water flow along the coast.

In the southern summer the Somali current flows south along the coast, driven by the north-east monsoon. It joins the Equatorial current, which reaches the African coast just south of the Equator, to produce the strong southward flowing Mozambique current, known as the Agulhas current off the eastern coast of South Africa.

In the southern winter, the south-west monsoon reverses the flow of the Somali current and the Equatorial current moves further north. This results in a diminished flow southwards which in turn reduces the flow of the Mozambique and Agulhas currents and according to the findings of Menaché (1963), these appear to form rather discrete circulatory systems at this time of year, with little confluence between them.

The Agulhas Current

Off the Natal coast the Agulhas current usually flows at a speed of between 1 and 2 m/second. The distance of its western edge offshore is variable, but in broad terms it may be said to follow the edge of the continental shelf. Thus off the Zululand coast, where the shelf is very narrow, it flows within a few kilometres of the shore and off the Natal coast, where the shelf reaches a maximum of 45 kilometres, the current is considerably further offshore. The western edge of the current appears to have a sinuous motion which undulates southward and generates eddies between it and the shore. As a result of these undulations, the distance of its western edge from the shore may vary over a short period. Mean surface temperature is approximately 23°C in winter and 28°C in summer (Anderson pers. comm.).

Inshore Currents

On the Natal coastal shelf, between the Agulhas current and the shore, there is a system of short term reversing currents which change direction of flow at fairly regular intervals of one to three days. This repeated reversal is thought to be due to movement of eddies generated by the sinuous motion of the western edge of the southward flowing Agulhas current. The speed of flow of these inshore currents averages between 0.1 and 0.4 m/second and despite the alternations of direction, there is a slow nett movement northwards. Temperature of the inshore water mass has a range of approximately 18 - 26°C, and is generally somewhat less than that of the Agulhas. This is attributed to upwelling of cooler subsurface water in the centre of the eddies.

The inshore current system is most pronounced in the region of the Tugela Bank between Port Durnford and Umhlanga where the shelf is widest, but it probably also occurs along the Natal South Coast. Off the northern Zululand and southern Mozambique coasts, no regular current measurements have been made, but it seems likely that a similar system of inshore currents generated by the Mozambique - Agulhas current may exist, particularly where the shelf is comparatively wide.

Northward flowing inshore currents were noticed while diving throughout these regions and MacNae (1962) comments on a northward going current and cool water at Xai Xai (Mozambique), which is probably the result of upwelling caused by eddy currents.

The Surf Zone

The following account of circulation in the surf zone is based on the work of Harris et al (1962).

In this area water movement results mainly from wave action and circulation is dependant on the angle at which waves strike the shore. When wave-approach is normal to the shore, 'cells' of circulation are set up, each being composed of longshore currents, rip currents and recycled water. The rip currents flow seaward at intervals of about 600m and are fed by longshore currents. The water of one 'cell' is discharged in approximately one hour. When wave approach is oblique to the shore the same system operates but the cells of circulation become asymmetrical.

Water temperatures taken in the surf zone during 1968 and 1969 ranged from 16.7° - 26.1°C and the mean temperature was 21.4°C . Oxygen content was usually in the region of saturation point and a mean of 6.98ml/l was obtained. Oliff (pers. comm.) found the salinity to range between approximately 35.0‰ and 35.3‰ but after flooding of rivers in midsummer, salinity dropped temporarily to about 34.0‰ in some localities.

Influence of Currents on the Coast

MacNae (1962) has discussed the relation of flora and fauna of the south-east African coast to Ocean currents and poses the problem: "..... how can the Mozambique - Agulhas current affect a shore it does not actually bathe?" He continues "it runs along the edge of the continental shelf, and between it and the shore is the cooler water of the counter current: water sufficiently cool to kill off larvae drifting in the warmer water of the stream current." The present concept of a reversing inshore system generated by eddies of the Agulhas current now offers an explanation as to how larvae may enter the inshore water where the continental shelf is wide, such as in Natal. This reversing inshore water may also form a sufficiently distinct and permanent system for local repopulation of some species with pelagic larvae to occur. Off the Zululand coast and some of the southern Mozambique coast, the continental shelf is narrow and the absence of a well developed inshore current system, as is found off Natal, may result in the Agulhas current having a more direct influence on the coast north of the Cape St. Lucia area. This might account for the more tropical fauna found in these regions as exemplified by fairly extensive coral growth.

Effects of Swell and Tidal Range

Up the east coast of southern Africa the south-west swell generated in the 'roaring forties' becomes deflected and progressively weaker, resulting in low energy swells striking the Natal, Zululand and Southern Mozambique coasts from the south-east (George et al, 1970). This expanse of coastline is subjected to continuous surf breaking on the shore, which becomes reduced in intensity northwards, in southern Mozambique.

The entire east coast of southern Africa has a semi-diurnal tidal pattern (Patullo, 1966) and the tidal range increases considerably northwards as illustrated by an increase in the mean spring range from 1.8m at Durban to 3.3m at Lourenco Marques, a distance of only 350km. It was observed in this investigation that tidal range is an environmental feature which becomes progressively more important along the southern Mozambique coast than surf action.

Influence of Topography of the Hinterland on Water Turbidity

In Natal, the interior rises to an altitude of more than 2000m over a distance of only some 200km from the coast. The rivers have been subject to flash flooding in a summer rainfall area and have scoured inland from the coastal belt, giving rise to the present day eroded topography.

As seven major and fifteen minor rivers drain into the sea along a coastline of only about 330km, it seems likely that the inshore marine environment has been subject to some degree of turbidity even before the situation was aggravated by modern agricultural practices. In Natal the width of the shelf and distance of the Agulhas current offshore does not result in quick removal of turbid water.

A somewhat different situation is found in Zululand and southern Mozambique, where there are flat, sandy, coastal plains and extensive local run-off into the sea does not occur. Moreover, fewer rivers flow into the sea over a much longer coastline than in Natal, resulting in predominantly clearer water conditions. It therefore appears that the biota occurring off Natal may be limited by the requirement of some degree of tolerance or adaptation to turbid water conditions.

A generalised summary of the main physical features which may affect the marine environment of Natal and Zululand is given in Table 1 overleaf.

Table 1. Generalised summary of the major physical features which may affect the marine environment of Natal, Zululand and southern Mozambique

Physical features	Natal (approx. 330 km)	Zululand and southern Mozambique (from Cape St. Lucia to Barra Falsa) (Approx. 1060 km)
Rivers entering sea	7 major, 15 minor	5 major, 4 minor
Inland topography	Steep, highly eroded	Flat, coastal plain with little runoff and erosion
Continental shelf	Wide (max. 45 km)	Very narrow in some regions
Inshore water	Turbid	Clear
Tidal Range	Low	High, becoming progressively higher northwards
Surf Action	Continuous, strong	Continuous becoming progressively weaker northwards

3. THE ROCK LOBSTERS RECORDED OFF THE EAST COAST
OF SOUTHERN AFRICA

The Palinuridae are currently divided into two groups, namely the 'Stridentes' and the 'Silantes', on the basis of the presence or absence of a stridulating apparatus. The palinurid list consisting of the following eight genera, recognised by George and Main (1967), is followed in this investigation:

Silantes Group: Jasus and Projasus.

Stridentes Group: Panulirus, Palinurus, Linuparus, Puerulus, Justitia and Palinustus.

All these genera are represented off the coast of Africa, south of the Tropic of Capricorn, with the exception of Justitia which occurs off Mauritius. An account of the genera and species recorded from the east coast of southern Africa is given below with notes on habitat-preference and behaviour of each.

GENUS PANULIRUS WHITE, 1847

George and Main, (1967) recognise nineteen species within this genus, in tropical and subtropical waters of the Indian, Pacific and Atlantic Oceans.

Seven of these occur in the Indian Ocean and five have been recorded off the east coast of South Africa, namely P. homarus, P. penicillatus, P. longipes, P. ornatus and P. varicolor.

Panulirus homarus

Holthuis (1946) proposed that P. bürgeri was a synonym of P. homarus and somewhat doubtfully recognised the identity of P. dasypus. P. homarus was referred to P. bürgeri by Barnard (1950) who expressed the opinion that the closely similar species P. dasypus should be recorded merely as a variety of P. bürgeri. Subsequently, as a result of examining the specimens of P. homarus and P. dasypus in the British Museum, Gordon (1953) stated "I am forced to conclude that these twelve specimens belong to a single variable species, P. bürgeri (de Haan), which according to Holthuis must now be called P. homarus (L.)". Her view has now been widely supported and in the present investigation all specimens were assigned to the single species, P. homarus. However, it is considered that the possibility that more than one species is represented in the Indian Ocean cannot be discounted and this is discussed in Section 2.

In the south-east African region P. homarus is distributed from Port Elizabeth in the south (Heydorn 1969a), at least as far north as Barra Falsa in Mozambique, where it was recorded in this investigation.

However it is most abundant off the Natal coast and reduction in numbers is evident southwards along the Transkeian coast and is particularly marked northwards along the Zululand and Mozambique coasts, where it is so scarce that adequate samples could not be collected for study of the life history.

Notes on habitat and behaviour

The following notes on habitat preference refer specifically to P. homarus occurring in Natal waters, where its abundance suggests that conditions are particularly favourable.

This species is essentially an inhabitant of reef in the surf zone and immediately beyond. It is a robust rock lobster with stout, strong legs which enable it to cling to rocks under extremely turbulent conditions. The water it inhabits is often highly turbid during the summer months, due to suspended silt carried down by rivers and even in winter some degree of turbidity is maintained by storms which periodically churn settled silt into suspension. It is also particularly tolerant of coarse sand particles, churned up and held in suspension by the surf which breaks continuously in the shallow water it inhabits. Animals were frequently observed completely buried by sand except for the frontal cephalothorax and antennae.

The optimal depth range is 1 - 5m, and vertical distribution and abundance seems to be correlated with the availability of its chief food organism, the brown mussel (Perna perna), which is most prolific in the surf zone. With increase in depth this mussel becomes less abundant and is seldom found deeper than 10m, which may account for the small numbers of P. homarus encountered below this depth. The deepest record of this species was from 35m on the Tugela Bank where three specimens were obtained in a prawn trawl. However, these had curiously elongated antennae, perhaps due to reduced light penetration and were obviously not living under typical conditions.

P. homarus is essentially a nocturnal species and during daylight it inhabits cracks, crevices and overhangs in reef. Its habitat in the surf zone is subject to substantial shifts of sand with the result that reef regularly becomes covered, only to have the sand scoured away a few days later. This has a marked effect on the local concentration of rock lobsters and as cover becomes reduced, shelters containing dense aggregations occur, whereas when sand has been scoured away the animals are more dispersed, though still gregarious.

During the day the animals may usually be observed with their antennae protruding from their shelters.

The antennae are directed towards any moving object and if danger threatens, the abdomen and tail fan are held extended, ready to propel the animal rapidly into cover. Fish and other rock lobsters may be warded off with the antennae whose armature of forward directed spines acts as a deterrent. When approached with a gloved hand, P. homarus remains at the edge of its shelter and tries to touch it with outstretched antennae. On contact with the glove the animal darts backwards with a few flaps of its abdomen and withdraws into a closely fitting recess with its abdomen folded beneath it. If the floor of the shelter is sandy, clouds of sand are shot out by flapping of the tail fan, temporarily obscuring the animal as it braces itself against the roof of its shelter with its legs. (Similar behaviour has been described in Jasus lalandii by Heydorn (1969b), who suggests that the cloud of murkiness acts as a deterrent to predators). Attempts to dislodge the animal by gripping the antennae or legs may result in autospasy or autotomy of these appendages. Meanwhile loud stridulation is emitted which causes all other rock lobsters in the vicinity to withdraw into their shelters. Stridulation was never heard on any other occasion.

On being confronted by an octopus which appears to be its chief natural predator, P. homarus reacts completely differently, and instead of withdrawing into cover it comes out and stands ready to abandon its shelter.

If the octopus advances the animal immediately takes flight by backward propulsion with its tail. This reaction is obviously due to the fact that a rock lobster is easy prey for an octopus when trapped in its shelter. The method of using a dead octopus tied to a stick to flush P. homarus out of inaccessible shelters was used with great effect in this investigation.

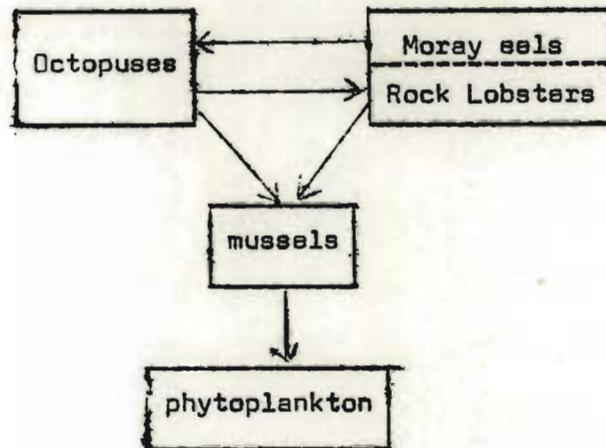
Moray eels (Lycodontus sp.) are frequently found living in association with P. homarus and it is a common sight to see a specimen of P. homarus at the mouth of its shelter with an eel's head protruding from beneath it, (see Fig. 2). Any attempts by a diver to disturb the rock lobsters in the vicinity resulted in immediate attack by the eel. The method of using an octopus to flush out rock lobsters has been mentioned above and it was noticed that if a moray was present, it immediately attacked the octopus and devoured it. That eels prey on octopuses naturally was substantiated by several instances where eels were found feeding on dead octopuses which they had obviously killed. Moray eels are attracted by the stridulation of rock lobsters and even if not actually present in a shelter with them, may appear and attack an intruder.



Fig 2. Moray eel and rock lobster sharing the same shelter on "Limestone Reef".

Octopus sp. appears to be the chief natural predator on P. homarus and on several occasions octopuses were found devouring rock lobsters which they had presumably captured. Judging by the piles of empty shells outside their shelters, octopuses also seem to feed on substantial quantities of the mussel P. perna and as this is the chief food organism of P. homarus, some degree of competition must exist for food.

Predation between Lycodontus sp., Octopus sp., P. homarus and P. perna is summarised diagrammatically below.



It is suggested that further study would probably show that this forms the basis of a self-regulatory situation which maintains a numerical balance between mussels, rock lobsters, octopuses and eels.

Panulirus penicillatus

According to George (1968), P. penicillatus is the most widely distributed member of the genus and occupies 240° of longitude, from the Red Sea (30°E) to the Galapagos Islands (90°W).

Barnard recorded a specimen from Mozambique Island, but had no records from the coast of South Africa.

During the present investigation only three immature specimens were collected in Natal over a three year period, but a further twenty-one were obtained from the Zululand coast and two from the Mozambique coast, the majority of which were sexually mature and breeding.

Notes on habitat and behaviour

P. penicillatus was most abundant at a locality off northern Zululand known as Island Rock, where it was the only species occurring. This is a large mussel covered outcrop measuring approximately 100m x 25m with a flattish top, but which falls away steeply into deep water on the seaward side. It is situated about 180m from the shore and there is a deep channel and very strong current running between it and the beach. It is almost entirely covered at high tide, but its top becomes exposed at low tide and P. penicillatus can be caught in shallow gullies and hollows in the walls of pools left as the tide recedes. This species was also occasionally found living on reef in the surf zone at various other localities on the northern Zululand and southern Mozambique coasts, within a few metres of P. homarus. Occurrence of both these species living in close proximity in the surf zone has also been recorded in Ceylon by De Bruin (1962) and on the south-east coast of Madagascar by Charbonnier and Crosnier (1961).

In this investigation P. penicillatus was found to occur near the seaward edge of the reef in holes and cracks in the roofs of large inaccessible caves at a depth of 1 - 4m. The floors of these caves were either rocky or covered with rounded pebbles and it was never found near sandy bottoms. It thus appears that P. penicillatus occupies a habitat where suspended sand does not occur in quantities, whereas P. homarus occurs where it may be subjected to a considerable amount of sand in suspension. Examination of the stomach contents of P. penicillatus showed that mussels were the predominant food organism.

P. penicillatus has extremely robust legs which are an adaptation for clinging to the rock in turbulent water. As mentioned by George (1968) it does not retreat from a gloved hand but clings to the rock and large specimens are difficult to pull off. The olive-black coloration also provides excellent camouflage in the dark recesses this species inhabits and it is easily overlooked if the protruding antennae are not seen.

Panulirus longipes longipes

Barnard (1950) referred to this species as P. japonicus and had a single record from Mozambique but none from South Africa. In their revision of the P. japonicus group, George and Holthuis (1965) have shown that Barnard's specimen was probably the spotted legged variety, P. longipes longipes.

In the present investigation this species has been found in various localities off the Zululand and Natal coasts and while it is by no means common, it is the second most abundant species in the region next to P. homarus. Twenty-five specimens, all of the spotted legged variety were collected, but P. longipes proved difficult to capture and many more were seen.

Notes on habitat and behaviour

George, (1968) commented on the wide variety of environmental conditions and depth range at which P. longipes occurs and this has been substantiated in the present investigation. In Natal, this species was most abundant on offshore reef, and particularly the Aliwal Shoal, where it was recorded at a depth of 18m in clear Agulhas current water. However, it was also obtained in the turbid conditions of Durban Harbour and seven specimens were recorded at a depth of only 1m from the Isipingo tidal swimming pool.

Off the Zululand coast, breeding specimens were obtained on offshore coral covered reef, in clear water at a depth of 12m. In addition, nine specimens (including ovigerous females) were found at a depth of 1m in a deep cave, only about 10m from the shore. In this case they were sheltered from direct wave action and the habitat was similar to that in the Isipingo tidal pool.

P. longipes was found to show preference for deep, inaccessible caves, making capture most difficult. An interesting morphological feature of this species is the large size of the cornea when compared with true surf dwelling species such as P. homarus and this may be an adaptation to living in deeper water or else to reduced light intensity in the caves it inhabits. From the observations made, it appears that P. longipes prefers clear water but can tolerate slightly turbid conditions, and where it occurs in the surf zone it inhabits protected areas not subjected to wave action. That it is not a true surf inhabiting species is substantiated by its less robust build and thinner legs than either P. homarus or P. pencillatus.

Panulirus ornatus

P. ornatus is the predominant rock lobster in East Africa where it constitutes the bulk of the commercial catch (Hall, 1960). Barnard (1950) recorded it from Delagoa Bay and also from Durban Bay (probably Durban Harbour), where it was found to be rare in this investigation but the predominant rock lobster occurring. The only other record of this species from South Africa is a single specimen caught off Tongaat.

In Mozambique P. ornatus was found in Delagoa Bay and Inhambane Bay.

Notes on habitat

In Durban Harbour juveniles specimens of P. ornatus were found living gregariously amongst rock piles at a depth of 1 - 4m, whereas adults were found sheltering singly or in pairs on a muddy substratum between large concrete blocks at a depth of 5 - 8m. No evidence of breeding was obtained and the origin of this population is puzzling. However it is interesting to note that in May and June of 1968 and in May 1969, large numbers of puerulus larvae of P. ornatus were found on the offshore shark nets at Durban.

In Delagoa Bay, Mozambique, five breeding specimens of P. ornatus were found on a fine sandy bottom, sheltering under coral on the reef off the west side of Inhaca Island at a depth of 3m. Another specimen from Delagoa Bay was obtained from a fish kraal on muddy, Cymodocea covered flats outside a mangrove swamp. No sign of rock or coral for shelter was evident and according to fishermen they are frequently captured in these kraals off the mangrove-lined south end of Delagoa Bay. Specimens obtained from Inhambane Bay were also captured in fish kraals and this species was never encountered by the author while diving off the shore in Mozambique.

George (1968) noted that P. ornatus is tolerant of fairly turbid conditions and in fact appears to prefer them. This is confirmed by its occurrence in Delagoa Bay, Inhambane Bay and Durban Harbour where turbidity is caused by fine, suspended organic material, much of which is washed out of mangrove swamps at low tide. However the striking feature of the occurrence of this species in these three localities and its apparent absence offshore, is its preference for non-turbulent conditions.

Panulirus versicolor

P. versicolor was recorded by Barnard (1950) from Durban Bay and Port St. Johns. This investigation has shown that the adults are the rarest species of Panulirus occurring on the east coast of South Africa and only two specimens were captured, both on the outside of Durban Harbour's North Pier. Surprisingly, juveniles with a carapace length ranging between 7.0mm and 25.0mm are common, particularly on wrecks or rock faces where they live in closely fitting holes with their conspicuous white antennae protruding. It appears that after attaining a certain size, environmental conditions are not suitable, moreover specimens kept in captivity did not survive for long after attaining a carapace length of about 25mm.

In Mozambique, one adult specimen was collected (although others were seen) from the estuary mouth at Barra Falsa. The animals were living on the undercut bank of the deep channel leading from the sea into the estuary. The bank was composed of compacted lagoonal sediment which was breaking off in large clods and the rock lobsters were found in shelters amongst these clods at a depth of about 3m. The channel was about 4m deep and on the incoming tide clear sea water flowed into the channel at a considerable speed. On the outgoing tide the water tended to carry organic matter resulting in more turbid water conditions.

Adult P. versicolor were also found at Ponta Torres on Inhaca Island at a depth of 6m where it inhabits a steep rocky slope on the edge of a channel. Extremely fast currents sweep along this channel which connects Delagoa Bay with the Indian Ocean and at the outgoing tide the water may be fairly turbid.

GENUS PALINURUS FABRICIUS, 1798

Four extant species of Palinurus are currently recognised, three of which occur in the eastern Atlantic, namely P. elephas, P. mauritanicus and P. charlstoni. The fourth species, P. gilchristi was originally described from False Bay in the Cape (Stebbing 1902), but Barnard (1926) recognised two further varieties of this species from Mozambique and Natal i.e. var. delagoae and var. natalensis.

However, in this investigation it has been found that specimens from both Mozambique and Natal showed variation in the criteria on which Barnard distinguished his varieties, and specimens which could be assigned to either var. delagoae or natalensis were obtained from both regions.

In a taxonomic revision of the genus Palinurus in the Indian Ocean currently being undertaken by the present author and Dr. R.W. George, two distinct species are recognised, namely P. gilchristi occurring off the south coast of the Cape and P. delagoae from off Mozambique and Natal. It should be noted that Barnard (1926) himself commented that "The examination of a large amount of material might show that natalensis should be merged into delagoae, and the latter raised to specific rank".

For the purpose of this thesis the species of Palinurus occurring off Mozambique and Natal has therefore been referred to as P. delagoae.

The following material was examined in this study:

Natal and Mozambique

- (1) Several thousand specimens from various localities obtained in the course of an investigation of the life history of this species, represented by O.R.I. Specimens no. B1 - B10.

- (2) S.A. Museum no. A6811, off Delagoa Bay.

Cape

- (1) S.A. Museum no. A970 - A980, off False Bay, Nanguas Pk., Fish Point Lighthouse, Cape Infanta, Cradock Bay and Mossel Bay fishing grounds.
- (2) D.R.I. specimens no. A1 and A2, off Skoenmakers Kop, Algoa Bay and False Bay.

Palinurus delagoae

Distribution, notes on habitat and behaviour

Information on the distribution of P. delagoae was obtained in interviews with trawler skippers and from trawling by the Oceanographic Research Institute's research vessel, DAVID DAVIES. This species has been recorded from various localities between Moma (at. 17°S) in northern Mozambique and Umkomaas in Natal. Knowledge of its distribution is limited to trawlable areas, but it appears to extend continuously over this range, on trawlable grounds. South African based vessels have not trawled north of Moma and its extreme northern most limit of distribution is unknown. In the south, no specimens of Palinurus have been obtained between Umkomaas and Port Elizabeth and this region appears to separate P. delagoae and P. qilchristi.

P. delagoae inhabits the edge of the continental shelf where the temperature ranges between about 12 - 14°C. In northern Mozambique waters its optimum depth is about 300m, whereas in Natal it is about 260m. Sexually mature specimens have been recorded over a depth range of 180 - 324m. However juveniles are often trawled somewhat deeper with Nephrops, at depths of down to 400m.

P. delagoae occurs on extensive open areas devoid of rocks on a substratum consisting of mud with a high organic content and varying quantities of sand or coral fragments. It appears to be gregarious and migratory so that at times, presumably during migrations, such dense local aggregations occur that a single trawler may fill its net with a 'jackpot' of tons of rock lobsters, whereas others working alongside catch nothing. Such exceptionally large catches are usually made during the breeding season towards the shallow extreme of the depth range. As they consist predominantly of ovigerous females this may indicate a movement towards the edge of the Agulhas current before hatching of the larvae.

Observations on captive specimens of P. delagoae kept at the Oceanographic Research Institute, Durban, help to substantiate the impressions of the habits of this species gained from trawling.

The animals were very active walkers and remained on the open floor of the tank avoiding all obstructions. When confronted by rocks they showed no inclination to take shelter but climbed over them in a somewhat ungainly manner until the highest point was reached, where they remained perched, sometimes one on top of another. When disturbed they made no attempt to shelter under rocks and formed a tightly packed group, each animals abdomen protected by the cephalothorax of the one behind it. The antennae were directed upwards thus giving protection from attack from above. This behaviour is not unlike the single - file migrations of Panulirus argus recorded by Herrnkind (1969) and must be an important means of protection on the exposed areas P. delaquae inhabits.

Palinurus gilchristi

Distribution, notes on habitat and behaviour

P. gilchristi has been recorded off the south coast of the Cape in False Bay and at various localities on the Agulhas Bank as far east as Port Elizabeth. It is rare however, and does not support a commercial fishery. Although this species does not occur on the east coast, an account of its habitat and behaviour is given, to illustrate the differences between it and P. delaquae.

In False Bay P. gilchristi has been captured in traps by the Division of Sea Fisheries on Rocky Bank and according to Day et al (1970) occurs at a depth of 55 - 102m. On the Agulhas Bank specimens are occasionally caught by trawlers fishing for soles at a depth of about 70m and specimens have also been obtained from the stomach of a Cape Fur Seal. On the basis of the data available the depth range of this species cannot be adequately established, but the indications are that it is considerably shallower than that of P. delagoae.

It was noticed that specimens of P. gilchristi in the East London Aquarium shelter in crevices in rocks and prevent themselves from being withdrawn by bracing against the roof of the crevice with their legs in the manner typical of Jasus lalandii or P. homarus. This behaviour, the fact that they occur on Rocky Bank and are not trawled in quantities suggests that P. gilchristi may inhabit rocky areas.

GENUS PROJASUS GEORGE AND GRINDLEY, 1964

A single male specimen of Projasus parkeri (carapace length 53mm) was trawled at a depth of 407m on the Nephrops fishing ground off the Durban Bluff. As the previous records are from off East London, this extends the known limits of distribution northwards to approximately 30°S.

However, as no other specimens have been recorded from Natal waters despite intensive trawling, this record probably reflects an extreme fringe of distribution.

GENUS PALINUSTUS A. MILNE-EDWARDS, 1880

There are three named species of Palinustus, including P. mossambicus which was described by Barnard (1926) from Mozambique (25°S, 33° 10'E). However, this position must be incorrect, being on land, and as no further specimens have been obtained, despite intensive trawling off Mozambique, the distribution of this species remains unknown.

GENUS PUERULUS ORTMAN, 1897

Numerous specimens of the genus Puerulus have been obtained from commercial trawlers operating in southern Mozambique waters and two specimens were trawled off Durban. Two species are represented in this material and have been identified as P. angulatus (Bate) and P. carinatus Borradaile. As P. carinatus was only previously known from a single specimen, briefly described and subsequently lost, a neotype has been selected and described (Berry 1969b). In addition, the differences between P. carinatus and P. angulatus, which were synonymised by Holthuis (1966), have been enumerated in the former publication which forms the basis of the second half of Section 2.

Notes on habitat

All the specimens were obtained at a depth range of 280 - 320m by trawlers fishing for Palinurus delagoae. Although an overlapping distribution is indicated, it should be noted that this is the lower extreme of the depth range of this species and the optimal depth for Puerulus appears to be somewhat deeper.

Data on substratum are lacking other than that the specimens were trawled on soft mud containing some sand particles.

Although breeding populations of both P. anquilatus and P. carinatus were found in close proximity, the two species were never obtained together in the same trawl. Subsequent to the material initially described (Berry 1969b), many more specimens of P. anquilatus have been trawled further north along the Mozambique coast, particularly off Bazaruto Island, whereas only four more specimens of P. carinatus have been obtained from north-east of Inhaca Island at a depth of 290m. P. anquilatus therefore appears to be the more widespread and more abundant species of this genus off the east coast of southern Africa and P. carinatus, which seems rare in this area, is possibly a more tropical species as indicated by Borradaile's specimen from the Saya de Malha Bank.

GENUS LINUPARUS WHITE, 1847

There are two named species of Linuparus: L. trigonus, originally described from Japan and L. sordidus from the South China Sea. Barnard (1950) recorded a specimen taken at 320m off Inhambane, Mozambique which he assigned to L. trigonus. However, George and Main (1967) suggested that the east African and north-eastern Australian specimens may be distinct species, in which case four geographically isolated species might exist. The south-east African species of Linuparus does in fact differ from the descriptions of L. trigonus and L. sordidus and its status is being investigated in a revision of the genus currently being undertaken by Dr. R.W. George and the present author.

A total of twenty-two specimens were obtained from the following localities: North of Bazaruto Island (approx. $21^{\circ} 30'S$ and $35^{\circ} 40'E$, depth 234m), off the Limpopo (approx. $25^{\circ} 20'S$, $33^{\circ} 55'E$, depth 272m), "the corner" (approx. $25^{\circ} 50'S$, $34^{\circ} 35'E$, depth 234 - 243m), off Tongaat (approx. $29^{\circ} 40'S$, $31^{\circ} E$, depth 288 and 298m) and S.E. of the Bluff, Durban (approx. $30^{\circ} 15'S$, $31^{\circ} 10'E$, depth 324m).

Notes on habitat

Single specimens of Linuparus sp. were occasionally obtained in trawls for Palinurus delagoae and it appeared to be more abundant in Mozambique than in Natal.

Its rarity in trawls suggests that it was probably not obtained in its typical habitat which may well be rocky areas, avoided by trawlers. This view is substantiated by the fact that no ovigerous females were obtained and several reliable fishermen report that they have never seen one. Linuparus sp. has never been obtained deeper than 324m and appears to be totally absent on the Nephrops and prawn trawling grounds (i.e. deeper than 350m), whereas the shallowest record was at 234m.

4.

DISCUSSION

Dispersal in rock lobsters is achieved by phyllosoma larvae which have a relatively long pelagic life, and it is particularly necessary to distinguish between distributional limits of breeding populations and fringe distributions where struggling, non-breeding populations may occur in habitats which are far from optimal. This is evident off the east coast of southern Africa where distributional limits of rock lobsters are greatly extended by the southward flowing Mozambique - Agulhas currents and of the five species of Panulirus occurring, four were recorded breeding off southern Mozambique, three off Zululand and one off Natal, (see Table 2). It has been noted previously that the inshore marine environment of the Zululand coast shows more similarity to that of the southern Mozambique coast than that of the Natal coast.

From the present observations on rock lobsters it is suggested that a more generalized ecological study may show that there is a transition from a more tropical fauna to the typical fauna of the Natal coast in the region of Cape St. Lucia, on the Zululand coast.

On the basis of abundance and records of breeding of the deep water palinurid species obtained in this investigation, it appears that P. angulatus and Linuparus sp. have a more tropical distribution than P. delagoae. The overlap in depth distribution of these three genera is possibly associated with adaptation to specific types of substratum, as over the depth range they inhabit the substratum changes progressively from being predominantly sand of terrestrial origin, with a low organic content in the shallower extreme, to mud with a high organic content of marine origin in the lower depth range. Occurrence of P. angulatus in the deepest extreme of the depth range inhabited by P. delagoae therefore indicates a possible preference for a softer more muddy substratum than P. delagoae. The indications are that Linuparus sp. inhabits a muddy substratum in the vicinity of rocks which would account for its rarity in trawls on clear grounds from whence P. angulatus and P. delagoae are obtained.

Ecological separation of the five species of Panulirus recorded off the east coast of southern Africa is considered below in terms of turbidity, temperature, depth and tidal range and is summarised in Table 2.

Occurrence of P. homarus under somewhat different environmental conditions off the Natal and Zululand coasts enables the type of turbid water it inhabits to be more critically assessed. In Natal turbidity is caused by sand held in suspension in the surf zone and also by suspended silt carried into the sea by flooding rivers. This differs from the situation off northern Zululand and much of the southern Mozambique coast, where there is little or no suspended silt originating from rivers, and turbid conditions are restricted to churning sand in the surf zone. The extension of a breeding population of P. homarus into Zululand and southern Mozambique therefore suggests that this species is adapted primarily to turbidity caused by sand in the surf zone.

In the comparatively silt-free water of the Zululand and southern Mozambique regions, another surf inhabiting species, P. penicillatus, displaces P. homarus in some areas where suspended sand is absent. However, in Natal P. penicillatus is only known by a few specimens and the absence of a breeding population, even in areas where there is no sand movement, suggests that this species is unable to tolerate turbidity caused by silt.

Thus it appears that clear water is a prerequisite for this species, which is in agreement with the views of George (1968), who considers that P. penicillatus is found in optimal conditions around oceanic islands.

Distribution and abundance of P. homarus off the east coast of Africa indicates that this species occurs optimally in subtropical water with a temperature below 24°C. However, perhaps a factor more important than temperature in determining its distribution may be tidal range. Off Natal and Pondoland where P. homarus is abundant, tidal range is low and the surf zone it inhabits remains virtually localised at all tides. This is not the case in the lower latitudes of East Africa where tidal range is high, resulting in some distance between high and low water marks and reduction of a localised, permanent surf zone. This reduction of suitable habitat is probably a major factor contributing to the falloff in abundance of P. homarus observed in the lower latitudes of Mozambique.

On first consideration, environmental factors separating P. longipes and P. ornatus are difficult to distinguish as both species are commonest in tropical waters and are usually found in association with madreporine corals. However, in this study P. ornatus was only found in non-turbulent conditions where the water was rather turbid and clouded with organic sediment.

This species might therefore be expected to inhabit the inside of coral reefs and P. longipes the outside, where clearer more turbulent conditions occur.

On the basis of the small numbers of adult P. versicolor obtained and absence of a breeding population, it is not possible to characterise the optimal habitat of this species, other than that in the localities where it was found, conditions were rather turbulent and invariably turbid due to fine suspended organic matter. This tolerance of turbidity and turbulence by P. versicolor has been noted by Postel (1966) and it is therefore suggested that it may occupy a habitat too turbulent for P. ornatus and too turbid for P. longipes in the tropical regions where these three species are abundant.

In considering the depth distribution of the five Panulirus species summarised in Table 2, the influence of tidal range seems to be a relevant factor. In this investigation P. penicillatus and P. homarus have been found to be shallow water species living optimally in areas subjected to substantial water movement caused by continuous wave action. Occurrence of such a habitat appears to be best developed in regions of low tidal range such as the Natal coast in the case of P. homarus and oceanic islands in the case of P. penicillatus.

Occurrence of P. longipes, P. versicolor and P. ornatus at a greater depth might therefore be associated with the high tidal range where these species are abundant.

The above discussion has dealt only with possible factors relating to ecological separation of the adults of various species of rock lobsters. As yet information on ecology and behaviour of the larvae of these species is virtually non-existent, but it is obvious that the relative abundance and distribution of adults is dependant on adaptation of the larval life of each species to specific hydrological conditions, and current systems in particular. Investigation of phyllosoma larvae in relation to these factors is therefore particularly necessary before the affinities between populations of rock lobsters in the Indian Ocean can be fully understood.

Table 2. Summary of some environmental factors which appear to constitute the optimal habitat of the five species of Panulirus occurring off south-east Africa, together with their southernmost breeding and distributional range recorded.

Species	Depth (m)	Temp.	Water Clarity	Water Movement	Tidal Range	Southernmost Distribution	
						Breeding	Non-breeding
<u>P. homarus</u>	1-5(optimal) 1-36	mean 21°C 17°-24°C	turbid	continuous surf	low	Quoha Mouth, Transkei	Port Elizabeth E. Province
<u>P. penicillatus</u>	1-4 (1-10, Fourmanoir et al, 1960)	23° - 25°C	clear	surf	low	Island Rock, N. Zululand	Umhlanga Natal
<u>P. longipes</u>	1-18	23° - 25°C	clear	no direct surf; some turbulence	high	Sordwana Bay N. Zululand	Aliwal Shoal Natal
<u>P. ornatus</u>	1-8 (1 ->25 Postel, 1964)	? >25°C	turbid	calm	high	Delagoa Bay, Mozambique	Durban Harbour
<u>P. versicolor</u>	1-16 with optimal at 4-12 (Postel, 1964)	? > 25°C	turbid/clear	strong current	high	nil	Port St. Johns, Transkei

SECTION 2

VARIATION IN PANULIRUS HOMARUS AND A TAXONOMIC
STUDY WITHIN THE GENUS PUERULUS

1.

VARIATION IN PANULIRUS HOMARUS

On the Transkeian coast of South Africa, Heydorn (1969a) found that rock lobsters fitting Barnard's description of "P. burgeri" predominated, but a specimen clearly fitting the description of "P. dasypus" as well as two specimens intermediate between these two "species" were also found. In the present investigation of P. homarus in Natal waters, the population sampled was also found to consist of specimens which could be assigned to these three categories. However, in order to initially avoid any taxonomic or evolutionary implications in the following text they have been referred to as 'forms'.

The predominant form (see Figs. 1 and 2) occurring in Natal, Zululand and southern Mozambique has no median interruptions in the abdominal transverse grooves which bear particularly well developed, rounded squamae of fairly uniform size along the posterior margins. In some specimens there may be a number of smaller, poorly defined squamae immediately behind these large ones and there may also be a few present on the posterior margins of the transverse grooves, but these are variable features.

The overall colour is red which becomes slightly browner and darker as the individual approaches a moult. On the basis of the well developed abdominal squamae, this will be referred to as the 'megasculpta' form, following the terminology used by Gordon (1953).

Quite distinct from the megasculpta form, are green-coloured specimens in which the squamae on the abdominal grooves range from being at best poorly developed, tending to be truncate and irregular in size, to so minute as to be virtually indistinguishable (see Figs. 3 and 4). When present these are best developed laterally and become reduced in size and usually disappear medianly, where the abdominal grooves are often interrupted. These median interruptions are normally present in at least one segment and sometimes in up to four, although in occasional specimens where the small squamae persist medianly, interruptions may be indistinct or absent in all segments. These specimens, which will be termed the "microsculpta" form, are always bright olive-green in colour and the ones with well defined median interruptions conform to what was previously regarded as a distinct species, namely P. dasypus.

These two forms are easily distinguishable because of the linking of green and red colouration with microsculpta and megasculpta morphology respectively.



Fig. 1. Typical example of the megasculpta form of P. homarus from Natal.



Fig. 2. Well developed squamae on the abdominal transverse grooves of the megasculpta form.



Fig. 3. Typical example of the microsculpta form of *P. homarus* from Natal.



Fig. 4. Minute squamæ on the abdominal transverse grooves of the microsculpta form. Note the median interruptions of the groove in segments 2 and 3.



Fig. 5. Example of a specimen intermediate between the megasculpta and microsculpta forms in colour and degree of development of the squamae on the abdominal transverse grooves.



Fig. 6. Intermediate specimen between the megasculpta and microsculpta forms showing poorly developed squamae on the transverse abdominal grooves.

No red microsculpta or green megasculpta specimens were found in over 5,800 specimens examined but there was a third, extremely small category of specimens which could not be assigned to either the megasculpta or microsculpta forms, being intermediate both in colouring and degree of development of the abdominal squamae (see Figs 5 and 6). During the course of two years sampling only 6 out of a sample of 5,800 specimens from Natal, 3 out of a sample of 120 specimens from Zululand and 4 out of a sample of 51 specimens from Mozambique, obviously bridged the gap between the red megasculpta and green microsculpta forms. Although this classification of specimens into separate categories is artificial and tends to be subjective, it was considered that the megasculpta and microsculpta forms were sufficiently distinct to enable valid comparison to be made between frequencies of each in samples from Natal, Zululand and Mozambique, (see Table 1) and for the frequencies to be determined on a monthly basis in Natal, (see Table 2).

These two tables show a very constant, low proportion of the microsculpta form in Natal waters, but in Zululand and Mozambique a somewhat higher frequency is evident.

Using a chi-squared test, it was found that the frequencies of the megasculpta and microsculpta forms in samples from Zululand did not differ significantly from those in samples from Mozambique. However, a highly significant difference was evident between the frequencies of the two forms from Natal and from Zululand/Mozambique combined.

Table 1. The frequency of specimens with megasculpta, microsculpta and intermediate morphology and colouration in the total samples from Natal, Zululand and Mozambique.

Locality	Megasculpta form		Intermediate specimens		Microsculpta form		Total
	No	%	No	%	No	%	
Natal	5832	98.3	6	0.1	92	1.6	5930
Zululand	106	88.3	3	2.5	11	9.2	120
Mozambique	63	79.7	4	5.1	12	15.2	79

A comparison of counts of the number of joints in the exopod flagella of samples of megasculpta and microsculpta specimens from south-east Africa with counts from East Aden (George, 1964b) and Ceylon (De Bruin, 1962) is presented in Table 3. These authors noted variation in counts on the left and right flagella of single specimens which was also found in the present investigation.

Table 2. Monthly frequency of the microsculpta form in samples from Natal.

Month	1968 - 1969			1969 - 1970		
	Numbers of microsculpta form	Numbers of megasculpta form	Percentage of microsculpta form	Numbers of microsculpta form	Numbers of megasculpta form	Percentage of microsculpta form
Feb.	3	282	1.1	4	176	2.3
March	2	159	1.3	7	300	2.3
April	1	122	0.8	3	182	1.6
May	0	155	0	5	276	1.8
June	4	154	2.5	6	165	3.6
July	1	180	0.5	4	259	1.5
Aug.	2	352	0.6	6	259	2.3
Sept.	8	251	3.2	3	214	1.4
Oct.	7	315	2.2	7	325	2.1
Nov.	5	458	1.1	3	303	1.0
Dec.	6	318	1.9	1	261	0.3
Jan.	2	184	1.1	2	274	0.7

Table 3. Number of joints in the flagellum of the exopod of the third maxilliped in samples of Panulirus homarus from South-east Africa, Aden and Ceylon.

No. of joints	South-east Africa				E. Aden (George 1964)		Ceylon (De Bruin 1962)	
	megasculpta		microsculpta		megasculpta		microsculpta	
	No.	%	No.	%	No.	%	No.	%
0	271	86	102	76	74	35	101	43
1	36	11	27	20	29	14	98	42
2	7	2	0	0	50	24	19	8
3	1	0.3	5	3.7	27	13	6	3
4	0	0	0	0	15	7	6	3
5	1	0.3	0	0	11	5	3	1.3
6	0	0	1	0.7	3	1.4	3	1.3
7	0	0	0	0	1	0.5	0	0
Totals	316		135		210		236	

The sample of the megasculpta form from south-east Africa shows considerable reduction in the number of joints compared with the samples from Aden and Ceylon. Counts on the sample of the microsculpta form from south-east Africa are also considerably lower than in the Aden or Ceylon samples, but show a tendency to be somewhat higher than the south-east African megasculpta sample. However due to the small size of the south-east African microsculpta sample, no meaningful comparison seems possible with samples from the other localities.

World Distribution and Possible Geographical Variation

The world distribution of P. homarus is presented in Table 4, where an attempt has been made to assess the predominance of specimens conforming to either the megasculpta or microsculpta morphology in each locality. From most regions it has not been possible to examine specimens, making it necessary to rely on photographs, personal communication and whether specimens have been assigned to "P. dasypus" or "P. burgeri" in the literature, these two being taken to represent the microsculpta and megasculpta form respectively, unless otherwise stated.

Table 4. Distribution and relative abundance of the megasculpta and microsculpta forms of Panulirus homarus.

	MEGASCULPTA	MICROSCULPTA
S.E. AFRICA	+++	++
S.E. MADAGASCAR	++	
N.E. MADAGASCAR		+
E. AFRICA		+
SOCOTRA	+	
S. ARABIA	+++	
INDIA S.W. COAST	+	+++
CEYLON		+++
JAPAN	+	+
W. THAILAND		++
SUMATRA		+++
JAVA		++
N.W. AUSTRALIA		+

+++ = Occurring in commercially exploitable quantities; the dominant rock lobster in the region.

++ = Occurring regularly in small quantities; not the dominant rock lobster in the region

+ = Rare, irregular occurrence

Three specimens from Mukalla, East Aden, collected by Dr. R.W. George, were compared with megasculpta specimens from Natal. These differed morphologically from Natal specimens only in being more distinctly pitted on the posterior rim of the carapace and on the abdominal tergites, but a marked difference in colouration is evident between specimens from the two regions (see George 1963, Fig. 2a). In the Aden specimens the carapace is a more bluish-red giving it a darker appearance, while the overall colour of the abdomen is dark yellowish-green with numerous conspicuous yellow dots on the tergites; the posterior margins of the squamae and abdominal segments are distinctly edged with yellow. This Aden population is adapted to the local climatic influence of the south-west monsoon which results in cool, upwelled water, turbid conditions and heavy surf in summer, and clear water with no surf in winter. (George 1963 and pers. comm.). This is a very different situation from the conditions which prevail off the south-east African region.

The only other regions where megasculpta P. homarus appears to have been recorded in reasonable abundance are the west coast of India (Miyamoto and Shariff 1961), Socotra (George pers. comm.) and the south east-coast of Madagascar (Charbonnier and Crosnier, 1961).

It has not been possible to determine the natural coloration of the specimens from Socotra or India but the specimens from south-east Madagascar resemble the Natal megasculpta specimens in colour pattern as far as can be determined from the figure given by Charbonnier and Crosnier.

Off the east coast of equatorial Africa P. homarus is extremely rare and according to Postal (1966) and Hall (1960) only "P. dasypus" (i.e. presumably the microsculpta form) has been recorded. The reduction in abundance of the megasculpta form observed along the northern Zululand and Mozambique coasts found in this investigation suggests that it might disappear somewhere off the northern Mozambique coast, where only the microsculpta form appears to occur. It is interesting to note that at a similar latitude in north-east Madagascar only "P. dasypus" (i.e. presumably the microsculpta form) has been recorded (Postal 1966). A similar reduction in numbers of the Aden megasculpta form southwards along the Somali coast is also suggested by its apparent absence off the coast of tropical east Africa, indicating that there is probably no continuous distribution between the megasculpta populations of Aden and the Natal/Mozambique region.

On the south-west coast of India both "P. dasypus" and "P. bürgeri" are recorded by Miyamoto and Shariff (1961) and it seems possible that "P. bürgeri", which they indicate as being rarer than P. dasypus, may represent the eastern distributional range of the Aden megasculpta form.

In Ceylon, De Bruin (1962) apparently had no hesitation in assigning all his specimens to "P. dasypus" and on the basis of his comprehensive description, 232 out of 235 specimens could only have belonged to the microsculpta form as they had the abdominal tranverse grooves interrupted medianly. He also describes all the specimens as being olive-green in colour.

It has not been possible to examine specimens from Thailand, Sumatra or Java, but according to George (pers. comm.) the green microsculpta form is represented.

Specimens from N.W. Australia, in colour transparencies taken by Dr. R.W. George, were indistinguishable in colour or morphology from southern African green microsculpta P. homarus.

P. homarus is apparently so rare in Japan that the few specimens obtained there must be regarded as strays, although this is the type locality of "P. bürgeri". Kubo (1963) recorded two specimens which he assigned to "P. burgeri" and notes that there are only three other records of this species from Japan, viz, De Haan (1841), Herklots (1861), and Doflein (1906).

However from Kubo's figure there can be little doubt that the specimen illustrated was green in colour and while there are squamae on the abdominal transverse grooves, they are small, unequal and diminish in size medianly, where there is an indication of an incomplete median interruption in one segment. This specimen would thus appear to conform to the microsculpta form and not the megasculpta form, as is suggested by its having been assigned to P. bürgeri. There are several other localities in the eastern Indian Ocean listed by Holthuis (1946) where P. homarus has been recorded, but whether these specimens would conform to the megasculpta or microsculpta forms on the basis of colour and morphological criteria is difficult to assess.

Based on available evidence of abundance of the various forms, the overall distributional pattern which emerges is that the megasculpta form occurs predominantly in the western Indian Ocean, where two discontinuous and possibly distinct populations appear to be represented, one being most abundant off Natal and the other off Aden. Although there are records of what may be the megasculpta form from the eastern Indian Ocean, this form is certainly exceedingly scarce there, whereas the microsculpta form appears to occur in abundance, supporting commercial fisheries in Sumatra, Java and Ceylon. This form seems to have a wider distributional range than the megasculpta form, extending into the western Indian Ocean in small but fairly constant numbers.

Possible Explanations of Variation

George (1964b) states "... it might be considered that the East Aden and Ceylon populations of P. homarus are sufficiently distinct in their abdominal grooving to postulate that little mixing of larvae occurs. On the other hand, if it could be shown that larval mixing is extensive then the difference in these populations is merely the result of local phenotypic expression of a genetically mixed and widespread species."

On examination of variation in the south-east African population, the striking colour differences associated with the megasculpta and microsculpta forms might be considered to suggest a phenotypic response to particular environmental conditions. However the two forms were found to be distinct even in the smallest juveniles and both retained their colour and associated morphology when kept in tanks, indicating that these features are probably not gradually expressed in response to environment. Moreover, the fact that the megasculpta and microsculpta forms occur side by side in the same habitat in remarkably constant proportions is difficult to explain in terms of phenotypic expression.

In considering possible explanations of the megasculpta and microsculpta forms in terms of genetic differences, which seems to be more plausible than in terms of phenotypic expression, it was at first thought that P. homarus in Natal might exhibit polymorphism. It seemed possible that the microsculpta and megasculpta forms could simply reflect the expression of genetic factors determining morphology and colour, in which case natural selection could account for their frequency in samples. However, the presence of small numbers of intermediate specimens indicates that the microsculpta and megasculpta phenotypes are not discontinuous, but intergrade extremely steeply. Moreover, polymorphism is an intra-population phenomenon and if variation of P. homarus in the whole Indian Ocean is considered, regional distribution with virtually exclusive occurrence of a particular form (e.g. the megasculpta form in Aden or the microsculpta form in Ceylon) detracts from this hypothesis.

A more plausible alternative explanation of the various phenotypes of P. homarus off the east coast of southern Africa seems possible in terms of geographic isolation and intergradation. According to Mayr (1963) there are two types of intergradation which are rather different from the evolutionary viewpoint; in "primary intergradation", gradual development of the character gradient between two units occurred while the populations involved were in continuous contact, whereas in "secondary intergradation"

the units, now connected by a steeply sloping character gradient, were separated completely at one time and have now come into contact again, after a number of differences have evolved.

On the available evidence, the microsculpta form seems to occur in abundance in the eastern Indian Ocean but extends throughout the range of the species, whereas the two megasculpta forms each appear to have a more localised distribution one with a centre of abundance off the east coast of Aden and the other off Natal (see Table 4). This distribution pattern suggests that the larval life of the microsculpta form might be adapted to widespread dispersion in 'open' current systems, whereas the larvae of the megasculpta forms might be adapted to 'closed' local circulatory systems. However, at present there is no direct evidence of this and the more widespread distribution of the microsculpta form could also be due to its having a greater tolerance of environmental conditions.

The east coast of southern Africa probably represents a limb of distribution of P. homarus and it seems likely that gene flow has occurred in the past and still does occur southwards in the Mozambique/Agulhas current. It might be suggested therefore, that continuous recruitment of P. homarus stock, possibly similar to the present day microsculpta form, took place into the south-east African region where there was a suitable inshore habitat for the adults to survive.

However virtually no local repopulation would be expected to have occurred if the larvae were adapted to wide dispersion and not to conditions on the narrow shelf. In this case their ability to return to the same region after entering the Agulhas current would seem improbable. Environmental change, such as possibly the broadening of the shelf and development of the inshore reversing current system would have resulted in strong selection pressure for larval life to become adapted to local hydrological conditions and for local repopulation to occur, as there could be no adaptive selection of the adults to their inshore niche before this evolved. Once larvae evolved which were adapted to local repopulation, the potential for simultaneous selection of adults which were adapted to local environmental conditions would have been provided, as well as the potential for reproductive isolation and speciation. This could have resulted in evolution of the megasculpta form which, it is suggested, is adapted to environmental conditions typical of the Natal region and probably has a high degree of geographic isolation.

