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SOUTH AFRICAN ASSOCIATION FOR MARINE BIOLOGICAL RESEARCH



OCEANOGRAPHIC RESEARCH INSTITUTE

Investigational Report No. 34

Palinurid and Scyllarid Lobster Larvae of the Natal Coast, South Africa

by

P. F. Berry

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Abstract

Between September 1970 and March 1973 phyllosoma larvae were collected off Richards Bay and Durban. The majority (84%) were scyllarids, represented by the genera *Scyllarus* (4 spp.), *Scyllarides* (2 spp.), *Parribacus* (1 sp.) and *Ibacus* (1 sp.). Palinurids were represented by *Panulirus* (5 spp.), *Palinurus* (1 sp.) and *?Palinustus* (1 sp.). In addition, puerulus larvae of *Panulirus homarus*, *Panulirus ornatus*, *Projasus parkeri* and *Palinurellus* sp. were obtained. All these larvae are described and in the case of *P.homarus*, in which a complete developmental series was obtained, notes on seasonal abundance and distribution are included.

Introduction

This study of phyllosoma and puerulus larvae represents the final phase of a programme initiated in 1968 by the Oceanographic Research Institute (O.R.I.) Durban, to investigate the life histories of the commercially exploited spiny lobster species of the South African Natal coast; namely *Panulirus homarus* (Linnaeus) and *Palinurus delagoae* Barnard. Work on the adults has already been completed and reported upon (Berry 1969, 1970a, b, 1971a, b, 1973a and b).

Most work on palinurid and scyllarid larvae has been aimed at solving the problem of identification which is particularly complex in tropical and subtropical regions where numerous species are present. Only comparatively recently have attempts been made to investigate larval ecology, such as those of Johnson (1960), Lazarus (1967), Chittleborough & Thomas (1969), Johnson (1971) and Ritz (1972).

The objective of this investigation was primarily to identify and describe the stages of larval development of *P.homarus* and *P.delagoae* and to provide information on their distribution and ecology. However, early on in the sampling programme it became evident that insufficient numbers of larvae were being obtained to hope to gain much information on larval ecology and the cost of expanding the programme to obtain adequate samples proved to be prohibitive. Nevertheless by combining with the National Institute for Water Research (N.I.W.R.), which was undertaking an intensive hydrographical study off Richards Bay every second month, it was possible to increase the intensity of sampling and benefit from comprehensive physical data available, particularly on currents. Unfortunately Richards Bay $(28^{\circ}50'S)$ is towards