The occurrence of the microsculpta form in a low, fairly constant proportion in samples may simply reflect the rate of continuous larval recruitment into the south-east African region in the southward-flowing Agulhas current, as was postulated for the hypothetical ancestral stock.

The increase in the proportion of microsculpta specimens in samples from Zululand and Mozambique might be explained by the marked decrease in numbers of the megasculpta form due to reduction of suitable environmental conditions for the adults.

Occurrence of microsculpta specimens in Natal with deposited spermatophoric masses and fertilized eggs is considered to be strongly indicative that hybridization occurs, as the rarity of this form makes the probability of two specimens mating seem remote. In addition, interbreeding between megasculpta and microsculpta specimens has recently been demonstrated in captive specimens at the Oceanographic Research Institute. Two microsculpta females were introduced into a tank containing ten male and nine female megasculpta specimens. At the time of writing, which is at the beginning of the breeding season, both microsculpta females have mated with a megasculpta male and produced fertilized eggs. These have not yet hatched, but if they do, as certainly seems likely, interbreeding between these two forms will be conclusively proved. While it might be argued that there is no proof that the larvae would be viable, the presence of intermediate specimens in the feral population provides strong circumstantial evidence that hybrids are viable and do survive to adulthood. If in fact, the intermediates are hybrids, their presence provides strong evidence that local repopulations occurs in the south-east African region.

The higher proportion of intermediates in samples from the Zululand/Mozambique region (see Table 1) compared with Natal possibly reflects a higher rate of hybridization due to falloff in abundance of the megasculpta form. This level of intergradation between the megasculpta and microsculpta forms is probably maintained by a low level of repopulation and continuous recruitment of the megasculpta form from Natal.

If the above hypothesis accounting for the steep gradient between the megasculpta and microsculpta forms of P. homarus in south-east African waters is valid, the problem is to assess how far the megasculpta form has progressed towards full biological species status. According to Mayr (1963), the extent to which the following species characteristics are fulfilled must be considered: Reproductive isolation, ecological difference and morphological distinguishability. The present evidence suggests that no reproductive, isolating mechanisms exist and that the megasculpta and microsculpta forms interbreed freely in the south-east African region.

Ecological distinction between the Natal megasculpta and microsculpta forms is suggested by the climatic differences between the inshore marine environment of Natal, and conditions under direct influence of the monsoonal system elsewhere in the Indian Ocean, where the microsculpta form occurs in abundance.

Moreover, the falloff in abundance of the megasculpta form off Zululand and Mozambique and its absence off tropical East Africa, where only the microsculpta form appears to occur, might also indicate ecological separation. However, the fact that both megasculpta and microsculpta forms survive side by side in the same habitat indicates that ecological separation, if it does exist, is probably not particularly well developed. It must also be pointed out that the five species of Panulirus recorded from the south-east African region, namely P. homarus, P. penicillatus, P. longipes, P. ornatus and P. versicolor, show distinct ecological separation, described in Section 1, and on no occasion were any two of these found living together.

In the case of the third species criterion, there can be no doubt as to the morphological distinctness of the megasculpta and microsculpta forms and the steepness of intergradation between them. This can probably be attributed to a high degree of geographic isolation of the megasculpta form in south-east African waters. It must be stressed, however, that geographic isolation is not an isolating mechanism in terms of the definition of the latter. According to Mayr (1963), isolating mechanisms always have a partially genetic basis and are "biological properties of individuals that prevent the interbreeding of populations that are actually or potentially sympatric".

Recognition that there is a difference between the species as a category and the species as a taxon is essential in application of the biological species concept. Mayr (1963) outlines this as follows. "The species as category is characterised by the biological species concept. The practicing taxonomist, however, deals with taxa, with populations and groups of populations, which he has to assign to one category or another, for instance either to the category species or to the category subspecies. The non-arbitrary criterion of the category species, biologically defined, is that of interbreeding or non-interbreeding".

On the basis of the available evidence it is therefore concluded that the megasculpta form, occurring off south-east Africa, does not adequately fulfill the requirements to be placed in the category of full biological species, distinct and separate from the microsculpta form.

Bearing in mind that the "subspecies" is not an evolutionary unit and is a purely arbitrary taxon used for practical taxonomic purposes, it is considered that further study of geographical variation and possible intergradation of populations of P. homarus elsewhere in the Indian Ocean would be necessary, before it could be assessed whether subspecific recognition would serve any useful taxonomic purposes.

2. REDISCOVERY OF THE ROCK LOBSTER PUERULUS CARINATUS
BORRADAILE (DECAPODA, PALINURIDAE)

(Published - Berry, 1969b)

During 1968, twenty-eight specimens of the genus Puerulus Ortmann, 1897 were obtained by commercial trawlers in southern Mozambique waters. Two more specimens were trawled off Durban, Natal and a further dried specimen from an unknown locality near Mauritius was available for examination. Twelve of the specimens from Mozambique, the specimen from Mauritius and one specimen from Durban, conform to the description of Puerulus angulatus (Bate, 1888). However, the holotype was not seen and identification of these specimens as P. angulatus is largely based on the description of this species from the Phillipines given by Holthuis (1966). Subsequently this identification has been confirmed by Dr. Holthuis who kindly examined a specimen sent to him. The other eighteen specimens are assigned to Puerulus carinatus Borradaile, 1910.

Puerulus carinatus was only previously known by a single specimen from Saya de Malha, briefly described by Borradaile, which has subsequently been lost. In a revision of the genus Puerulus, Holthuis (1966) considered P. angulatus and P. carinatus to be synonyms. Two species are undoubtedly represented in the South African material and having had the opportunity of comparing specimens which conform to Borradaile's description of P. carinatus with specimens which fit the description of P. angulatus,

it is proposed that P. carinatus is a good species. A neotype has been selected and with two other specimens has been presented to the Rijksmuseum van Natuurlijke Historie, Leiden. The remaining series of fifteen specimens has been retained at the Oceanographic Research Institute, Durban.

In view of the rediscovery of P. carinatus, four species may be recognised within the genus and the key devised by Holthuis (1966) has been modified accordingly:

1. Post-orbital spine present. No teeth but 6 post-cervical and 6 intestinal tubercles on the median keel of the carapace. Tubercles on carapace low and largely obscured by pubescence. Eyes large, much broader than long P. velutinus
- Post-orbital spine absent. Median keel of carapace with 3 or 5 post-cervical and 2 to 4 intestinal teeth. Tubercles of carapace usually distinct and not obscured by the pubescence. Eyes smaller, longer than broad 2
2. Three or more teeth between supra-orbital horns and the cervical groove. Median keel of carapace with 3 post-cervical and 2 intestinal teeth. Fifth pereopod of male not chelate P. angulatus
- Two teeth between supra-orbital horns and the cervical groove 3
3. Median keel of carapace with 3 post-cervical and 2 (occasionally 3 or 4) intestinal teeth. Fifth pereopod of male chelate P. carinatus
- Median keel of carapace with 5 post-cervical and 2 or 3 intestinal teeth. Fifth pereopod of male not chelate P. sewelli

The morphology of P. carinatus is described below and as the colour pattern of Puerulus has not previously been described, a detailed description is given for both P. carinatus and P. angulatus.

Puerulus carinatus Borradaile, 1910

Puerulus carinatus Borradaile, 1910: 261, pl. 16 fig. 5 (Saya da Malha, East Africa), (not seen); Holthuis, 1946: 110.

Puerulus angulatus - Holthuis, 1966: 267 (partim).

non Puerulus carinatus - Ramadan, 1938: 133, fig. 6,7; McNeill, 1949: 337, fig.

Material examined (details and measurements are recorded in Tables 5 and 6).

1. N.E. of Ouro Point, southern Mozambique, approx. 26°50'S 33°00'E; depth 320 metres; "Tracy-Jon"; May 1968. Neotype (O.R.I. No. 12, now Rijksmuseum van Natuurlijke Historie, Reg. No. Crust. D 25535; male, lacking the distal portions of the antennal flagella; propodus and dactylus of fifth pereopod of left side detached) and O.R.I. specimens 1-5, 7-11, 13-18 (specimens 10 and 14 now Rijksmuseum van Natuurlijke Historie, Reg. No. Crust. D 25536).
2. S.E. of the Bluff, Durban, Natal, S. Africa, approx. 30°00'S 31°09'E; depth 320 metres; July 1968; "Illovo"; O.R.I. No. 6.

Description of neotype. - A small rock lobster showing all the characteristic features of the genus as described by Ortmann, 1897 (Plate I, Fig. 1; Plate II, Fig. 1).

The supra-orbital horns are spaced wide apart and between each horn and the cervical groove are two teeth which decrease in size posteriorly.

On either side of the anterior margin of the carapace at the base of each supra-orbital horn, a sharp 2-topped tooth is present. Between these teeth the anterior margin of the carapace is straight. A well developed infra-orbital tooth projects antero-laterally and is continuous with a shorter stout tooth below it. Posterior to the infra-orbital tooth is a longitudinal row of 3 small teeth, decreasing in size posteriorly. On the left side there is a slight interruption between the first of these teeth and those posterior to it. Between the supra-orbital and infra-orbital rows of teeth there are two longitudinal rows of minute spinules; the anterior half of the upper of these rows is double, slightly curved and the spinules are irregularly spaced; the lower row is single, short and consists of only two spinules which are not characteristic in the neotype, being closer together than is normal. Extending anteriorly from the cervical groove are two slightly converging submedial rows of 5 blunt knob-like teeth. Of these teeth, 2 are much larger than the others which are poorly developed and flattened. Between the large teeth there is a wide interruption approximately the same distance as between the rows which gives the impression of 4 knobs forming a square as described by Borradaile. In front of the anterior tooth in each row there is an interruption followed by a cluster of irregularly arranged tubercles. Behind the cervical groove the carapace is angular with a median keel bearing 3 large gastric and 2 smaller intestinal teeth.

All these teeth are blunt and resemble elongate tubercles. The median keel slopes laterally to branchial keels, each bearing irregularly spaced teeth which are largest anteriorly and become progressively smaller and blunter until they are reduced to tubercles posteriorly. The entire dorsal surface of the carapace behind the cervical groove is evenly covered with small pointed tubercles.

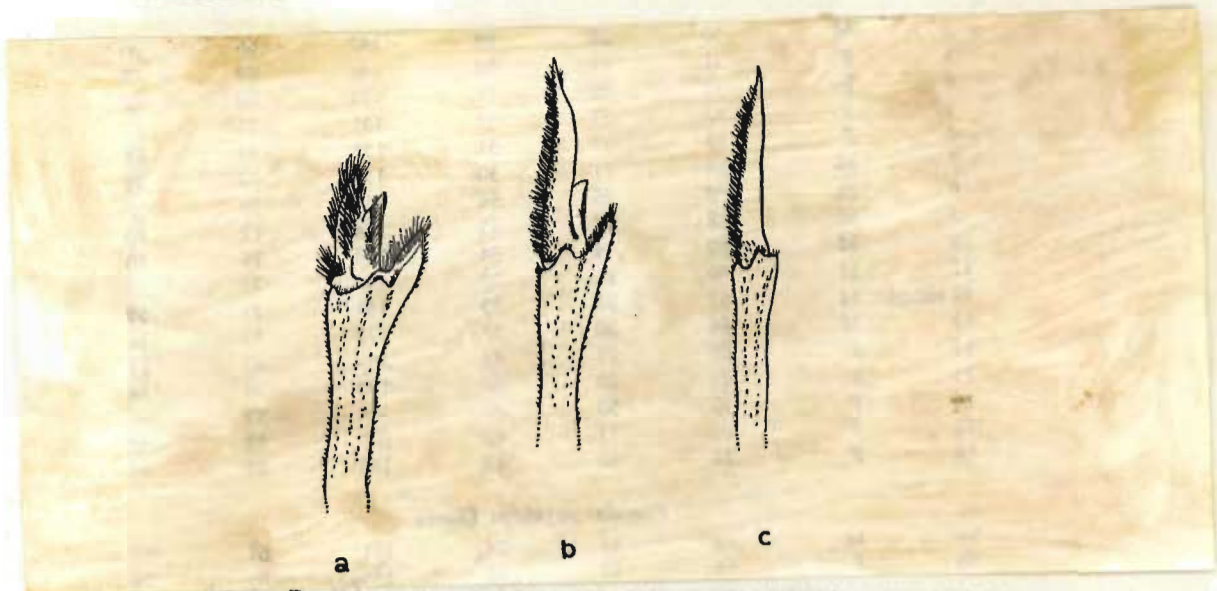


Fig. 7. Distal portion of the left fifth pereopod.
 a, Puerulus carinatus Borradaile, female;
 b, Puerulus carinatus Borradaile, male;
 c, Puerulus anquilatus (Bate), male.

Laterally the branchiostegite is covered with rows of blunt tubercles, but on the edge of the cervical groove adjacent to the last infra-orbital tooth, there is a region where the tubercles are enlarged and pointed.

The eyes are longer than broad; the peduncle is constricted in the middle and the cornea is kidney-shaped.

The antennular plate bears 2 minute, sharp spinules on either side of the mid-line. The lateral edges of the antennular plate form a stridulating organ with a process of the third segment of each antenna. There is a blunt angular elevation on the dorsal surface of the third segment of the antennal peduncle, just above the stridulating process, which is represented by a sharp spine in P. angulatus. A small spine is present just anterior to the stridulating process and almost on the inner margin of the segment; this spine is well developed on the left side only. On the outer margin of this segment there are 2 posterior teeth and 1 anterior tooth. On the lower surface of the segment there is 1 tooth on the inner margin, 1 on the outer, a large blunt subdistal tooth and numerous minute blunt tubercles.

On the left side, the fourth segment of the antenna bears 4 well developed, hooked teeth on its outer margin while 5 are present on the right side; the dorsal surface bears two oblique rows of teeth, the outer consisting of 3 teeth which decrease in size posteriorly, the inner consisting of 4 teeth of uniform size. Two terminal teeth are present on the inner anterior margin, the dorsal one being largest.

Table 5. Measurements of Puerulus carinatus Borradaile and Puerulus anquilatus (Bate) (in mm)

catalogue number	sex	carapace length	*pre-cervical width	*post-cervical width	total length	abdomen without telson	telson
<u>Puerulus carinatus</u> Borradaile							
1	M	48	19	31	135	62	25
2	M	50	20	28	142	66	26
3	F	51	21	30	149	69	28
4	F	52	20	31	150	69	29
5	F	52	21	32	151	72	27
6	F	53	22	31	155	74	28
7	M	54	21	30	153	70	29
8	M	58	25	34	164	76	30
9	M	58	24	35	164	77	29
10	M	60	24	34	164	74	30
11	M	60	25	35	166	75	31
12	neotype M	62	26	35	165	73	30
13	M	64	26	37	178	83	31
14	F	69	27	40	190	87	34
15	F	69	28	40	192	89	34
16	F	70	30	42	-	97	-
17	F	72	31	42	200	91	37
18	F	74	30	42	195	87	34
<u>Puerulus anquilatus</u> (Bate)							
19	M	48	17	24	131	61	22
20	F	53	18	27	144	65	26
21	M	54	17	27	150	71	25
22	F	57	20	30	157	73	27
23	M	57	20	29	155	74	24
24	F	59	21	31	167	79	29
25	F	60	21	32	166	77	29
26	M	60	21	30	164	76	28
27	M	61	21	31	164	75	28
28	F	63	22	32	174	82	29
29	F	67	24	35	173	75	31
30	F	67	25	36	185	86	32
31	F	73	25	38	207	98	36

* Precervical width was measured between the posterior bases of the supra-orbital horns; postcervical width was measured between the anterior extremities of the branchial keels.

On the lower surface of the segment there is a longitudinal row of 5 poorly defined, small teeth. The outer lateral margin of the fifth segment bears 3 spines, the anterior one being prominent; the inner lateral margin bears 3 small spines; there is a dorsal and a ventral spine on the anterior margin. The flagella are broken.

The peduncle of the antennule is approximately 0.75 times as long as the carapace. The flagella are short and the outer is broader and shorter than the inner one.

The epistome ends in a single strong median tooth.

The merus of the third maxilliped bears 5 poorly developed teeth; there is no sign of spination on the merus of the first or second pereopods. The first two pereopods are the stoutest and both bear scattered hairs particularly on the ventral surface of the propodus. The relative proportions of the pereopods are given in Table 6.

The dactyli of the fifth pereopods are chelate and are approximately $\frac{1}{5}$ of the length of the propodi; the chela is formed by a process of the propodus which opposes a process of the dactylus (Fig. 7).

Table 6. Pereiopod measurements of
Puerulus carinatus Borradaile

catalogue No.	pereiopods				
	1	2	3	4	5
1	41	55	74	92	-
2	-	-	-	-	-
7	50	64	84	103	112
8	56	70	-	111	120
9	55	74	-	-	-
10	54	69	82	109	-
11	55	74	95	119	125
12 (neotype)	68	75	94	115	124
13	57	74	93	115	123
3	46	59	76	93	97
4	44	60	86	101	104
5	47	60	79	95	99
6	49	63	81	98	101
14	61	81	98	115	115
15	62	80	102	117	116
16	-	-	-	-	-
17	77	82	-	-	-
18	-	-	-	-	-

The thoracic sternum bears a median tooth on all segments. At the bases of the second pereiopods a sharp spine is present and at the bases of the third, fourth and fifth pereiopods there are additional minute, blunt spines.

An elongate, tapering protrusion extends from each genital aperture.

The median keel of the first abdominal segment is poorly developed and is represented by a slight elevation. The broad transverse groove is filled with a short pubescence. The pleura bear a large single flattened tubercle and numerous poorly defined smaller ones.

In segments 2 to 5 the median keel is better developed than in the first segment and is twice interrupted to form three elongate flattened ridges; the middle ridge is largest and the anterior and posterior ones are small and ill-defined. While the middle ridges of segments 3 to 5 are slightly produced posteriorly they could not be described as being produced into posteriorly directed teeth as described in P. angulatus. The posterior ridge of the second segment shows signs of being divided into two. An anterior and a posterior transverse groove, filled with a short pubescence, runs adjacent and parallel to the anterior and posterior margins of the segment respectively. Two shallow oblique grooves without pubescence, extend from the anterior transverse groove to the posterior transverse groove on either side of the dorsum. The first of these grooves runs from approximately midway along the anterior transverse groove to about three quarters of the distance along the posterior transverse groove from the midline; the second connects the two transverse grooves along the base of the pleuron. The oblique rows of tubercles present on the dorsum in P. angulatus are almost indistinguishable. The pleura bear an oblique row of 1 to 4 ill-defined flattened tubercles running almost parallel to the oblique grooves on the tergite and terminate in two sharply pointed spurs. The anterior margins of the pleura of segment 2 bear two slight protuberances which correspond to the denticles described in P. angulatus.

The sixth abdominal segment has 2 poorly defined submedian rows of denticles which increase in size posteriorly. After a short interruption, these are followed by a posterior submedian denticle on either side of and just anterior to a single median tooth which is situated on the posterior margin of the segment. The lateral margins of the dorsum terminate in a large spine posteriorly. Along the base of the pleuron are 3 indistinct tubercles which increase in size posteriorly and there is a curved row of 3 flattened tubercles which are better defined than in segments 2 to 5. The pleura of the segment terminate in a well developed, anterior spur and a smaller posterior tooth.

The lateral margins of the calcified portion of the telson terminate posteriorly in a sharp spine and a minute blunt spine is present midway along each margin. On the dorsal surface there are two diverging rows of 3 blunt spines of irregular size. There is a single pair of submedian spines slightly anterior to the rows of spines.

The first abdominal sternite has two submedian and two lateral spines. In the second to the fifth segments only the submedian spines are present. The sternite of segment 6 has a poorly developed anterior pair of submedian tubercles, a well developed posteriorly directed posterior pair of submedial spines and slightly posterior to these and slightly wider apart, a posteriorly directed pair of spines on the posterior margin.

There are traces of a transverse row of minute tubercles.

No pleopods are present on the first abdominal segment. The pleopods are very similar on segments 2 to 5 and the exopods are leaf-shaped with rounded tips.

The calcified portions of the uropods terminate in a sharp spine and the inner margins bear irregular spines.

Colour pattern (Plate III, Fig. 1). - The supra-orbital horns are orange except for the distal third and lateral margins which are white. At the bases of each horn the white margin is expanded medially. The anterior teeth between the supra-orbital horns are bright red with white tips and the anterior margin of the carapace between these teeth is orange with a median red spot. Immediately posterior to this spot, a white patch extends to the anterior cluster of precervical tubercles. The basic colour of the dorsal surface of the carapace in the precervical region is orange. The two teeth between each supra-orbital horn and the cervical groove are bright red. The area immediately surrounding and between the two anterior large knob-like spines is red; medially the region between the posterior large knob-like spines is white. The tubercles of the anterior cluster are bright red.

Laterally, in the precervical region a longitudinal band of orange extends from the cervical groove to the orbit between the upper and lower longitudinal rows of spinules which are bright red. The area between the upper longitudinal row of spinules and the supra-orbital row of teeth is white. The region between the lower longitudinal row of spinules and the row of infra-orbital teeth is also white. The two large infra-orbital teeth are orange while the longitudinal row of small infra-orbital teeth is red.

The basic colour of the dorsal surface of the carapace posterior to the cervical groove is orange while the tubercles covering it are bright red. The median keel is white but the three gastric and two intestinal tubercles are bright red. Running above each branchial keel there is a narrow white strip. The teeth of the branchial keels are bright red. Continuous with the oblique regions on either side of the cervical groove and extending posteriorly on either side of the median keel to the level of the third gastric tubercle, is a broad white strip about the same width as the cervical groove. Running parallel to this is a narrow white strip which curves inwards and the strips of either side of the carapace meet behind the posterior gastric tubercle, to give a saddle-like effect. Below each branchial keel, the colour merges from orange dorsally to white at the ventral margin of the branchiostegite.

The tubercles on the branchiostegites merge similarly from orange dorsally to white in the ventral region. The enlarged tubercles adjacent to the posterior tooth in the infra-orbital row are bright red merging to orange posteriorly.

The peduncular segments of the second antennae are basically orange. Just anterior to the stridulating process on the dorsal surface of the third peduncular segment there is a white spot. The colour on either side of the row of teeth on the outer margin of the fourth segment is white. All the teeth on the peduncular segments are bright orange or red. The colour of the flagellum is plain red with no markings.

The antennular plate is orange with a wedge-shaped area of white in the midline. The spinules are bright red.

The antennule is uniformly pinkish-orange.

The cornea is dark brown; the peduncle is white with orange margins.

The segments of the pereopods are white with a trace of orange which becomes darker distally. The orange is most extensive on the merus and is conspicuous on the teeth of maxilliped 3. A bright orange spot is situated proximally on the dorsal surface of the propodus and carpus in pereopods 2-5.

The mouthparts and ventral surface of the carapace are white.

The anterior portion of the first abdominal segment, which slides under the carapace, and the transverse groove are orange. A transverse red band runs along the entire posterior margin of the transverse groove, through the ridge of the median keel. Immediately behind this red band is a transverse white band of approximately the same width which extends along the entire posterior margin of the segment. The pleura are white with red anterior margins and the large flattened tubercles are red. The pleural spurs are white.

In segments 2 to 5 the region between the anterior transverse groove and the anterior margin of the segment is red but where it slides under the preceding segment it is white. The anterior and posterior transverse grooves and the two oblique grooves on either side of the tergite are light orange. The entire dorsum between the anterior and posterior transverse grooves and the first oblique grooves is bright red, including the ridges of the median keel. On either side of the tergite the area between the transverse grooves and the first and second oblique grooves is also red. The colour pattern between the posterior margin of the transverse groove and the posterior margin of the segment is identical to that in the same region in segment 1.

The pleura are white, bordered by red on their anterior and posterior margins; the larger tubercles are red.

The anterior margin of segment 6 is white. The base of each pleuron is red, merging to orange medially. The teeth of the submedial rows and the area surrounding the rows are bright red. Running between the submedial rows of teeth from the anterior margin of the segment to the median tooth on the posterior margin is a white strip. The posterior margin of the segment is red except for the white median and lateral terminal spines. The red extends anteriorly on either side of the median white strip and merges into a broad transverse white band mottled with red which extends below the pair of submedian spines.

The lateral margin, two diverging rows of spines and the submedian spines of the calcified portion of the telson are red. The anterior margin and the area between the lateral margins and the diverging rows of spines are white, mottled with orange. The calcified portions of the uropods are red except for a white outer margin and terminal spine. The non-calcified regions of the telson and uropods are pale brownish-orange.

Variation within the series. - Little significant variation is present, the main differences being in the degree of development of the spines.

Small specimens have sharper, better developed spines than large specimens in which they tend to become flattened, tuberculate or even degenerate. The teeth on the anterior margin of the carapace at the base of the supra-orbital horns, which are normally two-topped may be one-topped or three-topped. The supra-orbital horns are normally followed by two teeth posteriorly but in one specimen a small third tooth is present on one side only. Rarely, an additional one or two minute teeth posterior to the two large intestinal teeth are present. The number of teeth on the outer margin of the fourth antennular segment is rather variable and up to six may be present. The flagella of the antennae are extremely long in specimens where they are unbroken, being approximately 12 times the carapace length. The carapace length averages 2.5 times the precervical width (measured between the posterior bases of the supra-orbital horns) and 1.5 times the postcervical width (measured between the anterior extremities of the branchial keels). The fifth pereopods (when intact) of all male specimens are chelate.

Description of female. - The fourth and fifth pereopods are approximately the same length, due to reduction of the dactylus of the chelate fifth pereopod (fig. 7a), which is only approximately 1/7 the length of the propodus. In the male the dactylus of the fifth pereopod is not reduced so that the fifth pereopod is longer than the fourth.

The pleural spurs are larger than those of the male and the anterior one is almost twice the length of the posterior one. This discrepancy in size between the anterior and posterior spurs is not as pronounced in the male.

No submedian spines are present on the sternite of abdominal segments 3 to 5 and they are poorly developed in the second abdominal segment. On the sternite of the sixth abdominal segment, the anterior tubercles are poorly developed or absent; the spines on the posterior margin of the sternite are better developed than in the male.

Pleopods are present on segments 2 to 5, but the exopods are larger than those of the male. Very slender endopods are present and a slightly shorter, wider stylamblys arises from the base of each.

Freshly spawned ova are bright orange, with a diameter of approximately 0.6mm.

Puerulus angulatus (Bate, 1888)

Material examined (details and measurements are given in Table 5).

1. "The corner", southern Mozambique, approx. 25°35'S 35°00'E; depth 280 metres; "Tracy-Jon"; September 1968; O.R.I. specimens 19-25, 28, 30 and 31.
2. N.E. of Milibangalala, southern Mozambique, approx. 26°17'S 33°07'E; depth 320 metres; "Tracy-Jon"; May 1968; O.R.I. specimens 26 and 29.
3. S.E. of the Bluff, Durban, Natal, S. Africa, approx. 30°10'S 31°07'E; depth 310 metres; "Tracy-Jon"; December 1968; O.R.I. specimen 27.

As far as can be determined from Bate's short description of the holotype of P. anquilatus (a juvenile of 36mm total length) and photographs of the specimen kindly supplied by the British Museum, the present specimens conform with the holotype in number and position of spines, but not in degree of development of spination. In the latter, the spines of the median thoracic keel and abdominal keel, are enormously developed in relation to the body size when compared with the South African specimens which is probably a juvenile characteristic.

As the South African specimens conform closely to the extensive description of P. anquilatus from the Philippines given by Holthuis (1966), only aspects which differ from Holthuis' description, variation within the series and some additional observations on the South African specimens are described below.

Description (Plate I, Fig. 2; Plate II, Fig. 2). - The supra-orbital horns are sharply hooked and the outer distal margins are crenulate (as in the holotype). The anterior margin of the carapace between the supra-orbital horns is concave. Between each horn and the cervical groove are 3 or more teeth decreasing in size posteriorly. The posterior tooth is considerably smaller than the preceding two teeth. The position and size of this posterior tooth is variable and in some specimens 2 or (as in the case in the holotype) 3 minute teeth are present instead of a single small tooth.

The carapace length averages 2.9 times the precervical width (measured between the posterior bases of the supra-orbital horns) and 1.9 times the postcervical width (measured between the anterior extremities of the branchial keels). These proportions of the carapace are the same as those of the holotype, although the measurements of the latter were taken from a photograph.

The median keel of the first abdominal segment is interrupted to form two elevated ridges. In abdominal segment 2, the median keel is divided into 4 elevated ridges, the second being the largest; the posterior ridge is very small. In segments 3 to 5 the median keel is divided into 3 elevated ridges; the second is the largest and is produced into a posteriorly directed tooth; the posterior ridge is also produced into a spine posteriorly, which is well developed in the fifth segment only.

The spinules on the anterior margins of the second pleura are minute.

The third segment of the antenna bears 4 to 6 (usually 5) teeth on its outer margin. On the ventral surface Holthuis describes two longitudinal rows of denticles, but only one row is clearly distinguishable in the South African specimens.

The fifth pereopod of the female is chelate; in the male it is not.

Colour pattern (Plate III, Fig. 2). The basic colour of the carapace is dull white with small scattered patches of dark red. The red of P. angulatus is darker and not as bright as it is in P. carinatus.

The supra-orbital horns are white with a faint pink tint along the inner margins.

The teeth between the supra-orbital horns on the anterior margin of the carapace are white. At the base of each supra-orbital horn is an irregularly shaped red patch which extends to the anterior margin of the carapace between the anterior teeth.

The white of the dorsal surface of the carapace extends to the midline of the anterior margin, separating the two red patches. The three teeth posterior to each supra-orbital horn are white with a little red posteriorly on their bases. The teeth of the two converging submedial rows are white with irregular red markings running along the outside of the rows. A red patch extends obliquely forward from each posterior supra-orbital tooth. The tubercles are white or pink.

Laterally the precervical region is white except for three red patches; a longitudinal red band extends below the upper longitudinal row of spinules; the spinules are pink or white; the lower longitudinal row of spinules is entirely surrounded by an oval red patch and the spinules are red;

the posterior tooth in the infra-orbital row is surrounded by another oval red patch. The large infra-orbital spine is white with a red base posteriorly while the lower infra-orbital spine and the anterior two spines in the infra-orbital row are white.

Posterior to the cervical groove the dorsal surface of the carapace is dull white with a slight orange tint surrounding the three gastric teeth. The gastric and intestinal teeth are white. The tubercles covering the dorsal surface are predominantly white with red and pink ones randomly interspersed. The teeth of the branchial keels are white. A strip of red extends dorsally along the length of the branchiostegite immediately below each branchial keel. Below this a second longitudinal red strip arises from near the posterior corner of the branchiostegite and extends along the middle of the branchiostegite for approximately half its length. The remainder of the branchiostegite is dull white. The tubercles are predominantly white with a few pink ones randomly interspersed; those in the region adjacent to the last spine in the infra-orbital row are red.

The peduncular segments of the second antennae are red, merging into pink and white. The teeth on these segments are white with a varying amount of red extending along their outer margins.

The entire spine on the dorsal surface of the third segment just above the stridulating process is white. Alternating irregularly shaped red and white bands extend along the length of the flagellum.

The antennule is uniformly pink.

The segments of the pereopods are pinkish-orange, becoming darker distally. The mouthparts and ventral surface are dull white.

The portion of the first abdominal segment which slides under the carapace is white, mottled with pink. The transverse groove is white. The posterior margin of the segment is red except for two submedian white bands. The anterior ridge of the median keel is white with a red base; the posterior, less pronounced ridge is entirely red. The pleura are white except for a single red spot and red margins.

In segments 2 to 5 the anterior margins are white mottled with red. The anterior and posterior transverse grooves and the oblique grooves are white. A narrow red band (narrower than the anterior transverse groove) extends along the entire posterior margin of the anterior transverse groove except for an interruption on either side of the tergite where the first oblique groove runs into the transverse groove. The red extends posteriorly along the first and second oblique rows of tubercles as far as the posterior transverse groove.

The region between the posterior transverse groove and the posterior margin of the segment is red. The remainder of the dorsal surface of the tergite is white. The ridges of the keel are white except for the posterior ones in segments 2 to 5 and the anterior ones in segments 4 and 5 which are red. The pleura are white with a few red tubercles; the anterior margins are red and there is a small patch of red on the posterior margins; the spurs are white.

The teeth of the two submedial rows in segment six are red with white tips. A patch of red extends laterally from each row. The lateral margins of the tergite are mottled red which extends inwards. The posterior margin of the segment is red except for the median and lateral terminal spines which are white. The colour of the pleura is as in segments 2 to 5.

The calcified portion of the telson is white except for the two red submedian spines, the lateral margins and the area surrounding the two diverging rows of spines which is also red. The spines of these rows are white. The calcified portions of the uropods are orange with white outer margins and terminal spines. The non-calcified portions of the telson and uropods are pale brown with a bluish-white margin.

Differences between P. carinatus and P. angulatus

1. P. carinatus has two teeth behind the supra-orbital horns whereas P. angulatus has three.
2. The outer distal margins of the supra-orbital horns of P. angulatus are crenulate whereas in P. carinatus they are smooth.
3. The anterior margin of the carapace of P. carinatus is straight (as figured by Borradaile, 1910) whereas in figures of P. angulatus by Kubo (1939) and Ramadan (1938) it is slightly concave as it is in the specimens of P. angulatus obtained off south-east Africa.
4. Although the spination of the two species corresponds closely, the spines of P. carinatus tend to be blunt, tuberculate and in some cases degenerate as opposed to the sharp well developed spines of P. angulatus. This is particularly marked in the gastric and intestinal tubercles and the ridges of the median keel where the median keel is almost non-existent in the first abdominal segment and the posterior ridge of the second segment is not divided into two as in P. angulatus. In P. carinatus the middle tubercles of segments 4 and 5 are not produced into posteriorly directed teeth as in P. angulatus. The oblique rows of tubercles on the tergites of the abdominal segments of P. angulatus are almost indistinguishable or absent in P. carinatus.

5. In P. angulatus there are two submedian converging rows of 3 to 5 large, and numerous small teeth on the dorsal surface of the carapace in the precervical region. In P. carinatus the two submedian rows consist of only 4 to 6 blunt knob-like teeth of which 4 (rarely 6) are well developed and the others are small and degenerate. This arrangement gives the impression of a square of 4 knobs as described by Borradaile. Anteriorly, quite isolated from the rows of knob-like teeth is a cluster of blunt tubercles. In small specimens of P. carinatus it is possible to distinguish that the spination has been derived from two converging rows of teeth as in P. angulatus.
6. The colour pattern of P. carinatus is basically orange with bright red spines while P. angulatus is basically white with dark red patches and red at the bases of white spines. The difference in colour pattern is so striking that commercial fishermen distinguished them as two species (Plate III).
7. The dactylus of the fifth pereopod is chelate in male P. carinatus which it is not in P. angulatus (fig. 7)
8. The disparity in size of the anterior and posterior pleural spurs in female P. carinatus is greater than in females of P. angulatus.
9. The carapace length averages 2.5 times the precervical width in P. carinatus whereas it averages 2.9 times the precervical width in P. angulatus.

The postcervical region of the carapace is also relatively wider in P. carinatus (see Table 5), the carapace length averaging 1.5 times the postcervical width in P. carinatus and 1.9 times the postcervical width in P. angulatus.

Discussion

Comparison of specimens of P. angulatus from the various widely separated localities where it has been recorded seems necessary in order finally to establish the taxonomic identity of this species. However, while the South African specimens designated as P. angulatus and P. carinatus appear to be closely related, the stability of distinguishing characteristics and lack of intermediate forms seems to eliminate the possibility that two varieties of a single species are represented.

Ramadan (1938) assigned a specimen of Puerulus from the Zanzibar area to P. carinatus but unfortunately in his description he does not define its measurements. However, the proportions of its carapace, measured from his figure, conform to those of the South African specimens of P. angulatus and as his specimen also has 3 spines between each supra-orbital horn and the cervical groove, it seems likely that it is P. angulatus as concluded by Holthuis (1966).

Puerulus gracilis Kubo (1939) has been synonymised with P. angulatus by Holthuis (1966).

Kubo's specimens differ from P. carinatus in that the fifth pereopod of the male is not chelate and there are three teeth between each supra-orbital horn and the cervical groove. According to Kubo, the antennae of the preserved specimens show signs of having red bands which are characteristic in the South African P. anquilatus, whereas P. carinatus has uniformly red antennae. From his description, Kubo's specimens cannot be P. carinatus and appear to conform to P. anquilatus.

Although P. anquilatus and P. carinatus were never taken in the same haul, the proximity of the localities where they were obtained poses the problem of explaining the mechanism of isolation between them, but in view of the lack of physical data from these localities, any explanation is purely speculative. As reptantian decapoda are very specific as to the substratum they inhabit and the nature of the bottom may change considerably within a short distance, it seems most likely that the two species occur on different types of substratum.

The chelate fifth pereopod of male P. carinatus, which is the most striking distinguishing feature of this species, appears to be unique not only within the genus but within the Palinuridae. While no definite explanation for this adaptation can be put forward, it seems possible that the chelae may be used in mating or courtship behaviour, in which case a behavioural isolating mechanism may exist between P. carinatus and P. anquilatus.

An unusual feature of both P. carinatus and P. angulatus is the remarkably long flagella of the antennae (12 times the carapace length).

The occurrence of P. angulatus in the western Indian Ocean is an interesting extension of its range. The extreme southern latitude distribution of the genus Puerulus given by George & Main (1967) is approximately 11°S and the specimens taken off Durban at 30°S extend this to the limits of the equatorial belt.

Appendix

A world revision of the genus Puerulus is currently being undertaken by Dr. R.W. George and the present author. The identity of P. angulatus and P. carinatus, described above, has been confirmed after examination of an assemblage of material which included the neotype of P. angulatus and all named species within the genus except P. gracilis (Kubo, 1939).

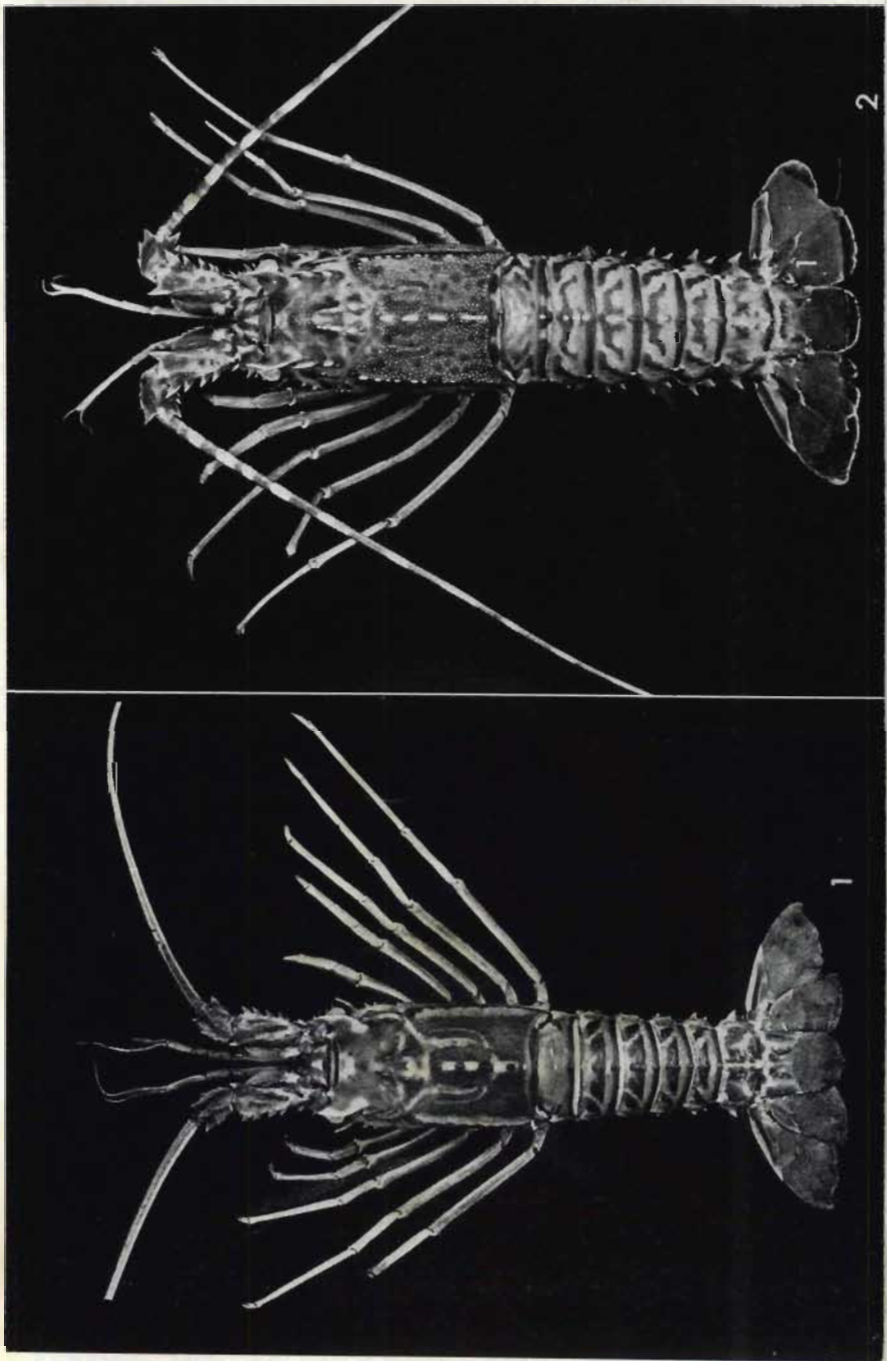


Plate I. Fig. 1. Puerulus carinatus Borradeille, male neotype, dorsal view.

Fig. 2. Puerulus anquilatus (Bate), female, no. 28, dorsal view.

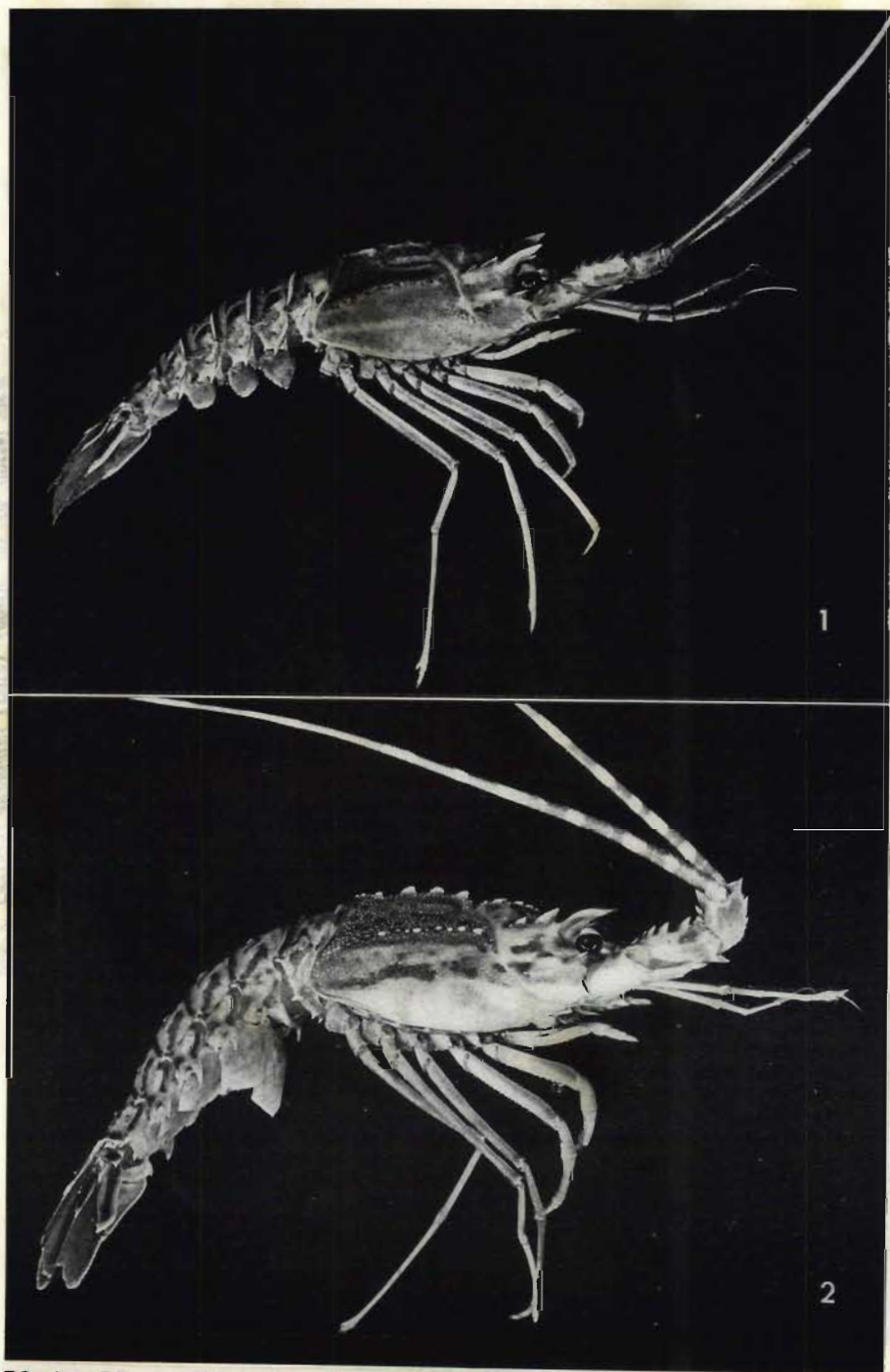


Plate II. Fig. 1. Puerulus carinatus Borradaile, male neotype, lateral view.

Fig. 2. Puerulus angulatus (Bate), female, no. 28, lateral view.



Plate III. Fig. 1. (left), Puerulus carinatus Borradaile, male in dorsal view.

Fig. 2. Puerulus angulatus (Bate), male in dorsal view.

SECTION 3

THE BIOLOGY OF PANULIRUS HOMARUS

This section deals with a study of the biology of the "megasculpta" form of Panulirus homarus in Natal waters, carried out during 1968, 1969 and 1970. Results are based on twenty-four consecutive monthly samples of the feral population, comprising a total of approximately 5,800 specimens. In addition, observations were made on rock lobsters kept in captivity at the Oceanographic Research Institute, Durban.

1.

MATERIAL AND METHODS

Sampling

All samples were collected by diving and each specimen was captured by hand. Due to the rough conditions in the surf zone, where the majority of specimens were obtained, it was not possible to employ any underwater breathing apparatus and basic skin-diving equipment was used; viz, mask, snorkel, flippers, a "wet" type sponge-neoprene suit, weight belt and gloves. In addition, each diver carried a bag around his waist in which to hold captured rock lobsters. SCUBA (Self Contained Breathing Apparatus) could only be used in deeper water outside the surf zone which was not subjected to strong wave action.

Collection of samples by diving eliminated selectivity inherent in various trapping methods, but in order to reduce possible subjectivity by the diver, a rule that every possible rock lobster should be captured within a shelter before moving on, was strictly complied with. As P. homarus is extremely gregarious, this system worked well and it is considered that provided sufficiently large numbers of specimens were captured, the samples obtained were adequately representative of the population.

All samples used for determination of biological cycles of P. homarus originated from the Natal coast, between Tugela River in the north and Umhlangankulu River at Port Edward in the south. Samples collected in Zululand and Mozambique and while diving from the research vessel MEIRING NAUDE were used for distributional and environmental studies only, as they were not obtained regularly and did not comprise large numbers.

Before this investigation was started, there were no sanctuaries for rock lobsters along the Natal coast, but in 1968 and 1969 certain areas were temporarily closed to exploitation for the period of a year, and one area was closed indefinitely. By confining research activity to these closed areas, the possibility of sampling immediately subsequent to exploitation by skin-divers was precluded. However, one year was insufficient time for the rock lobster stocks to return to a natural level and, particularly in the shallow water of the surf zone, where most diving for rock lobsters is done, the samples were affected to a greater or lesser extent by previous exploitation. The effect of exploitation on samples taken from offshore reefs was considered to be negligible, as depths greater than about 5 m are beyond the range of operation of the average skin-diver and use of artificial breathing apparatus is prohibited for capture of rock lobsters.

Collection of adequate samples from offshore reefs outside the surf zone necessitated use of SCUBA and due to the normally unfavourable diving conditions encountered along the Natal coast, only a single reef deeper than 5 m could be adequately, or regularly sampled.

This was "Limestone Reef" off Durban; an elongated flat-topped sandstone outcrop about 8 m deep at its base, with vertical sides rising up about 3 m to 4 m in height. It covers a considerable area, being at least 300 m long and about 25 m wide and has the advantage of being protected from the south-westerly wind by the Durban Bluff, making it possible to dive there on a few days each month. The fact that regular intensive sampling of offshore reefs had to be confined to a single locality is a limitation of this investigation. However, it is considered that the population of P. homarus on Limestone Reef is typical of that on other offshore reefs, as no difference was apparent between samples obtained there and the small samples taken from other reefs beyond the surf zone. The Limestone Reef area was proclaimed a rock lobster sanctuary for the duration of the sampling programme and collection of samples each month had no apparent effect on the population structure, probably due to continuous recruitment from extensive areas nearby, which are inaccessible to exploitation.

Although dives were made on reefs at depths of between 11 m and 42 m, very small numbers of P. homarus were encountered, thus suggesting that the sampling at Limestone Reef was done at a depth approaching the maximum at which P. homarus is still sufficiently abundant to make collection of a representative sample possible. It is therefore considered that the areas sampled in this investigation adequately cover the optimal vertical depth range of this species.

Treatment of Samples

Each monthly sample was stored in a deep-freeze until it was subjected to biometric analysis.

Unless otherwise stated, all observations were made on freshly thawed material and extensive periods in the deep-freeze were avoided to minimize weight loss due to dehydration.

Measurement and Recording of Data

Measurements were made to the nearest millimetre or gram and are defined as follows:

Carapace Length: The distance along the dorsal midline from the transverse ridge between the supra-orbital horns to the posterior extremity of the cephalothorax. This was used as the standard measurement of length.

Second Abdominal Segment Length: The minimum distance between the anterior and posterior extremities of the tergum.

Second Abdominal Segment Width: The maximum distance between the pleural spurs.

Total Length: The distance from the transverse ridge between the supra-orbital horns to the tip of the telson, measured along the dorsal midline. This measurement was made with a specially designed measuring board which held the animal straight, in order to minimize error due to the extensible abdomen.

Total Weight: Weight of the fully-thawed whole animal, excluding eggs in ovigerous females.

Tail Weight: Weight of the abdomen cut off flush with the anterior edge of the first abdominal segment.

The degree of development of the ovaries and external eggs, as well as the state of the exoskeleton in the moulting cycle and the state of the spermatophoric mass were each classified according to arbitrary scales and recorded as numerical values.

Although morphological relationships were determined largely for the applied aspects of this project, they are described below, as they demonstrate sexual dimorphism.

2.

MORPHOLOGICAL RELATIONSHIPS

Heydorn (1969a) described the following morphological relationships in P. homarus, but due to the small size of samples he had available, imperfect specimens with missing appendages were incorporated.

- (1) Carapace length/total weight,
- (2) Carapace length/tail weight ,
- (3) Tail weight/total weight.

The regression equations expressing the relationships in 1 and 2 above were recalculated in this investigation, incorporating data over a wider size range and using perfect specimens only. The following relationships were calculated in addition:

- (4) Carapace length/total length.
- (5) Carapace length/second abdominal segment length.
- (6) Carapace length/second abdominal segment width.
- (7) Carapace length/length of the third walking legs.

The relationship in 4 facilitates comparison of results in this investigation with those of other workers, in which total length was taken as the standard measurement and 5,6 and 7 were included as they demonstrate sexual dimorphism.

These relationships, with the exception of carapace length/leg length, were determined using a method of weighted regression described by Steffens and D'Aubrey (1967). The equation $y = m \cdot x + c$ was used in the case of 4, 5 and 6 while the exponential equation $y = m \cdot x^B$ was used in its logarithmic form $\log y = \log m + B \cdot \log x$ in 1 and 2. The relationship between carapace length and leg length was computed by the National Institute for Mathematical Sciences of the C.S.I.R.

1. Carapace Length (x) / Total weight (y)

Males $y = 0.00243 \times x^{2.7767}$

(281 observations over a carapace length range of 37 mm to 109 mm).

Females $y = 0.00177 \times x^{2.8590}$

(216 observations; carapace length range 35 mm to 105 mm).

These relationships conform closely with the regressions calculated by Heydorn (1969a, Fig. 3). Total weight increases at a rate slightly less than the cube of the carapace length and becomes progressively heavier in females than in males of the same length.

2. Carapace Length / Tail Weight

Males $y = 0.0009147 \times x^{2.707}$

(293 observations over a carapace length range of 37 mm to 109 mm).

Females $y = 0.0007473 \times x^{2.7945}$

(207 observations over a carapace length range of 35 mm to 105 mm).

These also conform closely with the regressions calculated by Heydorn (1969a, Fig.4). Tail weight increases at a rate slightly less than the cube of carapace length and becomes progressively heavier in females than in males of the same length.

3. The relationship between tail weight/total weight was determined by Heydorn (1969a) and was not recalculated in this investigation.

4. Carapace Length/Total Length (Fig. 1)

Males $y = 17.7625 + 2.5819 . x$

(297 observations over a carapace length range of 40 mm to 111 mm).

Females $y = -0.2780 + 2.9491 . x$

(271 observations over a carapace length range of 43 mm to 99 mm).

Total length increases in direct proportion to increase in carapace length. The total length of females is greater than in males of the same carapace length.

5. Carapace Length/Second Abdominal Segment Length (Fig 2)

Males $y = 1.4973 + 0.3206 . x$

(326 observations over a carapace length range of 32 mm to 117 mm.)

Females $y = 1.2625 + 0.3372 . x$

(310 observations over a carapace length range of 29 mm to 105 mm).

The second abdominal segment is slightly longer in females than in males of the same carapace length.

6. Carapace Length/Second Abdominal Segment width (Fig. 3).

Males $y = 3.4980 + 0.6173 . x$

(331 observations over a carapace length range of 32 mm to 117 mm).

$$\text{Females } y = 0.1838 + 0.7177 \cdot x$$

(311 observations over a carapace length range of 29 mm to 105 mm).

The second abdominal segment is wider in females than in males of the same length.

7. Carapace Length/Leg Length (Fig. 4)

Male specimens of P. homarus exhibit striking allometric elongation of the walking legs, particularly the second and third pairs, whereas in females leg length increases in direct proportion to increase of carapace length (see Fig. 4). This has also been noted in P. ornatus (Gordon 1960) and in P. japonicus (Kubo 1938). It will be shown that this adaptation probably enables males to withdraw females from their shelters and also plays an important part in overturning the female for copulation.

$$\text{Males } y = 61.9189 - 0.6469 \cdot X + 0.02234 \cdot X^2$$

The number of observations was 300 and the standard deviation about the regression line was 8.9629.

$$\text{Females } y = 5.4429 + 1.5867 \cdot X$$

The number of observations was 309 and the standard deviation about the regression line was 3.9090.

The two regression lines differ at a 5% level of significance for carapace lengths exceeding 48 mm.

Heydorn (1969a) showed that whereas tail weight decreases in relation to total weight with increased size in males, a slight increase is evident in females. The relationships between carapace length and second abdominal segment width and length show that the relatively heavier abdomen in females, as compared with males of an equivalent size, is due to increased dimensions of the abdomen.

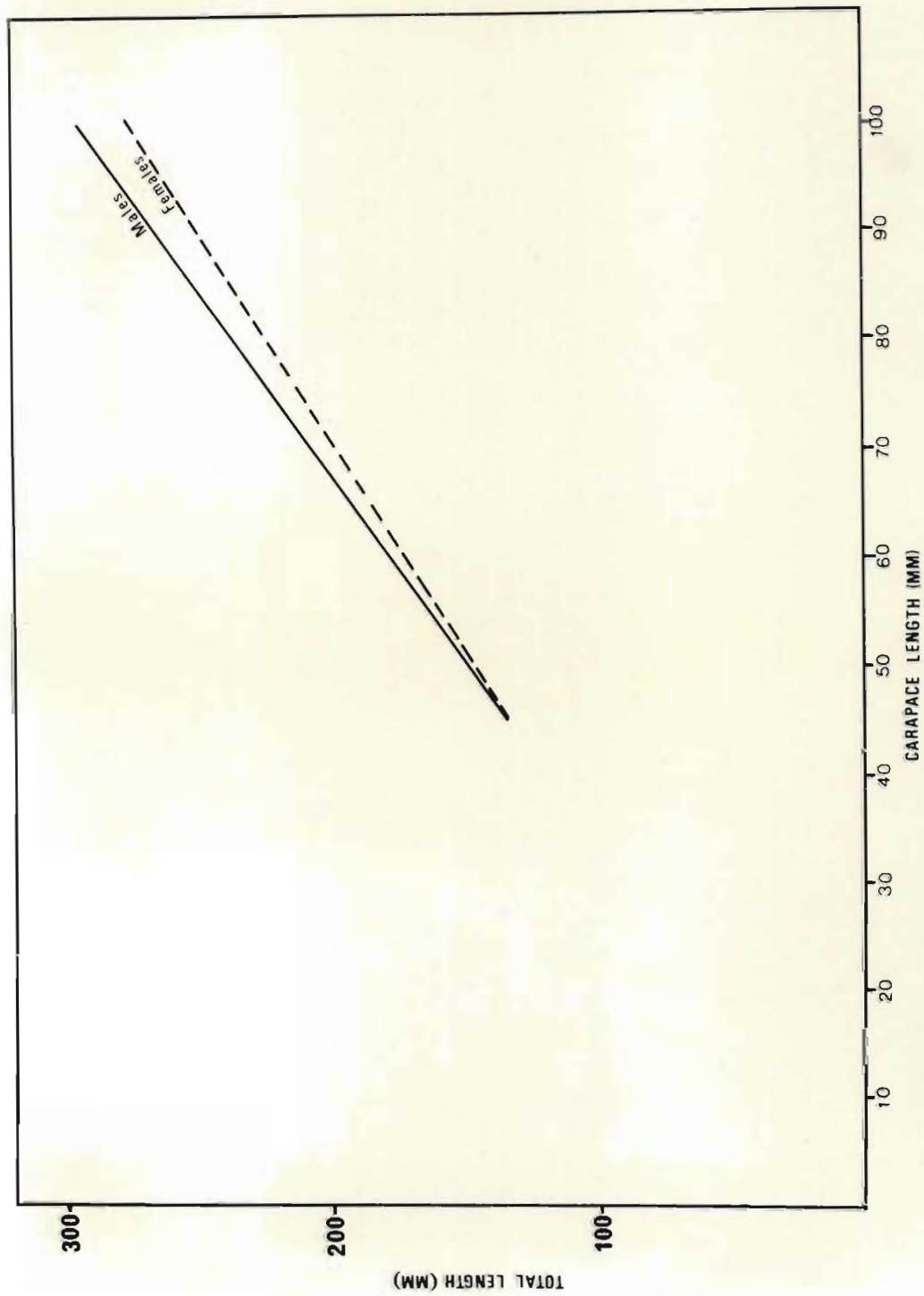


Fig. 1. Relationship between carapace length and total length.

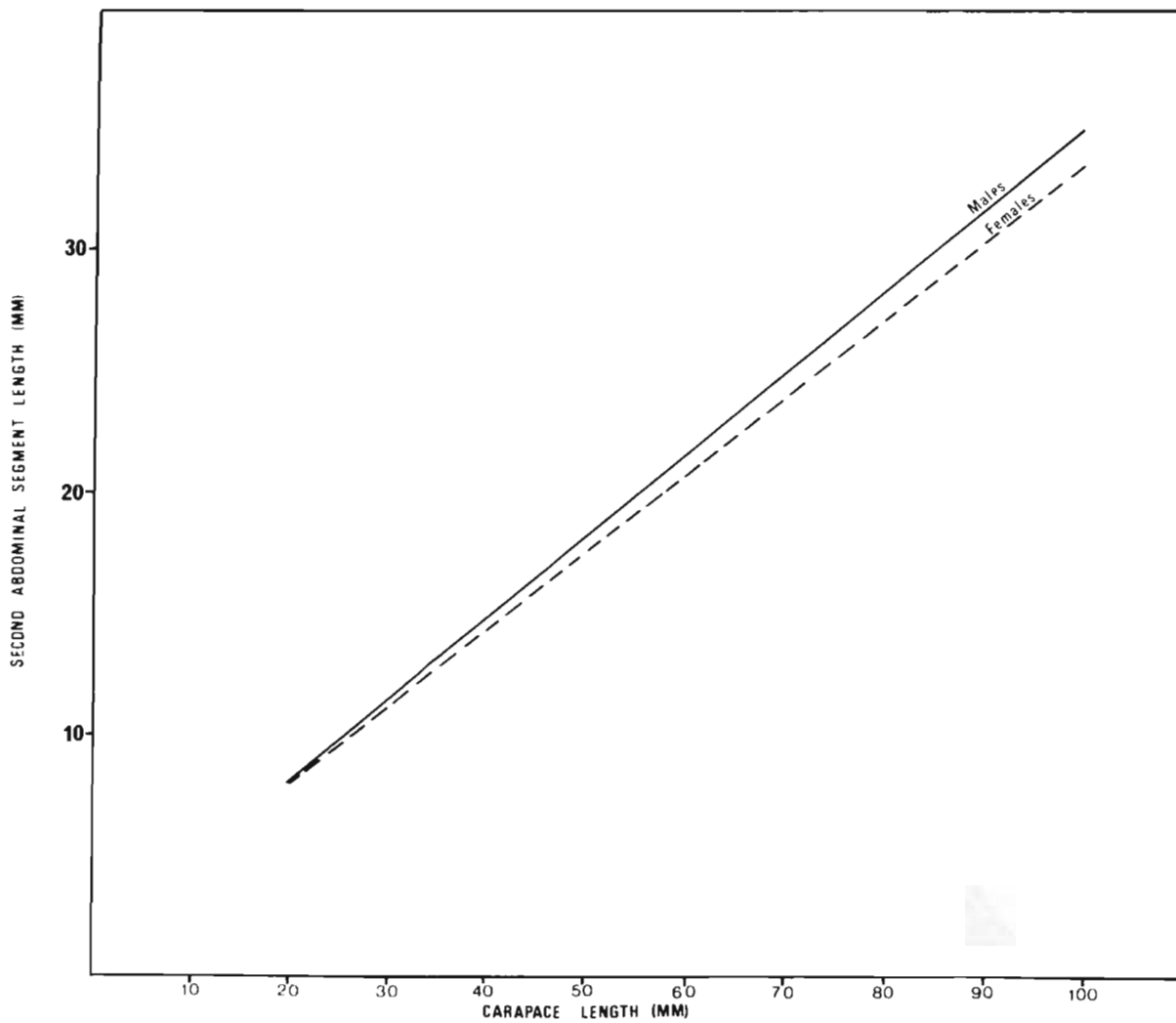


Fig. 2. Relationship between carapace length and second abdominal segment length.

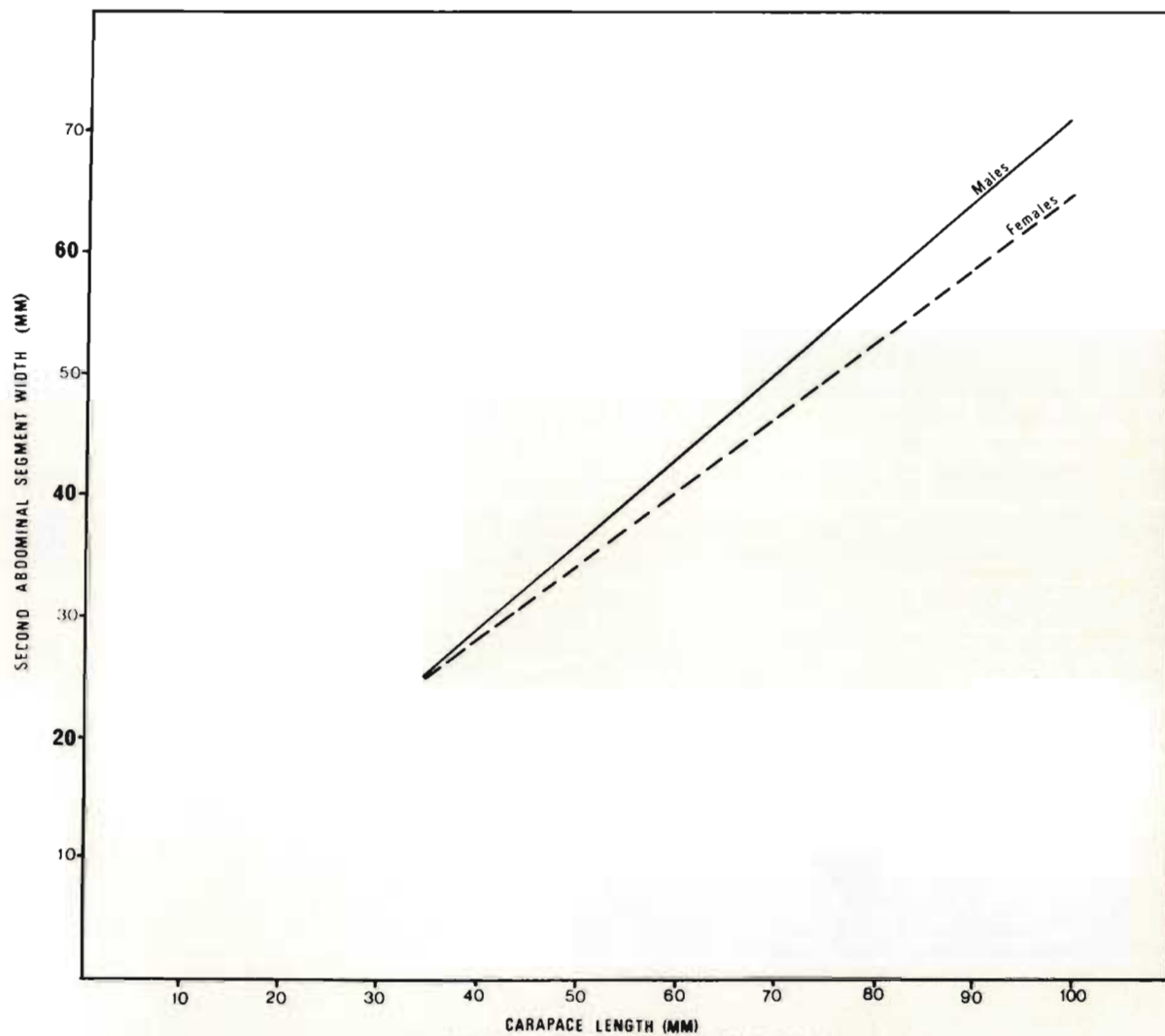


Fig. 3. Relationship between carapace length and second abdominal segment width.

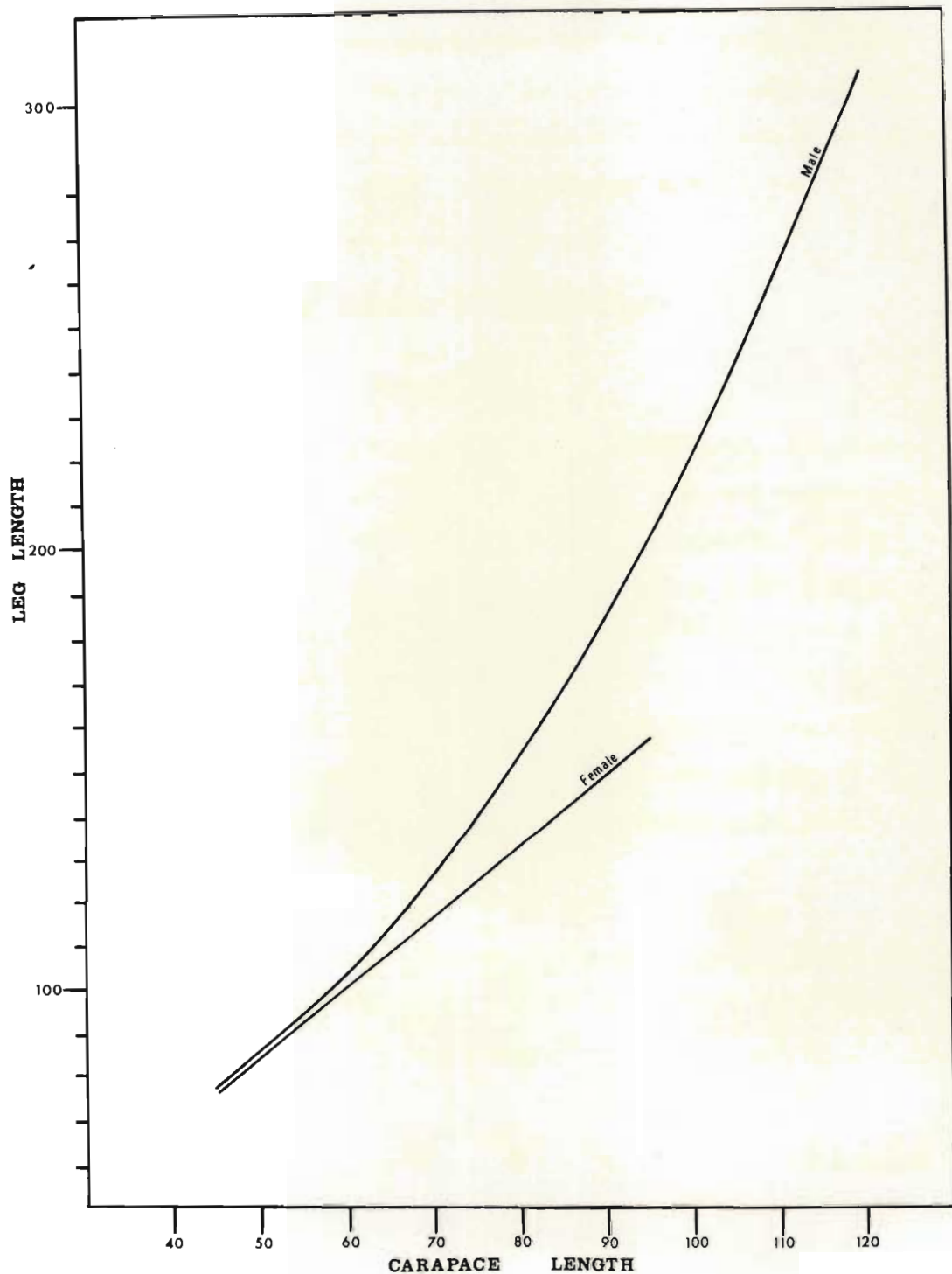


Fig. 4. Relationship between carapace length and length of the third walking leg.

This substantiates Heydorn's suggestion that the dimorphism may be related to egg-bearing in females. Elongation of the legs and enlargement of the cephalothorax would account for the decrease in tail weight relative to total weight with increased size in males.

3.

CHARACTERISTICS OF THE POPULATION

The Sex Ratio

The sex ratio in each size class, determined in the two years' samples combined, is shown in Table 1. Over the very small size range, in the 20 - 29 mm and 30 - 39 mm size classes, numbers are insufficient to be representative. From the 40 - 49 mm class to the 70 - 79 mm class, it is considered that a 50/50 ratio is reflected and the slight preponderance of females is attributed to a sampling artifact. Thereafter, a marked progressive increase in the proportion of males is evident, probably due to deceleration in the growth rate of females associated with egg production, and the larger maximum size attained by males.

The sex ratio on a monthly basis, combining the samples of the two years and incorporating the entire size range, shows little fluctuation and approximates closely to a 50/50 ratio, (Table 2).

Table 1. The sex ratio within each size class in the two years' samples combined.

Size Class	Numbers		Percentages	
	Males	Females	Males	Females
20 - 29	3	9	25	75
30 - 39	38	61	38	62
40 - 49	188	219	46	54
50 - 59	622	673	48	52
60 - 69	786	860	48	52
70 - 79	738	733	50	50
80 - 89	338	269	56	44
90 - 99	151	73	67	33
100 - 109	52	9	85	15
110 - 119	30	.1	97	3
120 - 129	1	0	100	0
TOTAL	2947	2907		

Table 2. The monthly sex ratio in the two years' samples combined.

Month	Number		Percentages	
	Males	Females	Males	Females
Feb.	250	211	54	46
March	271	189	59	41
April	138	163	46	54
May	219	211	51	49
June	147	170	46	54
July	208	230	47	53
August	299	282	51	49
Sept.	235	226	51	49
Oct.	307	332	48	52
Nov.	362	270	49	51
Dec.	291	282	51	49
Jan.	220	241	48	52
TOTAL	2947	2907	50	50

No difference in the sex ratio of samples from the surf zone or Limestone Reef was evident and it appears that no segregation of the sexes or movement of either sex from deeper to shallower water, or visa versa, occurs. This is substantiated by the fact that ovigerous females over the entire reproductive size range were obtained at all depths.

Size Composition

The size composition of samples from shallow water in the surf zone and deeper water at Limestone Reef was found to differ considerably. This is shown in Table 3 and Fig. 5, which are based on the total catch of the two year sampling period.

An important consideration in comparing the size frequency distributions shown in Fig. 5, is that the one in the surf zone reflects a certain degree of exploitation, whereas it is considered that exploitation has had a negligible effect on the Limestone Reef sample. The minimum legal size limit in the fishery for P. homarus falls in the 60 - 69 mm class and it seems likely that selection by skindivers for large rock lobsters, over the legal size limit, has resulted in a decrease in the proportion of large specimens in the surf zone compared with an unexploited situation. The rapid fall-off in numbers in the catch composition below the 50 - 59 mm class is a sampling artifact, due to inability to catch more than a small proportion of small rock-lobsters with gloved hands. The fall-off in numbers in the Limestone Reef catch composition cannot be attributed to the same cause as the majority of specimens are well above the size where this sampling artifact occurs.

The conclusion drawn from comparison of these size frequency distributions is that in the surf zone the entire size range is represented, whereas on Limestone Reef and probably all reefs beyond the surf zone, the majority of specimens are in the upper range of the size distribution. This is apparently not due to preference of deeper water by large rock lobsters, but seems rather to be due to confinement of small specimens predominantly to the surf zone. The reasons for this are not clear, but will be discussed further in the ~~chapter~~ dealing with feeding.

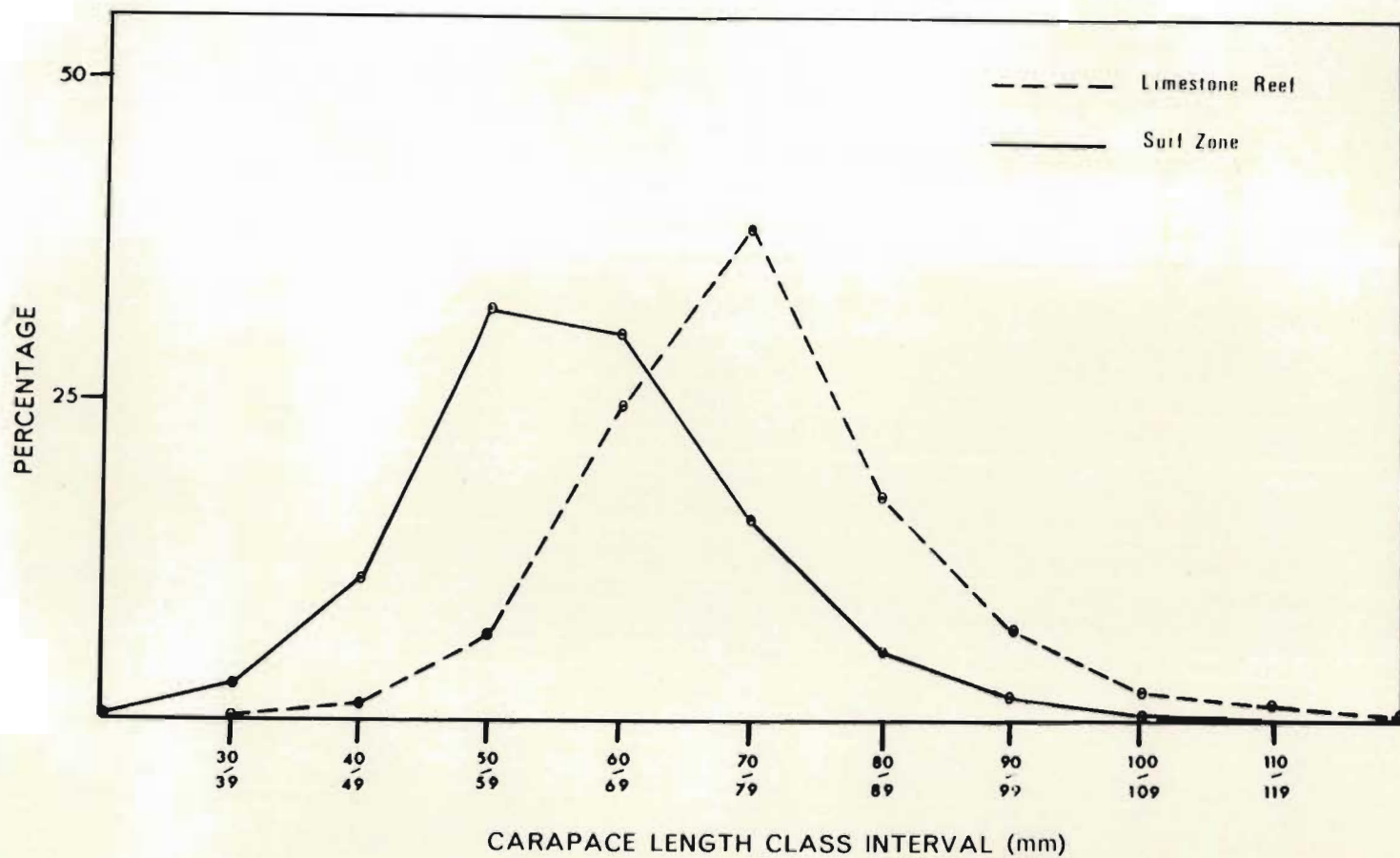


Fig. 5. Size frequency distributions for Limestone Reef and the surf zone, based on the total catch of both sexes over the two year sampling period, (see Table 3).

Table 3. Frequencies in each size class at Limestone Reef and from the surf zone over the entire two year sampling period.

		20	30	40	50	60	70	80	90	100	110
		29	39	49	59	69	79	89	99	109	119
Limestone Reef	No	0	9	29	159	568	899	407	168	50	30
	%	0	0.4	1.3	6.8	24.5	38.8	17.5	7.2	2.2	1.3
Surf Zone	No	12	97	399	1142	1075	562	196	62	7	2
	%	0.4	2.7	11.2	32.1	30.2	15.8	5.5	1.7	0.2	0

The numbers of males and females in each size class, in samples from Limestone Reef and the surf zone were recorded on a monthly basis, (Tables 4 - 11) and are illustrated in Figs. 6 - 9, expressed as percentages.

In samples from the surf zone, examination of Figs. 6 and 7 show that the modal size class is the same for both sexes in most months, and varies between the 50 - 59 mm and 60 - 69 mm classes. Attainment of a larger maximum size by males is evident virtually every month.

Figs. 8 and 9 show that at Limestone Reef, the 70 - 79 mm size class is the mode in both sexes in most months. Attainment of a larger maximum size by males is evident virtually every month.

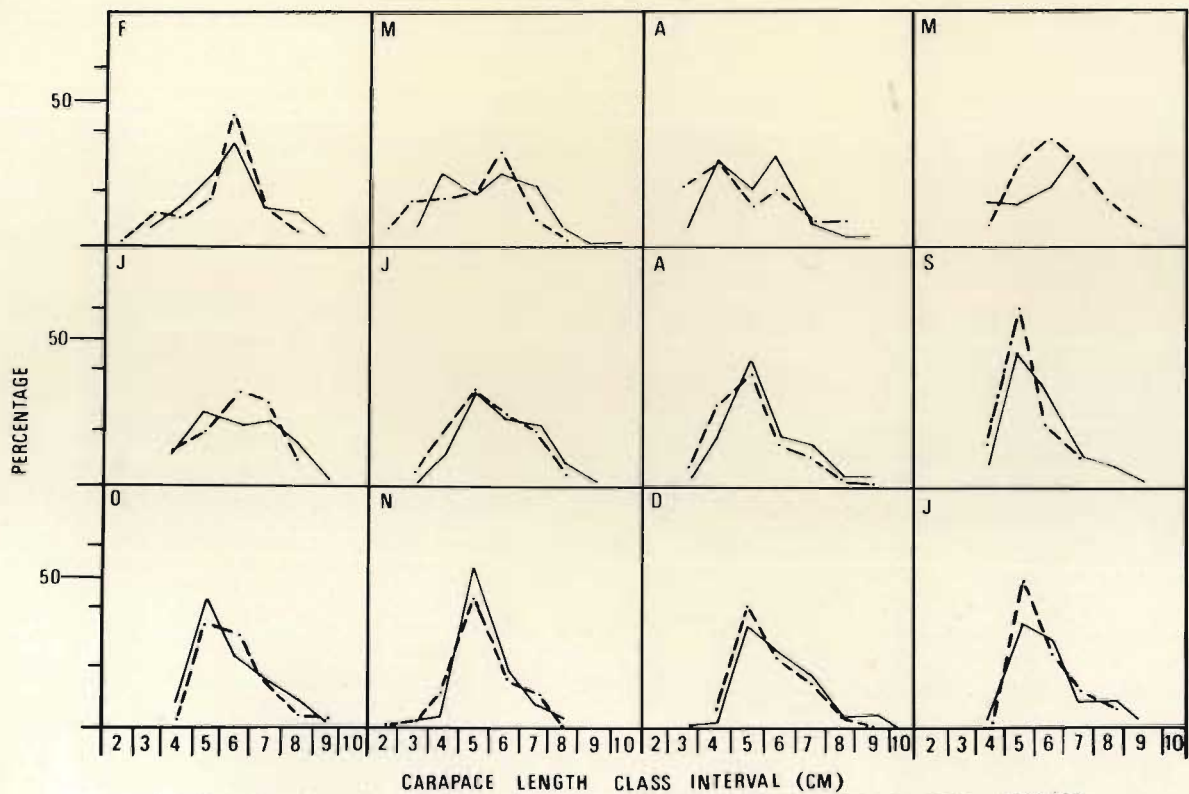


Fig. 6. Monthly size frequencies of males and females from the surf zone, 1968/69.
 (Solid lines = males, broken lines = females).

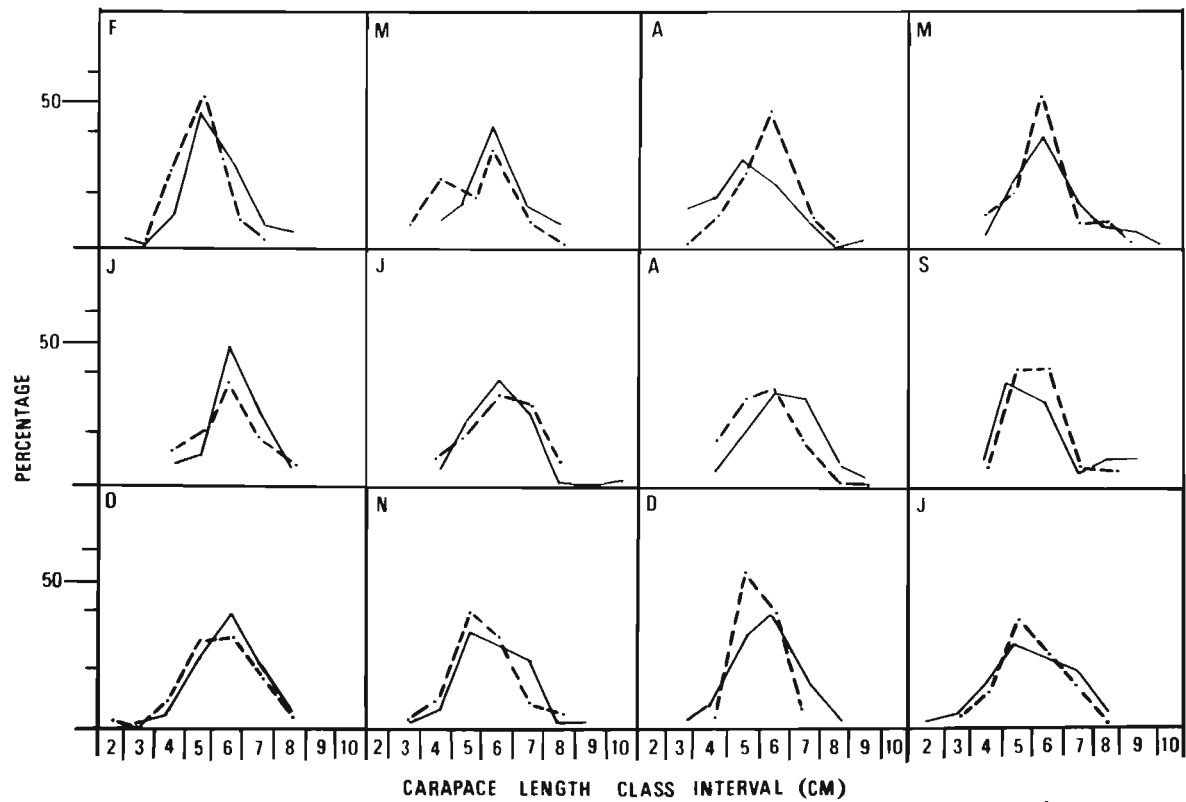


Fig. 7. Monthly size frequencies of males and females from the surf zone, 1969/70.
 (Solid lines = males, broken lines = females).

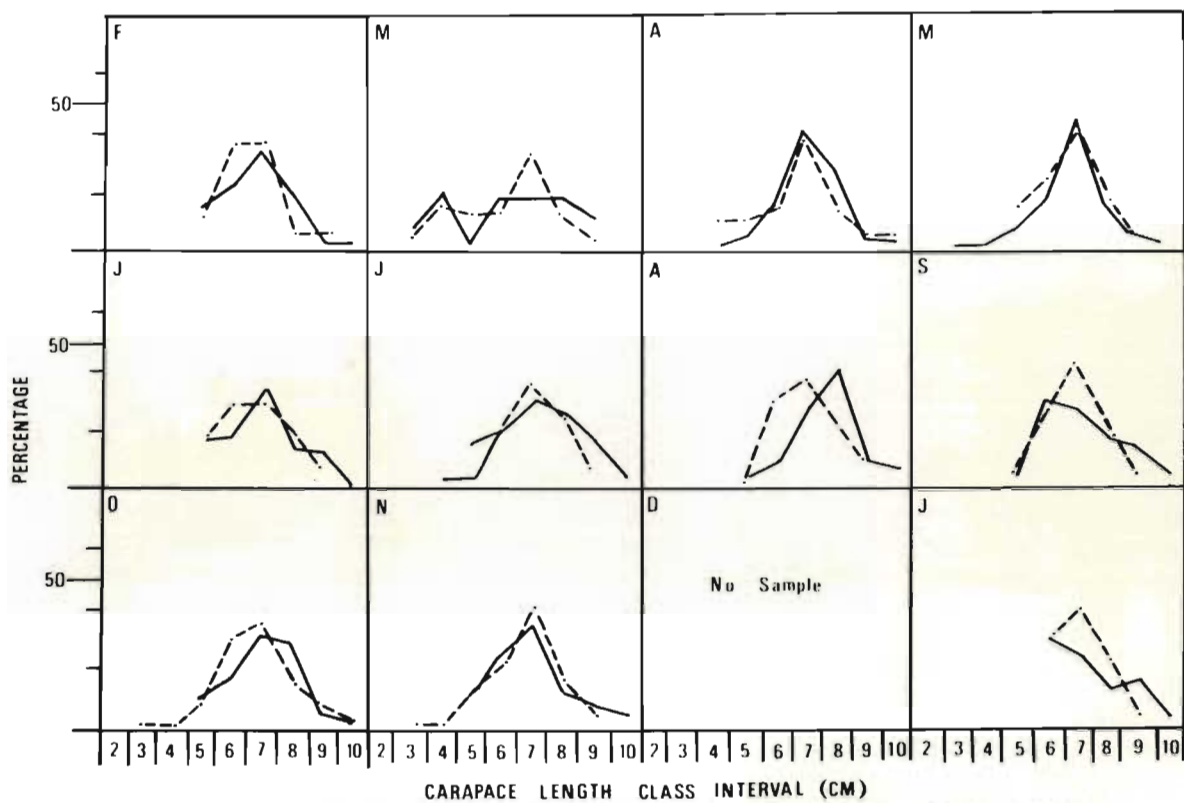


Fig. 8. Monthly size frequencies of males and females from Limestone Reef, 1968/69.
 (Solid lines = males, broken lines = females).

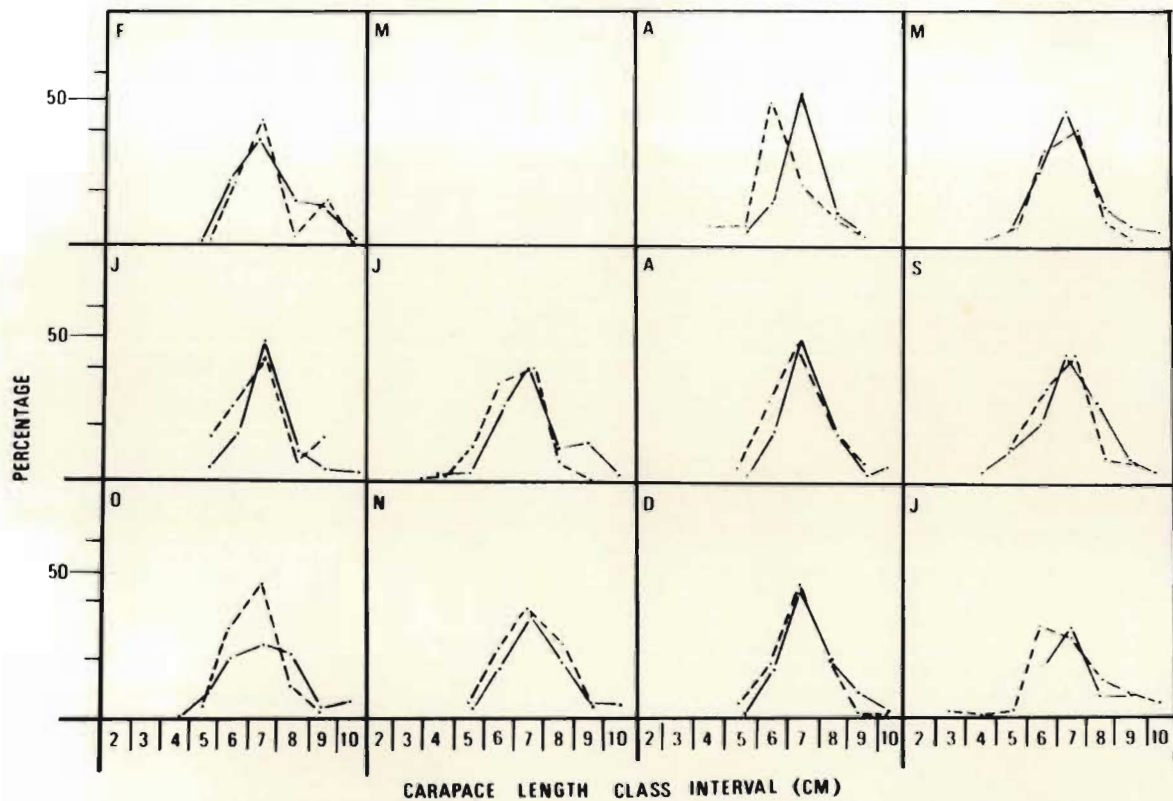


Fig. 9. Monthly size frequencies of males and females from Limestone Reef, 1969/70.
 (Solid lines = males, broken lines = females).

Table 4. Numbers of females in each size class in monthly samples from Limestone Reef, (1968/69).

Size Class	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	Total
Feb.			4	11	11	2	2		30
Mar.	2	5	4	4	10	4	1		30
Apr.		2	2	3	8	3	1	1	20
May			8	13	24	10	3		58
Jun.			5	9	9	6	2		31
Jul.			3	4	7	5	1		20
Aug.			1	28	33	20	8		90
Sep.			3	16	26	12	3		60
Oct.	1		5	21	24	12	5	2	70
Nov.	1		9	17	30	11	4		72
Dec.				No	Sample				
Jan.				7	9	5	1		22
Total	4	7	44	133	191	90	31	3	503

Table 5. Numbers of females in each size class in monthly samples from Limestone Reef, (1969/70).

Size Class	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	Total
Feb.			2	9	17	2	6	1	37
Mar.				No Sample					
Apr.		2	2	14	6	3	1		28
May		1	5	28	31	7	2		74
Jun.			6	12	19	3	7		47
Jul.	1	2	10	29	33	6	1		82
Aug.			2	16	30	13	4		65
Sep.		2	11	26	40	7	4		90
Oct.			4	22	32	8	1		67
Nov.			3	16	26	19	4		68
Dec.			4	12	31	16	2	1	66
Jan.	1		1	15	14	10	6		47
Total	2	7	50	199	279	94	38	2	671

Table 6. Numbers of males in each size class in monthly samples from Limestone Reef, (1968/69).

Size Class	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	Total
Feb.			4	6	9	5	1	1	1	27
Mar.	2	5	1	5	5	5	3			26
Apr.		1	2	5	14	9	2	1		34
May	1	1	4	10	26	9	4	1		56
Jun.			7	7	13	6	4		1	38
Jul.		1	1	5	8	6	4	1		26
Aug.			2	6	16	24	6	4	3	61
Sep.			3	22	19	12	10	4	2	72
Oct.			4	7	12	11	2	1	2	39
Nov.			8	18	25	9	6	4	2	72
Dec.				No Sample						
Jan.				9	7	4	5	1	3	29
Total	3	8	36	100	154	100	47	18	14	480

Table 7. Numbers of males in each size class in monthly samples from Limestone Reef (1969/70).

Size Class	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	Total
Feb.		1	14	24	11	10	2	2		64
Mar.				No	Sample					
Apr.		2	6	20	5	2	1			36
May		4	15	27	8	4	3			61
Jun.		2	7	19	5	2	1	2		38
Jul.	4	3	19	31	9	11				77
Aug.	1	2	15	40	14	2	4	1		79
Sep.	1	6	13	29	15	3		1		68
Oct.	1	6	16	18	15	4	6	1		67
Nov.		2	15	28	16	6	5	5	1	78
Dec.		1	10	26	12	5	2	2		58
Jan.			7	13	13	3	3	2		41
Total	7	29	137	275	123	52	27	16	1	667

Table 8. Numbers of females in each size class in monthly samples from the surf zone, (1968/69).

Size Class	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	Total
Feb.	1	12	11	18	45	14	6		107
Mar.	3	8	8	9	16	5	1		50
Apr.		7	10	5	7	3	3		35
May			1	4	5	4			14
Jun.			6	9	15	13	4		47
Jul.		3	14	25	19	15	4		80
Aug.		4	25	35	13	11	3	1	92
Sep.			7	32	11	5			55
Oct.			5	38	34	18	8	1	104
Nov.	2	6	21	13	34	23	6		165
Dec.		2	11	67	40	26	10	2	158
Jan.			2	34	18	8	4		66
Total	6	42	121	349	257	145	49	4	973

Table 9. Numbers of females in each size class in monthly samples from the surf zone, (1969/70).

Size Class	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	Total
Feb.		1	9	18	6	1			35
Mar.		7	27	20	38	12	4		108
Apr.		1	9	21	38	11	2		82
May			7	12	34	6	6	1	66
Jun.			7	10	17	9	4		47
Jul.			5	10	16	14	4		49
Aug.			10	20	21	11	2	1	65
Sep.			1	6	6	1	1		15
Oct.	3	2	10	28	29	16	4		92
Nov.		3	8	29	24	8	4		76
Dec.		1	1	34	24	3			63
Jan.		5	15	42	27	16	1		106
Total	3	20	109	250	280	108	32	2	804

Table 10. Numbers of males in each size class in monthly samples from the surf zone, (1968/69).

Size Class	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	Total
Feb.	6	15	24	42	16	12	4		119
Mar.	3	13	9	13	11	3		1	53
Apr.	2	9	6	9	3	1	1		31
May		4	4	5	8	4	2		27
Jun.		4	10	8	9	6	1		38
Jul.	1	6	18	12	11	5	1		54
Aug.	3	18	47	18	16	4	3		109
Sep.		5	29	19	6	4	1		64
Oct.		7	44	24	15	10	2		102
Nov.	4	10	80	32	14	5	3		148
Dec.	3	5	55	46	31	8	10	2	160
Jan.		2	25	21	8	8	3		67
Total	22	98	351	249	148	70	31	3	972

Table 11. Numbers of males in each size class in monthly samples from the surf zone, (1969/70).

Size Class	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	Total
Feb.	1		4	18	12	3	2			40
Mar.			19	33	84	28	16	11	1	192
Apr.		5	6	11	8	5		1		36
May			4	17	29	13	6	5	1	75
Jun.			3	4	16	8	2			33
Jul.			3	12	19	14	1		2	51
Aug.			3	9	17	15	4	2		50
Sep.			2	7	6	1	2	2		20
Oct.		2	8	22	40	21	6			99
Nov.		1	5	23	22	16	2	2		71
Dec.		1	6	23	28	13	2			73
Jan.	2	4	10	20	17	14	3			70
Total	3	13	73	199	298	151	46	23	4	810

The mean carapace length, the size range and the modal size class are summarised on a monthly basis in Tables 12 and 13. Comparison of these Tables shows that the mean carapace length of samples from Limestone Reef is considerably larger than in samples from the surf zone and in both areas it is slightly higher in males than in females. Over the two years sampled, the carapace length was found to range from 7 mm in postpueruli to a maximum of 102 mm in females and 127 mm in males.

It is considered that the composition of the monthly samples shows no evidence of migratory behaviour, although P. homarus probably does undertake short movements associated with sanding up of shelters and local availability of food.

Comparison of characteristics of the population of P. homarus obtained from Natal waters in the present investigation with those obtained in Transkeian and Eastern Province waters by Heydorn (1969a), is limited by difference in sampling methods. The majority of samples used by Heydorn were obtained from local Africans and are probably only representative of shallow water in the surf zone, where it is possible to catch rock lobsters on lines baited with limpets, or by wading out and catching them by hand. These samples are therefore best compared with those taken in the exploited surf zone in Natal, and examination of Fig. 10 shows that a higher incidence of large specimens, and a larger maximum size was recorded from Natal waters. However, in view of the difference in sampling methods, this does not necessarily mean that P. homarus is smaller in Transkeian waters, although a decrease in maximum size attained might be expected near its distributional limits.

Table 12. A summary of the mean carapace length, size range and modal size class in monthly samples from Limestone Reef.

	Number		Mean carapace length		Modal carapace length		Size Range	
	M	F	M	F	M	F	M	F
Feb. 1968	27	30	75	70	70-79	60-79	51-117	50-96
1969	64	37	78	75	70-79	70-79	57-115	55-102
Mar. 1968	26	30	68	64	60-79	70-79	38-98	38-95
1969								
Apr. 1968	34	20	75	72	70-79	70-79	47-101	44-105
1969	36	28	76	69	70-79	60-69	57-102	41-93
May 1968	56	58	73	72	70-79	70-79	31-104	50-97
1969	61	74	75	71	70-79	70-79	59-102	45-93
Jun. 1968	38	31	74	71	70-79	60-79	50-112	51-93
1969	38	47	76	72	70-79	70-79	51-114	50-98
Jul. 1968	26	20	74	73	70-79	70-79	47-108	52-96
1969	77	82	74	69	70-79	70-79	46-97	35-90
Aug. 1968	61	90	83	75	80-89	70-79	58-115	58-96
1969	79	65	76	74	70-79	70-79	40-119	50-99
Sep. 1968	72	60	77	73	60-69	70-79	53-114	52-95
1969	68	90	74	70	70-79	70-79	47-111	45-96
Oct. 1968	39	69	74	73	70-79	70-79	51-112	30-102
1969	67	67	76	71	70-79	70-79	43-116	52-90
Nov. 1968	72	72	75	72	70-79	70-79	52-116	38-94
1969	77	68	80	75	70-79	70-79	51-127	52-96
Dec. 1968								
1969	58	66	79	84	70-79	70-79	50-114	52-102
Jan. 1969	29	22	81	74	60-69	70-79	62-113	60-91
1970	41	47	82	75	70-79	60-69	64-110	38-93

Table 13. A summary of the mean carapace length, size range and modal size class in monthly samples from the surf zone.

	Number		Mean carapace length		Modal carapace length		Size Range	
	M	F	M	F	M	F	M	F
Feb. 1968	119	107	61	55	60-69	60-69	32-90	29-87
1969	40	35	60	54	50-59	50-59	23-81	34-70
Mar. 1968	53	50	59	50	40-49 60-69	60-69	31-100	26-84
1969	192	108	66	58		60-69	60-69	40-100
Apr. 1968	31	35	54	49	40-49 60-69	40-49	38-99	39-80
1969	36	82	60	60		50-59	60-69	39-98
May 1968	27	14	60	58	70-79	60-69	41-94	46-78
1969	75	66	67	64	60-69	60-69	40-103	41-90
Jun. 1968	38	47	66	47	50-59	60-69	46-91	40-85
1969	33	47	65	62	60-69	60-69	41-83	41-85
Jul. 1968	54	80	64	59	50-59	50-59	39-97	34-85
1969	51	49	67	68	60-69	60-69	42-104	48-87
Aug. 1968	109	92	59	57	50-59	50-59	33-97	32-90
1969	50	65	53	61	60-69	60-69	40-99	40-99
Sep. 1968	64	55	61	57	50-59	50-59	44-95	43-75
1969	20	15	65	61	50-59	50-69	48-92	48-83
Oct. 1968	102	104	63	63	50-59	50-59	40-98	43-92
1969	99	92	66	60	60-69	60-69	30-89	20-83
Nov. 1968	148	165	71	68	50-59	50-59	37-99	56-89
1969	71	76	62	59	50-59	50-59	32-95	35-89
Dec. 1968	160	158	65	61	50-59	50-59	35-104	37-98
1969	73	63	61	59	60-69	50-59	32-82	36-96
Jan. 1969	67	66	66	61	50-59	50-59	45-98	46-87
1970	70	106	59	58	50-59	50-59	23-80	38-81

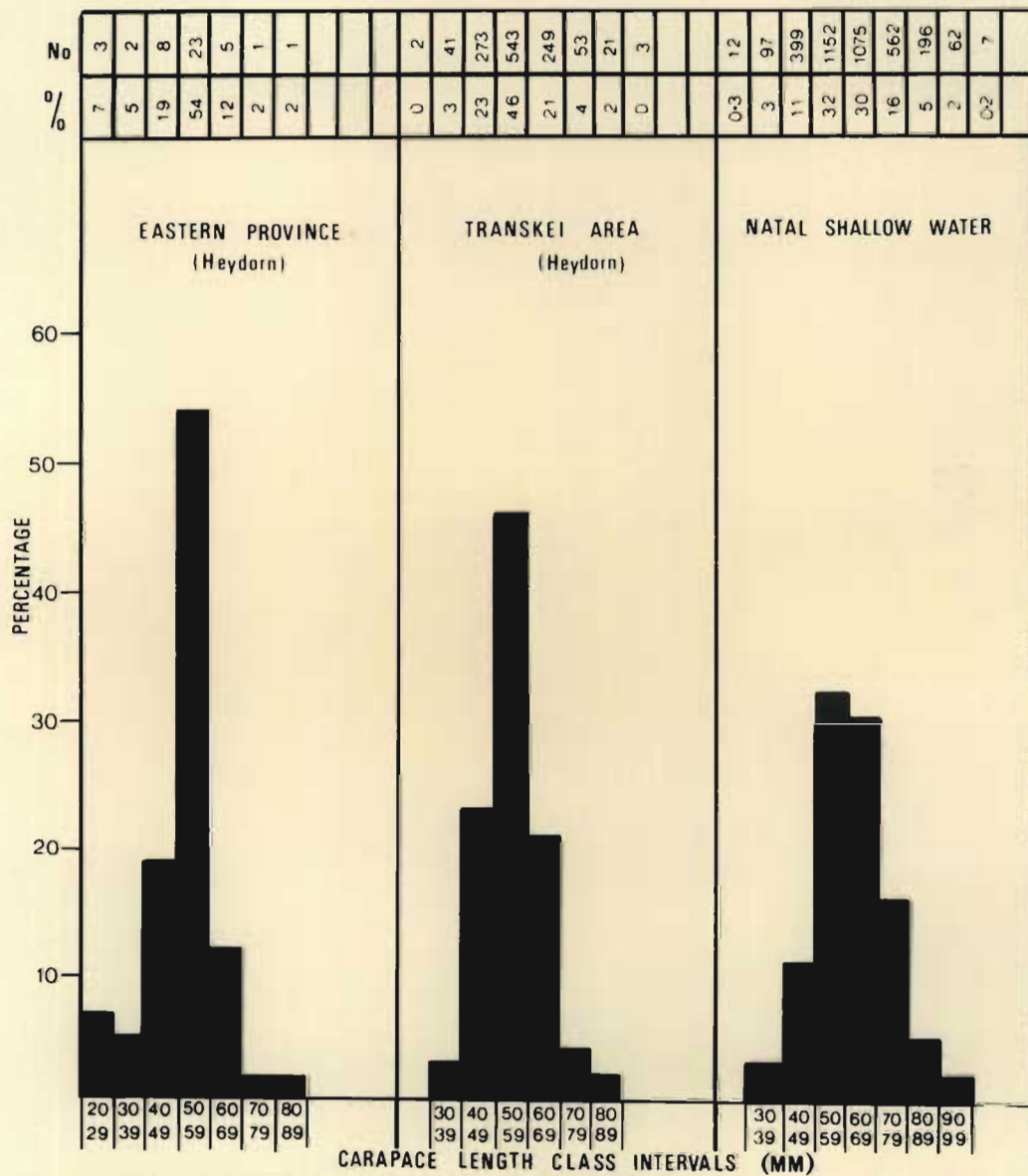


Fig. 10. A comparison of the size frequency distribution of samples from the Eastern Province, Transkei area (Heydorn, 1969a) and the surf zone in Natal.

Comparison of the size of P. homarus from Natal, Aden and Ceylon is presented in Table 14. This shows a very similar situation in these three regions and if in fact the same species is represented, the samples from Natal do not appear to show signs of reduction in size which might be attributed to occurrence in marginal conditions, as suggested by Heydorn (1969a).

Table 14. Comparison of carapace length in samples of P. homarus from Natal, Aden (George, 1963) and Ceylon (De Bruin, 1962).

Locality	Carapace length size range (mm)	Modal size class
Natal	7 - 127	50 - 59 (Surf) 70 - 79 (Limestone)
E. Aden	30 - <120, >130	80 - 89
Ceylon	39 - 112	70 - 79

4.

MATING BEHAVIOUR, OVIPOSITION AND FERTILIZATION

The following account of mating behaviour, oviposition and fertilization has been published in the Investigational Report Series of the Oceanographic Research Institute, Durban (Berry, 1970).

Little has been written of reproductive behaviour within the Palinuridae and from the brief descriptions in the literature, summarised by Fielder (1964a) and Heydorn (1969a), it appears that deposition of the spermatophoric mass has not previously been observed.

Fortunately, P. homarus thrives in captivity, and during 1967 and 1968 a study of mating behaviour, oviposition and fertilization was possible in rock lobsters kept in tanks at the Centenary Aquarium, Durban. During this period spermatophoric masses were deposited on seventeen females, courtship behaviour was observed on eleven occasions, mating on three occasions and oviposition on five occasions.

Method

Thirty rock lobsters, comprising fifteen of each sex were maintained in a tank measuring 3 m x 1.5 m x 1 m with a natural setting of rocks under which they could take refuge. A continuous flow of filtered sea water was pumped into the tank from an offshore well-point system and seasonal temperature changes offshore were reflected in the tank. In order to minimise algal growth on the exoskeletons of the lobsters, infra-red insolation was reduced by covering the tank with translucent sheets of green fibreglass. Copper sulphate is toxic to rock lobsters and cannot be used as an algicide. The lobsters were fed on live black mussels (Perna perna) and chopped fish. Observations were made through a large glass viewing window and mating behaviour was recorded on ciné film which was used for subsequent analysis.

Courtship behaviour and mating

In the present investigation all seventeen matings took place with the exoskeleton of both the male and female in a hard condition, but most of the females were recorded to have moulted a short while prior to mating (Table 15).

Table 15. Interval (in days) between moulting, mating and oviposition

Specimen	Interval between moulting and mating	Spermatophoric mass in postcopulatory stage	Spermatophoric mass in prefertilization stage	Interval between mating and oviposition
A	30	42	2	44
B	24	38	1	39
C	32	5	2	7
D	27	7	1	8
E	24	6	2	8
F	33	6	3	9
G	24	8	1	9
H	24	3	2	5
I	22	4	2	6
J	32	1	2	3
K	28	1	5	6
L	?	3	2	5
M	?	10	2	12
N	?	6	1	7
O	?	6	2	8
P	?	11	5	16
Q	?	5	5	10

Male lobsters were observed to show sudden attraction to particular sexually mature females, two of which were dissected and found to have ripe ovaries. Moreover, as the other attractive females oviposited shortly after mating, their ovaries must also have been ripe and it appears that the males were only attracted by females which had attained a reproductively receptive condition.

The presence of an attractive female resulted in the formation of a reproductive hierarchy of males in which one was dominant and showed aggression to all other males. During the breeding seasons of both 1967 and 1968, all mating was done by the same dominant male which was the largest perfect specimen in the tank and had a carapace length of 94 mm in 1967, and 95 mm in 1968. Two larger males were present which were subordinate, probably as they had missing and regenerated legs. Although the dominant male showed aggression of varying intensity towards different subordinate individuals, these exhibited no aggression towards one another and no ranks could be detected amongst them.

The reproductive hierarchy of males is distinct from the dominance order for shelter observed in P. homarus, which included both sexes and in which a basically straight line order of dominance existed (where specimen A was dominant to B which was dominant to C etc.), largely determined by size.

Courtship behaviour can be divided into two phases of activity.

1 Pre-copulatory phase

On the eleven occasions that courtship behaviour was observed, the dominant male took up a position in front of a particular female which remained in her shelter. All males in the immediate vicinity of the female were ejected from their shelters, but non-attractive females were ignored.

The male constantly flicked his antennules over the exposed frontal portion of the female and occasionally scraped at her tentatively with the dactyls of his third legs. Subordinate males showed attraction to the female but were vigorously driven off by the dominant male who immediately recognised their sex if they chanced to come into contact with his antennae or legs. No visual recognition appeared to be shown.

The attendant male scraped at the female with increasing frequency which usually resulted in the female leaving her shelter. However, if she would not move the male attempted to withdraw her by hooking the dactyls of his second and third legs under her coxae and branchiostegites and pulling her out. Once in the open, the male walked at the female's side, keeping close contact with her and often straddled her with his legs, while constantly brushing her with his antennules and scraping her lightly with the dactyls of his third legs. The female walked with her abdomen tightly flexed and her sternum close to the ground giving a "hunched" appearance, whereas the male walked with abdomen uropods and pleopods extended. The female showed little inclination to remain in the open and after a few minutes would return to her original shelter or enter a new one. The male would then take up a position in front of her and the sequence would be repeated until the intensity of the male's scraping again drove the female out. This phase of behaviour lasted for 5-13 hours and the periods for which the male allowed the female to remain "holed up" became increasingly shorter.

If the dominant male came into contact with another male while following the female, he would immediately drive it off for several feet, thus losing contact with the female. He would then return to where the female had been, coursing from side to side with antennules flicking violently until he had located her again.

2 Copulatory Phase

This phase which lasted for 3-12 hours was characterised by extreme activity of the attentive male which extricated the attractive female as soon as she entered a shelter. Aggression towards subordinate males was intensified. Three basic patterns of activity can be recognised.

The moving female elicited a following response in the male as described in the precopulatory phase. However, the male did not remain at the female's side but made repeated attempts to move ahead of her and confront her head on, whereupon the female immediately stopped with her anterior cephalothorax and antennules lowered and touching the ground. This position usually culminated in an attempt at copulation, but should the female have stopped in such a position that the male was prevented from making a frontal approach by some obstruction, he approached her from the side and began to scrape and claw at her dorsum, while constantly brushing her with his antennules. After a brief period the male gripped the female's legs with his and pulled her towards him. Alternatively he placed his legs over the female's carapace, hooking the dactyls under her branchiostegite and pulled her towards him, sometimes almost turning her over in the process. The side approach of the male did not appear to be an attempt at copulation but an attempt to dislodge the female prior to manoeuvring her for a frontal approach.

After stopping the female by confronting her head on, the male took up a position in front of her with his legs widely extended laterally. If the female remained stationary for about

30 seconds the male drew back a few inches and assumed a position with abdomen elevated and the frontal region of the cephalothorax and the antennules lowered. After 2-5 seconds during which the male showed progressively more intense agitation by clawing at the ground, he rushed at the female with legs stretched forwards and lifted her frontal cephalothorax with his rostral plate and antennae, while gripping her legs with his second and third legs and pulling them towards him. In this way he lifted the female up and exposed her sternum. The female was driven backwards by this rush and usually escaped by giving a few flaps with her abdomen. Such attempts at copulation failed repeatedly but as the male's activity became progressively more intense, the female appeared to become more submissive.

On the three occasions when mating was observed, the male made a frontal rush, driving the female backwards and lifting her up with her tail flexed beneath her. In one case the female was forced into a corner and in the other two cases the female's abdomen caught against rocks. These obstructions stopped her backward progress and enabled the male in each case to "embrace" her, bringing the two animals sternum to sternum in an almost vertical position, although on one occasion the female was completely overturned. In this embrace, which lasted approximately 5-8 seconds, the male flapped his abdomen violently before releasing the female, who darted across the tank with a freshly deposited spermatophoric mass on her sternum.

Courtship activity continued apparently unaffected through daylight and darkness which is surprising as P. homarus is normally nocturnal.

On attainment of sexual maturity, male specimens of P. homarus exhibit striking allometric growth of the second and third legs, (see page 104). This is apparently an adaptation which enables large males to withdraw females from deep crevices and also plays an important part in overturning the female for copulation. It seems unlikely that males are capable of copulating with females larger than themselves and it is significant that males attain a considerably larger size than females.

The suddenness with which females became attractive to males and the ability of males to locate an attractive female has led the author to suspect that reproductively receptive females exude a sex attractant. Ryan (1966) has demonstrated the production of a sex attractant pheromone in the urine of pre-moult female crabs of the species Poftunus sanguinolentus. He found that male crabs responded with characteristic searching behaviour when placed in water in which sexually attractive females had been kept. If the excretory openings of attractive females were plugged, the water did not induce searching activity in males. Attempts to repeat Ryan's experiments with P. homarus during 1969 were inconclusive due to the fact that specimens which were isolated in small experimental tanks (measuring 150 cm X 57 cm X 47 cm) did not become sexually attractive or mate. Water taken from the large tank (described previously), in which a sexually attractive female was present, failed to induce searching behaviour in males, isolated in a small volume of water. This could have been due to dilution of the attractant in the large tank or lack of sexual response in closely confined males. Moreover, when sexually attractive females were removed from the large tank they became unattractive to males for at least a day, even if replaced immediately into the same tank. This was probably due to trauma resulting from catching/
catching/

them which was extremely difficult as they would take refuge in a shelter and it was almost impossible to extricate them without damage. Thus no meaningful results could be obtained by plugging the excretory openings. Sexually attractive females were, however, found to be continuously producing urine, much in excess of that produced by non-attractive females. This urine was collected in capillary tubes but failed to induce a sexual response in males, even when a tube was attached to a non-attractive female. It must be concluded therefore, that if a sex attractant pheromone is released in the urine, the female must be able to arrest its production. Ryan's findings, in fact, suggest that this occurred in P. sanguinolentus, although production of the attractant was resumed after only about two hours.

In P. homarus, the dominant male is able to distinguish between subordinate males, non-attractive females and attractive females on contact with his antennae or legs. Moreover the impression was gained that actual contact was necessary before recognition occurred and contact with any part of another animal enabled the dominant male to make this recognition. This indicates that the sex attractant may not be localised in a particular area. If this is so the tegumentary glands seem to be possible sites for release of a substance involved in chemo-recognition, as according to Yonge (1932), they are scattered unevenly over the body, they open to the exterior by ducts, and being involved in cuticle secretion, their activity is presumably under hormonal control.

Thus although there is strong circumstantial evidence that P. homarus produces a sex attractant, conclusive proof of its existence and its site of production has yet to be obtained.

The Spermatophoric Mass

The spermatophoric mass of the genus Panulirus is typically composed of a matrix in which are embedded two highly convoluted tubules, the spermatophores, containing the spermatozoa. The mass is formed from the products of the paired gonads of the male and a single spermatophore with its surrounding matrix is extruded simultaneously from each gonopore during copulation. The component from each gonopore is plastered to the female's sternum and the two coalesce medially, giving the spermatophoric mass a bilaterally symmetrical appearance (Fig. 11).

The only detailed study of the spermatophoric mass of a rock lobster is that by Matthews (1951) on P. penicillatus. Heydorn (1969a) has briefly described the spermatophoric mass of P. homarus immediately after deposition and subsequent to fertilization. He also compares its gross morphology and colour with descriptions of spermatophoric masses of other species within the genus, and agrees with Matthews that spermatozoa are liberated by mechanical means. The spermatophoric mass of P. homarus has been studied in more detail in the present investigation and further observations on the mechanism of liberation of spermatozoa have been made.

In sexually mature females the posterior two sternal plates each has a soft uncalcified "window" on either side of the midline (Fig. 14). The anterior uncalcified windows are smaller and more rounded than the posterior ones which are oval and cover a large area of the sternal plate. An elevated

calcified ridge extends along the base of each posterior window. These uncalcified regions appear similar to those described in P. interruptus by Lindberg (1955) who states "... the posterior segments of the sternum of mature females are soft and fleshy, presumably as an adaptation for reception and retention of the spermatophore". Sexually immature females do not have these uncalcified areas but at puberty the posterior windows begin to develop and only after a certain size is attained do the anterior windows appear. At present their function is still open to conjecture but Lindberg's suggestion that they are an adaptation for retention of the spermatophoric mass seems unlikely, as a soft surface seems less suitable for adhesion of the spermatophoric mass than the calcified portions with elevated ridges and grooves. A more plausible explanation seems to be that the soft areas enable the male to locate the correct position for deposition of the spermatophoric mass with his copulatory organs, both of which are supplied with tufts of sensory setae.

Large males have sufficient spermatophoric material within their vasa deferentia for several matings. Observations on mating behaviour suggest that they are polygamous and are probably only able to mate with females smaller than themselves. As the size of the spermatophoric mass relative to the size of the female bearing it is approximately the same in all females, with the exception of some very small ones, it seems probable that males are able to control the size of the spermatophoric mass deposited. It is possible therefore, that the degree of development of the windows, which shows a positive correlation with the size of the female, may supply the stimulus for this regulation. If males can only mate with females smaller than themselves, presumably the situation would not arise where too

small a spermatophoric mass is deposited relative to the size of the female. It seems unlikely that very large males would be able to mate successfully with very small females, and an extreme difference in size of animals involved may account for occasional small females which were found with an excessively large spermatophoric mass covering the entire sternum, coxopodites and gonopores. This appears to be exceptional and regulation of the size of the spermatophoric mass probably failed to occur.

The spermatophoric mass undergoes considerable changes in appearance subsequent to deposition on the female and the following three stages are recognised in the present investigation.

- (1) An unscraped post-copulatory stage.
- (2) A scraped pre-fertilization stage.
- (3) A fragmented post-fertilization stage.

(1) Post-copulatory stage (Fig. 11)

The freshly deposited spermatophoric mass covers the entire surface of the posterior two sternal plates of the female's cephalothorax, and although it may extend further forward, the position of the spermatophores is always posterior to the gonopores. When freshly deposited it is dull white and extremely sticky, but hardens after four to six hours. This stage is characterized by the fact that the spermatophoric mass shows no signs of having been scraped by the female. The duration it remains unscraped varies from twenty-four hours to forty-two days, (see Table 15) which is similar to the findings of Sutcliffe, (1922) who reported oviposition to occur a few days to a month after mating in P. argus.

Difficulty was experienced in sectioning the spermatophoric mass and the best results were obtained from frozen sections. Transverse frozen sections cut to a thickness of 10 μ were stained with haemalum and eosin. The deposited spermatophoric mass of P. homarus was found to be composed of the following three distinct horizontal matrix layers (see Fig. 12).

- (1) An outer crust-like layer, termed the protective matrix in this investigation.
- (2) A middle layer bearing the spermatophore, termed the spermatophoric matrix.
- (3) A basal spongy layer, termed the adhesive matrix.

The protective matrix is composed of minute granules and shows a tendency to fracture in a vertical plane when sectioned, giving it a striated appearance. It is strongly eosinophilic and a few agarophilic granules scattered sparsely throughout it indicate the possible presence of a calcium salt.

The spermatophoric matrix is clearly demarcated from the overlying protective matrix. It is slightly eosinophilic but shows a strongly positive agarophilic reaction, suggesting more calcification than the protective matrix. It also has a more highly compacted granular appearance than the protective matrix, and as it does not fracture in the same manner, it is likely that it is of a different consistency. Embedded in the spermatophoric matrix are the spermatophores, which are remarkable in that they lie in one plane with their tops just projecting into the overlying matrix.



Fig. 11. Spermatophoric mass in the post-copulatory stage showing (a) the unpicked matrix (x 1 approx.).

The adhesive matrix cements the spermatophoric mass to the sternum of the female. Where it comes into contact with the female it is composed of compacted granules which are, however, larger than those of the protective and spermatophoric matrices. These granules become progressively larger and more globular towards the junction with the spermatophoric matrix. The adhesive matrix tends to have a striated appearance and as it is also strongly eosinophilic on its basal margin it shows similarities with the protective matrix.

(2) Prefertilization Stage (Fig. 13)

Shortly before oviposition, the female starts scraping at the outer protective matrix of the spermatophoric mass with the

dactyls of the fifth legs, so that just prior to oviposition the spermatophores are exposed as two highly convoluted open grooves, situated posteriorly to the gonopores (see Fig. 13). This stage is characterized by the scraped appearance of the mass. The remarkable ability of the female to scrape away the overlying matrix and perfectly expose the spermatophores is explained by the layered structure of the spermatophoric mass. By scraping the protective matrix away until the underlying spermatophoric matrix is reached, the tops of the spermatophores are opened, thus exposing the spermatozoa to the exterior (see Fig. 12). Whether the female is able to differentiate between the matrix layers by some sensory means, and thus remove the protective matrix to leave the spermatophoric matrix exposed, or whether the physical properties of the spermatophoric matrix prevent her from removing it, is open to speculation. However, the latter explanation seems more likely as the spermatophoric matrix is more compacted than the protective matrix and therefore probably has a harder consistency. Once the spermatophores have been completely opened the female is ready to oviposit. However the spermatophores are not exposed evenly, and up to three days may elapse with portions of the spermatophores exposed to the exterior while the female is still opening the remainder. During this period it seemed puzzling that the exposed spermatozoa did not wash out of the spermatophore, particularly as P. homarus lives in turbulent water. However microscopic examination showed that the spermatozoa are embedded in a gel, which retains them within the spermatophore until fertilization.



Fig. 12. Transverse section through the deposited spermatophoric mass in the region of the spermatophore showing (a) the protective matrix, (b) the spermatophoric matrix, (c) the spermatophore and (d) the adhesive matrix. The spermatozoa have been lost from the spermatophore during sectioning (x 50 approx.)

(3) Post-fertilization Stage (Fig. 14)

This stage is characterised by the empty spermatophores and fragmented nature of the matrix. The female continues to scrape at the spermatophoric mass after oviposition, resulting in partial removal of the spermatophore-bearing and spongy layers of matrix. Ultimately the sternum is scraped clean, except for small pieces of matrix which adhere to the concavities between the sternal plates and are lost with the exoskeleton at ecdysis.

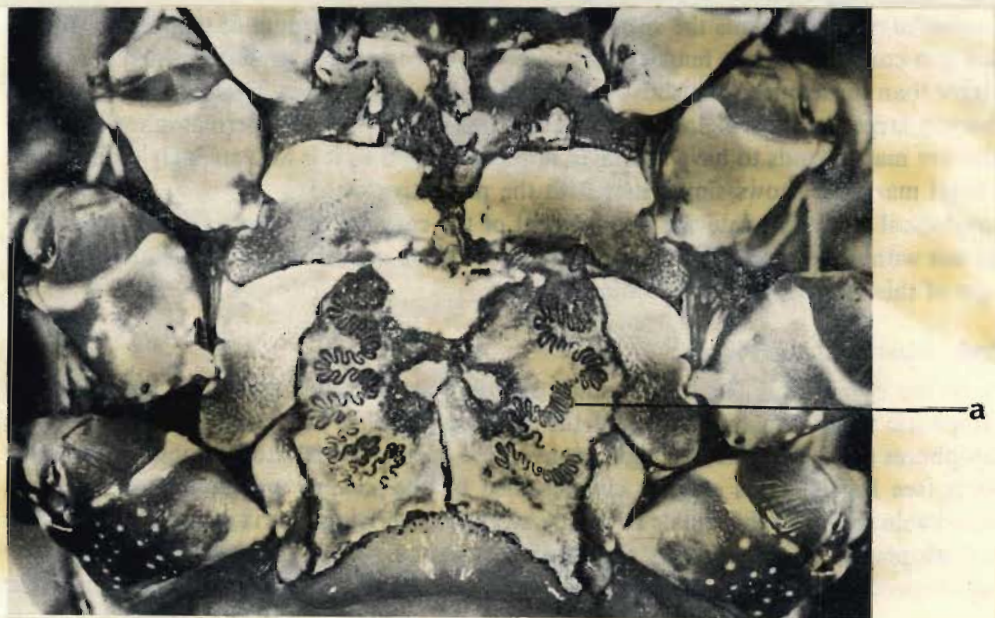


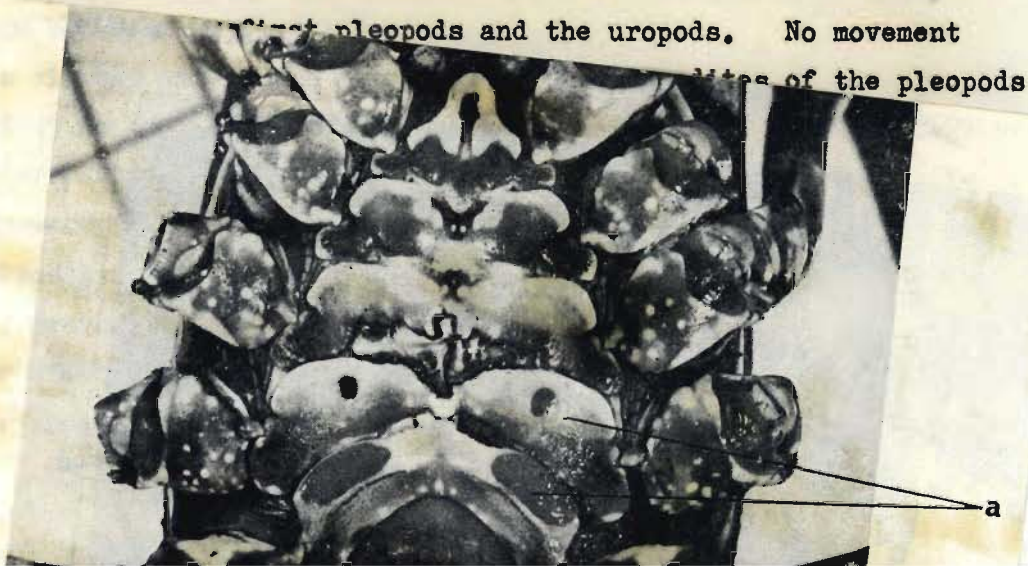
Fig. 13. Spermatophoric mass in the prefertilization stage showing the picked matrix and (a) exposed spermatophores (x 1.5 approx.).

Fig. 14. Spermatophoric mass in the post-fertilization stage showing the remnants of the matrix and (a) the uncalcified "windows" (x 1 approx.).

Oviposition

Oviposition has been described in both P. interruptus (Lindberg, 1955) and P. argus (Crawford and De Smidt, 1922). Both these species are said to assume a normal "erect" posture and to pick intermittently at the spermatophoric mass during oviposition. The eggs are reported to be carried over the spermatophoric mass from the gonopores to the exopodites, by a current set up by the pleopods. Similarly Von Bonde (1936) states: "In Jasus the female does not lie on her back when laying her eggs". Presumably it remains in an upright posture.

These observations differ in various respects from oviposition in P. homarus, which was observed on five occasions. In the first observation the female stopped picking at the spermatophoric mass, which she had been doing intermittently since about a day after it had been deposited, but continued combing her ovigerous setae for about twenty minutes. She then climbed up the side of a rock, thus assuming a vertical position with her abdomen bent under her body and the tail fan spread and held tightly against the thoracic sternum (see Figs. 15A and 15B). The first signs that oviposition had commenced were given by a few ova which escaped from the first pleopods and the uropods. No movement of the exopodites of the pleopods



some presumably unattached or unfertilized eggs.

In the second observation a female was noticed lying on her back and was presumed dead. On removal from the tank she was found to be alive and in the process of spawning. When replaced in the tank, she again turned onto her back by climbing up the wall and lay with her legs stiffly held upwards at an angle of about 30 degrees to her body. In this position it was possible to obtain a ventral view of the lobster as she oviposited. The abdomen was bent, with the telson and inner uropods pressed against the first pleopods, which were directed forward and lay covering the posterior portion of the spermatophoric mass (Fig. 15B). The outer uropods curved round the branchiostegites laterally. Thus an entirely enclosed brood chamber was formed, being closed above and below by the tail fan and abdomen respectively, and laterally by the overlapping pleopods. In this position most of the spermatophores remained exposed. Three to five batches of 15-20 ova were extruded alternately, first from one gonopore, and then after about two to three minutes from the other. The ova rolled slowly over the spermatophores and passed into the brood chamber through a channel formed between the extended first pleopods and the junction of the telson and inner uropods (see Fig. 15B). They were apparently drawn in by a current set up by the endopodites of the posterior pleopods which could be seen beating rhythmically through the telson. The exopodites of the pleopods moved slightly with the beating of the endopodites and at no time did the female scrape the spermatophoric mass. The horizontal position assumed by this female was probably due to the fact that no rocks were present in the tank and the smooth concrete walls prevented her from assuming a vertical position. This view is substantiated by the fact that in the other three observations

the females assumed vertical positions to oviposite. The exact duration of oviposition was only noted in the first observation.

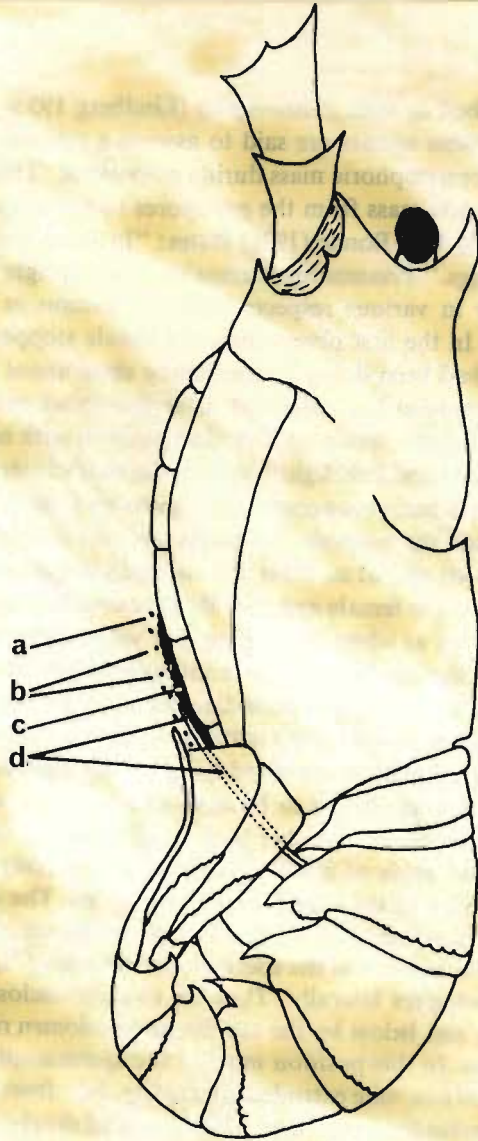


Fig. 15A. Diagrammatic lateral view of ovipositing female showing (a) the position of the gonopore, (b) ova, (c) spermatophoric mass and (d), the position of the first pleopod.

Three specimens caught during field sampling were found to be in the process of spawning. In these specimens only the endopodites of the posterior pleopods bore the full number of eggs while the anterior ones bore very few, and it appears therefore, that eggs became attached from the fifth pair of pleopods progressively forwards. This is unlike Jasus in which Von Bonde (1936) reports that egg attachment is in the opposite sequence.

It appears that mating is not a necessary stimulus for oviposition as five specimens oviposited in the tank without any deposited spermatophoric mass. The ova became attached in the normal manner but within a week had all been picked from the ovigerous setae. Sutcliffe (1953) records the same phenomenon in P. argus.

Fertilization

Since the early accounts of the morphology of the crayfish spermatozoon, such as Huxley's (1896), the typical rayed structure of reptantian decapod spermatozoa has caused speculation amongst zoologists. Opinions as to whether the spermatozoa are actively motile or not are conflicting and no entirely satisfactory explanation of the function of the spines has been put forward.

The spermatozoa of P. homarus are similar to those of J. lalandii described by Heydorn (1965). Smears of seminal fluid taken from spermatophores within the spermatophoric mass, revealed numerous spermatozoa (Fig. 16), which are roughly spherical in shape with a diameter of 10-15 μ . Using phase contrast microscopy, it was possible to distinguish a clear, oval, peripheral body and the spermatozoa tended to become orientated with this body facing in the same direction.

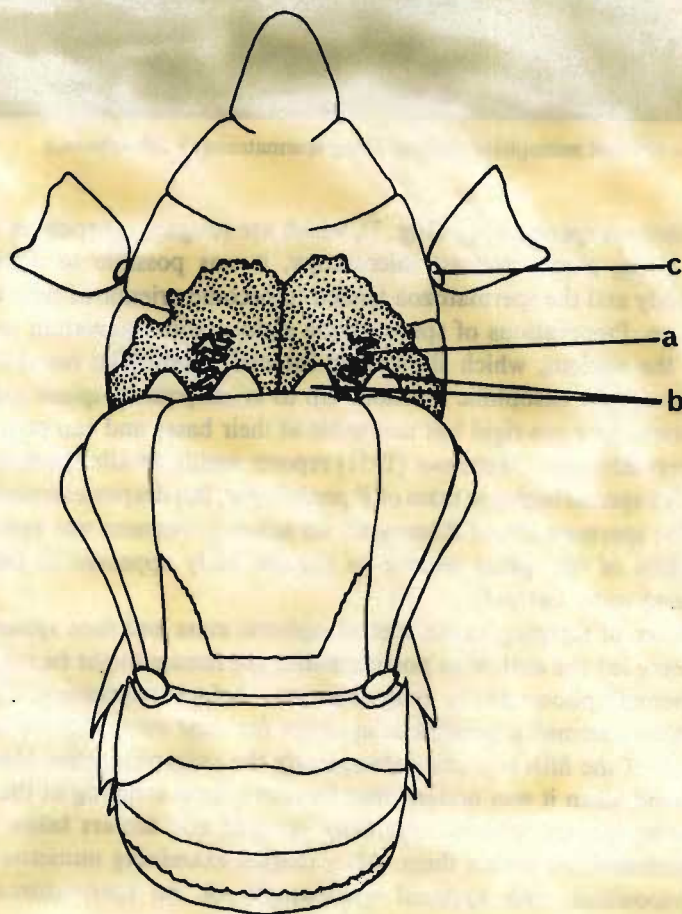


Fig. 15B. Diagrammatic ventral view of ovipositing female showing the spermatophores (a), first pleopods (b), and gonopores (c).

Preparations of spermatozoa stained with haemalum revealed this peripheral body to be the nucleus, which showed an intensely basophilic reaction; the rest of the cell showed only a slight basophilic reaction. Up to seven pointed spines radiate from the mature spermatozoon. These are rigid but moveable at their bases and can protrude at various angles from the spermatozoon. Matthews (1951) reports seeing motile spermatozoa in preparations taken from the spermatophoric mass of P. penicillatus, but despite

examining numerous preparations of living spermatozoa of P. homarus, no active movement was ever observed; movement and orientation of the spines relative to the cell body appeared to be caused by Brownian movement and water currents.

The sequence of scraping at the spermatophoric mass and then systematically combing the ovigerous setae led the author to postulate that the female might be transferring spermatozoa from the spermatophores to the ovigerous setae before oviposition. The spined structure of the spermatozoa seemed a possible adaptation for their entanglement in the bristle-like setae of the dactyls of the fifth legs and subsequently the ovigerous setae.



Fig. 16. Phase contrast microphotograph of living spermatozoa (x 500 approx.).

However, this hypothesis was abandoned when it was noticed that females ceased scraping at the spermatophoric mass as soon as the spermatophores were fully exposed and smears taken at this stage revealed abundant spermatozoa within them. Also, despite examining numerous females immediately prior to oviposition with exposed spermatophores, no spermatozoa were found on the ovigerous setae.

It has been mentioned that the spermatozoa are contained in a gel within the spermatophores, which probably prevents them from being washed out in turbulent water. In order for the spermatozoa to be released, the consistency of this gel must change. As the spermatophores are empty on completion of oviposition, it seems probable that release of the spermatozoa is brought about by an enzyme exuded by the female at oviposition which changes the gel to a sol. Attempts to bring about this change artificially were not successful and evidence for the existence of such an enzyme remains circumstantial.

Microscopic examination shows that spermatozoa adhere to freshly exuded ova with their spines and there can be little doubt that many spermatozoa stick to ova as they roll over the open spermatophores. However, the spermatophoric grooves are deep relative to the size of spermatozoa and as they are also narrower than the diameter of the ova, this must preclude all but the topmost spermatozoa in the grooves from coming into contact with ova. For this reason, it is suggested that the spines of the spermatozoa serve to increase their surface area, making them more susceptible to being carried by water currents. As the current which draws the relatively heavy ova from the gonopores to the brood chamber is localised directly over the exposed spermatophores, it probably

draws in spermatozoa at the same time. In this case, ova and spermatozoa must come into contact primarily in the brood chamber as they are swirled about together by the beating endopodites of the pleopods. Fertilization must occur before the egg capsules are secreted by the tegumentary glands of the pleopods as suggested by Burkenroad (1947).

Discussion

Although observations on mating behaviour were primarily confined to the activities of a single dominant male specimen, subordinate males reacted in the same way to receptive females when allowed to do so. No variation in the pattern of mating behaviour was observed and there is no reason to believe that it was in any way unnatural, although substantiation by field observations would be desirable.

The time recorded between mating and oviposition was variable (Table 15), but in most cases oviposition occurred within about one week. The considerably longer period taken by specimens A and B may be due to their having been transferred to another tank after mating. In all the specimens there is a possibility that trauma, caused by daily examination of the spermatophoric masses, may have delayed oviposition.

As noted by Heydorn (1969a), the spermatophoric mass of P. homarus appears to be unique in that it does not turn black to form the characteristic "tar spot" described in other members of the genus. Examination of the spermatophoric mass of a specimen of P. penicillatus showed that the black appearance of the mass was due to an additional outer layer and that if this was scraped

away the typical white colouration of the spermatophoric mass of P. homarus was reached. In P. cygnus the interval between mating and oviposition is considerably longer than in P. homarus (George, pers. comm.). It is possible, therefore, that the black layer may give additional protection to the spermatophoric mass in species with a longer period between mating and oviposition.

P. homarus is extremely gregarious and observations on mating behaviour suggest that dominant males are polygamous and prevent subordinate males from mating. However, it seems unlikely that small males would be physically capable of withdrawing females larger than themselves from their shelters or overturning them for copulation. Dominance and polygamy by large males may therefore result in intensification of selection for characters involved in successful mating, i.e. allometric elongation of the second and third pairs of legs of males and their attainment of a larger size than females. While limited, observations on mating behaviour in P. homarus indicate that the reproductive potential and contribution of large males may be considerably greater than that of small males, a fact that bears consideration in fisheries management.

In all cases that oviposition was observed the eggs were fertilized. It must therefore be concluded that oviposition in P. homarus naturally takes place with the female in a vertical position and that the one occasion when a female oviposited while lying on her back was due to her inability to assume a vertical position. While Lindberg (1955) and Crawford and De Smidt (1922) respectively reported P. interruptus and P. argus to oviposit in a normal "erect" position, they do not specify whether the female was vertical or not. This seems likely as it is difficult to believe

that the current set up by the endopodites of the pleopods could be sufficiently strong to draw ova, which are denser than water, from the gonopores to the brood chamber if the female was in a horizontal position.

5.

GONADS AND THEIR PRODUCTS

Male

The reproductive organs conform to the typical palinurid pattern. The morphology of the vas deferens is described and illustrated in Section 5, together with an account of the spermatophoric material it contains. The structure of the deposited spermatophoric mass prior and subsequent to fertilization and the morphology of ^{the} rayed spermatozoon has been described on pages 132-136 and 146.

Female

The ovaries resemble an elongated H, with the vertical lobes joined by a transverse bridge just anterior of the heart. In the majority of animals the right posterior lobe does not extend as far posteriorly as the left one, as it is folded ventrally at the level of the posterior end of the heart.

Development of the ovaries was initially classified into five stages, but when it became apparent that P. homarus may breed more than once a year it became necessary to make a finer distinction as to when the ovaries started to develop, and an extra stage, namely stage 2A, was defined and added. Development of the ovaries was therefore classified into the following six macroscopically

distinguishable stages, the validity of which was confirmed histologically:

Stage 1. Immature.

Ovaries flattened and strap-like; ova when seen with a hand-lens tend to be uniform in diameter; overall colour white with a slightly granular appearance.

Stage 2. Inactive.

Ovaries flattened dorso-ventrally; ova not uniform in diameter when seen with a hand lens, the smaller ones being white and the larger ones being pale pink or light orange, giving an overall pinkish-orange colouration.

Stage 2A. Active.

Ovaries slightly swollen, tending to become rounded in cross section; ova just visible to the naked eye and not of uniform diameter; colour deep orange.

Stage 3. Active/ripe.

Ovaries swollen to fill most of the available space in the cephalothoracic cavity; ova easily visible to the naked eye and not uniform in diameter; colour bright coral red.

Stage 4. Ripe.

Ovaries grossly swollen filling all available space in the cephalothoracic cavity; ova easily visible, tending to be uniform in diameter and some are usually present in the oviducts; colour bright coral red.

Stage 5. Spent.

Ovaries similar in appearance to stage 2, but may be distinguished macroscopically by the presence of a few large residual ova from stage 4, usually retained at the extremities of the ovary lobes and in the oviducts. These ova are soon resorbed, in which case this stage is indistinguishable macroscopically from stage 2.

Ovaries in stage 1 occur only in sexually immature rock lobsters. At the onset of sexual maturity the ovaries develop progressively through the stages from 2 to 5, after which the cycle begins again from stage 2. Development may begin immediately if the animal is shortly going to breed again but if no further breeding is imminent the ovaries remain quiescent in stage 2.

In order to avoid confusion between the ova within the ovary and those carried externally on the ovigerous setae of the female, the latter will be termed "eggs" and they have been classified into four macroscopically distinguishable stages according to their degree of embryonic development. However, to give a complete picture of the stage of a female in her egg-bearing cycle, two additional stages were added, denoting whether she was actually carrying eggs and if not, whether this was because she had not yet oviposited or because her eggs had hatched.

Stage 0. Not yet oviposited.

No eggs on ovigerous setae which are clean, pale yellow and silky, denoting that oviposition has not yet occurred.

Stage 1. Freshly oviposited eggs.

Eggs round and bright orange; no embryonic development visible macroscopically; mean diameter 0.54 mm.

Stage 2. Early embryonic development.

Eggs round and deep orange; embryo first visible; mean diameter 0.56 mm.

Stage 3. Well formed embryo.

Eggs slightly oval in shape and light brown due to growth of the embryo and reduction of the quantity of orange yolk; eyes of the embryo, which now occupies two thirds of the egg, are conspicuous; mean diameter of long axis 0.58 mm.

Stage 4. About to hatch.

Eggs brown and oval in shape; little or no yolk present, the whole egg capsule being occupied by the embryo; mean diameter of long axis 0.58 mm.

Stage 5. Eggs hatched.

Initially the ovigerous setae are matted by a mass of egg stalks and empty capsules. These are detached by the female within a few days, after which this stage can only be distinguished from stage 0 by the dark colour of the ovigerous setae and absence of a clean silky appearance.

6.

ATTAINMENT OF SEXUAL MATURITY

Female

A female capable of carrying fertilized eggs was regarded as being sexually mature. However in specimens not carrying eggs, ovary state can also be used as a criterion of attainment of sexual maturity as sexually immature females have ovaries in stage 1.

The incidence of egg-bearing in each size class is presented in Table 16 in which it may be seen that there is a gradual progressive increase in the incidence of egg-bearing, with no marked increase at any particular size and even in the larger size classes egg-bearing does not reach a particularly high level. This is in contrast to the situation recorded by Heydorn (1969b) in Jasus lalandii, which shows a sharp increase in frequency of egg-bearing after a certain size has been attained and over 90 percent of the females in the larger size classes are egg-bearing. The results obtained for

TABLE 16. Incidence of egg-bearing females in each size class during the two years of sampling.

Carapace length	50	51	52	53	54	55	56	57	58	59	60-69	70-79	80-89 £	90-99	100-109	110-119
No. examined	60	37	63	68	57	92	74	80	74	68	860	733	269	73	9	1
No. egg-bearing	2	5	11	13	17	24	24	37	35	28	374	388	174	48	2	
Percentage egg-bearing	3	14	17	19	30	26	32	46	47	41	43	53	65	66	22	

TABLE 17. Incidence of females in each size class in which the adult ovarian cycle has started (stages 2-5).

Carapace length	47	48	49	50	51	52	53	54	55	56	57	58	59
No. of females	23	38	31	60	37	63	68	57	92	74	80	74	68
No. in stages 2-5	3	5	8	13	17	32	37	35	56	55	61	62	60
Percentage	13	13	26	22	46	51	54	61	61	74	76	84	88

P. homarus can probably be attributed to repetitive breeding during the course of a year, which does not occur in J. lalandii. This would have the effect of lowering the overall frequency of egg-bearing and masking the true incidence in each size class. Nevertheless, on the basis of these results, it is considered that while some females are capable of breeding at a size of 50 mm, the majority probably only attain sexual maturity at a carapace length of about 54 mm and greater.

The incidence of females in each size class in which the adult ovarian cycle has started (i.e. those animals with ovaries in stages 2-5), is presented in Table 17. Examination of these data shows that the majority of females have developing ovaries indicating approach of sexual maturity at a carapace length of 51 mm and greater. This is a somewhat smaller size than the estimate of size at onset of sexual maturity based on the incidence of egg-bearing, but it will be shown that oviposition is invariably preceded by a moult, so that an animal would be expected to be slightly larger when actually carrying eggs. Using ovary development as a criterion of attainment of sexual maturity has the advantage of being unaffected by repetitive breeding and the results obtained substantiate the view that the majority of females are capable of egg-bearing at a carapace length of about 54 mm.

The Natal population of P. homarus appears to attain sexual maturity at a slightly larger size than the Transkeian population investigated by Heydorn (1969a), who estimated the population as a whole to become sexually mature at a carapace length of 50 mm. Breeding also appears to start at a smaller size in Transkeian waters as the smallest berried female recorded by Heydorn had a carapace length of 43 mm as opposed to 50 mm, which was the smallest recorded from Natal.

De Bruin (1962) estimated that the Ceylon population attains sexual maturity after a carapace length of between 55 and 59 mm is reached, which is similar to the Natal population. George (1963), working on the East Aden population, had insufficient data to make an accurate assessment, but suggested that sexual maturity might be attained between a carapace length of 60-70 mm.

Male

On the basis of a study of development of the vasa deferentia and mating organs of P. homarus in Transkeian waters, Heydorn (1969a) considered that sexual maturity is attained at a carapace length of between 50 and 59 mm. In the present investigation the mating organs of 209 specimens from Natal were examined and it was concluded that they also become fully developed within the same size range. Examination of the seminal fluid revealed the presence of spermatozoa in animals from 47 mm upwards and it is therefore concluded that males are capable of mating between a carapace length of 50-59 mm.

Another morphological change in males, associated with the onset of sexual maturity, is elongation of the legs and in Fig. 4 it can be seen that divergence of the male and female leg lengths first becomes marked at a carapace length of about 55 mm. However, as it is not known by how much the leg length of males must exceed that of females before successful mating can take place, this cannot be used as a criterion of attainment of sexual maturity. Observations on captive animals suggest that extreme elongation of legs in males plays an important role in aggressive behaviour, courtship and mating. Therefore unlike females, which probably breed at the smallest size at which they are physiologically capable of doing so, males may have to attain a considerably larger size before they are capable of making any reproductive contribution to the population.

7.

INCUBATORY PERIOD

The period of incubation, during which the eggs were carried attached to the ovigerous setae of the females, was recorded in fifteen specimens which oviposited and produced larvae in captivity. There was no protracted interval between the start and completion of hatching as recorded in J. lalandii by Paterson (1969) and, in each case, hatching was completed overnight, except in one outsize female with a carapace length of over 90 mm, in which a few eggs were still hatching the following morning. It seems likely that release of larvae at night may reduce predation by reef fish.

Water temperature was taken daily in the tanks containing the experimental animals. Determinations of oxygen levels revealed values varying from 4.5 to 6.0 mg/l. This was somewhat lower than in the surf zone inhabited by P. homarus where the water is usually slightly supersaturated (approx. 7.0 mg/l). It therefore appears that under natural conditions oxygen content would not be as important a factor influencing the incubatory period as water temperature.

The results obtained appear in Table 18 and show a marked reduction in the incubatory period with increase in water temperature. This can probably be attributed to an increased metabolic rate at higher temperatures. It is not known to what extent these results were influenced by the low oxygen content of the tank water, but the incubatory period obtained is compatible with observations on the intermoult period and also indirect estimates of its length based on samples of the feral population.

TABLE 18. The incubatory period of eggs in captive rock lobsters.

Mean temp. °C	Incubatory period (days)	Carapace length (mm)
20.2	59	95
20.9	54	66
21.0	53	70
21.0	54	61
21.4	53	71
21.7	56	76
22.4	46	75
22.5	50	96
23.9	41	78
24.4	43	72
24.5	38	65
25.6	34	70
25.9	29	67
?	50	93
?	47	94

Paterson (1969) found that in J. lalandii the incubatory period in small females showed a tendency to be shorter than that of large ones. A similar tendency is not obvious in the present results except in the case of one outsized female with a carapace length of over 90 mm which appeared to have a rather longer incubatory period than smaller ones.

Based on the present results the incubatory period of P. homarus appears to be similar to that recorded in some other sub-tropical palinurid species; it is thought to be about one month in P. japonicus (Terao, 1929 and Nakamura, 1940) and P. argus (Sutcliffe, 1952). However, it appears to be somewhat shorter than in some colder water species in which an incubation of about nine to ten weeks was recorded by Allen (1916) in P. interruptus and about three months by Paterson (1969) in J. lalandii.

8.

THE REPRODUCTIVE CYCLE

Observations on the breeding cycle of P. homarus are based on twenty four consecutive monthly samples, comprising a total of 2608 females within the reproductive size range. It will be shown that in Natal, females breed more than once per season, which has also been recorded in P. japonicus (Ino, 1950) and P. argus (Sutcliffe, 1953).

Frequency of Egg-bearing

Heydorn (1969a), found that in Transkeian waters no egg-bearing occurred in July but that the incidence increased until a peak was reached in January. He concluded that the peak

period of spawning was during the summer months and on the basis of his four seasonal field trips, found no indication of more than one spawning during the year.

In this study, the numbers of egg-bearing females in each size class were determined every month over the two years sampled. Examination of Tables 19 and 20 shows that small females had a different seasonal pattern of egg-bearing from larger ones. Those with a carapace length of 50-59 mm were therefore grouped and considered separately from the ones with a carapace length of 60 mm and over, in determination of the monthly frequency of egg-bearing. This grouping is artificial, as with increase in size, females become capable of breeding more times per year, which progressively extends the breeding season. However, this will be elaborated later and the present division of the females into two groups suffices in giving an overall picture of the seasonal incidence of breeding. In both years sampled, the number of egg-bearing females each month was expressed as a percentage of the total number of sexually mature females (taken as all females excluding those with immature ovaries).

Examination of Figs. 17 and 18 shows that in the larger size group (carapace length of 60 mm and greater), the lowest incidence of egg-bearing was in Autumn and early Winter. In both years sampled, the first marked increase in the incidence of egg-bearing was in June. Egg-bearing reached its highest levels during the summer months and thereafter, an extremely rapid drop-off was recorded in March.

TABLE 19. Numbers of egg-bearing females in each size class in the monthly samples of 1968/69.

Month	Size Class	51	52	53	54	55	56	57	58	59	60 69	70 79	80 89	90 99	100 109	TOTAL
FEB				1	1	1	1	1	3		42	22	6	2		80
MAR										1	14	7	3			25
APR												1	3			4
MAY														1		1
JUN											1	4	3	1		9
JUL											6	10	6			22
AUG											12	17	14	7		50
SEP										1	14	21	9	1		46
OCT			1		2	1		4		3	33	32	19	5		100
NOV			1		2	2	7	6	8	3	40	42	13	4		128
DEC				5	1	6	2	6	5	5	28	18	10	1		87
JAN				1	4	2	2	4	6	2	21	15	7	1		65
TOTAL			2	7	10	12	12	21	22	15	211	189	93	23		617

TABLE 20. Numbers of egg-bearing females in each size class in the monthly samples of 1969/70.

Month	Size Class	50	51	52	53	54	55	56	57	58	59	60 69	70 79	80 89	90 99	100 109	TOTAL
FEB							1		7	3	1	10	12	2	6	1	43
MAR											2	2	2	2			8
APR												2	2				4
MAY													5	4	1		11
JUN													11	4	4		19
JUL												16	23	9	1		49
AUG			1									8	27	10	3		49
SEP						1					1	18	15	5	1		42
OCT					1		2	3			3	23	22	8	1		63
NOV		1	3		1	1	2	3	3	1	2	24	25	17	3		87
DEC				5	1	2	2	3	2	4	3	27	26	10		1	86
JAN		1	1	4	3	3	5	3	4	5	1	33	26	10	5		104
TOTAL		2	5	9	6	7	12	12	16	13	13	163	199	81	25	2	565

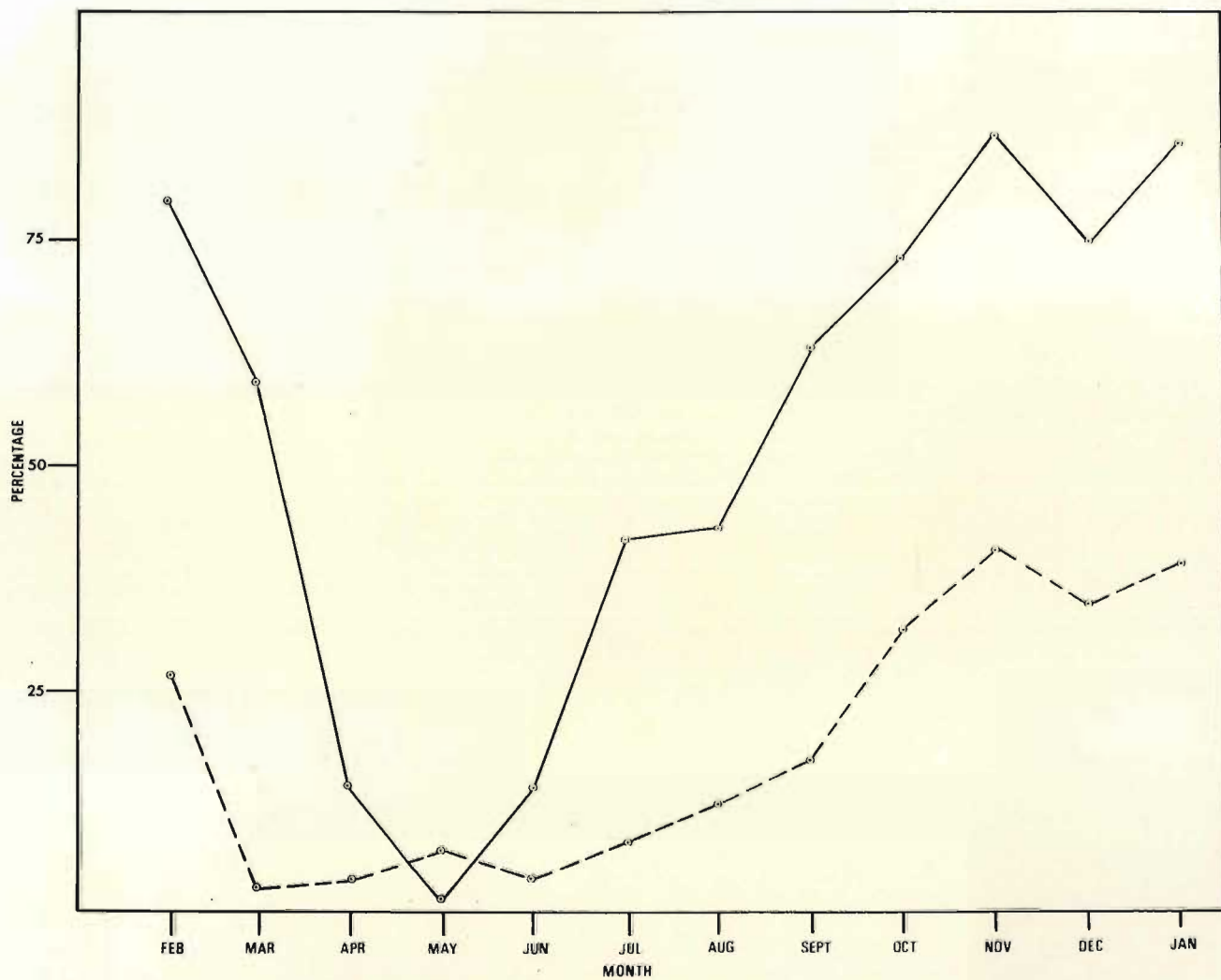


Fig. 17. Monthly frequency of egg-bearing in females of carapace length 60 mm and greater (solid line) and the percentage of these which show evidence of breeding again shortly (broken line). 1968/69.

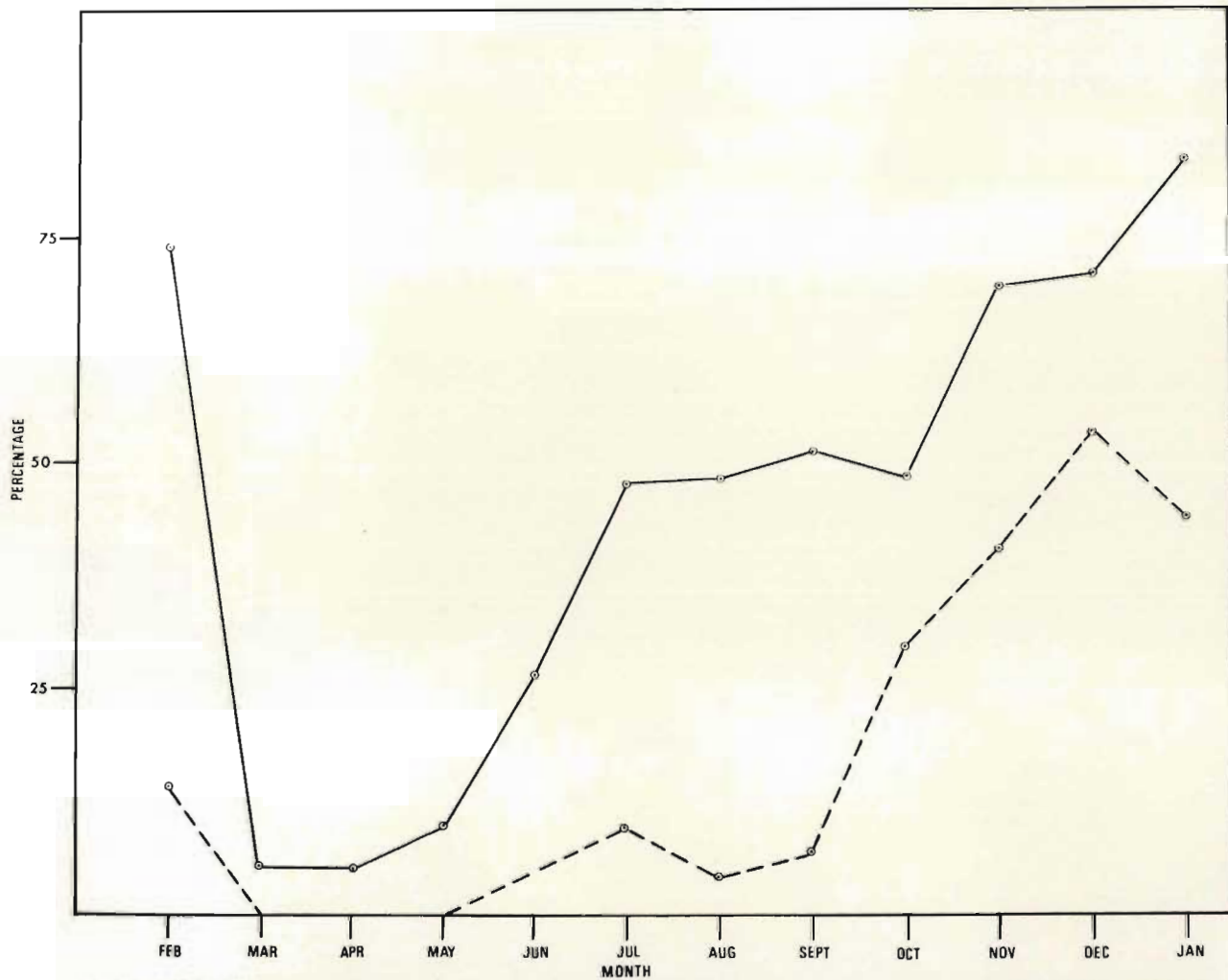


Fig. 18. Monthly frequency of egg-bearing in females of carapace length 60 mm and greater (solid line) and the percentage of these which show evidence of breeding again shortly (broken line). 1969/70.

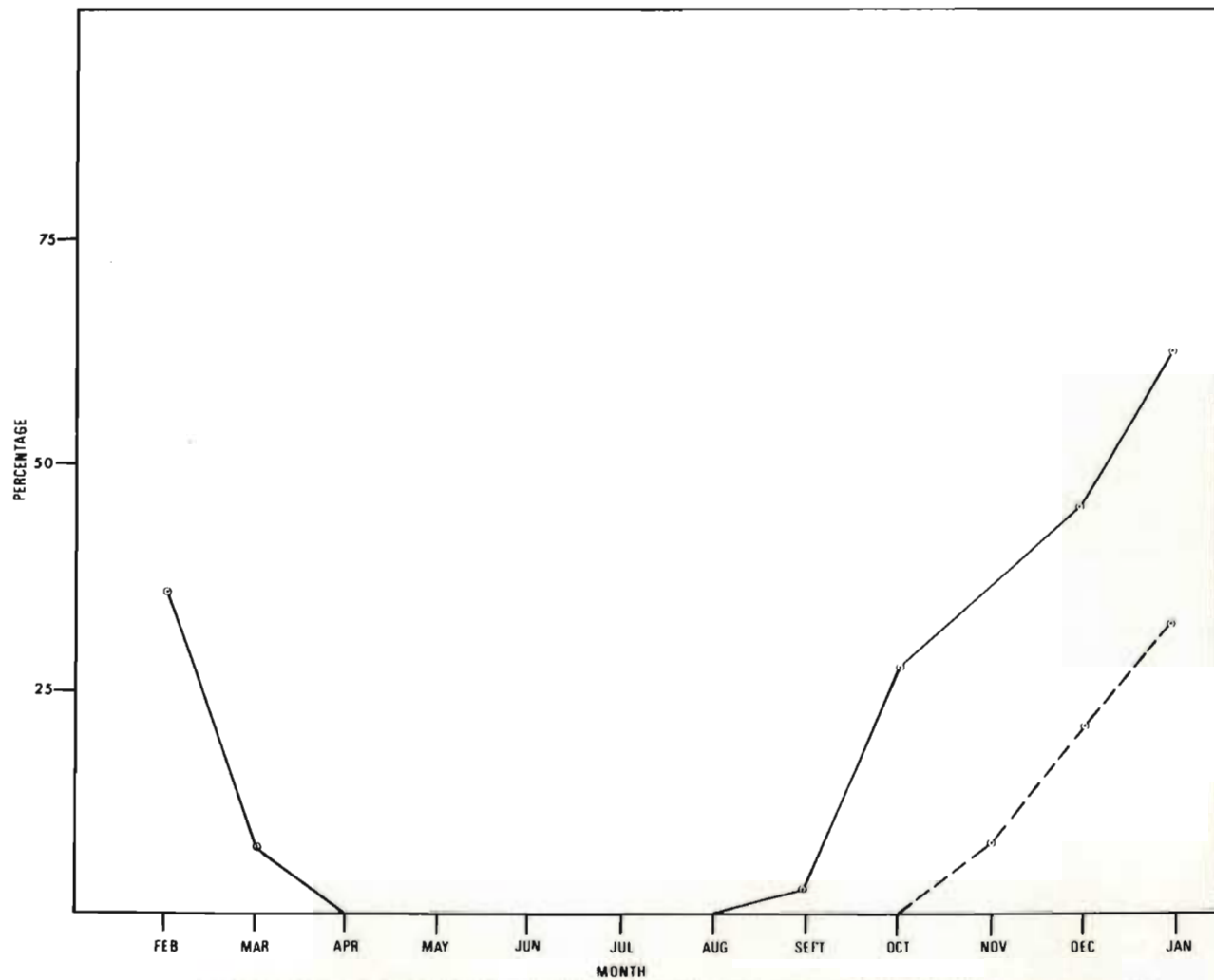


Fig. 19. Monthly frequency of egg-bearing in females of carapace length 50 - 59 mm (solid line) and the percentage of these which show evidence of breeding again shortly (broken line). 1968/69.

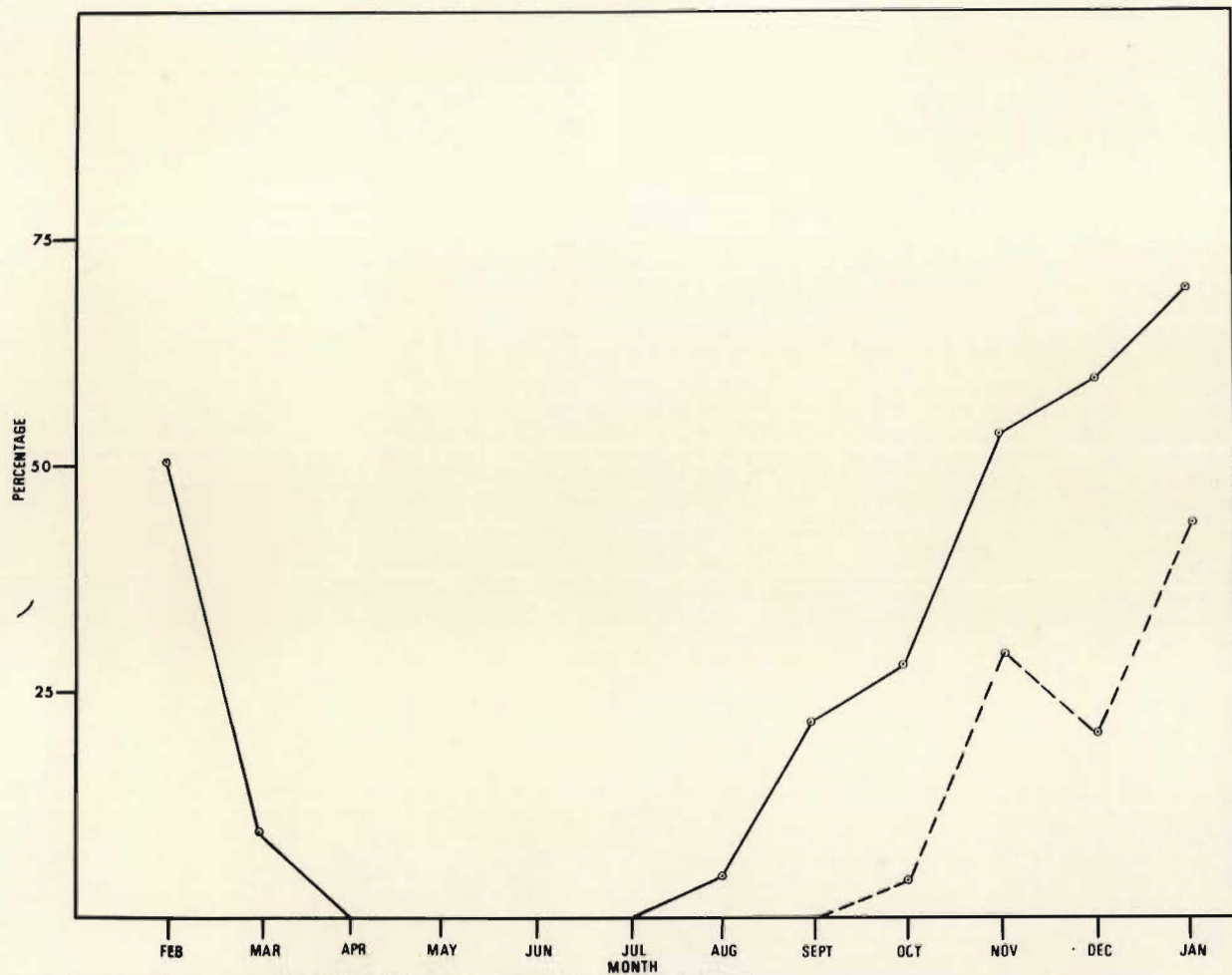


Fig. 20. Monthly frequency of egg-bearing in females of carapace length 50 - 59 mm (solid line) and the percentage of these which show evidence of breeding again shortly (broken line). 1969/70.

In both years sampled, inflection occurs in the graphs after July, although it is not as distinct in 1968/69, marking a sudden change in the rate of increase in egg-bearing. This can probably be attributed to hatching of a sufficiently large number of eggs to result in a drop in the overall frequency of egg-bearing females. Repetitive breeding and the gradual increase in the number of females ovipositing, has a masking effect so that it is not possible to distinguish how many times the majority of females breed per year from these graphs.

Breeding in the smaller size group (carapace length 50-59 mm) starts about three months later than in the larger specimens and examination of Tables 19 and 20 shows that females within the group appear to start breeding 'en bloc' with no differentiation in timing according to size. Figs. 19 and 20 show that egg-bearing also builds up to its highest level in the summer months and a peak was recorded in January in both years. Slight inflection is evident in the graphs for both years, but is particularly distinct in Fig. 20. It is attributed to the same cause as in the larger size group.

Repetitive Breeding

Evidence of repetitive breeding during the year was obtained both in the feral population and in captive specimens.

The reproductive activity of ten captive females is summarised in Table 21. Of these, four oviposited once in twelve consecutive months, four twice, one three times and one four times.

TABLE 21. A record of oviposition in ten captive rock lobsters, over a period of twelve consecutive months.

Initial Carapace Length	SPRING			SUMMER			AUTUMN			WINTER			Total number of broods
	S	O	N	D	J	F	M	A	M	J	J	A	
61				+			+		+				3
63					+								1
63					+								1
65			+			+							2
68				+									1
73	+			+									2
74		+			+								2
75					+								1
75				+				+					2
93		+			+			+		+			4
TOTAL	1	2	1	4	5	1	1	2	0	1	0	0	

In the feral population, evidence of repetitive breeding is based on a combination of three criteria; namely the degree of development of the ovaries, the state of the spermatophoric mass and the presence or absence of externally carried eggs. Consider a female which has recently oviposited for the first time in the breeding season. Its ovaries will be spent (stage 5) or may have recovered to an inactive stage (2). The spermatophoric mass will be in a post-fertilization stage and the eggs will show no macroscopic signs of embryonic development (stage 1). However, a female with eggs in an advanced state of embryonic development with a post-fertilization spermatophoric mass and ripe ovaries will clearly breed again when her eggs have hatched. The criteria on the basis of which a female which was considered to show signs of repetitive spawning are summarised in the third category of Table 22. In the case where a female's ovaries are just starting to become active (stage 2A), it might be argued that ovarian development has not advanced sufficiently to be sure that repetitive breeding will take place, as reversion to an inactive state could occur due to resorption, as was reported in captive J. lalandii by Heydorn (1969b). However, while resorption of ova might occur in P. homarus it seems that the number of cases in the feral population would be negligible.

It must be pointed out, however, that on the basis of the criteria outlined in Table 22, it is not possible to distinguish whether a female is about to breed for the first, second, third or fourth time in the year.

The monthly proportion of egg-bearing females showing signs of producing another brood is presented in Tables 23 and 24 and Figs. 17-20. As in the previous section, an arbitrary

TABLE 22. Summary of the combinations of criteria by which a female which has yet to oviposite, has oviposited, but shows no signs of producing another brood or has oviposited and does show signs of producing another brood, may be detected.

Class	1 Yet to oviposite	2 Oviposited with no signs of further breeding	3 Oviposited with evidence of repetitive breeding
Ovary stage	Inactive to ripe (2, 2A, 3 and 4)	Inactive or spent (2 or 5)	Active to ripe (2A, 3 or 4)
Egg stage	None (0)	Just oviposited to recently hatched (1, 2, 3, 4, and 5)	With eggs or recently hatched (1, 2, 3, 4 and 5)
Stage in moulting cycle	Premoult, intermoult or postmoult (A, B or C)	Intermoult or pre-moult (A, B or D)	Intermoult or premoult (A, B or D)
State of spermatophoric mass	Postcopulation or prefertilization (0, 1 or 2)	Postfertilization (3)	Postfertilization (3)

distinction has been made between small specimens (c.l. 50-59 mm) and the larger specimens (c.l. 60 mm and over).

During March, April and May of 1969 there was no evidence of repetitive breeding in the larger group, although a low incidence was recorded during these months in 1968 (see Figs. 17 and 18). It seems likely however, that these specimens in 1968 represent late breeders of the previous years cycle which had not yet moulted prior to their first spawning in the new cycle. During the winter months a slight increase of the incidence of repetitive breeding was recorded followed by a marked increase in spring, building up to a peak in summer (November in 1968 and December in 1969) and followed by a rapid fall off during February.

In the case of the small females, no signs of repetitive breeding were recorded from February to October in 1968 and February to September in 1969 (see Figs. 19 and 20). Thereafter there was a rapid increase until a peak was reached in January followed by a complete drop off to nil in February.

It is interesting to note that in both years, the first evidence of what must be second breeding was obtained two months after egg-bearing was recorded for the first time in the season. This agrees with the minimum interval between breeding recorded in captive specimens. Also the peak frequency of small females showing evidence of repetitive breeding coincides with the peak month of egg-bearing.

TABLE 23. Numbers of females in which there is evidence of repetitive breeding each month 1968/69.

Month	Size Class	51	52	53	54	55	56	57	58	59	60 69	70 79	80 89	90 99	100 109	TOTAL
FEB											12	8	3	1		24
MAR												1				1
APR														1		1
MAY												3		1		4
JUN												1	1			2
JUL												2	2			4
AUG											1	5	4	4		14
SEP											1	7	4			12
OCT											8	19	9	3		39
NOV					1		2	3	1	1	23	19	3	1		54
DEC				1	1	4	2	1		3	9	10	6	1		38
JAN					3	2	1		3	1	9	8	3			30
TOTAL				1	5	6	5	4	4	5	63	83	35	12		223

TABLE 24. Numbers of females in which there is evidence of repetitive breeding each month 1969/70.

Month	Size Class	50	51	52	53	54	55	56	57	58	59	60 69	70 79	80 89	90 99	100 109	TOTAL
FEB													2		3	5	5
MAR																	
APR																	
MAY																	
JUN													2	1			3
JUL												1	6	2	1		10
AUG													2	1			3
SEP												1	2	1			4
OCT								1				11	15	6	1		34
NOV			1		2			1	1			10	14	1	3		33
DEC				2		1			1			12	14	8			38
JAN			2	3	1	1		2		2	2	13	14	4	1		45
TOTAL			3	5	3	2		4	2	2	2	48	71	24	9		175

The monthly frequency of egg-bearing in each size class, expressed as a percentage of the total number of sexually mature females in each, is presented in Table 25 and 27. These data demonstrate a tendency for the frequency of egg-bearing and the length of the breeding season to increase, as female become larger. This can almost certainly be attributed to the ability of females to produce more broods per year as size increases. Observations on breeding frequency in captive animals show that there is no doubt as to the feasibility of females producing three broods a year and the eggs of even a fourth may be produced, although in the single case recorded in captivity they did not hatch until early in the following year.

The problem posed by repetitive breeding in P. homarus is how to determine what proportion of females in each size class produce one, two, three or even perhaps four broods per year.

In the case of the 50-59 mm class the evidence of repetitive breeding can safely be regarded to indicate production of a second brood, as the short duration of the breeding season precludes the possibility of any but perhaps a few exceptional animals producing three broods. By determining the difference in areas beneath the graphs illustrating the frequency of egg-bearing and the frequency of repetitive breeding, in Figs. 19 and 20 it was possible to obtain an estimation of the proportion of females producing one or two broods in each year sampled.

The results are as follows:

1968/69

- A Area beneath graph of frequency of egg-bearing = 215 units² (from Fig.19)
 B " " " " repetitive breeding = 65 units²

The difference between A and B gives the area covered by those breeding once = 150 units². Therefore approx. 57% bred once and approximately 43% bred twice.

1969/70

- A Area beneath graph of frequency of egg-bearing = 297 units² (from Fig.20)
 B " " " " repetitive breeding = 96 units²

The difference between A and B gives the area covered by those breeding once = 201 units². Therefore approx. 52% bred once and 48% bred twice.

On the basis of these data it is thus concluded that within this size class, almost half of the reproducing females produce two broods per annum. This is not surprising, as examination of Tables 23 and 24 shows that even the smallest females are capable of producing a second brood.

In the larger size classes the breeding season is sufficiently long for more than two broods to be produced. However, as demonstrated by breeding in captive animals, the number of times females breed cannot necessarily be inferred from the length of the period in which a particular size class is egg-bearing, as all females may not breed in every intermoult period (see Table 21). In view of these considerations only an approximation of the number of broods produced each year by the majority of females in each size class was considered to be possible.

TABLE 25. The monthly percentage of egg-bearing females in each size class during 1968/69 (corrected to the nearest decimal point). The total numbers of sexually mature females from which this was calculated, are presented in Table 23 below.

	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN
50-59	36	8						3	26	35	45	62
60-69	76	67			4	27	30	52	60	87	70	84
70-79	85	47	9		18	48	38	68	76	88	72	88
80-89	75	60	50		30	67	61	82	95	76	100	78
90 +	100			33	50		78	33	83	100	50	100

TABLE 26. The total numbers of sexually mature females in each size class during 1968/69.

	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN
50-59	22	13	8	11	14	29	18	35	42	82	67	34
60-69	55	20	10	17	24	22	40	27	65	46	40	25
70-79	26	15	11	29	22	21	45	31	42	48	25	17
80-89	8	5	6	11	10	9	23	11	20	17	10	9
90 +	2	1	1	3	2	1	9	3	6	4	2	1

TABLE 27. The monthly percentage of egg-bearing females in each size class during 1969/70, (corrected to the nearest decimal point). The total numbers of sexually mature females from which this was calculated, are presented in Table 25 below.

	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN
50-59	50	10					5	22	28	53	59	70
60-69	67	3	4			36	22	59	45	61	75	79
70-79	67	8	12	16	39	49	63	46	46	74	74	87
80-89	100	50		31	57	90	66	63	67	74	63	91
90 +	100			33	55	100	60	25	100	75	33	83

TABLE 28. The total numbers of sexually mature females in each size class during 1969/70.

	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN
50-59	22	20	23	16	14	19	22	18	32	82	37	43
60-69	15	38	52	62	29	45	37	32	51	40	36	42
70-79	18	12	17	37	28	47	41	41	48	34	34	30
80-89	2	4	5	13	7	10	15	8	12	23	16	11
90 +	7	0	1	3	7	1	5	4	1	4	3	6

The number of months of the year in which the frequency of egg-bearing was over 50 percent of the maximum frequency recorded during the year was determined from Tables 25 and 27. Females only carry eggs between moults and using the duration of intermolt periods recorded for each class in a study of moulting in captive animals, (described on page 194) it was possible to estimate whether over 50 percent of females in each class were breeding for a sufficient period to suggest that one, two or three broods were produced in the year. For example, in the 60-69 mm carapace length size class, over 50% of females were found to be egg-bearing for approximately 190 days of the year. Therefore, as the mean intermolt period for this class (the period during which each brood of eggs is produced), was found to be about 80 days, there would be sufficient time for the majority to produce two broods, but not three. The results, based on the combined data from two years sampled are presented in Table 29.

TABLE 29. A tentative estimate of the proportion of females in each size class producing one, two, three or four broods per year.

Size class (mm)	Approx. no. of days when over 50% are egg-bearing/year	Approx. duration of intermolt period (see Table 36)	Number of broods produced per year			
			1	2	3	4
50-59	120	70	majority	some	very few	nil
60-69	190	80	some	maj.	few	nil
70-79	255	80	few	some	maj.	few
80-89	300	100	few	some	maj.	few

Examination of Table 27 shows that the 70-79 mm class, is the smallest class in which females were recorded breeding throughout the year (although this was in 1969/70 only), so it appears possible that a fourth brood may be produced by a few females in this class. Production of a fourth brood almost certainly occurs in the 80-89 mm class but the intermoult period is probably too long for the eggs to hatch in the same year. The 90-99 mm class was omitted from the estimate due to insufficient data, but it seems probably that the situation in these large females would be as suggested in the 80-89 mm class, possibly with a higher frequency ovipositing in the fourth intermoult period each year.

The Ovarian Cycle

The monthly frequency of sexually mature females in each stage of ovarian development was determined and the results are presented in Figs. 21 and 22. It must be pointed out, however that the majority of females complete several ovarian cycles during the course of one year and the pattern of ovarian development shown in these figures over a twelve month period reflects a composite picture of repetitive breeding activity.

The general seasonal pattern of breeding activity which emerges from the ovarian development during the two years of sampling is as follows: Breeding is at its lowest level during Autumn (March-May) when for two to three months the majority of females have inactive ovaries (stage 2) and the low incidence of spent ovaries (stage 5) indicates that there is little or no breeding. Thereafter, during the winter months (June-August) the ovaries start to develop rapidly and the first high incidence of spent ovaries shows that a significant level of breeding activity.

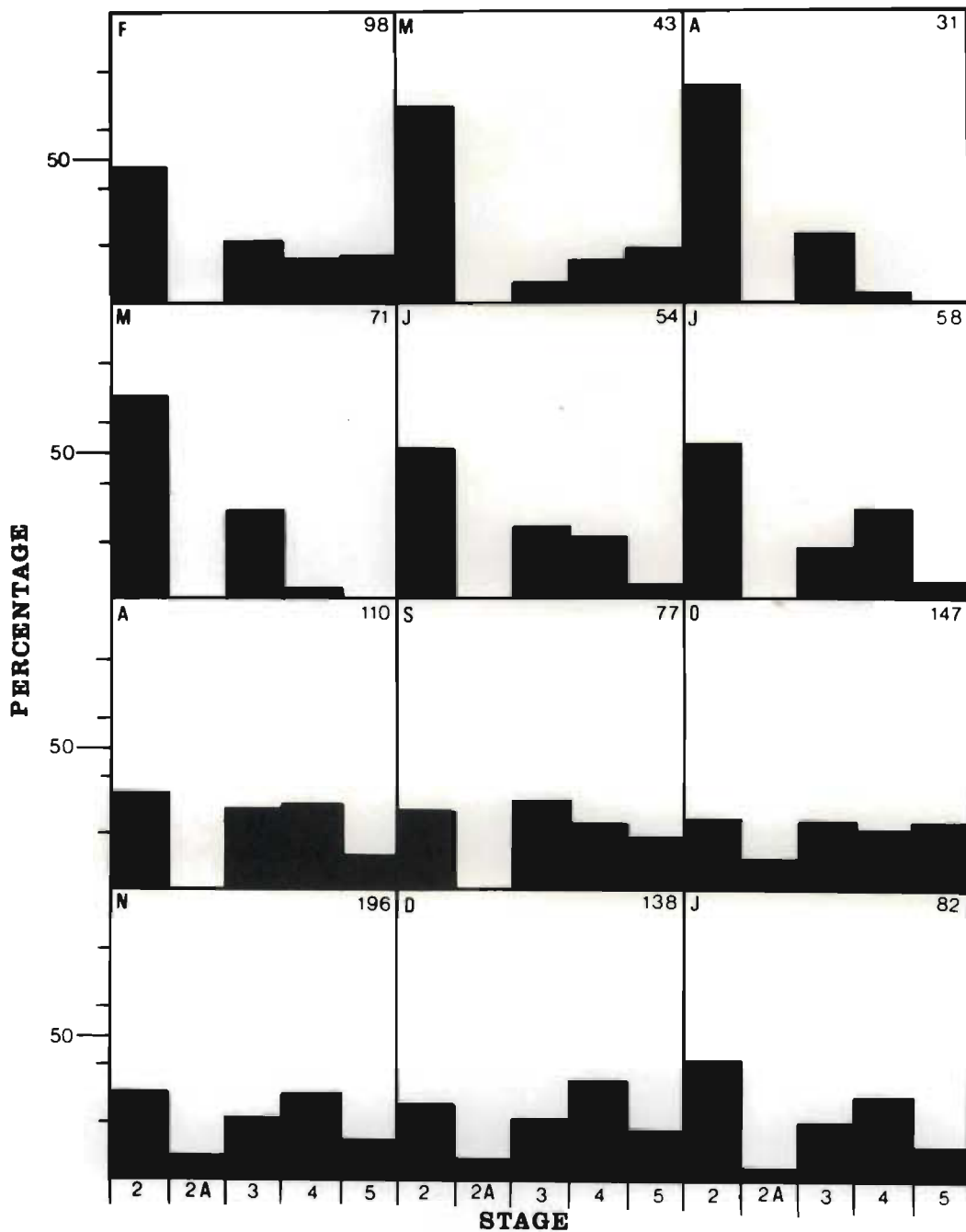


Fig. 21. Frequency of each stage of ovary development, expressed as a percentage of the total monthly catch of sexually mature females. (1968/69).

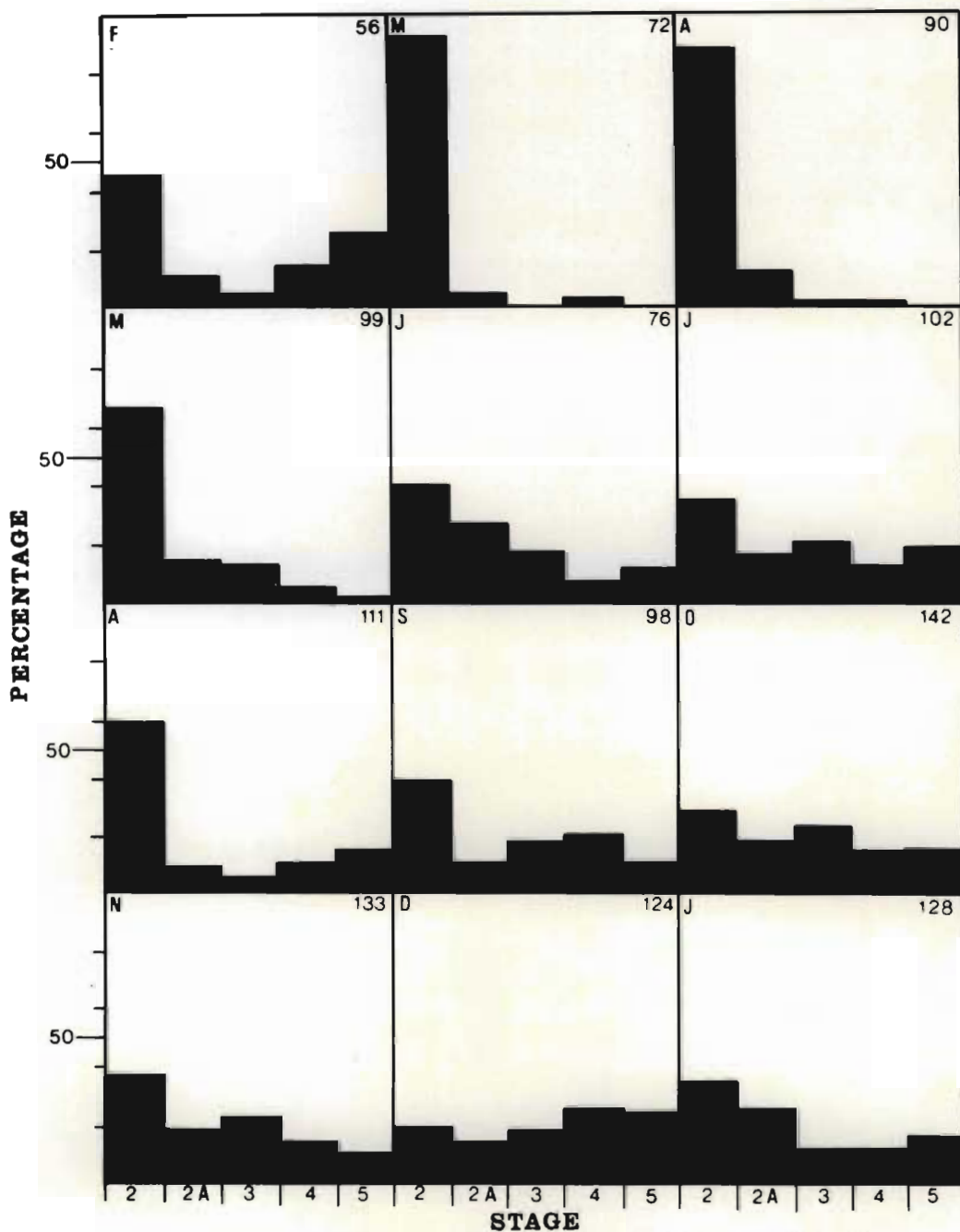


Fig. 22. Frequency of each stage of ovary development, expressed as a percentage of the total monthly catch of sexually mature females. (1969/70).

has started. Throughout the spring and summer the monthly pattern of ovarian development remains rather constant, apart from minor fluctuations. This constancy and the persistence of inactive ovaries reflects repetitive development of the ovarian cycle over the period of highest breeding activity.

Seasonal Changes In The Spermatophoric Mass

In order to distinguish between females which had not yet mated, a stage 0 was introduced in addition to stages 1, 2 and 3, denoting the postcopulatory, prefertilization and post-fertilization stages of the spermatophoric mass, which have been described on pages 132-136.

The frequency of occurrence of each of these stages was determined on a monthly basis in both years sampled and the results are presented in Figs. 23 and 24.

The highest incidence of females with no spermatophoric masses, (stage 0) coupled with the lowest incidence of stages 1, 2 and 3 was recorded in autumn and early winter, indicating the period of least reproductive activity. A low frequency of stage 0 was recorded throughout the year and the presence of this stage even in the peak months of breeding can be attributed to frequent moulting and loss of the spermatophoric mass between production of consecutive broods of eggs. For eight to nine months of the year, when breeding activity is at a high level, the proportions of stages 1-3 remained fairly constant with a low frequency in stages 1 and 2 and a somewhat higher frequency in stage 3. This is attributed to the short period in which the spermatophoric mass remains in stages 1 and 2, a mean period of five and two days respectively,

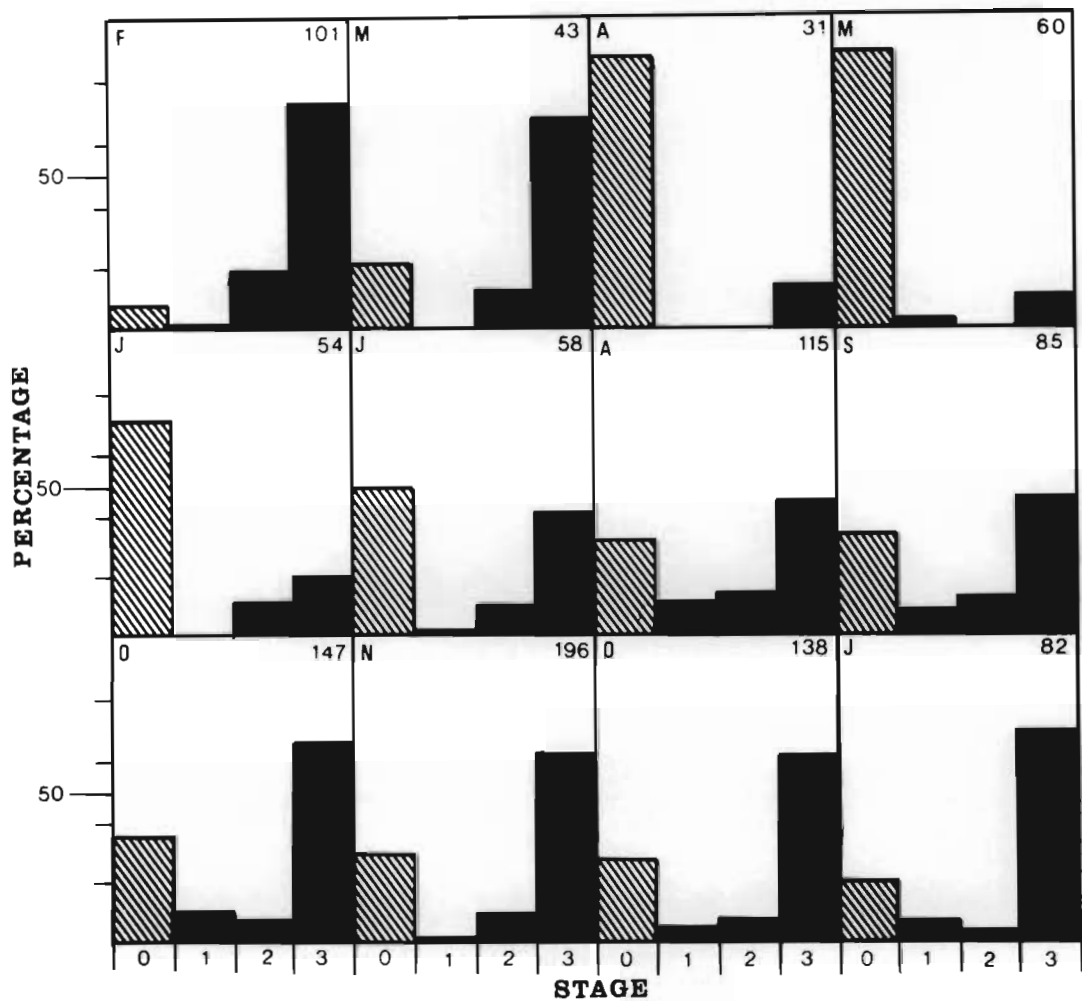


Fig. 23. Frequency of each stage of the spermatophoric mass and the incidence of females in which it was absent, (stage 0), expressed as a percentage of the total monthly catch of sexually mature females, (1968/69).

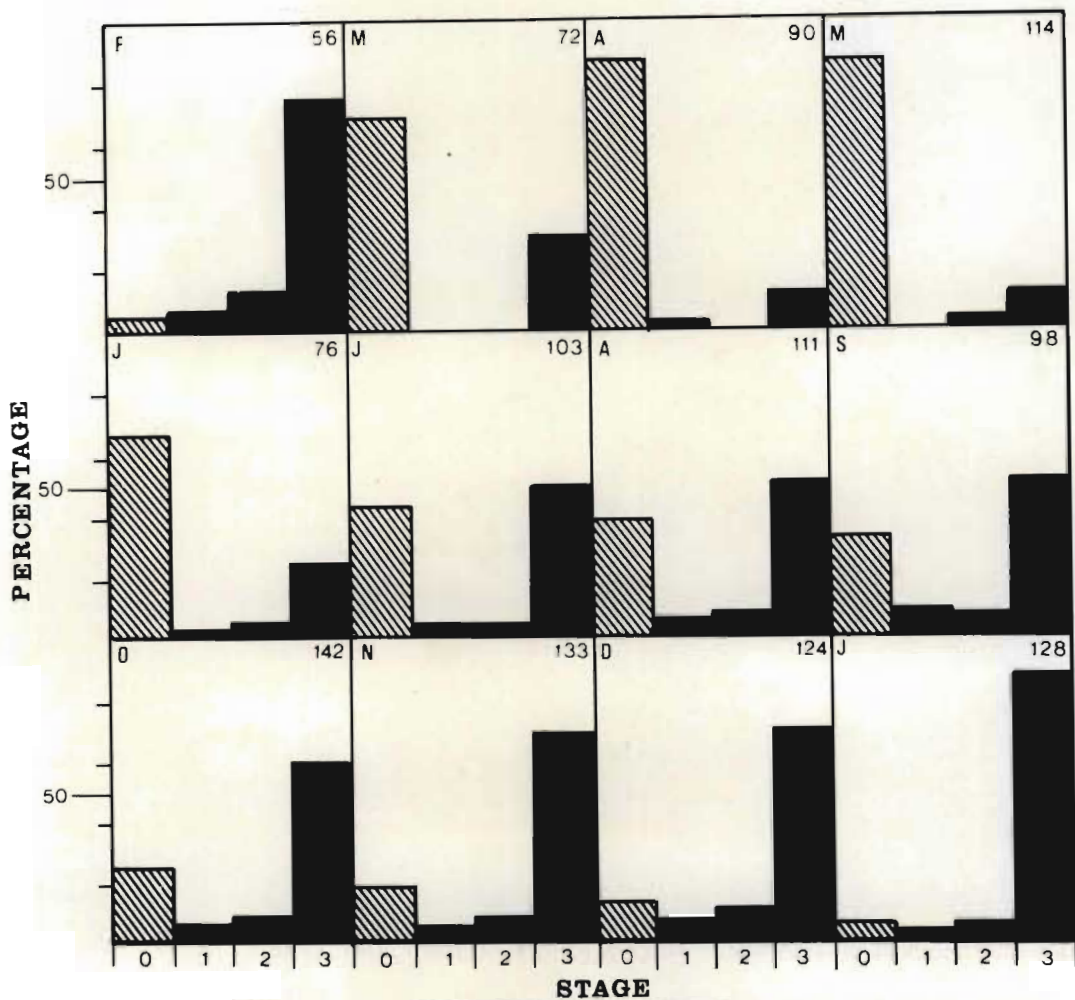


Fig. 24. Frequency of each stage of the spermatophoric mass and the incidence of females in which it was absent (stage D), expressed as a percentage of the total monthly catch of sexually mature females, (1969/70).

based on observations on captive animals, whereas the mean period it remains in stage 3 was ten days.

Development Of The Eggs

The frequency of females in stages 0 to 5 as defined on page 149 was determined on a monthly basis and the results of the two years of sampling are presented in Figs. 25 and 26.

The first increase in the frequency oviposited eggs (stage 1), indicating initiation of the breeding season is evident in June of the first year sampled and in May the following year. The rapid embryonic development observed in captive animals is substantiated by the first appearance of eggs about to hatch (stage 4) only one month later in both years. Thereafter, throughout the spring and summer months, the frequencies of stages 1 to 4 remained rather constant, due to repetitive breeding. The gradual decrease in the frequency of females with no eggs (stage 0) from the start of the breeding season to the lowest level in January and February, reflects the gradual increase in the frequency of egg-bearing which reaches a peak in these months.

The masking effects of repetitive breeding makes it impossible to determine the exact length of the incubatory period or how many broods are produced per year. The high frequency of eggs in stage 1, relative to the other stages indicates unequal distribution in time, due to inability to detect initial embryonic development in the yolky eggs macroscopically.

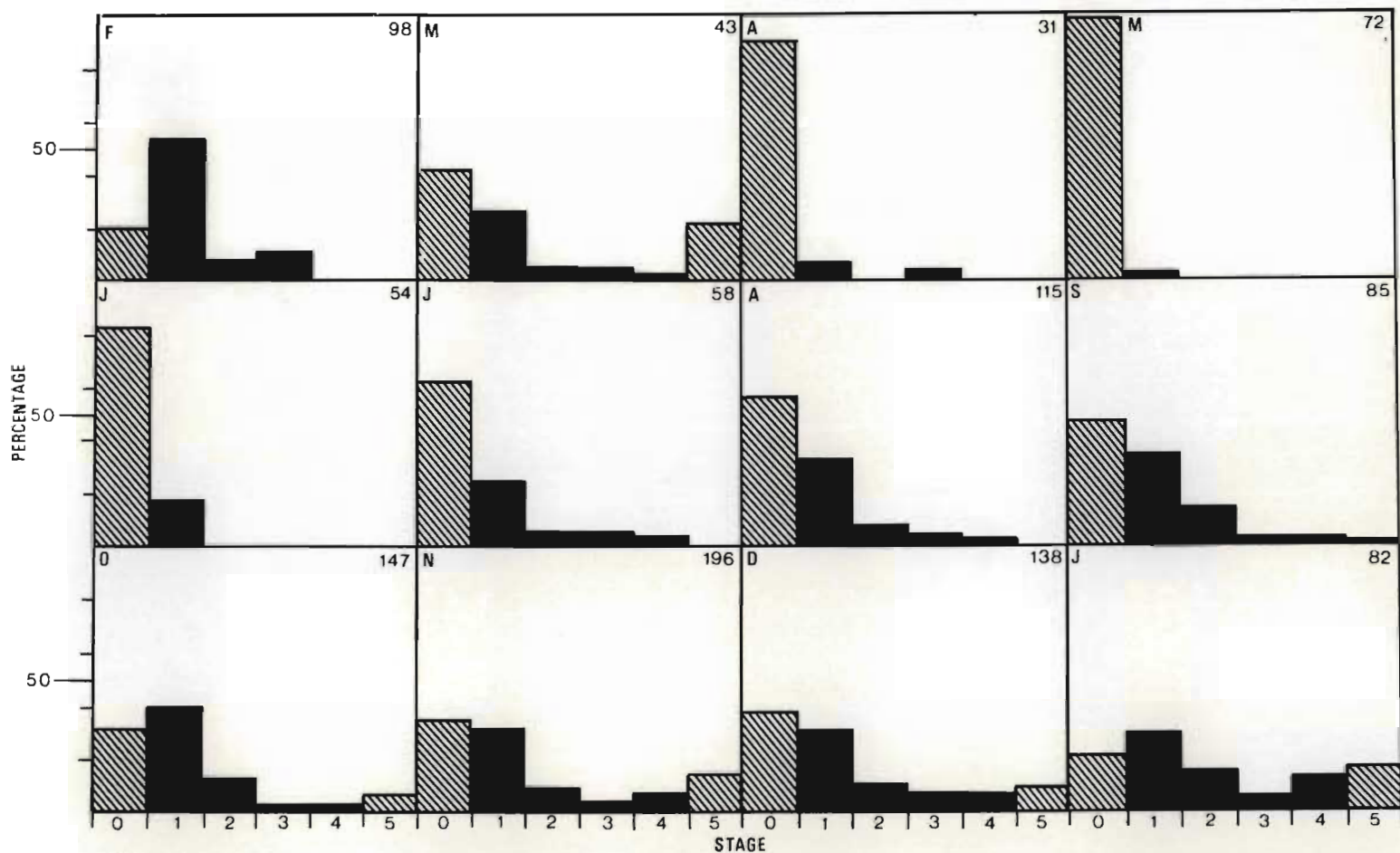


Fig. 25. Frequency of each stage in the egg-bearing cycle, expressed as a percentage of the total monthly catch of sexually mature females, (1968/69). (Stages 0 and 5 represent females without eggs, i.e. before oviposition and after hatching).

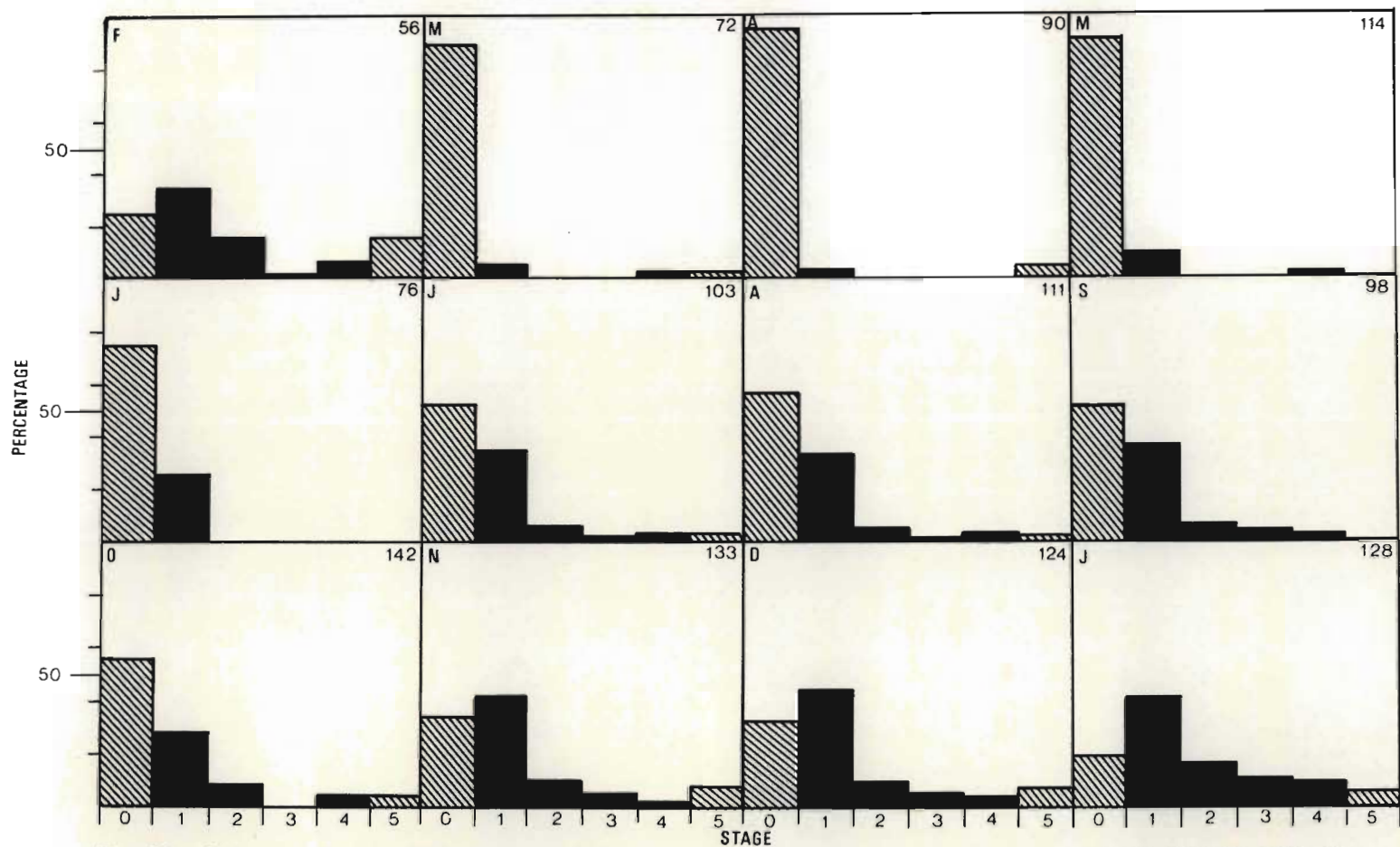


Fig. 26. Frequency of each stage in the egg-bearing cycle, expressed as a percentage of the total monthly catch of sexually mature females, (1969/70). (Stages 0 and 5 represent females with no eggs, i.e. those before oviposition and subsequent to hatching).

9.

FECUNDITY

Egg counts were made on thirty-nine randomly selected specimens over the sexually mature size range using the following method:

Approximately 1 gm of freshly spawned eggs was removed from the ovigerous setae and counted. They were then carefully dried on filter paper until they no longer stuck to it or left any signs of moisture, before they were weighed to an accuracy of 0.01g. All the remaining eggs left on the female were then carefully stripped off and dried as described above, before being added to the small sample to obtain the total weight. The total number of eggs carried was then calculated by simple proportion.

For practical purposes, the number of eggs carried may be taken to increase in direct proportion to increase in carapace length (see Fig. 27). The relationship of egg number to carapace length is given by the equation $y = -523443 + 11905.x$ which was calculated using Bartlett's method (Simpson et al, 1960).

The egg counts on P. homarus are similar to counts made in other members of the genus Panulirus; e.g. P. japonicus of carapace length 71 mm produces approximated, 524,000 eggs (Ino, 1950) and in P. interruptus between 50,000 and 800,000 eggs are carried (Lindberg, 1955). In comparison with the egg counts of various species of Jasus quoted by Kensler (1967), P. homarus appears to be considerably more fecund for its size, particularly when it is considered that it may produce several broods per year as opposed to the single brood recorded by all investigators of Jasus so far.

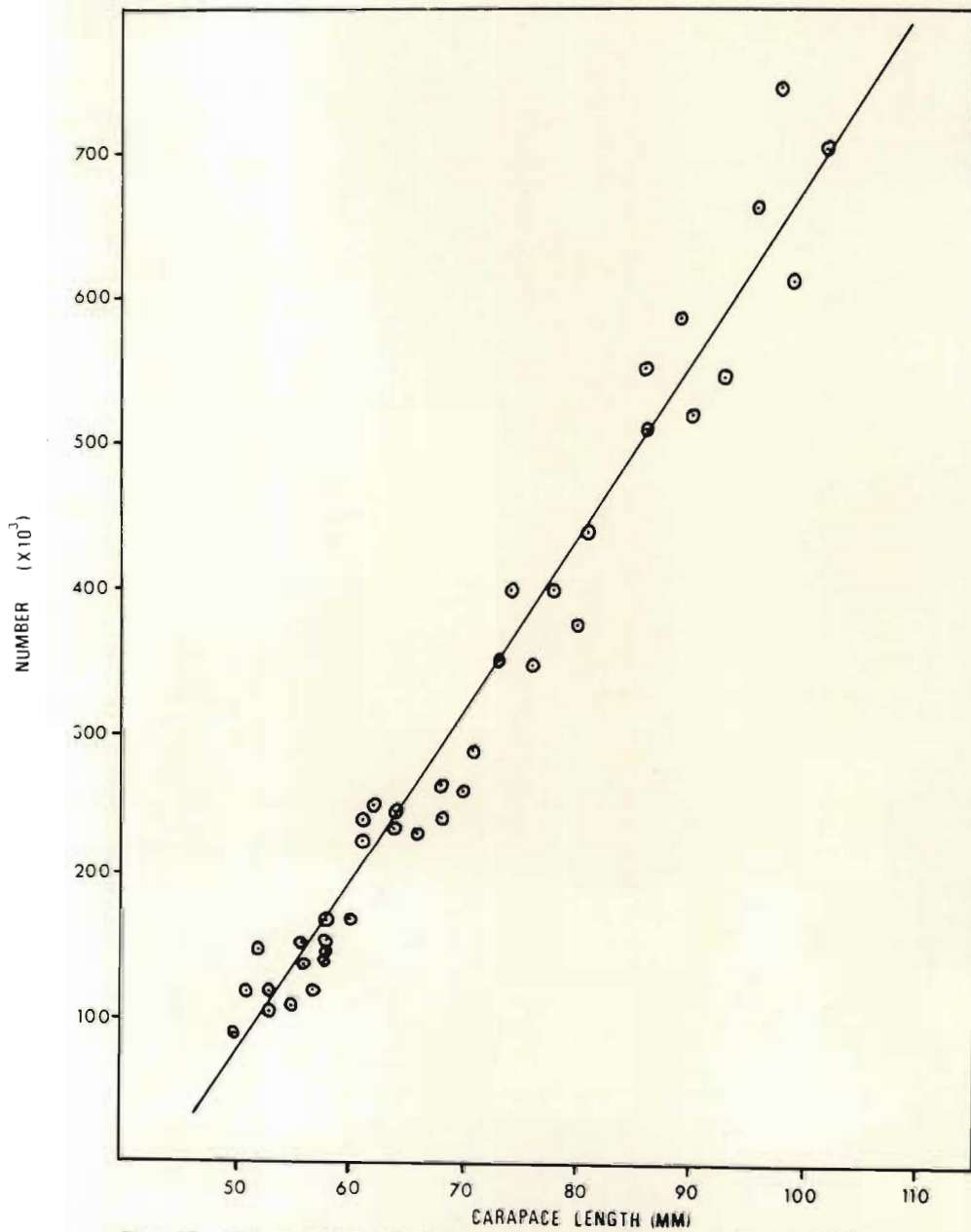


Fig. 27. The relationship between carapace length and the estimated number of eggs carried on the abdomen.

Ino (1950) found that four out of 61 captive specimens of P. japonicus produced second broods of eggs and that these averaged less than half the size of the first brood. No direct comparison was made of the size of the first and subsequent broods produced during the year by captive specimens of P. homarus; but there was no obvious reduction in size, nor was there any obvious reduction in egg counts made late in the breeding season on what must have been second, third or fourth broods.

It was possible to make an approximation of the relative fecundity of different sized females, taking into account the number of eggs produced in each size class (see Fig. 27), the number of broods produced by the majority of animals in each size class per year (see Table 29) and the approximate proportion each size class constitutes within the sexually mature section of the population. The proportion which actually breed within each size class per year was taken to be constant, as it seemed unlikely that it would vary significantly, except perhaps in the 50-59 mm class. An accurate determination of this factor was not possible due to the complications of repetitive breeding.

The proportion each size class constitutes within the population as a whole is not known and relative fecundity was estimated from Limestone Reef and surf zone samples separately. The size frequency distributions, based on random samples taken over the entire two year sampling period were used, (see Table 30) and it seems reasonable to assume that over the sexually mature size range, (taken as the 50-59 mm class and larger), the proportion of females in each size class in the samples bears a close approximation to that in the actual population sampled. Relative fecundity of each size class was calculated as shown in Tables 31 and 32.

TABLE 30. Frequency of females in each size class at Limestone Reef and the surf zone.

Size class	50-59	60-69	70-79	80-89	90-99	100-109
Limestone Reef	No 94 %	332 28.8	470 40.7	184 15.9	69 6.0	5 0.4
Surf zone	No 599 %	537 36.4	253 17.1	81 5.5	6 0.4	- -

Examination of these Tables shows that both in the Limestone Reef and the surf zone populations, the 70-79 mm size class was estimated to be the most fecund. In actual fact, the relative fecundity of the 80-89 mm and larger classes would be higher than is shown, as an unknown proportion of each probably produces four broods per year. Nevertheless even if the majority produced four broods, they would still be relatively less fecund than the 70-79 mm class which, according to this estimate, make the major contribution to the reproductive potential of this species in Natal.

Table 31. An estimate of relative fecundity of each size class in the Limestone Reef population, taking into account the proportion each constitutes within the population, the numbers of eggs produced by each and the number of broods produced by the majority in each class per year.

	Size class (mm)	50-59	60-69	70-79	80-89	90-99	100-109
A	Percentage each class constitutes in the sexually mature size range.	8	29	41	16	6	0.4
B	Number of eggs ($\times 10^3$).	131	250	379	488	608	727
C	Number of broods produced by the majority per year	1	2	3	3	3	3
	$A \times B \times C$ ($\times 10^3$)	1048	14500	46617	23424	10944	875
	Percentage contribution i.e. relative fecundity	1	15	48	24	11	1

Table 32. An estimate of relative fecundity of each size class in the surf zone population, taking into account the proportion each constitutes within the population, the number of eggs produced by each and the number of broods produced by the majority in each class per year.

	Size class (mm)	50-59	60-69	70-79	80-89	90-99
A	Percentage each class constitutes in the sexually mature size range.	41	36	17	6	0.4
B	Number of eggs ($\times 10^3$).	131	250	379	488	608
C	Number of broods produced by the majority per year.	1	2	3	3	3
	$A \times B \times C$ ($\times 10^3$)	5371	18000	19329	8784	730
	Percentage contribution i.e. relative fecundity	10	34	37	17	1

10.

SUMMARY OF REPRODUCTION

Mating behaviour was studied in thirty captive specimens. Females became sexually attractive to males, whose behaviour suggested that a pheromone sex attractant was produced. Presence of a sexually attractive female resulted in dominance of one male over all others and observations suggest that males are polygamous and prevent subordinates from mating.

The structure of the spermatophoric mass prior and subsequent to fertilization is described. Changes are brought about by the female which picks away an overlying matrix layer to expose the spermatophores as two open, highly convoluted grooves containing the spermatozoa.

Oviposition was observed on five occasions and it is suggested that spermatozoa and ova are drawn into the brood chamber by a water current set up by the abdominal endopods.

Based on observations on samples of the feral population it is considered that sexual maturity is attained by the majority of females at a carapace length of about 54 mm, although some females are capable of reproduction at a carapace length of only 50 mm. Males are considered to become physically capable of reproduction at a carapace length of between 50 mm and 60 mm.

The duration of incubation of eggs ranged between 29 and 59 days in fifteen captive females. Water temperature appeared to be an important factor in determining the incubatory period.

Observations on the breeding cycle were based on 24 consecutive monthly samples, comprising a total of 2608 females over the sexually mature size range. Egg-bearing was recorded throughout the year but maximum breeding activity was recorded in the summer months (November, December, January and February) P. homarus was found to breed repetitively during the year and with increased size, females become capable of producing more broods. The estimated number of broods of eggs produced per year by the majority of females in each size class is as follows:

50-59 mm, 1 brood

60-69 mm, 2 broods

70 mm and larger, 3 broods.

Large females were found to be capable of producing a maximum of four broods. In the upper extremes of the size range, breeding appears to be independent of seasonal environmental change.

Cyclical development of the ovaries and eggs, as well as the frequency of the various structural stages of the spermatophoric mass, confirm the seasonal pattern of breeding observed in the frequency of egg-bearing. However, repetitive breeding had a masking effect so that it was not possible to determine the frequency of breeding from these observations.

Egg counts were made on thirty-nine randomly selected females over the sexually mature size range. The smallest size class (50-59 mm) was estimated to produce about 100,000 eggs and the largest class (90-99 mm) about 900,000 eggs.

An estimate of relative fecundity was made taking into account the number of eggs produced by each size class and the proportion each class constitutes in the total of sexually mature females. It was concluded that the 70-79 mm class makes the major contribution to the reproductive potential of P. homarus in Natal.

11.

MOULTING

Comprehensive descriptions of the act of moulting (ecdysis) in rock lobsters have been given by Travis (1954), Thomas (1966), and Paterson (1969). The account given here deals mainly with aspects observed during moulting in P. homarus which differ slightly from accounts given for other species.

Moulting was observed in captive rock lobsters on nine occasions and was recorded on cine film twice.

In the premoult condition, a longitudinal resorptive line extends obliquely along the length of each branchiostegite. In addition to this line there is another shorter resorptive line from the longitudinal one to the margin of each branchiostegite, at the level of the third maxilliped. As recorded in P. argus (Travis, 1954), P. cygnus (Thomas, 1966) and J. lalandii (Paterson, 1969), the exoskeleton of P. homarus does not break along the longitudinal resorptive line, as has been reported by some observers and this line serves as a pliable area which allows the normally rigid edge of each branchiostegite to bend outwards during the moult. The short perpendicular resorptive lines do break during the moult, however, and by doing so they split the edge of each branchiostegite into two portions which is

clearly visible in a photograph of moulting in P. cygnus (Thomas, 1966, Fig. 2). This facilitates the outward bending of the curved branchiostegites which could not otherwise bend far outwards in one piece.

The first indication that moulting was imminent was the bulging appearance of the arthrodistal membrane, between the carapace and the first abdominal segment. According to Drach (1939) this is caused by water absorption which increases pressure in the pericardial pouches. This appears to be a gradual process in P. homarus, as slight swelling was usually noticed the afternoon before moulting and in one animal swelling was evident three days prior to moulting. It appears also to be irreversible, as the normal sequence of moulting continued in two animals after being captured and transferred to other tanks for photographic purposes. Similarly two animals captured while sampling at sea, moulted in the divers holding bag.

During the period of initial swelling of the arthrodistal membrane, the animals were observed to avoid contact with other rock lobsters and continuous and varied movement of the appendages was evident, such as flexing the legs, scratching the dactyls on the substratum and running the flagella of the antennules between the opposed third maxillipeds. No particularly violent movements were observed, as have been recorded by some workers and it is considered that the extent and type of movement, is probably dependant on the degree of difficulty experienced in loosening the old exoskeleton from the new, underlying one.

The arthrodistal membrane between the carapace and abdomen eventually became so swollen that the posterior edge of the old

exoskeleton of the carapace separated from the new one. At this stage the arthroial membrane ruptured dorsally and the old exoskeleton of the carapace started to rise, hinged from the anterior end, slowly and imperceptibly at first, but at a progressively increasing rate. The abdomen now started a rhythmic telescoping movement and its foreshortening by muscular contraction probably served to increase hydrostatic pressure within the cephalothorax and its appendages. When the old cephalothoracic exoskeleton had risen to an angle of about 60 degrees, the eyes were withdrawn from it. At this stage the sternum became detached and the legs started to be withdrawn from the old exoskeleton, held hanging loosely downwards. As has been reported in other palinurid species, no muscular movement was apparent in the rising of the cephalothoracic exoskeleton, but once the peduncles of the antennae became visible it was evident that the animal was using them with alternate pushing motion to force the old exoskeleton forwards. In the absence of any other muscular movement visible in the cephalothoracic region it is therefore considered probably that the process of raising the old cephalothoracic exoskeleton is largely brought about by muscular movement of the antennae, once loosened within the old exoskeleton.

When the peduncles of the antennae were almost fully withdrawn, the animal increased the frequency of telescoping movement of the abdomen, resulting in its partial withdrawal from the old exoskeleton. This was probably facilitated by reduction in the pressure within the abdomen and a resultant reduction in its size, due to the almost complete release of the cephalothorax from its old exoskeleton. At this stage with the legs partially withdrawn, the animal fell onto its side. The extremities of the legs and abdomen were now withdrawn simultaneously,

as the animal gave a few flaps with its abdomen, "jackknifed" out of the old exoskeleton and swam off a short distance.

The whole process of shedding of the exoskeleton, from initial rupturing of the arthroal membrane took approximately three to seven minutes. This duration is similar to the findings of Paterson (1969) in large species of J. lalandii and is slightly shorter than duration given for P. argus (Travis, 1954), P. interruptus (Lindberg, 1955) and P. cygnus (Thomas, 1966). All nine observations of moulting in P. homarus were made on sexually mature specimens and it is not known whether the duration is shorter in juveniles as was found in J. lalandii (Paterson, 1969) and in P. argus (Travis, 1954).

It was noticed that rock lobsters would congregate round an animal in the act of moulting but would quickly retreat on contact with it. However, as soon as moulting was completed they would eagerly devour portions of the discarded exoskeleton. No instance of cannibalism was ever recorded in P. homarus unlike other species, such as J. lalandii (Paterson, 1969) and it seems that some form of inhibitory mechanism exists, which prevents cannibalism during moulting when animals are temporarily defenseless.

12.

THE MOULTING CYCLE

The moulting cycle in rock lobsters is a continuous process with which metabolism, the reproductive cycle, sensory acuity and behaviour are closely associated. The crustacean moulting cycle has been divided into four basic stages by Drach and Tohernigoutzeff, (1967) who subdivided these further into a total of thirteen stages. This subdivision was considered to

be beyond the requirements or scope of this investigation in which the intention was only to be able to distinguish animals in which moulting was just about to occur or had just occurred. Bearing in mind the large number of specimens to be examined in monthly samples, the moulting cycle of P. homarus was divided into only four macroscopically distinguishable stages which are defined below. Although this a coarse division, transition from stage A to B and C to D takes place quickly making stages A and D reasonably well defined.

TABLE 33. Classification of the moulting cycle into four stages.

Stage	Description	Approximate duration
A	Immediately after moulting; exoskeleton soft and pulpy.	24-48 hrs. approx.
B	Shortly after moulting; exoskeleton hardening but the upper branchiostegal regions of the carapace and the pleural spurs can be depressed.	2-10 days approx.
C	Exoskeleton fully hardened; not depressible as in B; if the exoskeleton is cut there is no fully pigmented underlying layer evident.	Varies according to size.
D	Moulting imminent; exoskeleton thin and brittle; an underlying fully pigmented layer can be exposed by cutting the carapace or breaking off the tip of an antenna.	11-15 days approx.

Information on the frequency of moulting and on growth was based on a study in captive animals, due to inability to obtain satisfactory results on these aspects from the monthly samples. Although the incidence of stages A and D was determined in these samples, the level of moulting tended to be very constant throughout the year, with no marked peaks of activity, making accurate interpretation of moulting frequency impossible. This was considered to suggest that P. homarus moults several times per year, probably in association with repetitive breeding. In contrast to this situation, Heydorn (1969b) found that in J. lalandii, sampling of the feral population gave a clear indication of a single moult per year with a well defined period of moulting activity.

Ovigerous Setae

Paterson (1969), working on captive J. lalandii, found that in most mature females there was an almost regular, biannual development and loss of ovigerous setae. Similarly, in the genus Panulirus, Nakamura (1940) on P. japonicus, Sutcliffe (1953) on P. argus, and George (1962) on P. cygnus indicate that females moult twice annually and shed the ovigerous setae at the moult following breeding. No evidence, however, was obtained of loss of ovigerous setae in P. homarus either from field observations or observations in captive animals.

13.

MOULTING AND GROWTH IN CAPTIVE ANIMALS

Material And Methods

Many practical difficulties would be involved in growing rock lobsters in captivity from post-*puerulus* to the maximum size attained, as such an experiment would have to last for the full life-span of the species. Moreover, after such a prolonged period in captivity it seems doubtful whether a natural rate of growth would be recorded.

A more practical approach attempted in this investigation, was to start a study of growth with a number of animals in several size classes, suitably spaced over the size range. The intention was to record growth until each class had overlapped the initial size of the one above, thus enabling a composite estimation of growth rate to be made over the entire size range in the period of approximately one year. It was considered that this would have the advantage of reducing effects of prolonged captivity on growth.

The carapace length of *P. homarus* ranges from about 7.0 mm to approximately 100 mm and a total of 47 experimental animals were divided into three separate size groups for this study. Group 1 consisted of 7 animals, in which carapace length ranged between 7.1 and 8.2 mm, Group 2 consisted of 10 animals with a carapace length range of 18.4 to 22.8 mm and Group 3 was composed of 15 animals of each sex ranging in carapace length from 61 mm to 93 mm in females and 65 mm to 87 mm in males.

The sexes were not distinguished in the first two groups, as they were composed entirely of juveniles. The numbers of experimental animals used was determined by the availability of suitable tanks.

Details of the tank in which the animals in Group 3 were kept and the methods used are given on page 122. Identification of each animal was made possible by coded punch marks in the tail fan. Quick drying, acetone-based paint was also daubed on the carapace of each animal, so that one which had moulted was conspicuous by the absence of a paint spot. Over a fourteen month period a record was kept of the date of moulting of each specimen and linear increase in carapace length was measured to the nearest tenth of a millimeter with vernier calipers.

The animals in Group 1 were kept in a tank measuring 75 mm X 58 mm X 50 mm and the dimensions of the tank in which Group 2 were kept were 150 mm X 58 mm X 50 mm. Both tanks operated on the same water circulatory system as the large tanks used for the adults. The juveniles were identified with paint marks until they were large enough to have a code punched in the tail fan.

The animals were fed on as natural a diet as possible, which consisted of ground fresh mussels (Perma perna) for very small juveniles and whole, live mussels for larger animals, supplemented with chopped fish. Particular care was taken to ensure a supply of mussels as it had been noticed previously that animals deprived of them for several intermolt periods gradually lost their pigmentation and eventually died while moulting.

Although extreme caution was exercised when handling animals, loss of appendages was unavoidable due to autospasy, particularly in juveniles. Growth records of animals which had lost more than one leg or any other appendage were discarded, but as loss of a single leg appeared to have no discernable effect on growth, and this was considered to be a fairly frequent natural occurrence, growth records were included where regeneration of only leg was involved.

Mortalities and loss of appendages seriously disrupted the original design of this experiment. No animals in Group 1 survived for more than a few moults, probably due to some dietary deficiency. In Group 2 the animals were able to feed on whole mussels and grew well. However, of the original ten animals only three survived without serious loss of appendages for the full duration of the study and of the original thirty animals in Group 3, eight males and nine females were alive at the end of the study.

These setbacks necessitated filling in gaps in the data by capturing suitable sized animals and recording growth increment after a single moult in most cases, or one inter-moult period. However, it is considered that this probably provided a better approximation of the natural growth rate than in animals kept for longer, as during the short period, adverse effects of confinement and inadequacies in diet would have been minimal. Newly captured animals fed within hours of being placed in a tank and the moulting cycle appeared to remain unaffected.

Although the results of this study are based on rather composite data, some animals were kept for up to sixteen months in captivity and these continuous records serve as a useful check on the accuracy of the estimated growth rate made.

Increase In Carapace Length

The carapace length was measured only when the exoskeleton had completely hardened after moulting and a record of growth in individual animals was obtained by comparing the premoult and postmoult carapace lengths.

Growth increments per moult in juvenile specimens, in which the sexes were considered together, and of adult males and females are presented in Tables 34, 35 and 36, respectively. Mean percentage increase per moult is illustrated in Fig. 28.

In post-*pueruli* and very small juveniles the initial low growth increments may possibly be associated with morphological and physiological change involved in transition from pelagic to benthic life. However, as these specimens did not survive long, there is the possibility that the low growth rate might reflect unfavourable environmental conditions in captivity.

It is of interest to note that the sharp drop in mean carapace length increment per moult between the 45-49 mm and the 50-54 mm size classes corresponds to the size of initial onset of sexual maturity.

TABLE 34. Average carapace length increment per moult in juveniles of both sexes.

Carapace length (mm)	Number of moults	Range of increase (mm)	Mean increase (mm)	Mean % increase (mm)
7 - 9	11	0.3 - 1.0	0.7	9.7
10 - 14	4	0.6 - 1.9	1.3	9.7
15 - 19	8	0.6 - 4.4	2.5	13.5
20 - 24	8	2.9 - 4.2	3.6	16.6
25 - 29	4	2.8 - 4.3	3.7	15.2
30 - 34	6	3.6 - 6.2	4.6	14.2
35 - 39	7	2.1 - 6.0	3.7	9.5
40 - 44	11	2.2 - 5.9	3.5	8.4
45 - 49	5	2.7 - 5.4	3.7	8.3

TABLE 35. Average carapace length increment per moult in adult males.

Carapace length (mm)	Number of moults	Range of increase (mm)	Mean increase (mm)	Mean % increase (mm)
50 - 54	3	1.6 - 3.5	2.3	5.3
55 - 59	3	1.2 - 2.9	2.1	4.8
60 - 64	2	1.4 - 3.5	2.5	4.0
65 - 69	8	1.4 - 3.0	2.2	3.2
70 - 74	13	1.3 - 3.5	2.2	3.0
75 - 79	10	1.4 - 3.5	2.3	2.9
80 - 84	6,	1.1 - 3.6	2.4	2.9
85 - 89	8	0.9 - 3.5	2.3	2.6
90 - 94	1	1.4	1.4	1.5

TABLE 36. Average carapace length increment per moult in adult females.

Carapace length (mm)	Number of moults	Range of increase (mm)	Mean increase (mm)	Mean % increase (mm)
50 - 54	5	1.4 - 3.2	2.0	3.8
55 - 59	1	2.1	2.1	3.6
60 - 64	5	0.6 - 3.8	2.3	4.0
65 - 69	13	0.4 - 3.2	1.7	2.6
70 - 74	8	1.1 - 3.8	2.2	3.0
75 - 79	8	0.8 - 3.5	2.0	2.6
80 - 84	2	2.0 - 2.1	2.0	2.5
85 - 89	1	1.1	1.1	1.3
90 - 94	3	0.6 - 0.8	0.7	0.7

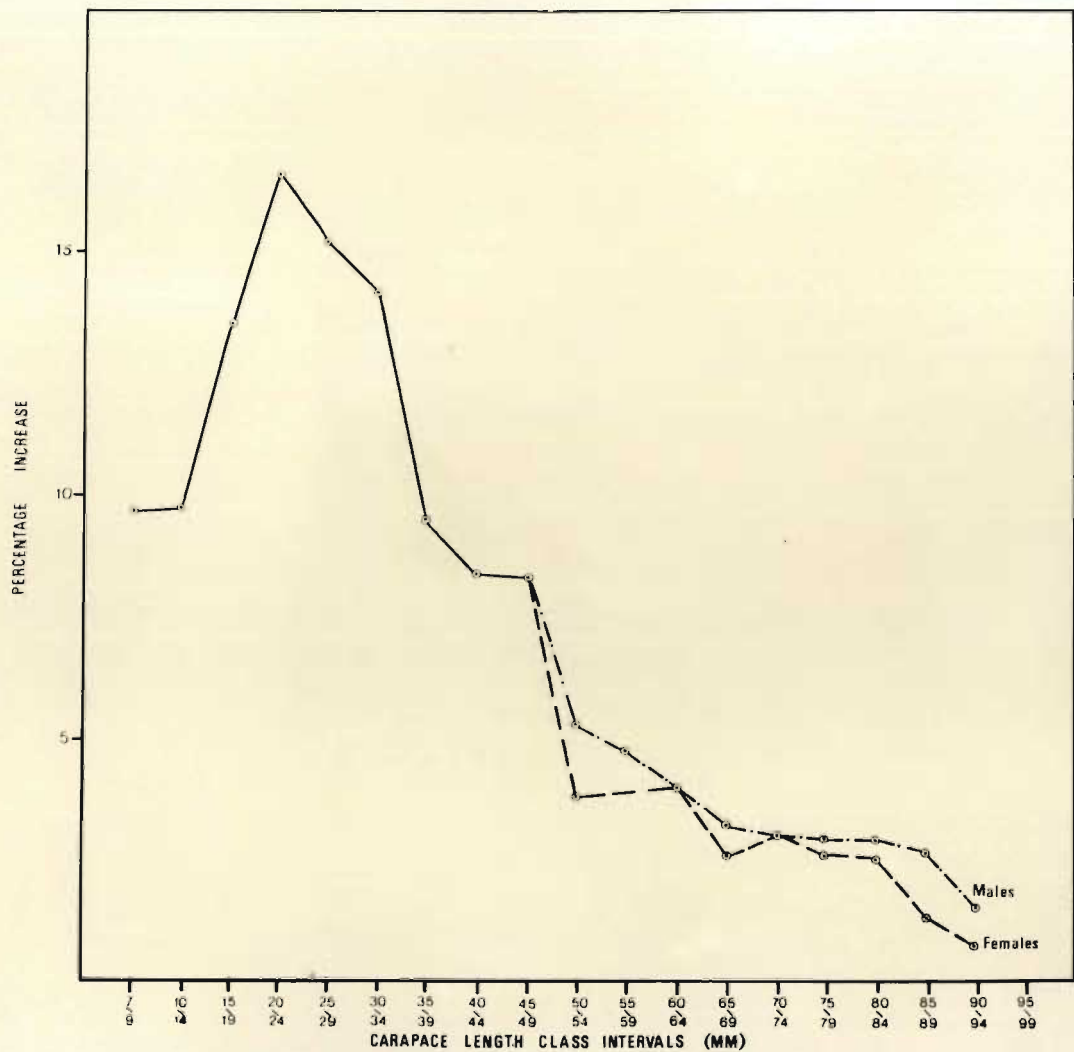


Fig. 28. Mean percentage increase per moult in each size class.

A feature of these results is that to some extent within the juveniles, and particularly over the entire adult size range except the very largest classes, a tendency is evident for the mean amount by which the carapace length increases each moult to remain fairly constant. This means that the progressive decrease in the mean percentage size increment per moult which occurs as animals become larger, is basically a function of the animals' size and is not due to a progressive decrease in carapace length increments each moult, as might have been expected. A slightly lower mean increment per moult is evident over the size range of adult females when compared with males which is attributed to an energy drain in females, associated with egg production.

The results of Paterson's (1969) study of growth in captive J. lalandii show a similar tendency for the amount by which the mean carapace length increases per moult to remain constant, and in fact the growth increments Paterson recorded in sexually mature animals are of the same order as those obtained in this study. In juveniles however, the increments she recorded were considerably lower than in juvenile P. homarus.

Frequency Of Moulting

Duration of the intermoult period is recorded in Tables 37, 38 and 39. These results show that there is a tendency for progressive increase in the mean intermoult period with increase in carapace length and that the mean intermoult period of females is slightly longer than in males.

TABLE 37. Intermoult periods over the juvenile size range with the sexes combined.

Carapace length (mm)	No. of intermoult periods recorded	Range of duration of intermoult periods (days)	Mean duration of intermoult periods (days)
7 - 9	5	30 - 43	36
10 - 19	3	21 - 34	26
20 - 29	7	21 - 28	24
30 - 39	5	25 - 39	33
40 - 49	6	36 - 47	44
50 - 59	13	59 - 86	68

TABLE 38. Intermoult periods over the sexually mature size range of males.

Carapace length (mm)	No. of intermoult periods recorded	Range of duration of intermoult periods (days)	Mean duration of intermoult periods (days)
60 - 69	2	74 - 75	75
70 - 79	22	61 - 69	73
80 - 89	10	67 - 103	85
90 - 99	-	-	-

TABLE 39. Intermoult periods over the sexually mature size range of females.

Carapace length (mm)	No. of intermoult periods recorded	Range of duration of intermoult periods (days)	Mean duration of intermoult periods (days)
60 - 69	10	66 - 96	79
70 - 79	18	61 - 91	79
80 - 89	4	79 - 127	99
90 - 99	3	88 - 124	107

Paterson (1969) recorded a similar progressive increase in the intermoult period with increase in size in J. lalandii, but the duration of the intermoult period she recorded was consistently longer than that of P. homarus and she suggests that in mature animals a recurrent, regular biannual moulting rhythm is established. This is not, however, in accord with Heydorn's (1969b) findings, based on samples of the feral population of J. lalandii, in which he concludes that moulting occurs only once per year. In any event, a very much slower rate of moulting than in P. homarus is indicated, which has been recorded in other palinurid species which inhabit colder water than P. homarus, such as P. interruptus (Lindberg, 1955) and P. cygnus (George, 1962). This can probably be attributed to their having a lower metabolic rate, associated with low water temperatures.

A continuous record of moulting in the specimens kept over a period of between eleven and sixteen months is summarised in Tables 40, 41 and 42. These results confirm those above and show that the majority of sexually mature animals moulted four times per annum.

TABLE 40. Records of moulting and growth in sexually mature females kept in captivity.

Initial carapace length (mm)	Final carapace length (mm)	Time (days)	No. of moults	Mean intermoult period (days)	Mean frequency of moulting per annum
64.8	72.4	446	5	89	4.1
65.0	73.7	458	5	92	4.0
66.5	80.0	398	5	80	4.7
66.7	76.2	344	5	69	5.2
68.2	80.3	421	6	84	4.4
76.2	80.4	409	5	82	4.5
74.4	77.8	351	4	88	4.1
76.4	85.3	461	5	92	4.0
93.2	97.1	419	4	108	3.4

TABLE 41. Records of moulting and growth in sexually mature males kept in captivity.

Initial carapace length (mm)	Final carapace length (mm)	Time (days)	No. of moults	Mean intermoult period (days)	Mean frequency of moulting per annum
68.0	75.4	381	5	76	4.8
71.0	79.2	413	5	82	4.5
71.1	81.4	489	7	67	5.4
77.5	89.8	334	4	83	4.4
77.0	87.2	376	5	75	4.9
88.0	90.2	367	4	92	4.0
84.5	91.4	409	5	82	4.5
87.7	92.8	340	4	85	4.3

TABLE 42. Records of moulting and growth in juvenile specimens kept in captivity.

Initial carapace length (mm)	Final carapace length (mm)	Time (days)	No. of moults	Mean intermoult period (days)	Mean frequency of moulting per annum
21.1	52.1	381	8	47	7.8
23.0	54.0	251	7	36	10.0
34.3	55.6	343	7	49	7.4

The moulting cycles of the specimens referred to in Tables 40 and 41 appeared to be unaffected by breeding and the only alteration observed in the intermoult periods was a slight increase in length during the winter months, which is similar to the findings of Travis (1954), working on P. argus. This can probably be attributed to a decrease in metabolic rate associated with lower water temperatures in that season. It was also found that moulting did not take place at the same time in consecutive years, apparently being continuously displaced by increase in the duration of the intermoult period as the animal increased in size. Thus moulting does not appear to be a seasonably synchronised event in P. homarus.

Growth

A tentative estimate of the linear growth rate was made by cumulatively adding the mean carapace increment per moult in each size class and doing the same with the mean intermoult periods. The resulting growth curve is presented in Fig. 29, in which each point represents the estimated size attained in each consecutive moult. This estimate is subject to the limitation that any inaccuracy, particularly over the smaller size range where data were somewhat meagre, will have been carried forward and have adversely affected the estimate in the larger size classes. However, because of the large carapace increments and short intermoult periods in juveniles, it is considered that inaccuracy over this size range would have had very slight adverse effect on the overall estimate. Moreover, the fact that the growth rate of individual specimens, most of which were kept in captivity for at

least a year, conform to the above estimate of the mean growth rate, adds reassurance that the degree of accuracy achieved is at least within the possible range of variation in growth rate in P. homarus.

Fig. 29 shows that the most rapid rate of growth occurs at a carapace length in the region of between 15 and 50 mm. The marked inflection recorded at a size of 50 mm corresponds to the size at initial onset of sexual maturity, after which growth rate appears to remain constant over the sexually mature size range until the upper extreme of the range is attained and a slight decrease in growth rate is evident.

The majority of females appear to become sexually mature at a carapace length of approximately 54 mm, although a few may breed at a carapace length of 50 mm (see page 150). According to the estimated growth rate, the majority would therefore attain sexual maturity early in their third year, although it does seem possible that some females may breed late in their second year.

Although P. homarus breeds throughout the year there is a definite peak of breeding activity in the summer months. It therefore seems probable that after the pelagic larval life there is corresponding peak period of larval settlement. As the breeding season of small adults is short, starting later and ending earlier than in larger animals it seems probable that the time of year at which larval settlement occurred would determine whether sexual maturity was attained during this comparatively short breeding season and thus whether females bred in their second or third years.

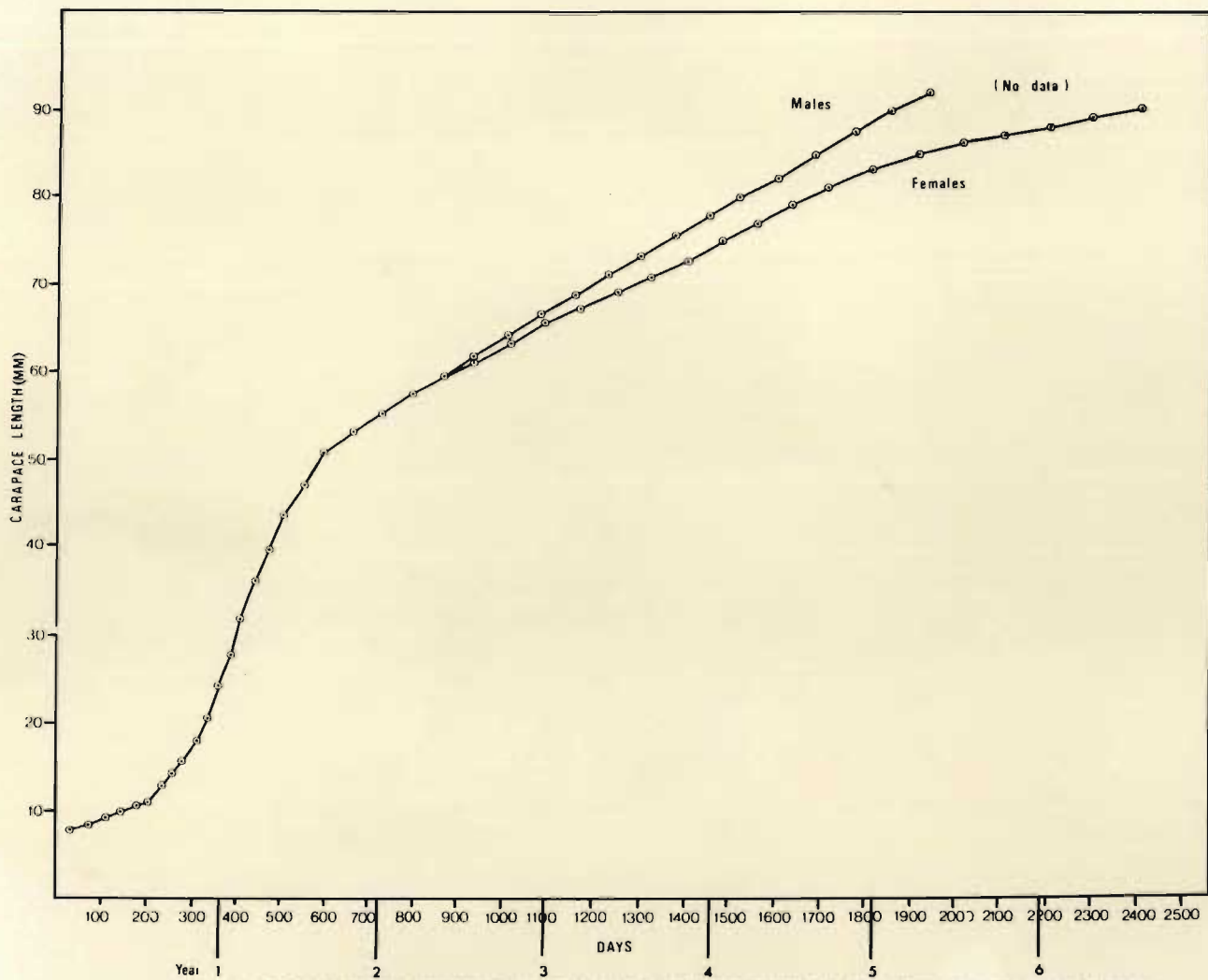


Fig. 29 Estimate of linear growth rate made by cumulatively adding the mean carapace length increment per moult in each size class and doing the same with the mean intermoult periods.

As small females start breeding in September/October when the majority have a carapace length of about 54 mm, it is possible to interpolate from Fig. 29 that the peak of larval settlement occurs in the same months two years earlier.

As the peak of hatching of eggs is in March/April this would mean that the larval life lasts for six to seven months. This is however, a very tentative estimate and it is hoped that it will be possible to determine the length of larval life and peak period of settlement more accurately from the study of phyllosoma and puerulus larvae, currently being undertaken. If this is possible it will serve as a useful check on the time scale shown in Fig. 29.

According to the estimate of relative fecundity described on page 176, females within the 70-79 mm size class make the largest contribution to the reproductive potential of this species, and this size would be attained in the fourth year after settlement according to the present estimate of growth rate. It is interesting to note in Fig. 29 that in this size range, females would be appreciably older than males of the same size. This is apparently due to deceleration of the growth rate in females which becomes evident soon after the size of attainment of sexual maturity and results in an increasing divergence of the growth curves of males and females with increase in size. Assuming the level of predation to be equal in both sexes, this probably accounts for the larger maximum size attained by males, as females would have to be subjected to predation for a longer period in order to attain the same maximum size.

14.

SUMMARY OF MOULTING AND GROWTH

The act of moulting is described, based on observations made on captive rock lobsters.

The number of moults per year could not be determined from monthly samples of the feral population, as moulting was recorded at a fairly constant level throughout the year with no peaks of activity.

There is no evidence that P. homarus sheds its ovigerous setae after breeding, as has been recorded in other members of the Palinuridae.

A study of moulting was made in captive animals, in which it was found that the mean intermoult period became progressively longer with increase in carapace length and over the sexually mature size range it was slightly longer in females than in males. Sexually mature animals moulted four or five times per year.

Over the juvenile and adult size range there was a tendency for the mean carapace increment per moult to remain fairly constant, but a marked drop was evident at the size of attainment of sexual maturity. The mean percentage increment per moult reached a peak in the 20-24 mm size class. Thereafter it decreased progressively with increase in size and was slightly higher in males than in females.

The study shows that moulting is a continuous cyclical process and that ecdysis does not take place at the

same time in consecutive years, being continuously displaced by the increase in intermoult duration. Thus moulting does not appear to be synchronised with seasonal environmental conditions, although a slightly longer intermoult period was evident over the winter months. The moulting cycle appeared to be unaltered by breeding activity.

A tentative estimate of the linear growth rate was made by cumulatively adding the mean carapace increment per moult in each size class and doing the same with the mean intermoult periods. The most rapid rate of growth was found to be between a carapace length of 45 mm and 50 mm. At 50 mm, which corresponds to the size of first onset of sexual maturity, a marked decrease in the growth rate was evident and throughout the sexually mature size range it remained fairly constant, except in the upper extreme of the size range in which the rate decreased slightly. Over the sexually mature size range the growth rate of males is slightly higher than that of females.

It is estimated that the majority of females attain sexual maturity at the beginning of the third year after settlement of larvae, although some may breed late in the second year. Females in the 70-79 mm size class, which appear to make most reproductive contribution to the population are estimated to achieve this size in the fourth year after settlement.

The majority of females appear to attain sexual maturity in September/October and by interpolation from the growth rate it was possible to estimate when the peak of larval settlement occurs. Knowing the peak months of hatching of eggs it is

suggested that the larval life lasts six or seven months. However, this requires confirmation of a study of the phyllosoma and puerulus larvae.

15. CORRELATION AND DISCUSSION OF THE MOULTING AND REPRODUCTIVE CYCLES

Development of the ovarian cycle in relation to the moulting cycle is summarised in Table 43. Although a tendency of progressive development of the ovaries to maturity in the premoult and postmoult stages is evident, the ovarian cycle does not appear to be particularly closely synchronised with the moulting cycle. This is well illustrated by the fact that moulting can clearly take place with the ovaries varying in degree of development from stage 2A to 4 (see stage A in the Table).

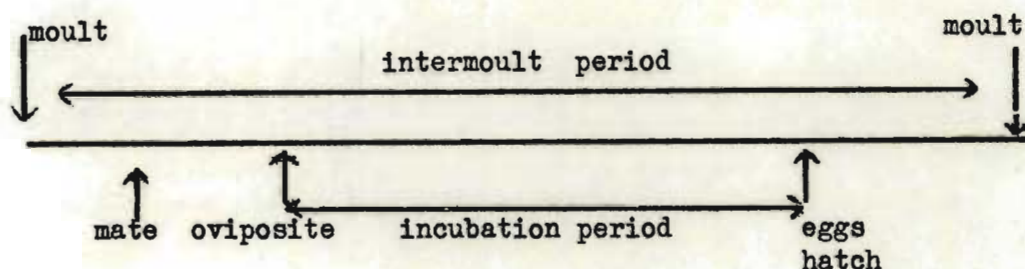
Analysis of the stage of exoskeleton in the moulting cycle in all females with freshly deposited spermatophoric masses showed that 94 percent mated with the exoskeleton fully hardened and in stage C and only 8 percent mated with the exoskeleton not yet fully hardened and in stage B. This analysis was based on 111 observations, made over the two year period of field sampling. In all observations of captive animals, mating took place with the exoskeleton in stage C.

TABLE 43. Summary of the relationship between the moulting and ovarian cycles.

Stage in the moulting cycle	Premoult				Postmoult								Intermoult			
	D				A				B				C			
Ovary stage	2A	3	4	5	2A	3	4	5	2A	3	4	5	2A	3	4	5
No.	39	87	54	1	5	31	21	-	10	39	44	-	178	261	289	298
%	22	48	30	1	9	54	37	-	12	42	47	-	17	25	28	29

The relationship between the moulting and reproductive cycles is summarised in Table 44, based on the direct observations made on captive rock lobsters and evidence obtained by sampling the feral population.

TABLE 44. Summary of the relationship between the moulting and reproductive cycles.



The timing of reproductive activity in relation to the intermoult period is shown in Table 45, based on observations on captive rock lobsters. An example of the timing of the reproductive and moulting cycles in a females, which bred in five consecutive intermoult periods, is presented in Table 46.

TABLE 45. Timing of reproductive activity in relation to the intermoult period, based on observations on captive rock lobsters.

Duration (days)	Moulting to mating	Mating to oviposition	Incubatory period	Hatching to moulting
Mean	21	8	47	10
Range	17 - 42	3 - 16	29 - 59	6 - 33
No. of observations	23	21	15	12

TABLE 46. The actual interrelationship between the moulting and reproductive cycles and their synchronisation recorded from single female which bred during five consecutive intermolt periods. The animal grew from a carapace length of 93 mm - 97 mm during this period (each vertical line represents a moult).

Moult number	1	2	3	4	5	6
Intermolt duration (days)	?	92	88	123	128	
Incubation period (days)	50	47	?	59	50	
Interval between moult and oviposition (days)	?	25	?	31	36	
Interval between hatching and moult (days)	24	20	?	33	42	
Month of moult	June 1969	Sept 1969	Dec 1969	Mar 1970	July 1970	Nov 1970

Examination of Table 45 shows that the interval recorded between moulting, and oviposition varied considerably. As females moult with the ovaries in varying stages of development, (see Table 43), it seems possible that this interval might depend upon their degree of development when moulting occurs and their subsequent rate of maturation.

The incubation period of eggs appears to be dependant on environmental conditions and probably also the size of the female carrying them, although clear evidence of variation with size was not obtained.

The interval which elapses between hatching of the eggs and moulting is greatest in summer as the length of the incubatory period is shortest at this time. Although no females moulted while ovigerous, two did strip off fertilized eggs prematurely and one moulted three days and the other four days later. The date of oviposition was unknown in these specimens but the intermoult period in both cases appeared to be of normal duration which suggests that the eggs might have been removed due to the impending moult.

That the moulting cycle is a continuous process is demonstrated in Fig. 29, where progressive increase in the intermoult period is evident with progression of time. It was found that the intermoult periods do not appear to be synchronised with the seasonal environmental events and as a rock lobster grows, they are progressively displaced in consecutive years relative to any given time in the year. For example in Table 46, it may be seen that the animal did not moult in the same months in 1970 as it did in 1969. This would be expected to have the effect of a gradual change in the timing of the intermoult periods in relation to the seasons and thus prevailing environmental conditions. It therefore seems possible that the number of times an animal breeds per year might be determined by the degree of synchronisation of the intermoult periods (and thus potential breeds cycles) with favourable environmental conditions. Increase in the number of broods produced per year seems to be associated with the ability to start breeding earlier in the season and continue later as females increase in size. It appears therefore, that timing of the moulting cycle at the beginning and end of the season when conditions for breeding are marginal would determine whether

a female bred and thus how many broods she produced. Very large females, however, which breed in consecutive intermoult periods throughout the year appear to be unaffected by seasonal environmental changes. This suggests that breeding occurs as often as females are physiologically capable of doing so and not necessarily at a particular time when environmental conditions for phyllosoma larvae are optimal.

It seems likely that if more data had been available, a slight seasonal change in the length of the mean intermoult period might have been detected throughout the year besides the prolongation observed during winter months. Nevertheless the results of this investigation clearly demonstrate that the moulting cycle is not synchronised with seasonal environmental events, and moreover, it appears to be the basic cycle, with the sequence of activities involved in reproduction "superimposed" upon it.

P. homarus appears to be the only palinurid species which has been recorded to breed more than twice a year. This high fecundity suggests that larval mortality might be high, perhaps due to the local current systems. However, incidental observations made on the reproductive biology of P. longipes and P. penicillatus in this investigation indicate that they breed several times a year. It therefore seems probable that the situation regarding moulting and reproduction described in P. homarus, may prove to be typical of other tropical and sub-tropical spiny lobsters.

16.

FEEDING

Identification of the food items eaten by P. homarus was restricted by the fact that they are masticated both by the mandibles and in the gastric mill. Moreover, as feeding takes place at night, stomach contents of animals caught during the day are usually semi-digested. For these reasons, identification was largely limited to fragments of molluscan shell and calcareous crustacean remains.

The contents of the gastric mills of samples of P. homarus were lumped together, washed in running water and then sorted into various groups of food organisms. The percentage by volume of each classified group was then determined. A large proportion of the gastric mills were empty, probably due to regurgitation of the contents after capture, and large samples were needed before an adequate quantity of stomach contents was obtained for examination. The result of analysis of the gastric mills of over 1000 randomly selected specimens is presented in Table 47.

TABLE 47. Food items recorded in the gastric mill.

Food Items		Entire size range	Carapace length less than 50 mm
Phylum	Group	%	%
Mollusca	<u>Perna perna</u>	76	17
	other Pelecypoda and Gastropoda	1	5
Crustacea	Cirripedia (Thoracica)	12	47
	Decapoda	5	8
Other	Semi-digested tissue and sand particles	6	23

Examination of the Table shows that the gastric mills of small rock lobsters contained a higher proportion of barnacle remains and a lower proportion of mussel remains than in large lobsters. It appears that this might be due to inability of the small animals to open mussels, as in captivity it was noticed that they were only able to open the very smallest mussels and appeared to subsist to a large extent on the barnacles covering the mussel shells. This might explain why small rock lobsters are confined to the surf zone, as barnacles are particularly numerous there.

P. homarus appears to be essentially carnivorous and although some traces of plant remains were recorded, it seems likely that they were ingested incidentally, on pieces of mussel shell. Although it may feed on almost any dead animal, P. homarus cannot be regarded as a true scavenger, as its chief food organism is live brown mussels (Perna perna). In addition, barnacles, probably mainly growing on mussel shells, are an important food item. It seems probable that the majority of fragments of decapod crustacean exoskeleton originate from exuviae eaten for their calcium content, as feral rock lobsters have been observed eating the exuviae of their own species.

Feeding behaviour was observed in both feral and captive animals. P. perna occurs in dense aggregations in which the attaching byssus threads are protected by the neighbouring mussels. Rock lobsters usually select a mussel separated from, or on the edge of a group and detach it by severing the byssus threads with the dactyls of their stout third maxillipeds. The mussel is then turned with the maxillipeds and first walking legs and any large barnacles are bitten off with the mandibles

and ingested. The mussel is manipulated until the flattened end is brought between the mandibles with which the edge of the shell is crushed. When a sufficiently large aperture has been made in the shell, the dactyls of the third maxillipeds or the first walking legs are inserted, the adductor muscle is severed and the two valves are levered apart exposing the flesh for ingestion. On occasions when mussels are eaten without being detached from the rock, the same method of opening them is employed. Large numbers of mussel shells opened by P. homarus are washed up on Natal beaches.

SECTION 4

THE BIOLOGY OF PALINURUS DELAGOAE

1.

INTRODUCTION

The investigation of the biology of Palinurus delagoae, on which this section is based, was of a preliminary nature and was not as intensive as that of P. homarus. However, it appears that no previous study of the life history of a member of the genus Palinurus has been undertaken which therefore makes comparison between P. delagoae and other comparatively well known genera, such as Jasus and Panulirus, particularly interesting.

2.

MATERIAL AND METHODS

Sampling

Monthly samples were obtained using the standard ottertrawl employed in the commercial fishery for P. delagoae. This had a 24 m headrope and 7.6 cm stretched mesh in the cod-end. In the initial phases of the programme, the Oceanographic Research Institute's research vessel DAVID DAVIES, a stern trawler of 72 gross tons was used for sampling. However, this vessel was later sold to a commercial fishing concern which undertook to trawl for P. delagoae each month and to retain complete drags of rock lobsters for research purposes. A total of eighteen monthly samples were obtained of which sixteen were considered to be adequately large for study of the life history. Of these sixteen samples, which comprised a total of 4830 specimens,

... taken in 1968, eleven in 1969 and two in 1970.
As possible, all samples were obtained in the first week
of the month.

The samples were frozen aboard the vessel and unless
otherwise stated, all data were recorded on freshly thawed
material which was examined on shore. Measurements were
made by the author only, and carapace length, which was used
as the standard measurement of length in this investigation, is
defined as the distance along the dorsal midline from the base
of the median spine on the anterior margin of the carapace,
to the posterior extremity of the carapace. The measurement
was not made from the tip of the anterior median spine as this
was so frequently damaged.

The moulting, ovarian and egg-bearing cycles were
classified into arbitrary stages of development which were
each recorded as a numerical value.

The Research Area

All samples originated from trawling grounds off the
Natal coast at a depth of between 180 and 324 m. These grounds
extend discontinuously from Isipingo in the south to the Tugela
river in the north.

3.

CHARACTERISTICS OF THE POPULATION

A brief account of the habitat where P. delagoae occurs, its depth distribution and behaviour is given on pages 28 and 29. in Section 1.

Interpretation of the population structure of this species from a single sample each month is difficult, due to the very variable catch composition. This is attributed to segregational behaviour and some samples consisted predominantly of sexually immature specimens, sexually mature specimens or egg-bearing females. Moreover, although sampling was concentrated as far as possible to the optimal depth at which sexually mature rock lobsters occur, the constant local movement of P. delagoae made it impossible to ensure that the same section of the population was sampled consecutively. This segregational behaviour and movement is not understood at this stage but a tendency for small, sexually immature rock lobsters to occur in the deepest extreme of the depth range was evident, whereas sexually mature animals and particularly dense aggregations of egg-bearing females tended to occur in shallower water near the edge of the continental shelf. While it seems probable that local movement and segregation may be determined by availability of food and reproductive behaviour, an extremely intensive sampling programme would be necessary before any correlation between distribution and behaviour of the various sections of the population would be possible.

Size Frequency Distribution

The size frequency distributions of males and females on a monthly basis are presented in Fig. 1, which illustrate the variability in composition of the samples. However, it is considered that the sexually mature section of the population was adequately sampled in sufficient number of months for interpretation of the breeding cycle.

The size frequency distributions of the total catch of males and females taken over the entire sampling period are presented in Fig. 2. The absence of juvenile specimens smaller than the 50 - 59 mm size class from the catch is conspicuous. This suggests that they have a different distribution or occur in a different habitat, as at least small numbers would be expected to have been caught if they were present with the adults, due to clogging of the meshes of the trawl. Moreover, no juveniles were obtained even by using a prawn trawl with a 40 cm mesh in the cod-end. The low numbers of the smallest size class (50 - 59 mm) caught may be attributed partially to their ability to escape through the trawl mesh, but may also reflect their scarcity on the trawling grounds as it is in this size range that recruitment to the adult population appears to occur. The only hint of where the juveniles may occur is given by the exclusive presence of specimens in the 50 - 59 mm size class in the lower extreme of the depth range down to 400 m, which suggests that the bulk of the juvenile population may inhabit a still greater depth.

Over the larger size range, from the 70 - 79 mm size class upwards, fishing characteristics of the trawl seem unlikely

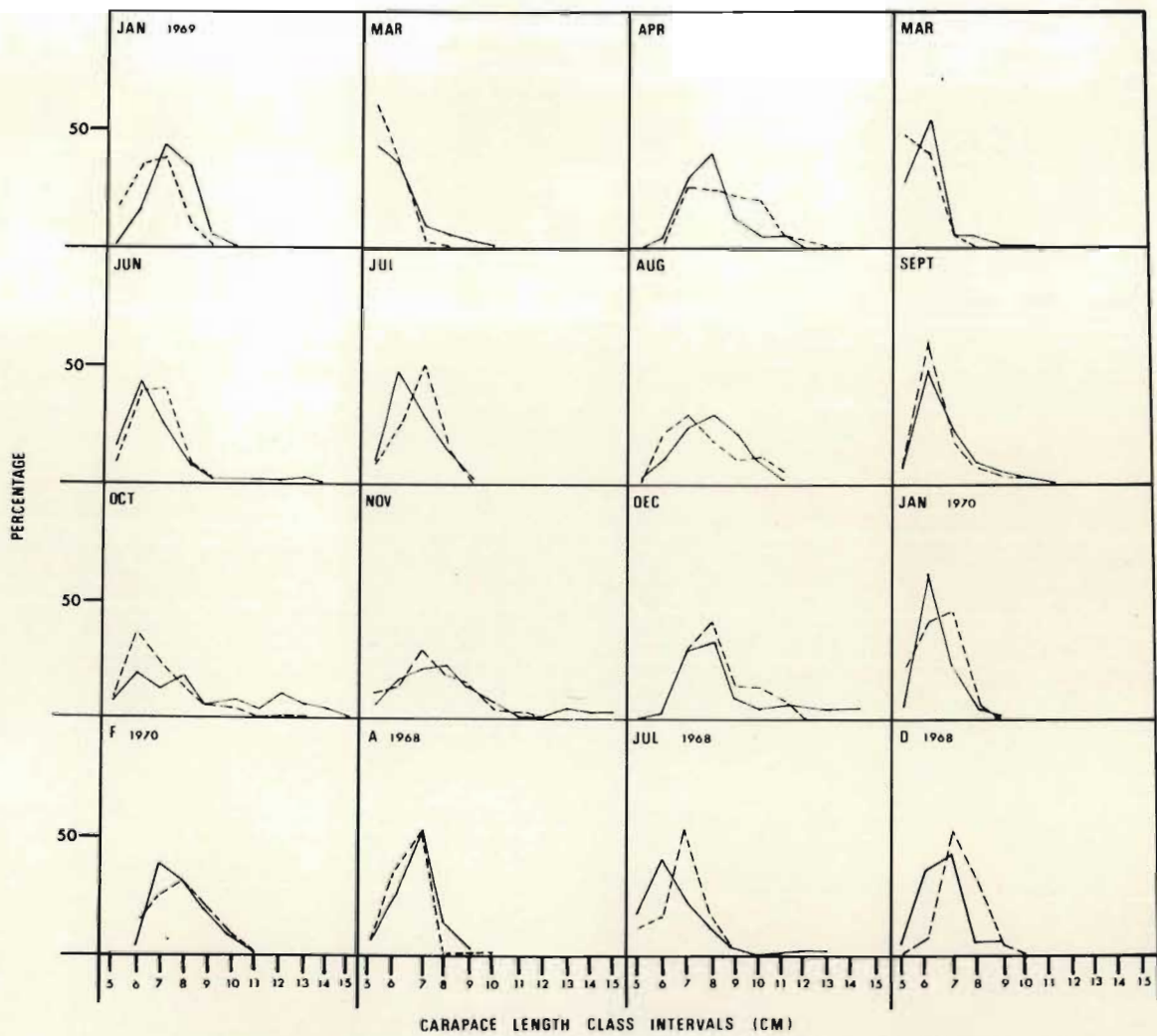


Fig. 1. Monthly size frequency distributions (males = solid line, females = broken line). (See Tables 1 and 2).

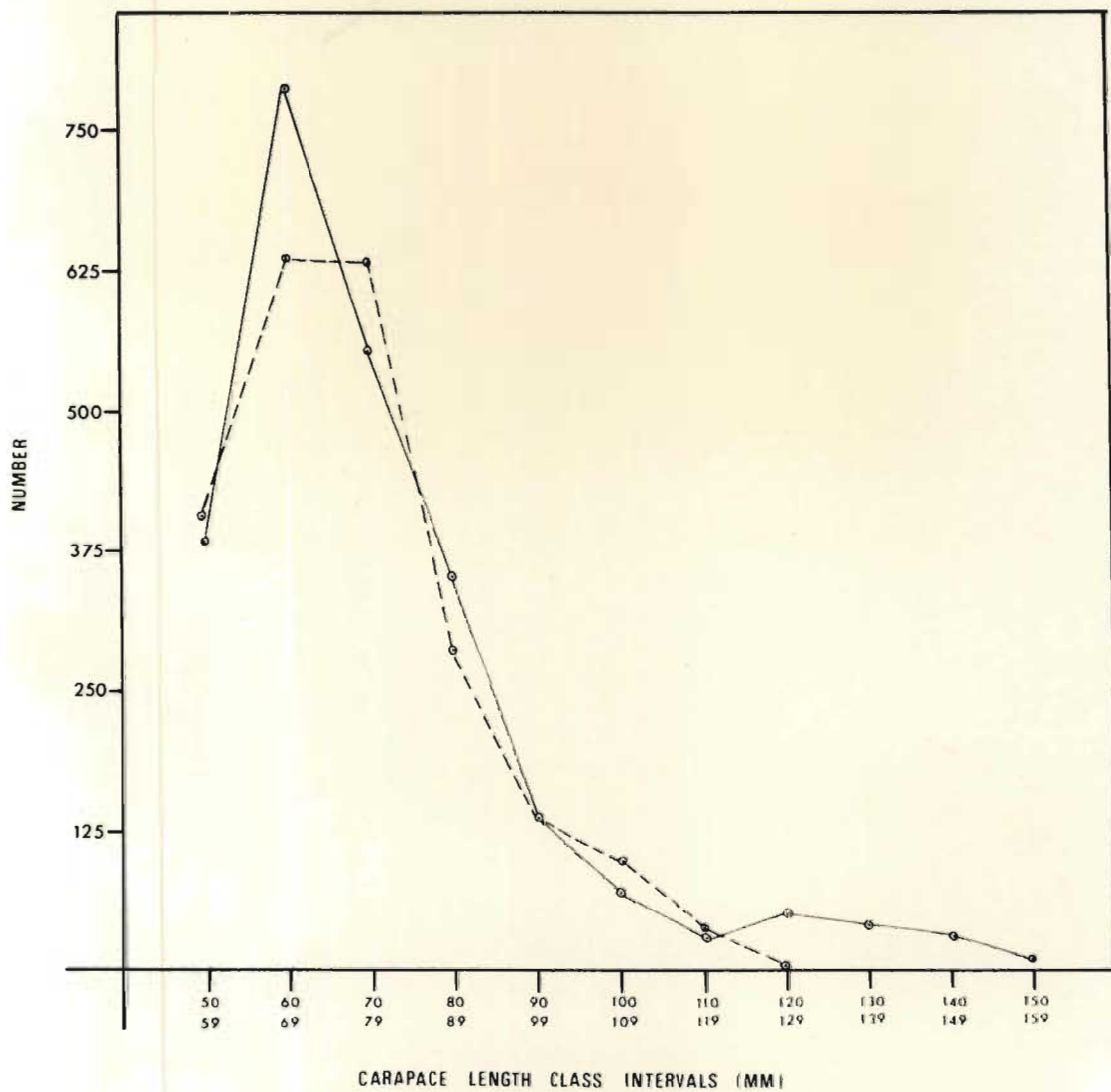


Fig. 2. Numbers of males (solid line) and females (broken line) in each size class in the combined monthly samples.

Table 1. Monthly frequency of males in each size class.

Size Class	50		60		70		80		90		100		110		120		130		140		150		Total
	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	
Apr. 1968	5	2.4	53	25.9	109	53.4	29	14.2	7	3.4	1												204
Jul. 1968	7	16.7	17	40.4	10	23.8	5	11.9	1	2.4			1	2.4	1	2.4							42
Dec. 1968	1		6		7		1		1														16
Jan. 1969	2	1.9	17	15.7	47	43.5	37	34.3	5	4.6													108
Feb. 1969							No		S	a	m	p											
Mar. 1969	249	43.3	206	35.8	51	8.9	34	5.9	20	3.5	4	0.7	4	0.7	5	0.9	2						575
Apr. 1969	0	0	1	5.0	6	3.0	8	4.0	13	1.5	1	5.0		0			1	5.0					20
May. 1969	34	17.3	102	52.3	45	23.0	8	4.1	0	0	2	1.0	1	.5	2	1.0	1	.5	1	.5			196
Jun. 1969	24	15.7	66	43.1	39	25.5	12	7.8	3	2.0	2	1.3	1	0.7	3	2.0	1	0.7	2	1.3			153
Jul. 1969	12	9.4	59	46.4	37	29.1	17	13.4	2	1.6				0		0							127
Aug. 1969	2	2.3	9	10.2	21	23.8	26	29.5	18	20.4	8	9.1	3	3.4	0		0				1	1.1	88
Sep. 1969	11	7.1	76	49.0	35	22.6	14	9.0	8	5.1	4	2.6	1	0.6	1	0.6	0		3	1.9	2	1.3	155
Oct. 1969	19	7.1	50	18.8	35	13.2	53	19.9	19	7.1	22	8.3	8	3.0	29	10.9	19	7.1	11	4.1	1		266
Nov. 1969	8	5.1	25	16.1	32	20.6	36	23.2	21	13.5	12	7.7	2	1.2	3	1.9	7	4.5	5	3.2	4	2.6	155
Dec. 1969	0		3	2.6	34	29.8	37	32.5	11	9.6	5	4.4	7	6.1	6	5.2	6	5.2	5	4.4	0		114
Jan. 1970	10	4.8	130	62.2	48	23.0	13	6.2	5	2.4	0		1	0.5	0		1	0.5	1	0.5	0		209
Feb. 1970	0		3	3.9	30	38.9	24	31.1	13	16.9	5	6.5	1	1.3	0		0		1	1.3	0		77

Table 2. Monthly frequency of females in each size class.

Size Class	50		60		70		80		90		100		110		120		130		140		150		Total	
	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%		
Apr. 1968	3	4.5	25	37.9	35	53.0	1	1.5	1	1.5	1	1.5	0	0	0	0	0	0	0	0	0	0	66	
Jul. 1968	9	11.1	13	16.0	44	54.3	14	17.3	0		1	1.2	0	0	0	0	0	0	0	0	0	0	81	
Dec. 1968	0		3	7.9	20	52.6	13	34.2	2	5.3	0		0	0	0	0	0	0	0	0	0	0	38	
Jan. 1969	5	17.2	10	34.4	11	37.9	3	10.3	0		0		0	0	0	0	0	0	0	0	0	0	29	
Feb. 1969	No Sample																							
Mar. 1969	269	61.1	157	35.7	10	2.3	2	0.5	0		0		2		0	0	0	0	0	0	0	0	440	
Apr. 1969	0		6	2.1	73	25.3	71	24.7	64	22.2	58	20.1	15	5.2	1	3.5	0	0	0	0	0	0	0	288
May. 1969	54		98		55		6		2		0		0		0		0	0	0	0	0	0	215	
Jun. 1969	14	8.6	63	38.9	65	40.1	17	10.5	2	1.2	0		1	0.6	0		0	0	0	0	0	0	162	
Jul. 1969	16	7.9	47	23.4	102	50.7	36	17.9	0		0		0		0		0	0	0	0	0	0	201	
Aug. 1969	0		15	22.1	20	29.4	12	17.6	7	10.3	10	14.7	4	5.9	0		0	0	0	0	0	0	68	
Sep. 1969	7	6.2	70	61.9	21	18.6	8	7.1	4	3.5	3	2.7	0		0		0	0	0	0	0	0	113	
Oct. 1969	10	10.3	37	38.1	23	23.7	14	14.4	6	6.2	5	5.2	1	1.0	1	1.0	0	0	0	0	0	0	97	
Nov. 1969	13	11.6	16	14.3	34	30.4	21	18.8	19	16.7	5	4.5	4	3.6	0		0	0	0	0	0	0	112	
Dec. 1969	1	1.4	2	2.8	20	27.8	30	41.7	10	13.9	6	8.3	3	4.2	0		0	0	0	0	0	0	72	
Jan. 1970	6	21.1	119	41.8	131	45.9	23	8.1	2	0.7	0		3	1.1	1	0.35	0	0	0	0	0	0	285	
Feb. 1970	0		8	12.9	15	24.2	19	30.6	12	19.4	6	9.7	1	1.6	1	1.6	0	0	0	0	0	0	62	

to have affected the size composition of the catch. The presence of what appears to represent almost an extension of the extremely large males in the catch composition graph, suggests that once a certain size is attained there may be a reduction in natural predation on them. Their occurrence in the population could also be interpreted to suggest that it has been little affected by exploitation. However, this is not consistent with the decrease in catch per unit effort in the fishery reported by trawlermen in recent years and the persistence of these extremely large specimens is possibly due to concentration of the fishery on the large aggregations of small specimens, which can be trawled in greater quantities and which usually occur in deeper water than the extremely large animals.

The Sex Ratio

The proportions of the sexes in each size class in the combined catch of sixteen months show what approximates to a 50/50 ratio over most of the size range (Table 3). However, in the 120-129 mm size class the larger size attained by males results in a sudden increase in their proportion and their exclusive occurrence in 130-139 mm size class and those above.

The ratio of sexes on a monthly basis shows marked fluctuation which is interpreted to reflect segregation of the sexes, possibly associated with reproductive behaviour, (see Table 4). For instance the sample in April, 1969 was composed virtually entirely of sexually mature females, over 90 percent of which were ovigerous.

TABLE 3. The sex ratio in each size class, based on the combined monthly samples.

Size class	Numbers		Percentages	
	Males	Females	Males	Females
50 - 59	384	407	48.5	51.5
60 - 69	823	689	54.4	45.6
70 - 79	586	679	46.3	53.7
80 - 89	354	290	55.0	45.0
90 - 99	137	131	51.1	48.9
100 - 109	66	95	40.9	59.1
110 - 119	29	34	46.0	54.0
120 - 129	50	4	92.5	7.5
130 - 139	39	-	100	-
140 - 149	28	-	100	-
150 - 159	8	-	100	-

TABLE 4. Sex ratio on a monthly basis.

Month	Numbers		Percentages	
	Males	Females	Males	Females
April 1968	204	66	75.	24.4
July	42	81	34.1	65.9
Dec	16	38	29.6	70.4
Jun 1969	108	29	78.8	21.2
Mar	575	440	56.7	43.3
Apr	20	288	6.5	93.5
May	195	215	47.6	52.4
June	153	163	48.4	51.6
July	127	201	38.7	61.3
August	88	68	56.4	43.6
Sept	155	113	57.8	42.2
Oct	266	97	73.3	26.7
Nov	155	112	58.1	41.9
Dec	114	72	61.3	38.7
Jan 1970	209	285	43.1	56.9
Feb	77	62	55.4	44.6

Size Range And Mean Carapace Length

The marked absence of juveniles smaller than the 50 - 59 mm size class in samples (with the exception of the single specimen with a carapace length of 39 mm) is evident in Table 5, which shows size range on a monthly basis. Over the entire period sampled, the carapace length of males ranged from 53 to 158 mm and in females it ranged from (39) 51 to 123 mm.

The mean carapace length is also presented in Table 5 and again reflects the variability of the catch composition. Considering the maximum size this species attains, the mean carapace length seems to be particularly low.

4.

GONADS AND THEIR PRODUCTS

Male

The general external morphology of the male reproductive organs conforms to the typical palinurid pattern. An account of the morphology of the spermatophoric mass is given below, based on a publication recording its occurrence in this species, (Berry, 1969a). At the time this was the only record of production of an external spermatophoric mass in a palinurid genus, besides Panulirus.

A total of 54 females were found carrying spermatophoric masses. The exoskeleton, in every case, was fully hardened and the intermolt stage in the moulting cycle had been attained.

TABLE 5. Size range and mean carapace length on a monthly basis.

Month	Size range (mm)		Mean carapace length (mm)	
	Males	Females	Males	Females
Apr 1968	58 - 100	58 - 108	75.0	72.0
Jul	55 - 136	51 - 101	72.0	72.0
Dec	59 - 95	67 - 90	70.4	78.0
Jan 1969	56 - 98	53 - 87	76.7	68.5
March	55 - 136	53 - 115	80.6	67.5
April	68 - 139	66 - 116	84.6	89.2
May	54 - 146	51 - 94	67.6	64.9
June	55 - 149	39 - 119	71.0	71.0
Jul	54 - 98	54 - 88	70.0	72.0
Aug	58 - 153	60 - 117	84.6	83.3
Sept	54 - 155	54 - 108	73.9	69.0
Oct	55 - 150	54 - 123	91.3	74.7
Nov	53 - 158	55 - 116	87.7	78.9
Dec	67 - 144	57 - 119	91.7	85.2
Jan 1970	56 - 99	55 - 122	68.6	71.4
Feb	68 - 146	62 - 120	84.2	84.7

The spermatophoric mass, which is opaque-white, soft and jelly-like, is spread evenly over the entire surface of the last sternal plate of the thorax and extends anteriorly onto the preceding sternal plate, posteriorly onto the arthrodial membrane of the abdomen, and laterally onto the coxopodites of the fifth pereopods. It is roughly bilaterally symmetrical and the portions extruded from each gonopore of the male are clearly distinguishable as two rounded patches (Fig. 3). The seminal fluid within each vas deferens consists of a clear matrix in which is coiled a white tube-like spermatophore containing spermatozoa. This is typical of descriptions of the seminal fluid in other palinurid genera (Heydorn, 1965). Microscopic examination of the external spermatophoric mass, however, shows that the spermatozoa are spread diffusely throughout the jelly-like matrix. It appears, therefore, that the delicate spermatophores rupture when the spermatophoric mass is spread onto the sternum of the female, thus releasing the spermatozoa. In Panulirus the external spermatophores do not rupture and the spermatozoa remain localized within them.

The thoracic sternum of the female lacks setae and the only apparent adaptation for attachment of the spermatophoric mass is the absence of a median tooth on the last sternal plate, thus making the surface flatter than in the preceding segments. The spermatophoric mass is sticky and adheres strongly to the sternum of the female.

In Panulirus the spermatophoric mass may be carried for several days or even weeks before fertilization and the hard protective matrix is probably an adaptation for shallow, turbulent water where an unprotected spermatophoric mass would be washed off.

Fig. 3. Palinurus delagoae, ventral view of the thoracic sternum of the female carrying an external spermatophoric mass.

In a deep-water environment it is unlikely that the spermatophoric mass of P. delagoae would require a specialised protective matrix, particularly if fertilization and oviposition occurred sooner after mating than in Panulirus. The apparently unspecialised spermatophoric mass of P. delagoae may well represent a primitive condition, which would be in keeping with the views expressed by George and Main (1967), that the deep-water palinurid genera of the Stridentes group are primitive and the genus Panulirus, which has invaded shallow water, is the most recently evolved genus.

Female

The ovaries resemble an elongate H and the right posterior lobe is folded ventrally at the level of the heart with the result that it does not extend as far posteriorly as the left lobe.

Development of the ovaries was initially classified into five stages but one of these was subsequently subdivided so that initial ovarian development could be more accurately distinguished, resulting in the following **six** macroscopically distinguishable stages.

Stage 1. Immature.

Ovaries flattened and strap-like, terminating posteriorly in the thoracic cavity; general colour white with a slightly granular appearance. Ova as seen with a hand-lens tend to be uniform in diameter.

Stage 2. Inactive.

Ovaries flattened, showing no signs of swelling with usually one lobe extending into the first abdominal segment; ova not uniform in diameter when seen with a hand-lens, the smaller ones being white and the larger ones being pale yellow, resulting in a general cream or light yellow colouration.

Stage 2A. Active.

Ovaries showing first signs of swelling, tending to become more rounded in cross-section; the shorter lobe usually extends into the first abdominal segment and the longer one into the second abdominal segment; ova are not uniform in diameter and barely distinguishable to the naked eye; colour yellow.

Stage 3. Active/Ripe.

Ovaries obviously swollen; ova not uniform in diameter and easily distinguishable; lobes usually as in stage 2A but the longer one

may extend into the third abdominal segment; colour bright yellowish orange.

Stage 4. Ripe.

Ovaries grossly swollen, filling all available space in the cephalothoracic cavity; ova uniform in diameter and some may be present in the oviducts; the shorter ovary lobe usually extends into the second abdominal segment and the longer one into the third abdominal segment; colour deep orange.

Stage 5. Spent.

Ovaries similar in appearance to stage 2 but distinguishable macroscopically by the presence of a few large, residual ova which are retained at the extremities of the ovary lobes and in the oviducts. These ova are soon resorbed and this stage is then macroscopically indistinguishable from stage 2.

Ovaries in stage 1 are found only in sexually immature specimens. On attainment of maturity they develop from an inactive state (stage 2), through stages 2A, 3, 4 and 5 before returning again to stage 2, in which they remain quiescent until the following breeding cycle.

At oviposition the ova pass to the exterior where they become attached to the ovigerous setae on the endopods of the females pleopods. Once attached to ovigerous setae they have been termed "eggs" in this study to facilitate their distinction from ova within the ovaries.

The egg-bearing cycle was divided into six stages described below.

Stage 0.

No eggs on ovigerous setae which are clean, pale and silky, indicating that oviposition has not yet occurred.

Stage 1.

Eggs present on ovigerous setae; no embryonic development visible macroscopically; eggs rounded and light yellow; mean diameter 0.87 mm.

Stage 2.

Embryos just visible; eggs rounded and deep yellow; mean diameter 0.89 mm.

Stage 3.

Embryos well developed with conspicuous pigmented eyes; eggs oval in shape and light brown due to reduction of yellow yolk and growth of the embryos; mean diameter 0.92 mm.

Stage 4.

Embryos occupy most of the egg capsule with little or no yellow yolk present, eggs oval in shape; colour light brown; mean diameter of long axis 0.94 mm.

Stage 5.

Eggs hatched; ovigerous setae dark in colour and matted by egg stalks and empty egg capsules. After these have been detached by the female this stage is distinguishable from stage 0 by the darker colour of the ovigerous setae.

5.

ATTAINMENT OF SEXUAL MATURITYFemale

The incidence of egg-bearing in each size class was determined over the peak months of breeding. Although a gradual increase in the frequency of egg-bearing is evident, sexual maturity appears only to be attained by the population as a whole at a

size of 70 mm and greater (see Table 6).

It was also possible to determine the frequency of specimens with reproductively active ovaries (stage 2-5) in each size class in order to estimate size at onset of sexual maturity (see Table 7). This shows a gradual increase in the frequency of females with reproductively active ovaries, and the majority appear to attain sexual maturity at a carapace length of about 65 mm. This is a considerably smaller size than is indicated using the incidence of egg-bearing as a criterion, but can probably be attributed to moulting and subsequent growth prior to mating and oviposition.

Male

Unlike P. homarus, males of P. delagoae do not develop fleshy copulatory organs and no satisfactory method was found for accurate determination of the size of attainment of sexual maturity.

Heydorn (1965) was able to estimate size of attainment of sexual maturity in male J. lalandii by making sperm counts in smears of the seminal fluid from the vasa deferentia. This method was tried, but proved unsatisfactory in P. delagoae as it was not possible to obtain an even spread of spermatozoa on a slide. This was probably due to a difference in properties of seminal fluid in the two species which will be described in the next Section.

TABLE 6. Incidence of egg-bearing in small females over the peak breeding period (Dec-April).

Carapace length (mm)	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Number examined	14	12	22	13	19	27	33	31	35	29	41	40	30	46	25
Number egg-bearing	0	1	5	2	5	10	11	15	17	13	26	29	21	33	17
Percentage egg-bearing	0	8	23	15	26	37	33	48	49	45	63	73	70	72	68

TABLE 7. Incidence of females in each size class in which the adult ovarian cycle has started (stages 2-5)

Carapace length (mm)	60	61	62	63	64	65	66	67	68	69	70/79
Number examined	57	42	77	56	60	80	53	67	68	58	632
Number in stages 2-5	4	12	20	17	24	47	32	51	52	48	619
Percentage	7	29	26	30	40	59	60	76	77	83	98

The smallest male in which mature spermatozoa were found had a carapace length of 57 mm but spermatogenesis probably occurs at a considerably smaller size than that at which males are physically capable of mating.

6.

THE REPRODUCTIVE CYCLE

The frequency of egg-bearing was expressed as a percentage of the total number of sexually mature females each month. Fig. 4 shows that breeding starts in spring (September) and egg-bearing builds up to its highest level in late summer and early Autumn (February to April). Thereafter, in May, there is a sharp decline in the incidence of egg-bearing, presumably due to hatching of the eggs, which appears to continue at a very low level until July. The sharp decrease in the incidence of egg-bearing recorded in March is probably the result of inadequate data, as only fourteen female specimens were obtained that month.

The seasonal pattern shown in the egg-bearing cycle above is substantiated by the monthly development of the eggs (see Fig. 5). Freshly spawned eggs (stage 1) were first recorded in September and the low incidence of eggs in advanced stages of development probably represent the remnants of the previous years breeding cycle. Eggs about to hatch (stage 4) were first recorded in April and the first evidence of hatched eggs (Stage 5) was evident in May and continued until July. The reason that the incidence of eggs recorded in the more advanced stages was low is because they do not remain for the same period of time in each stage. As early embryonic development is difficult to detect macroscopically in such yolky eggs, they would therefore have been classified as being in stage 1 for a longer period.

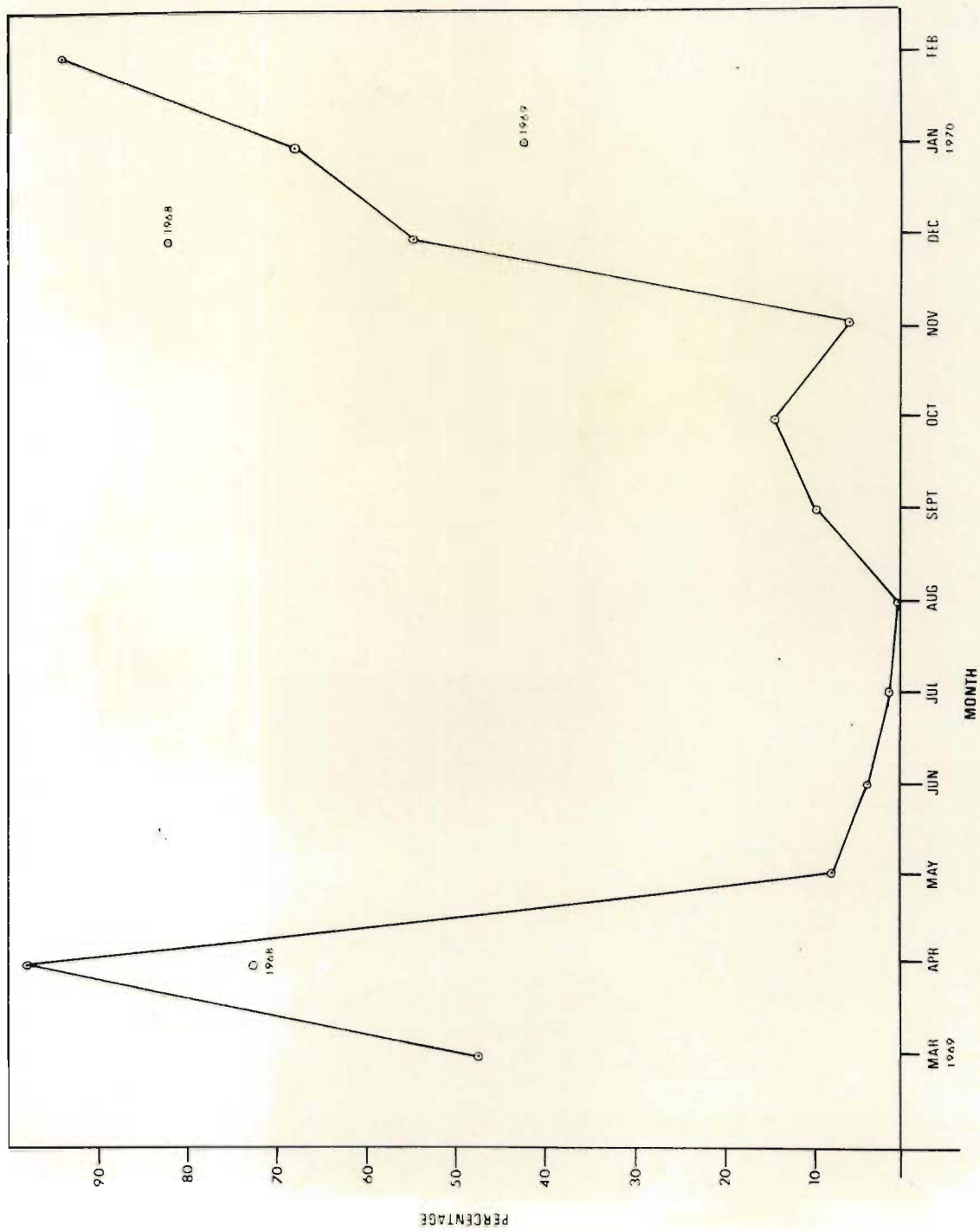


Fig. 4. Frequency of egg-bearing females in monthly samples.

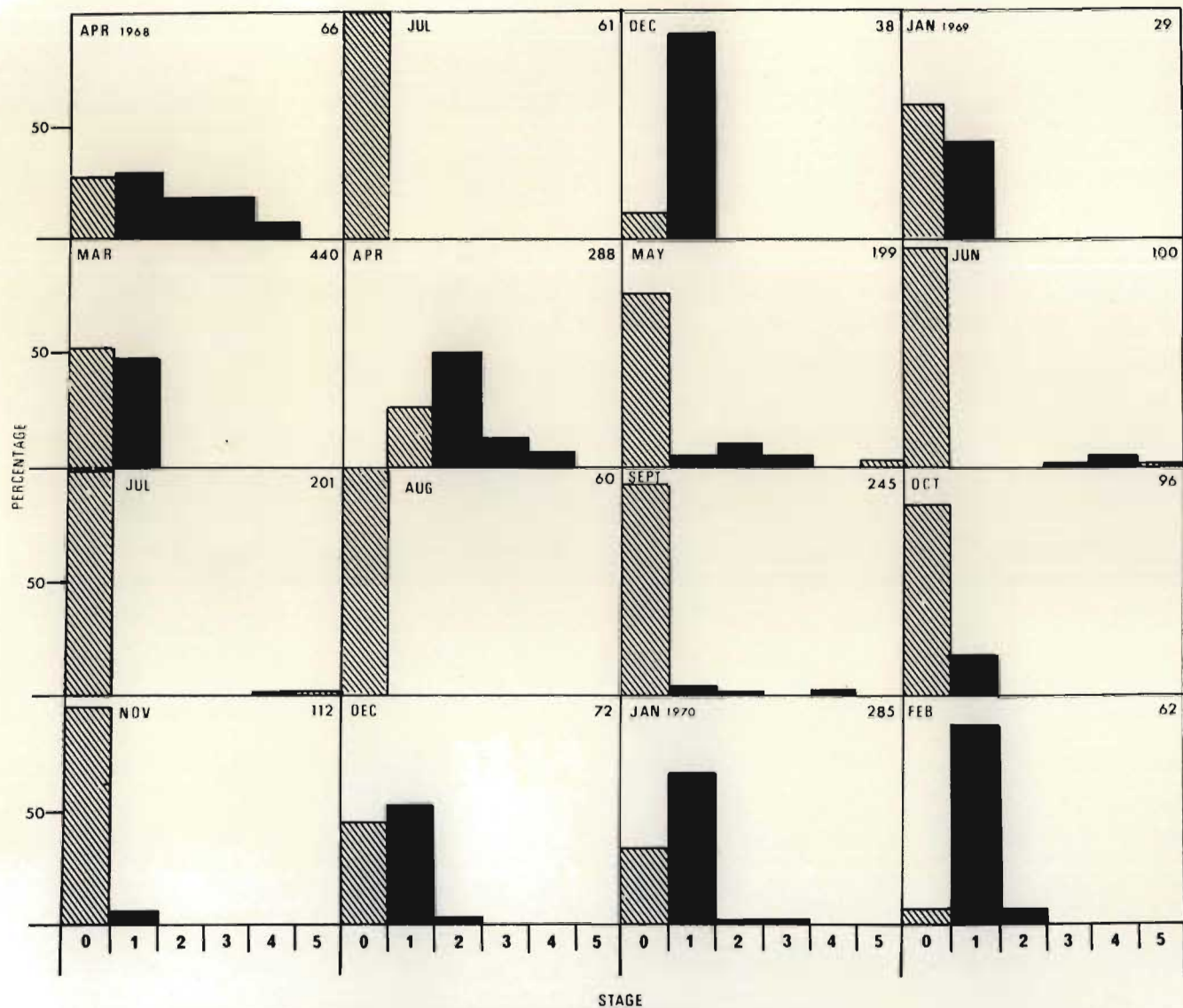


Fig. 5. Frequency of each stage in the egg-bearing cycle, expressed as a percentage of the total monthly catch of sexually mature females.

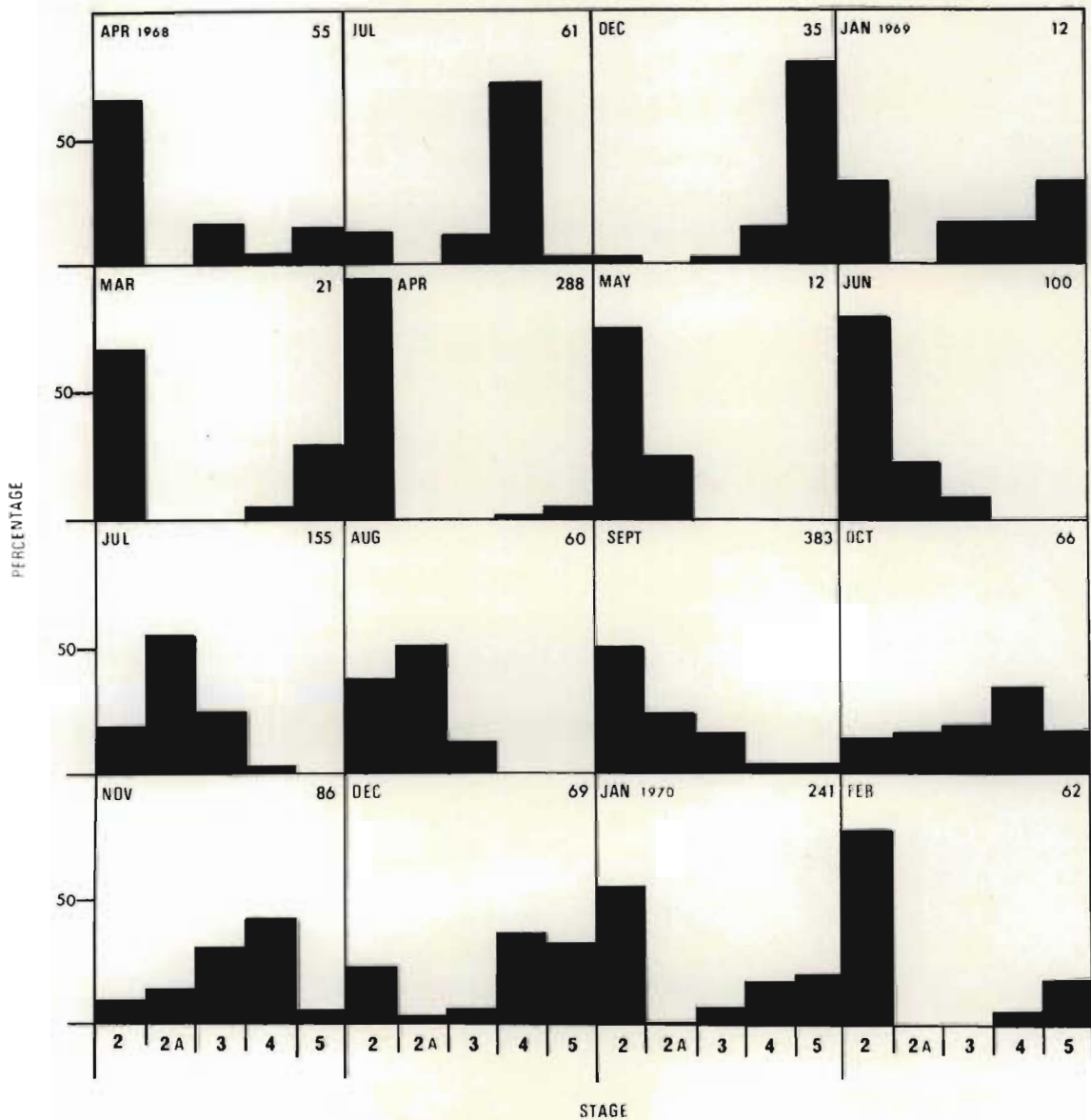


Fig. 6. Frequency of each stage of ovary development, expressed as a percentage of the total monthly catch of sexually mature females.

The ovarian cycle is recorded in Fig. 6, and in 1969, in which February was the only month not sampled, gradual development of the ovaries is evident from April, when over 90 percent of sexually mature females had inactive ovaries (stage 2), to November/December, when the highest incidence of ripe ovaries (stage 4) was recorded. Spent ovaries (stage 5), indicating spawning, were recorded from September to April in 1969, with a peak in December, which corresponds to the first high incidence of freshly spawned eggs (see Fig. 4). The patterns of ovary development in the three months sampled in 1968 conform to those of the same months in 1969, except in July, in which a higher incidence of ripe ovaries (stage 4) was recorded. These ripe ovaries seem very early in the season, as the 1969 samples indicate that first egg-bearing occurs in September. It therefore seems likely that this small sample consisted of late breeders in the previous year's breeding cycle.

No evidence of breeding more than once a year was obtained, nor was there any indication that small females commenced breeding later in the year than large ones which is the case in Panulirus homarus.

The monthly incidence of egg-bearing suggests that the incubatory period is long and in the region of five to six months. Some confirmation of this was obtained by keeping ovigerous females in a tank specially cooled to the temperature of their natural environment ($12^{\circ} - 14^{\circ}\text{C}$). Although five of the six specimens studied were already ovigerous when obtained and one specimen which oviposited in captivity died before its eggs hatched, at least some indication of the length of the incubatory period is evident from the results presented in Table 8. By

considering the time taken by the eggs of specimen F to develop to stage 2 and those of specimens B to progress from stage 2 to hatching, an incubation of approximately 180 days is indicated.

TABLE 8. Incubatory period recorded in captive specimens of P. delagoae.

Specimen	Initial stage of development of eggs and number of days elapsed before start of hatching	Interval between start and end of hatching (days)
A	stage 1 (21.10.69) 144 (14.3.70)	11
B	early stage 2 (10.12.69) 101 (21.3.70)	8
C	stage 2 (10.12.69) 65 (13.2.70)	7
D	stage 2 (10.12.69) 51 (30.1.70)	8
E	stage 3 (10.12.69) 45 (24.1.70)	6
F	stage 1 (spawned) 86 (died in (2.11.69) stage 2) (27.1.70)	

The considerable time recorded between the start and completion of hatching in Table 8 is interesting, as in Panulirus homarus it was found that hatching was completed overnight (see page 154). However, in J. lalandii Paterson (1969) recorded a mean interval of 32 days between start and completion of hatching which is particularly long, considering that her results suggest a total incubatory period of about two to three months duration. The factors influencing variability in the incubation of palinurids require study and it seems likely that availability of oxygen to the developing embryos might be found to be a critical factor in view of the constant movement of the eggs, apparently to obtain a circulation of water around them,

observed in both P. delagoae and P. homarus. This may account for the most exposed eggs near the surface of the egg mass hatching before the ones in the middle, particularly in females with very large broods.

7.

EGG COUNTS

Egg counts were made on twenty four females over the sexually mature size range. The method used is described on page 175 in Section 3 and the results are presented in Fig. 7, where it may be seen that the number of eggs carried increases in direct proportion to increase in carapace length, although in the extreme upper size range data were inadequate. The relationship of egg numbers (y) to carapace length (x) is given by the equation $y = -147200 + 2820 \cdot x$ which was calculated using Bartlett's method (Simpson et al, 1960).

P. delagoae carries far fewer eggs for its size than has been recorded in any other member of the Palinuridae, which is probably associated with the great depth at which it lives and the comparatively large size of its eggs.

8.

SUMMARY

Production of an external spermatophoric mass is recorded in P. delagoae. This is the first record of an external spermatophoric mass in a palinurid genus, other than Panulirus and a description is given of its morphology.

It is estimated that sexual maturity is attained by the female population, as a whole, at a carapace length of 70 mm and

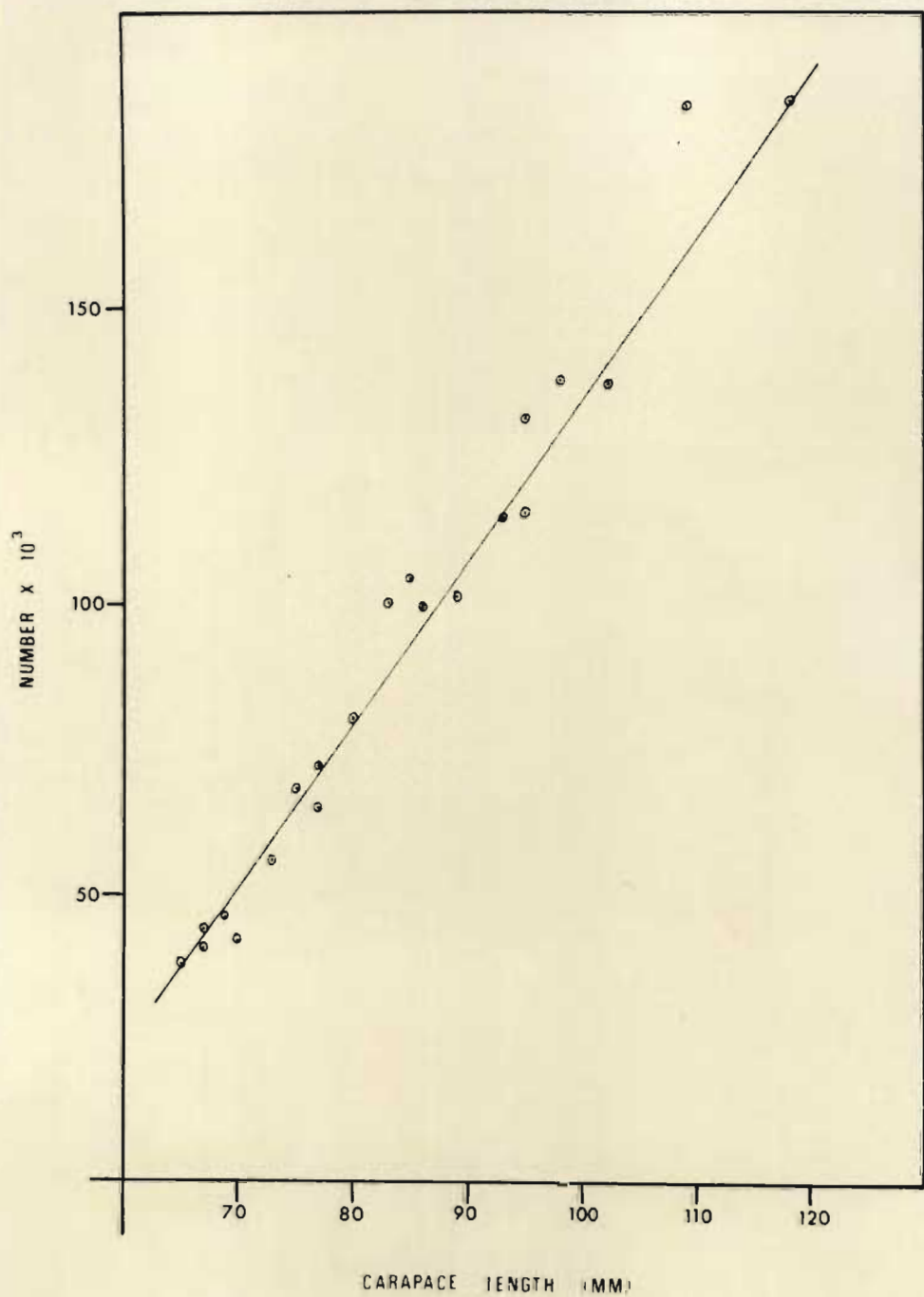


Fig. 7. The relationship between carapace length and the estimated number of eggs carried on the abdomen.

greater. No satisfactory method was found for determination of size at attainment of sexual maturity in males.

P. delagoae breeds once a year. Egg-bearing starts in spring (September), builds up to a peak in late summer and early autumn, (February-April) and falls off sharply in May.

The monthly incidence of egg-bearing in samples of the feral population indicate that the incubatory period of the eggs is at least four months and probably somewhat longer. Observations on captive animals suggest that it is at least 144 days and possibly as long as 180 days. An interval of 6-11 days was recorded between start and completion of hatching.

It was found that fewer eggs were carried, relative to the size of the animal, than seem to have been recorded in any other member of the Palinuridae. A small female with a carapace length of 70 mm was estimated to produce about 50,000 eggs and a large one of 120 mm about 190,000. The comparatively low number of eggs produced is thought to be due to their large size.

9.

THE MOULTING CYCLE

The moulting cycle was divided into four macroscopically distinguishable stages, described below.

TABLE 9. Description of the four stages in the moulting cycle.

Stage	Description
A	Immediately subsequent to moulting; exoskeleton soft and pulpy.
B	Shortly after moulting; exoskeleton hardening but depressible on dorsum of carapace; pleural spurs depressible.
C	Exoskeleton fully hardened; not depressible as in stage B; no fully pigmented layer underlying exoskeleton.
D	Preparation for moulting evident; exoskeleton thin and brittle; an underlying fully pigmented layer can be exposed by cutting the carapace or breaking off the tip of an antenna.

The monthly frequency of sexually mature rock lobsters, (with a carapace length of 70 mm and greater) in stages A, B and D of the moulting cycle is shown in Table 10 and Fig. 8. This gives an indication of the approximate period when moulting occurs. In females, moulting was recorded from July to December, with a single, well defined peak in September. In males, the pattern of moulting activity was very similar to that of females, with a peak in September, but a smaller peak was also recorded in May.

TABLE 10. Frequency of sexually mature specimens moulting each month.

	MALES		FEMALES	
	Percentage	Number examined	Percentage	Number examined
JAN	0	69	0	160
FEB	0	72	0	54
MAR	0	120	0	14
APR	1	165	0	320
MAY	17	60	0	63
JUN	0	63	0	85
JUL	4	74	2	197
AUG	0	77	2	73
SEP	31	64	51	68
OCT	4	197	6	50
NOV	4	122	2	83
DEC	2	120	1	104

These results suggest that adult females moult once per year, and adult males twice. This however, hardly seems likely and examination of Fig. 8 shows that the two peaks of moulting recorded in males are only four months apart and not more or less equally spaced, as might be expected if moulting occurred biannually. It therefore seems possible that the smaller peak represents a continuation of the sub-adult moulting cycle, in which several moults probably occur per year. Moreover, examination of the data showed that those males moulting in May were all small, the largest having a carapace length of 78 mm. That a similar secondary moulting peak was not recorded in females, could be due to deceleration of growth rate associated with egg

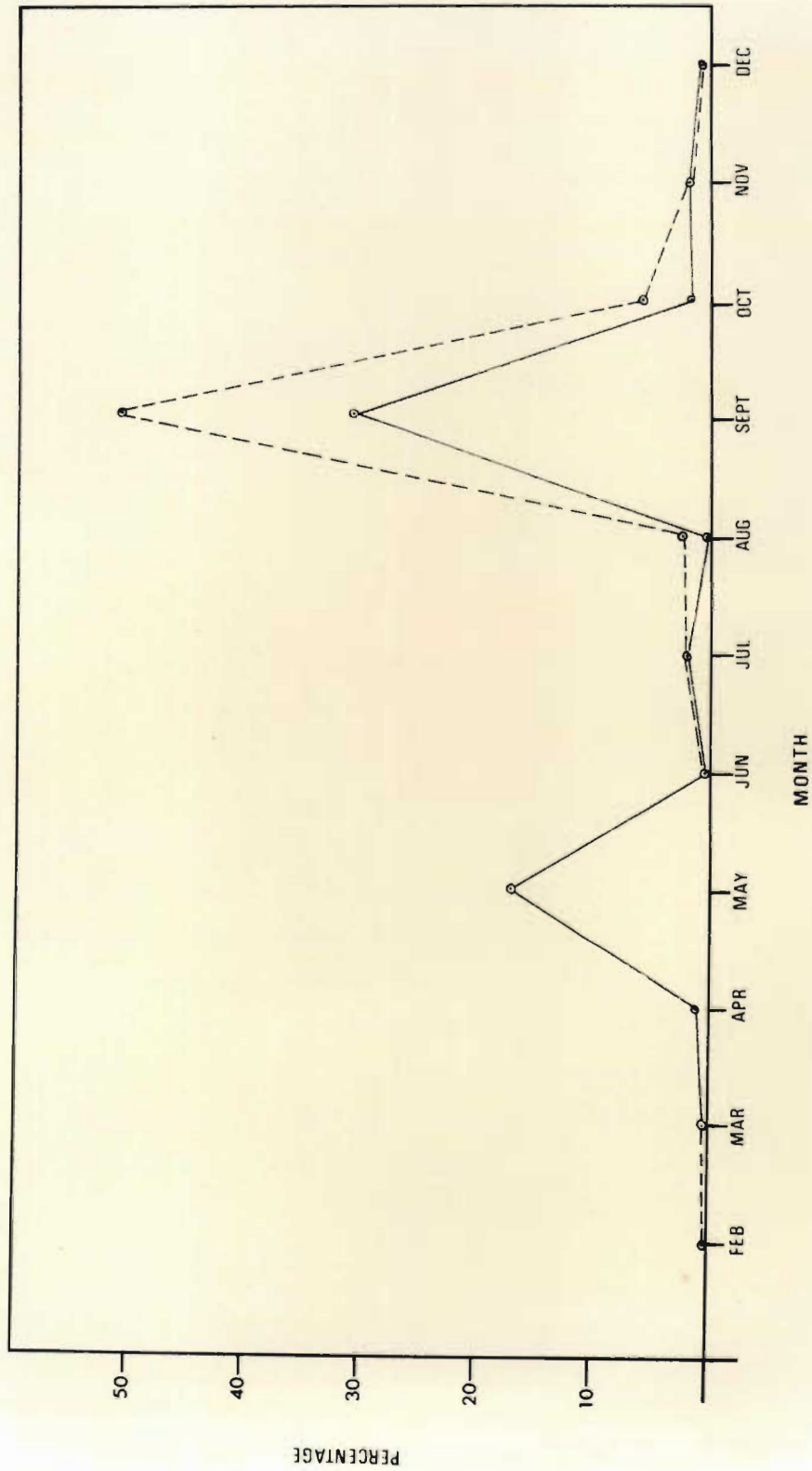


Fig. 8. Frequency of sexually mature rock lobsters moulting each month (males = solid line, females = broken line).

production, and attainment of sexual maturity at a slightly smaller size than males.

Specimens of P. delagoae did not survive long enough in captivity to enable determination of whether one or two moults occur per year. On the basis of the samples of the feral population it therefore appears that after attainment of sexual maturity this species moults once annually.

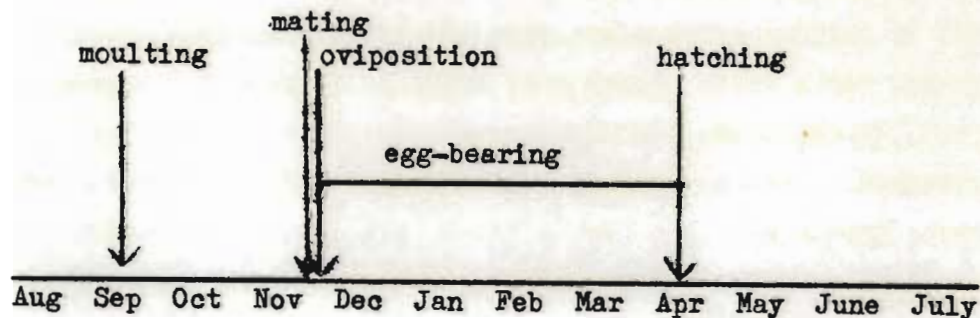
The Ovigerous Setae

No sexually mature female was recorded without long ovigerous setae and it appears that they are never lost in P. delagoae.

10. CORRELATION AND DISCUSSION OF THE MOULTING AND BREEDING CYCLES

On the basis of the results obtained from samples of the feral population, timing and interrelationship between the moulting and breeding cycles is summarised in Table 11.

TABLE 11. Summary of the moulting and breeding cycles of Palinurus delagoae.



The duration of the incubatory period in this Table is based on the frequency of egg-bearing in samples of the feral population, but according to observations on captive specimens, it seems that this may be a slightly conservative estimate of its length.

Considering the large numbers of females examined, the 54 specimens found carrying spermatophoric masses represent a particularly low proportion compared with the high proportion recorded carrying spermatophoric masses in P. homarus. This is taken to indicate that the spermatophoric mass is carried by the female for only a short time in P. delagoae, a view which is substantiated by its jelly-like consistency.

Due to segregation and migration, the possibility cannot be precluded that a second peak of moulting occurs after hatching of the eggs, which was not detected due to sampling only once a month. However, examination of Table 11 shows that the intermolt period would be at least seven months long, even if a second moult took place immediately after hatching of the eggs. Moulting so soon after hatching of the eggs would certainly not be in keeping with the long interval between the first moult and oviposition and the extremely long incubatory period, both of which seem to indicate a low metabolic rate possibly associated with the deep, cold water habitat of this species. Moreover, if there is a second moult after hatching of the eggs, this non-breeding intermolt period would have to be shorter than the one in which breeding occurs. However, the shorter intermolt period would extend over the winter months which would be expected to prolong it, if anything, as is the case in P. homarus. It therefore seems reasonable to conclude

that a second moult does not occur, and sexually mature specimens of P. delagoae moult only once a year.

Information regarding frequency of moulting and breeding, and loss of the ovigerous setae in some members of the Palinuridae is summarised in Table 12.

This shows that the majority of species appear to moult biannually, produce one brood of eggs per year and lose the ovigerous setae at the moult subsequent to hatching of the eggs. However, this is by no means always the case as shown by repetitive moulting and breeding in P. homarus with no loss of setae, or production of two broods of eggs in P. argus, with no moult between each brood and loss of setae after the second brood only. It appears therefore, that the variability recorded probably reflects adaptation of each species to particular climatic conditions.

In P. delagoae the deep, cold water environment it inhabits appears to result in a low metabolic rate with only one moult per year and production of a single brood of eggs. Obviously no loss of ovigerous setae would be possible if females breed in consecutive intermoult periods. In addition, moulting and breeding activity seems to be closely synchronised with seasonal environmental events in this species. This is very different from the situation in P. homarus, which inhabits shallow, subtropical water and, probably associated with a higher metabolic rate, moults and breeds repetitively virtually throughout the year.

TABLE 12. Summary of information regarding frequency of moulting and breeding, and loss of ovigerous setae in some members of the Palinuridae.

Species and author	Number of moults/year	Number of broods/year	Ovigerous setae lost
<u>Palinurus delagoae</u> present author	1	1	No
<u>Panulirus argus</u> Sutcliffe (1953)	2	2	Yes
<u>P. japonicus</u> Nakamura (1940) Ino (1950)	?2	2	Yes
<u>P. interruptus</u> Lindberg (1955)	2	1	?
<u>P. cygnus</u> George (1962)	2	1	Yes
<u>P. homarus</u> present author	4	1-4	No
<u>J. lalandii</u> Heydorn (1969)	1	1	?
<u>J. lalandii</u> Paterson (1969)	2	1	Yes
<u>J. novaehollandiae</u> Fielder (1964a & 1964b)	2	1	No
<u>J. paulensis</u> Grua (1964)	2	1	No

Despite the differences in environment to which the adults of these two species respond, they both produce pelagic larvae which occur in the same offshore circulatory system. It is interesting to note therefore, that the larvae are produced at the same time of the year in both species and the peak of hatching is in April/May. In addition, Berry (1969c) found that in the lobster Nephrops andamanicus which occurs at a depth of 400 m off south-east Africa, the peak of hatching was also in May after an incubatory period of nine months. In this case, however, the larvae do not appear to be pelagic and probably settle soon after hatching. This suggests that there is some basic climatic or nutritional factor in the offshore water mass to which these three species of decapod crustacea are responding. As yet there is no indication of what this might be, but it is hoped that the recently started investigation of the phyllosoma larvae, which is being conducted in conjunction with hydrological and primary productivity studies by the C.S.I.R., will provide the answer.

11.

FEEDING AND PREDATORS

The contents of the gastric mills of 403 randomly selected specimens were examined and an estimate by volume was made of the proportion each of the major food items constituted (see Table 13).

TABLE 13. Analysis of the contents of the gastric mills of 403 randomly selected specimens.

Group	Percentage volume
Cephalopod	46
Teleost	33
Crustacean	6
Calcareous grit	7
Unidentified	8

The cephalopod remains could be matched with a small unidentified cuttlefish, which is caught in abundance in the same trawls as P. delagoae. The teleost remains could not be identified and the fragments of crustacean material consisted largely of fragments of Brachyuran exoskeletons.

The only predators of P. delagoae recorded were the dogsharks Dalatius licha and Cephaloscyllium sp.

SECTION 5

A COMPARATIVE STUDY OF THE SPERMATOPHORIC
MASSES AND MECHANISMS OF FERTILIZATION IN
SOUTHERN AFRICAN ROCK LOBSTERS

This section is based on work published in the Investigational Report Series of the Oceanographic Research Institute, Durban (Berry and Heydorn, 1970).

In many decapod crustaceans, the male is known to produce discrete aggregations of spermatozoa embedded in some form of protective covering. The entire structure, termed the spermatophoric mass is transferred to the female which then carries it externally or in some cases internally. This enables the spermatozoa to be retained in a viable state by the female until such time that her ova are ready for fertilization.

In the Palinuridae, the method by which fertilization is achieved is only known with certainty in two of the eight genera, namely Panulirus and Palinurus and both these genera produce spermatophoric masses which are carried externally by the female. The only other genus in which the mechanism of fertilization has received attention is Jasus and most workers have postulated that fertilization must be internal due to the apparent absence of an external spermatophoric mass (Von Bonde 1936, Fielder 1964a, and Heydorn 1969b). However, Paterson (1968),

working on J. lalandii considered that internal fertilization was unlikely to occur and has recently reported what is believed to be an external spermatophoric mass in a single specimen (Paterson 1969). This consisted of a transparent gelatinous substance, which unfortunately disintegrated rapidly in sea water before its structure could be investigated. The methods of fertilization in the remaining five palinurid genera do not appear to have been described.

In the present investigation a comparative study has been made of the products of the male reproductive systems of representative species of five palinurid genera, namely Panulirus homarus, Palinurus delagoae, Puerulus anquilatus, Linuparus sp. and Jasus lalandii. The paired vasa deferentia of these species conform to the typical palinurid pattern, consisting of a tube which is narrow and coiled proximally, but which becomes enlarged distally. In this enlarged distal portion, the male reproductive products are accumulated and stored ready to be extruded during mating. The object of this investigation has been to relate the arrangement of the spermatophoric material within the vasa deferentia of P. homarus and P. delagoae to the structure of the external spermatophoric masses as deposited on the female's sternum.

By comparison of the contents of the vasa deferentia of these two species with the contents of the vasa deferentia of J. lalandii, P. angulatus and Linuparus sp. it has been possible to assess whether in fact external spermatophoric masses are produced by these three species or whether fertilization is internal. This comparative study also affords an opportunity to determine whether changes in the mechanisms of fertilization have occurred in association with invasion of new environments and if so, whether they substantiate the evolutionary scheme for the Palinuridae postulated by George and Main (1967).

The first detailed investigation of the spermatophoric mass of a palinurid was that of Matthews (1951) working on Panulirus penicillatus, in which he concludes that it is formed by accumulation of materials derived from various regions of the male reproductive system. Subsequently, Berry (1970) has studied the structure of the external spermatophoric mass in relation to the mechanism of fertilization in Panulirus homarus (see Section 3). The morphology of the external spermatophoric mass of Palinurus delagoae has been described in section 4, and the mechanism of fertilization in this species is discussed in this section. The terminology originally used by Matthews has been adhered to in order to facilitate comparative description.

The spermatophoric masses of P. homarus and P. delaquoae show the same basic organisation. In broad terms they may be described as consisting of a matrix in which are embedded two highly convoluted tubules, the spermatophores, which contain the spermatozoa. In all Panulirus species examined this matrix is granular and hardens in sea-water, whereas in P. delaquoae it remains soft and gelatinous. The mass is derived from the products of the paired gonads of the male and a single spermatophore with its surrounding matrix is extruded simultaneously from each gonopore during mating. The component from each gonopore is plastered to the female's sternum and the two coalesce medially giving the spermatophoric mass a bilaterally symmetrical appearance, (see Section 3, Fig 11 and Section 4, Fig. 3).

1.

MATERIALS AND METHOD

Three sexually mature specimens of P. homarus, two of P. delaquoae and J. lalandii and one each of P. anquilatus and Linuparus sp. were used for study. Both vasa deferentia were removed from each specimen immediately after it had been killed with the exception of the specimen of P. anquilatus which was frozen. Fixation in Bouin's fluid and Heidenhein's Suza resulted in the vasa deferentia becoming very brittle and a 5% formaldehyde solution was found to be an adequate fixative without hardening the tissue to the same extent.

The tissue was embedded in paraffin wax and transverse sections were cut at 10 microns thickness. Good results were obtained by staining with Mayer's haemalum and eosin and periodic acid Schiff's reaction stain was also used as an aid in tissue differentiation.

2. DESCRIPTION OF THE VAS DEFERENS OF EACH SPECIES

Panulirus homarus

Two distinct portions may be recognised in the vas deferens; a proximal portion consisting of a narrow, coiled tubule and a distal portion in which the tube is greatly enlarged. The external morphology of the vas deferens and the regions where the illustrated sections were cut are shown in Fig. 1.

The proximal vas deferens (Figs. 1 and 2) is given a dull white colour by the matrix it contains. Transverse sections show that within its thin, muscular wall, the entire periphery of the tubule is lined by glandular epithelium which is slightly proliferated dorso-laterally. The epithelial cells are columnar and secrete a strongly eosinophilic granular matrix, which surrounds a core of tightly packed spermatozoa. This comprises the spermatophoric tubule or spermatophore described in P. penicillatus by Matthews (1951). Most active secretion of matrix is from the dorso-lateral epithelium which may account for the pear-like shape of the spermatophore when seen in cross-section.

Within the spermatophore the spermatozoa are embedded in a gelatinous substance (Section 3, page 135).

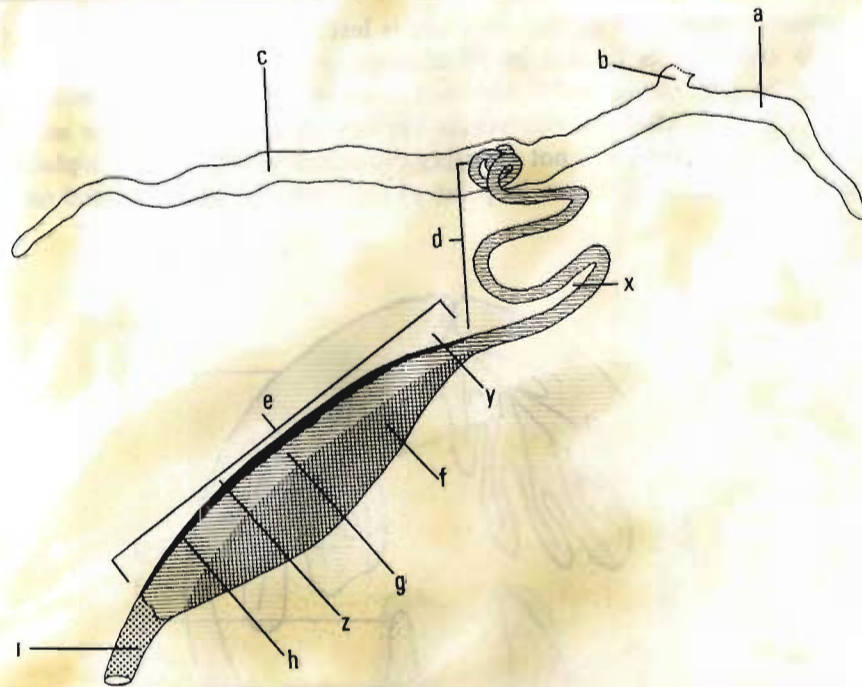
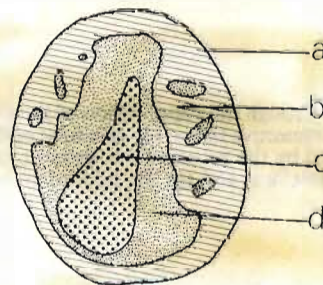


Fig. 1. Diagram of the right portion of the male reproductive organs of Panulirus homarus, showing (a) the anterior testis lobe, (b) portion of the transverse bridge (c) the posterior testis lobe, (d) the proximal vas deferens, (e) the distal vas deferens, (f) the region containing grey matrix, (g) the region containing white matrix, (h) the 'hyaline line' and (i) the terminal portion of the vas deferens containing no matrix. The illustrated sections were cut in the regions marked x, y and z.



0.5mm

Fig. 2. Diagram of a transverse section through the proximal vas deferens of Panulirus homarus (see Fig. 1, x), showing (a) muscle and connective tissue, (b) glandular epithelium, (c) spermatozoa and (d) matrix.

The distal vas deferens (Figs. 1,3 and 4) is dull white in appearance due to the matrix it contains, except for the ventral region which is light grey and the short muscular portion leading to the exterior which contains no matrix and is pale yellow. A pale yellow line runs dorsally along the entire length of the enlarged portion, termed the "hyaline line" by Matthews (1951).

Transverse sections show that the dorso-lateral proliferation of the glandular epithelium lining the proximal vas deferens becomes progressively more dorsal towards its distal end. In the region where the hyaline line first becomes visible externally, these proliferations merge to form a dorsal bilobed projection into the lumen of the tubule (Fig. 3). This structure is termed the "typhlosole" by Matthews (1951) and it runs dorsally along the length of the distal vas deferens, although its bilobed structure is lost towards the terminal end (Fig. 4). The typhlosole therefore, is formed by proliferation and invagination of the dorsal epithelial lining of the vas deferens and it continues to secrete a strongly eosinophilic, granular matrix into the lumen. Although this matrix appears to be similar to the matrix which surrounds the spermatophore, it is not as highly compacted and the spermatophore remains as a discrete tubule within it. From its point of entry into the enlarged distal vas deferens, the spermatophore becomes arranged in regular convolutions (Fig. 5) and is also forced towards the ventral periphery by the extensive dorsal production of the matrix by the typhlosole.

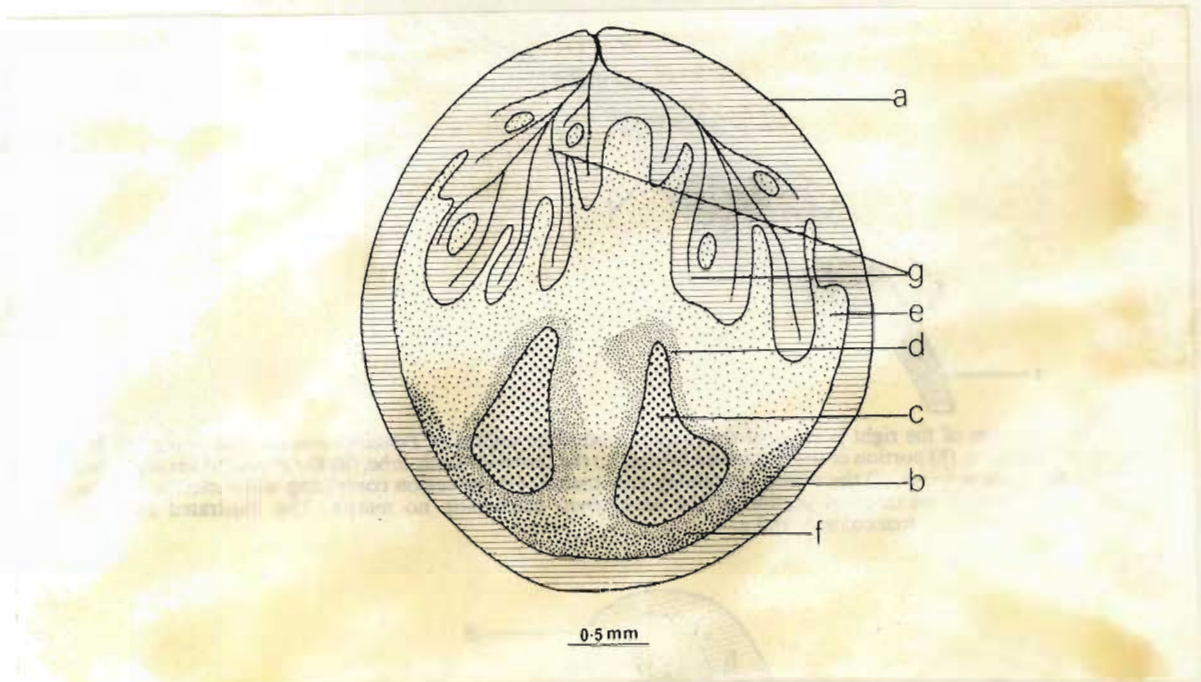


Fig. 3. Diagram of a transverse section through the upper region of the distal vas deferens of Panulirus homarus (see Fig. 1,y), showing (a) muscle and connective tissue, (b) glandular epithelium, (c) spermatozoa, (d) the wall of the spermatophore, i.e. matrix secreted by the proximal vas deferens (e) matrix secreted by the typhlosole, (f) matrix secreted by the peripheral epithelium and (g) the bilobed typhlosole.

The glandular epithelium of the ventral periphery of the vas deferens is composed of cells which are smaller and squarer than those of the typhlosole and they secrete a thin matrix layer of large, strongly eosinophilic granules below the spermatophore. This thin matrix layer is represented externally by the grey ventral portion of the vas deferens (Fig. 1,f) and it will be shown that its function is to cement the external spermatophoric mass to the sternum of the female.

Transverse sections through the middle region of the distal vas deferens show the spermatophoric mass in a state ready to be extruded and deposited on the female's sternum (Fig. 4). At this stage it has the same basic structure as in the upper region, but the spermatophore is more convoluted and the convolutions are so tight that the walls of the spermatophore tend to coalesce, probably due to compression (Fig. 6). As the matrix secreted by the typhosole, the wall of the spermatophore and the ventral globular matrix layer are all eosinophilic, they tend to become indistinguishable when stained and are only visible when unstained. This may be the reason why Matthews (1951) did not distinguish a ventral adhesive matrix layer in P. penicillatus.

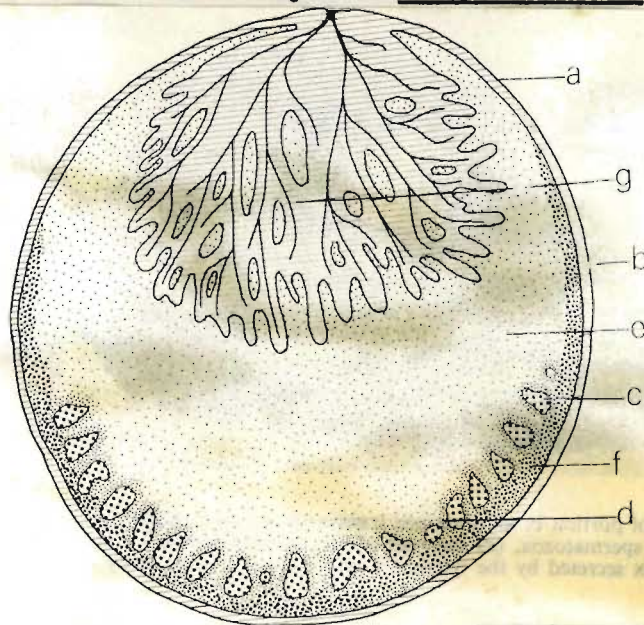


Fig. 4. Diagram of a transverse section through the distal vas deferens of Panulirus homarus (See Fig. 1,z), showing (a) muscle and connective tissue, (b) glandular epithelium, (c) spermatozoa, (d) the wall of the spermatophore, i.e. matrix secreted by the proximal vas deferens (e) matrix secreted by the typhosole, (f) matrix secreted by the peripheral epithelium and (g) the typhosole.

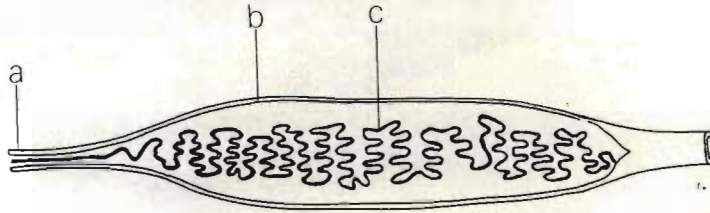


Fig. 5. Diagram showing the arrangement of the spermatophore (c) within portion of the proximal vas deferens (a), and the distal vas deferens (b) of Panulirus homarus. The vas deferens is shown dissected dorsally.

In Section 3, it was shown that the external spermatophoric mass of P. homarus is composed of the following three horizontal layers; an outer protective matrix layer; a middle spermatophoric matrix layer in which the spermatophores are embedded; and a basal adhesive matrix layer which cements the spermatophoric mass to the female's sternum (Fig. 7). This layered structure can be derived from the crescent-shaped arrangement of the spermatophoric material within the vas deferens (Fig. 4).

The matrix secreted by the typhlosole forms the outer protective layer; the matrix secreted in the proximal vas deferens, which forms the wall of the spermatophore, coalesces to form the the spermatophoric matrix. The layer secreted by the epithelium on the ventral periphery of the distal vas deferens forms the basal adhesive layer.

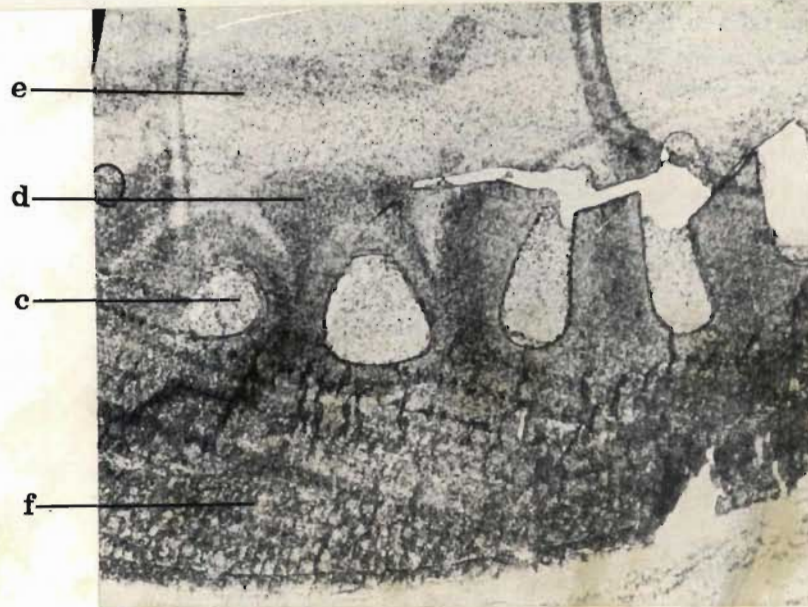


Fig. 6. Photograph of portion of an unstained transverse section through the distal vas deferens of Panulirus homarus showing (c) spermatozoa, (d) the wall of the spermatophore, i.e. matrix secreted by the proximal vas deferens, (e) matrix secreted by the typhlosole and (f) matrix secreted by the peripheral epithelium (x 25 approx.).

In the deposited spermatophoric mass the top of the spermatophore just projects into the overlying protective matrix (Fig. 7). This is probably due to pressure of the protective matrix which causes the spermatophore to protrude beyond the level of the spermatophoric matrix. This unique arrangement enables the female to pick away the overlying protective layer until the spermatophoric matrix is reached and thus expose the spermatophore as an open furrow (Section 3, Fig.13).

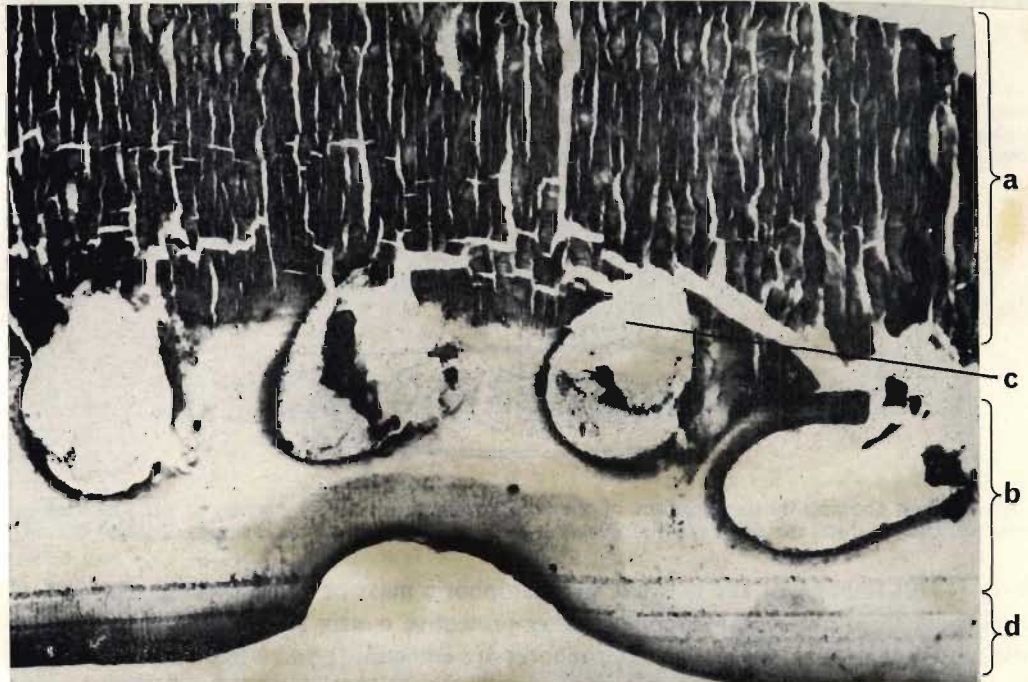


Fig. 7. Photograph of a transverse section through the deposited spermatophoric mass of Panulirus homarus in the region of the spermatophore showing (a) the protective matrix, (b) the spermatophoric matrix, (c) the spermatophore and (d) the adhesive matrix (x 50 approx.). The spermatozoa were lost from the spermatophore during sectioning.

Palinurus delaqaiae

The external morphology of the vas deferens is basically similar to that of P. homarus and the sections illustrated were cut in the corresponding regions to those shown in fig. 1. A proximal region, which is coiled and narrow and a distal region which is longer and not as wide as that of P. homarus can be recognised.

The proximal vas deferens (Fig. 8): Transverse sections through this region reveal an arrangement which is basically similar to that found in P. homarus. The spermatophore is triangular in cross section and its wall is composed of a homogeneous eosinophilic substance quite unlike the granular wall of the spermatophore of P. homarus. There is a dorso-lateral region of thickened epithelium but this thickening is due to elongation of the cells and not due to proliferation of cells as in P. homarus. The wall of the spermatophore is thickest opposite these enlarged cells. In the ventral region it is thin and between it and the ventral epithelium is a narrow layer of large eosinophilic globules, similar to those composing the adhesive layer in P. homarus. The matrix filling the lumen between the wall of the spermatophore and the epithelium is gelatinous and not granular as in P. homarus. There are scattered dense areas of agglutination within this gel which stain identically with the spermatophoric wall and in some instances can be seen to coalesce with this wall. It therefore appears that the gelatinous matrix moves from the glandular epithelium inwards to coalesce and form the wall of the spermatophore surrounding the spermatozoa.

The distal vas deferens (Fig. 9 and 10): This portion of the vas deferens is an opaque white colour and unlike in P. homarus, a terminal muscular portion without seminal fluid cannot be differentiated externally.

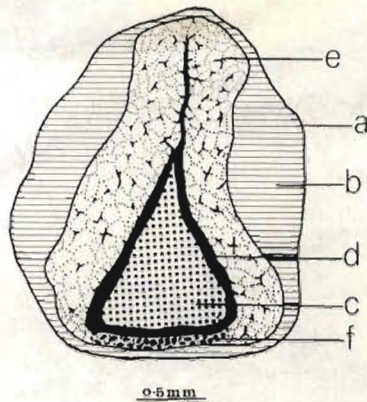


Fig. 8. Diagram of a transverse section through the proximal vas deferens of Palinurus delagoae, showing (a) muscle and connective tissue, (b) glandular epithelium, (c) spermatozoa, (d) the wall of the spermatophore, (e) gelatinous matrix with dense areas of agglutination and (f) the globular matrix layer.

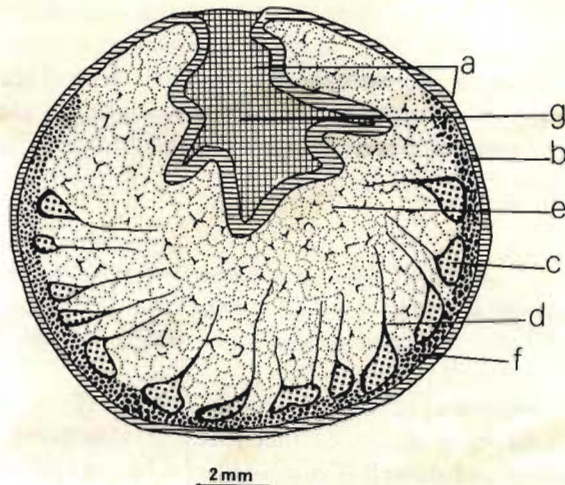


Fig. 9. Diagram of a transverse section through the distal vas deferens of Palinurus delagoae showing (a) muscle and connective tissue, (b) glandular epithelium, (c) spermatozoa, (d) the wall of the spermatophore, (e) gelatinous matrix with dense areas of agglutination secreted by the typhlosole, (f) globular matrix secreted by the peripheral epithelium and (g) the typhlosole.

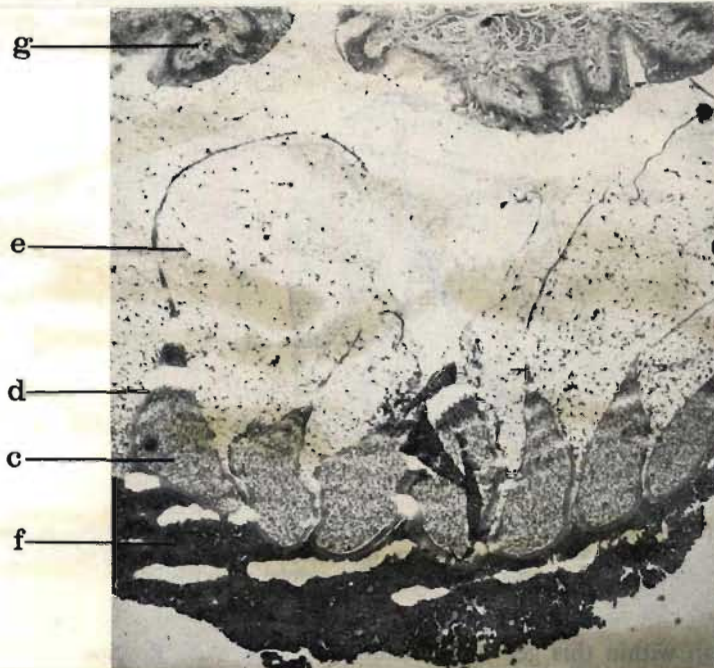


Fig. 10. Photograph of portion of a transverse section through the distal vas deferens of Palinurus delagoae showing (c) spermatozoa, (d) the wall of the spermatophore, (e) the gelatinous matrix secreted by the typhlosole, (f) the globular matrix secreted by the peripheral epithelium and (g) portion of the typhlosole (x 15 approx.).

A well developed hyaline line runs dorsally along its length and transverse sections cut in the region of the beginning of the hyaline line show a bilobed typhlosole and initial convolution of the spermatophore. However the typhlosole shows no extensive proliferation of the epithelium as in P. homarus and it consists of a central core of muscle and connective tissue which is merely lined with glandular epithelium. As in P. homarus the typhlosole loses its bilobed structure towards the terminal end of the vas deferens.

The spermatophore becomes highly convoluted in this region and still retains its triangular shape in cross section. At its apex the wall of the spermatophore extends dorsally into the overlying gelatinous matrix secreted by the typhlosole. This matrix fills the entire lumen dorsal to the spermatophore and as in the proximal vas deferens, scattered dense areas of agglutination are present. Ventral to the spermatophore there is a layer of eosinophilic globules secreted by the adjacent epithelium, which corresponds to the adhesive layer of P. homarus.

Jasus lalandii

The morphology and histology of the male reproductive organs has been described by Paterson (1969) and the nature of the seminal fluid by Heydorn (1965). Both the external morphology and anatomy of the vas deferens appears to be identical with that of Jasus novaehollandiae described by Fielder (1964b). The sections illustrated were cut in corresponding regions to those of P. homarus and P. delagoae and a proximal and a distal region of the vas deferens can also be recognised.

The proximal vas deferens (Fig. 11) is essentially similar to that of P. delagoae, consisting of an outer covering of muscle and connective tissue, lined internally by glandular epithelium.

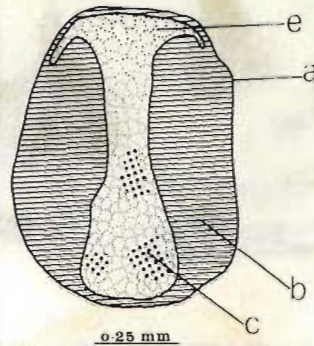


Fig. 11. Diagram of a transverse section through the proximal vas deferens of Jasus lalandii showing (a) muscle and connective tissue, (b) glandular epithelium, (c) spermatozoa and (e) gelatinous matrix.

Dorso-laterally, the epithelium is composed of extremely high columnar cells which are more glandular than the cells around the rest of the periphery. The lumen is filled with a gelatinous matrix which is more homogeneous than that of P. delagoae and does not have the same dense areas of agglutination. Embedded in the matrix is the spermatophore which is a thin continuous thread of spermatozoa with no surrounding wall as in P. delagoae and P. homarus. It is apparent that this thread-like spermatophore is somewhat convoluted in the matrix even in this portion of the vas deferens.

The distal vas deferens (Fig. 12 and 13) is not as enlarged as that of P. delagoae and has only a small wedge-shaped typhlosole projecting into its lumen. The columnar epithelial cells lining the typhlosole are higher than those around the rest of the periphery and secrete a gelatinous matrix which fills the lumen of the vas deferens.

The thread-like spermatophore is not localised ventrally as in P. homarus and P. delagoae, but is convoluted randomly throughout the matrix. Adjacent to the peripheral epithelium is a thin layer of strongly eosinophilic globules, similar in appearance to the somewhat thicker adhesive matrix layer underlying the convoluted spermatophore of P. delagoae.

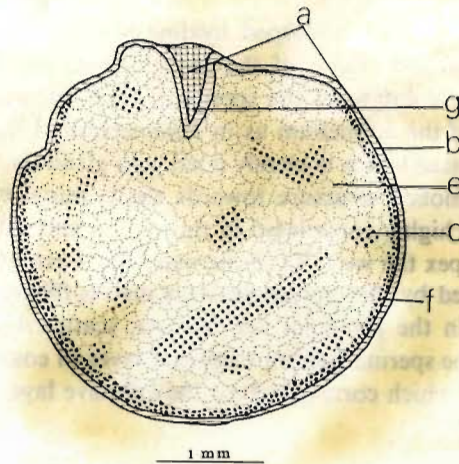


Fig. 12. Diagram of a transverse section through the distal vas deferens of Jasus lalandii showing (a) muscle and connective tissue, (b) glandular epithelium, (c) spermatozoa, (e) gelatinous matrix secreted by the typhlosole in the upper regions of the distal vas deferens (f) the globular matrix secreted by the peripheral epithelium and (g) the typhlosole. The thickness of the spermatophore and globular matrix layer is exaggerated in this diagram.



Fig. 13. Photograph of portion of a transverse section through the distal vas deferens of Jasus lelandii showing (e) the gelatinous matrix, (c) the thread-like spermatophore and (f) the globular matrix layer secreted by the peripheral epithelium (x 80 approx.).

Puerulus anquilatus and Linuparus sp.

Sections through the vasa deferentia of P. anquilatus and Linuparus sp. were cut in the regions corresponding to those of the preceding species (Fig. 1).

The external morphology and anatomy of the vasa deferentia of these two species resembles that of P. delagoae and the spermatophores show the same characteristic peripheral arrangement, with an underlying adhesive layer. The matrix is gelatinous but has a homogeneous consistency as in Jasus and the dense areas of agglutination found in the protective matrix of P. delagoae are not present. In both P. anquilatus and Linuparus sp., the spermatophore consists of a large, tightly compacted core of spermatozoa, embedded in an eosinophilic mucous which forms a distinct interface with the protective matrix. However, there is no wall surrounding the spermatophore as in P. delagoae. The spermatophore of P. anquilatus is roughly triangular in cross section and the underlying matrix layer has a similar consistency to that of P. delagoae (Fig. 14 and 15).

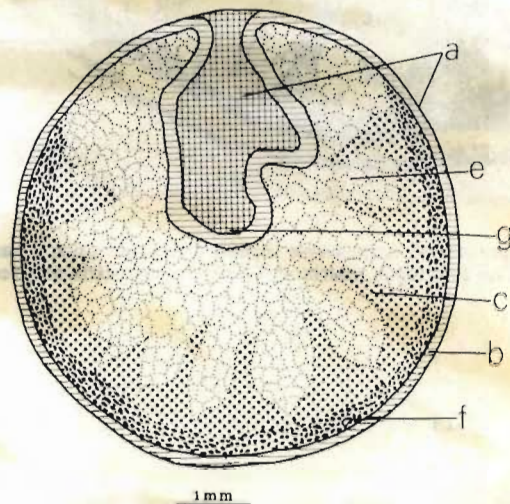


Fig. 14. Diagram of a transverse section through the distal vas deferens of *Puerulus anquilatus* showing (a) muscle and connective tissue, (b) glandular epithelium, (c) spermatozoa, (e) gelatinous matrix secreted by the typhlosole, (f) globular matrix secreted by the peripheral epithelium and (g) the typhlosole.

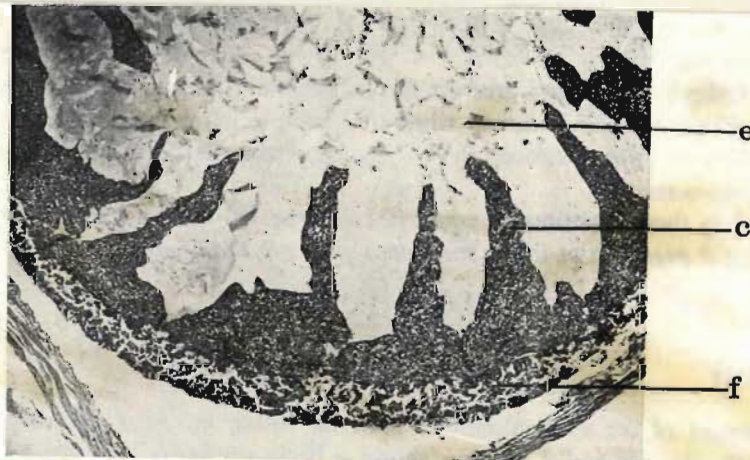


Fig. 15. Photograph of portion of a transverse section through the distal vas deferens of *Puerulus anquilatus* showing (c) spermatozoa, (e) gelatinous matrix and (f) globular matrix secreted by the peripheral epithelium (x 25 approx.).

The spermatophore of Linuparus sp. is more oval and extends almost to the typhlosole through the protective matrix (Fig. 16). The consistency of the peripheral matrix layer resembles that of Jasus and is similar to the mucous in which the spermatozoa are embedded.



Fig. 16. Photograph of portion of a transverse section through the distal vas deferens of Linuparus sp. showing (c) spermatozoa, (e) gelatinous matrix and (f) globular matrix secreted by the peripheral epithelium. (x 25 approx.).

3.

OTHER OBSERVATIONS

Although the matrices of the spermatophoric masses of P. delagoae, J. lalandii, P. anquilatus and Linuparus sp. have a similar gelatinous consistency, their properties differ in some cases on exposure to sea-water.

The matrix of the spermatophoric mass of P. delagoae changes from a viscous mucous-like consistency to a stiff gel when exposed to sea-water and smears on microscope slides remained intact for five days in running sea-water.

In J. lalandii the thread-like spermatophore is distinguishable in smears of the spermatophoric mass examined microscopically. If the coverslip is gently depressed the spermatozoa become dispersed but reform in a thread when the pressure is released, due to the viscosity of the surrounding matrix. However, if a drop of sea-water is placed on the seminal smear before a coverslip is put on and pressure is again exerted, the spermatozoa disperse as before but do not reform again in a thread when the pressure is released and can be seen moving freely according to water movement. This demonstrates that at least portion of the matrix is soluble in sea-water.

Unfortunately these experiments could not be repeated on the spermatophoric masses of Linuparus sp. and P. angulatus as living specimens were not obtainable.

4.

DISCUSSION

The arrangement of the spermatophoric material within the vasa deferentia of P. homarus, P. delagoae, P. angulatus and Linuparus sp. shows a basic similarity, and the following features are common to all these species:

There is a distinct thin matrix layer around the ventro-lateral periphery of the vas deferens, known to have an adhesive function in P. homarus and P. delagoae; the spermatophore is highly convoluted in a longitudinal plane and is arranged peripherally with its base resting on this adhesive matrix layer. It is enclosed laterally and above by a thick protective matrix layer which is gelatinous in P. delagoae, P. anquilatus and Linuparus sp. but is granular, with a putty-like consistency in P. homarus. The spermatophoric masses of P. anquilatus and Linuparus sp. show a close resemblance in structure and although they are also similar to the spermatophoric mass of P. delagoae they do not have a wall surrounding the spermatophore, a feature that P. delagoae has in common with P. homarus.

In the original description of the external spermatophoric mass of P. delagoae (Section 4) it was stated that the wall of the spermatophores was ruptured and that the spermatozoa were spread diffusely through the matrix. However, the specimen on which this description was based had been deep frozen and numerous unfrozen specimens with freshly deposited spermatophoric masses have subsequently been found with the spermatophores intact. It has now been confirmed that repeated freezing and thawing of the spermatophoric mass can rupture the wall of the spermatophore which accounts for the structure of the mass as initially described.

In view of these observations and the present study of the spermatophoric mass within the vas deferens, the deposited spermatophoric mass of P. delaqaos has now been found to consist of a basal adhesive layer which cements the mass to the female's sternum and resting on this layer is the spermatophore which is highly convoluted in a longitudinal plane, and is covered by a thick, gelatinous, protective matrix. Prior to fertilization this overlying protective matrix is not evenly scraped away to expose the spermatophore as in P. homerus, but was found to be broken up by deep scratches, presumably made by the dactyls of the fifth legs. This must break open the spermatophore and expose the spermatozoa.

As the peripheral matrix layer undoubtedly cements the spermatophoric mass to the female's sternum in P. homerus and P. delaqaos, the presence of this layer in P. angulatus and Linuparus sp. indicates that external fertilization also occurs in these species. Their external spermatophoric masses probably closely resemble that of P. delaqaos in view of the similarity of the masses within the vasa deferentia, and are probably also insoluble in sea-water.

In J. lalandii the arrangement of the contents of the vas deferens is quite distinct from the other four species in that the spermatophore is thread-like and has no specific orientation, being convoluted randomly throughout the matrix.

This matrix is gelatinous as in P. delagoae, P. angulatus and Linuparus sp.. The presence of a basal matrix layer in J. lalandii which is similar to, though much thinner than the basal adhesive layer of P. delagoae, now provides further evidence for external fertilization in Jasus. Remains of a spermatophoric mass have not been evident in Jasus except for a single record by Paterson (1969) and this may be accounted for by the fact that the mass disintegrates in sea-water. Because of this, oviposition must occur immediately after mating and presumably the spermatozoa are released as the matrix disintegrates.

To summarise, three basic types of spermatophoric masses can be distinguished among the species examined in the present investigation:

- (i) A spermatophoric mass which is gelatinous, and which disintegrates in sea-water. The highly convoluted spermatophore is randomly distributed throughout the protective matrix and is thread-like with no specific shape (e.g. J. lalandii).
- (ii) A spermatophoric mass which is gelatinous but does not disintegrate in sea-water. The spermatophore has a characteristic shape and a definite orientation and distribution within the protective matrix (e.g. P. delagoae, P. angulatus and Linuparus sp.)
- (iii) A spermatophoric mass which is granular with a putty-like consistency that hardens in sea-water. The spermatophore has a characteristic shape and a definite orientation and distribution within the protective matrix (e.g. P. homarus).

Characteristic convolution of the spermatophore, found in P. homarus, P. delagoae, P. angulatus and Linuparus sp. starts in the upper region of the distal vas deferens where the typhlosole first becomes bilobed and large in relation to the diameter of the tube. This convolution is apparently brought about by a combination of factors: Extensive production of the protective matrix by the typhlosole forces the spermatophore to the ventral periphery of the vas deferens and restricts its arrangement to the longitudinal plane. Thus as the spermatophore is accumulated within the relatively wide distal vas deferens, convolution is caused by this confinement to the longitudinal plane and the restriction of movement along the tube by its relatively short length. Apparently progress of the spermatophore towards the terminal end of the vas deferens is brought about by peristaltic movement, as the wall of the vas deferens contains both longitudinal and circular musculature.

In J. lalandii the typhlosole is small in relation to the diameter of the distal vas deferens. Thus the spermatophore is not restricted to a longitudinal plane by extensive dorsal production of matrix, which accounts for the random arrangement and lack of orientation of the spermatophore.

According to George and Main (1967) divergence into two lines, namely the Silentes to which Jasus belongs and the Stridentes to which Panulirus, Palinurus, Puerulus and Linuparus belong, took place at an extremely early stage in the course of palinurid evolution. This is therefore a basic consideration when comparing the spermatophoric masses of species belonging to the two groups.

It is significant that P. delagoae, Linuparus sp. and P. anquilatus which have a similar type of spermatophoric mass, are all deep-water species. George and Main (1967) postulate that these species represent surviving forms of a deep-water ancestral palinurid line and in their evolutionary scheme, these authors postulate that Puerulus and Linuparus diverged from a common ancestral stock on the Cretaceous. This is supported by the close similarity of the spermatophoric masses of P. anquilatus and Linuparus sp.

They also believe that Palinurus and Panulirus diverged from a common ancestral stock in the Miocene and propose that Panulirus is the most recently evolved genus which has invaded the sublittoral environment in the tropics.

This hypothesis is supported by the structure of the spermatophoric mass of P. delagoae which although it shows affinity to the spermatophoric masses of the other deep-water species P. anquilatus and Linuparus sp., has the spermatophore enclosed in a wall, a feature found in Panulirus. The adaptive significance of this wall in the spermatophoric mass of P. delagoae remains obscure in view of the fact that it is a deep-water species.

According to George (Pers. comm.) Jasus is an extremely old genus which has inhabited shallow temperate water in the southern oceans where the species have been adapted to the current systems controlled by the mid-latitude westerly winds. The extant species are similar morphologically and show a relict distribution pattern. It may therefore be expected that the reproductive systems and mechanism of fertilization would show little difference amongst the species and evidence of this is given by the identical structure of the spermatophoric mass within the vas deferens of J. novaehollandiae figured by Fielder (1946b) and J. lalandii described in this investigation. In accord with the supposed antiquity of this genus, the spermatophoric mass shows an unspecialised level of development and in extant species the mechanism and timing of fertilization is probably geared to environmental conditions very similar to those inhabited by the ancestral line.

On first consideration it would appear that the hard spermatophoric mass of the genus Panulirus evolved in response to shallow, turbulent water conditions where a soft spermatophoric mass would be liable to be washed off. However, development of a hard spermatophoric mass is apparently not a prerequisite for invasion of shallow water, as is illustrated by Jasus. In the case of P. delagoae, (and probably also Linuparus sp. and P. anquilatus) the gelatinous spermatophoric mass is insoluble in sea-water indicating a trend towards prolonging the interval between mating and oviposition. It is suggested therefore that in the Stridentes group, selection pressure resulting in prolongation of the interval between mating and oviposition originally led to the development of an insoluble spermatophoric mass, such as that of P. delagoae and turbulent conditions found in shallow water was a secondary factor leading to evolution of the resistant spermatophoric mass of Panulirus.

The mechanism of fertilization must be adapted to prevailing environmental conditions and in sublittoral waters Panulirus would have been subjected to severe environmental stresses during the Pleistocene ice ages, e.g. falling and rising of sea levels, changes in area of continental shelves, changes in water temperatures and strengthening and weakening of oceanic circulation (George and Main 1967).

Possession of a hard spermatophoric mass enabling great latitude of the interval between mating and oviposition may have contributed to the success of the genus during this period. The structure of the spermatophoric masses of the various Panulirus species could be expected to show structural differences determined by the prevailing climatic environment and water circulation systems, to which their reproductive cycles are geared. Little comparative work has been done on the spermatophoric masses of the species but a difference is exhibited in the spermatophoric mass of P. homarus which lacks the additional outer layer found in such species as P. penicillatus. The presence of the additional layer may well indicate a longer interval between mating and oviposition than occurs in P. homarus.

The similarity of the spermatophoric masses of P. delagoae Linuparus sp. and P. anquilatus may indicate that development of an insoluble spermatophoric mass originally developed early in the course of evolution of the Stridentes group and that in the deep-water environment of the basic structure of the spermatophoric mass has probably changed little over a great period of time. It seems reasonable to assume that the unspecialised internal arrangement of the spermatophoric mass of Jasus and its solubility in sea-water are primitive features.

While the ancestral Stridentes line may never have had a spermatophoric mass quite like that of Jasus, it seems likely that the mass must have passed through a similar level of development. It is only possible to speculate as to what selective forces originally led to the evolution of an insoluble spermatophoric mass, but the obvious result of its development is a greater flexibility in the period between mating and oviposition which makes the female independent of the presence of a male during oviposition. This could have had a selective advantage where population density was low. It could possibly also have had some survival value under particular climatic conditions, e.g. delay of oviposition until conditions were suitable.

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ACKNOWLEDGEMENTS

I am very grateful to all those who gave assistance in this investigation and my sincere thanks are expressed to the following people in particular:

My supervisor, Dr. A.E.F. Heydorn, Director of the Oceanographic Research Institute, for his advice and encouragement throughout the project and also his criticism of the manuscript.

Dr. R.W. George, of the Western Australian Museum, for stimulating discussions and criticism of parts of the manuscript.

Dr. N.F. Paterson, formerly of the South African Museum, who encouraged investigation of fertilization within the Palinuridae.

Mr. G. Newman, of the Division of Sea Fisheries, for his helpful criticism of Section 5 of the manuscript.

Dr. L.B. Holthuis, of the Rijksmuseum Van Natuurlijke Historie, who gave excellent advice in preparation of the paper on Puerulus.

Dr. A. Alexander, Senior Lecturer in the Department of Animal Biology, University of Natal, for her criticism of the paper on mating behaviour in P. homarus. Also Mr. D. Smith of the same Department for his advice on photography,

Mr. D. Yoxall for his capable assistance both in the diving programme and processing of data. Also Mr. T.P. More and N. Holliday, without whose frequent help as co-divers, many of the samples of P. homarus would have been smaller.

Prof. A.J. Burton and Prof. T.A. Villiers for the facilities provided in the Departments of Animal and Plant Biology.

All my colleagues at the Oceanographic Research Institute for their cooperation and assistance.

I am extremely grateful for the facilities provided and the administrative support of the Oceanographic Research Institute. I wish also to acknowledge the cooperation of the Coastal Fisheries Department of the Natal Parks, Game and Fish Preservation Board and the Division of Sea Fisheries.

Financial support of the East Coast Rock Lobster Programme was provided by the South African National Committee for Oceanographic Research.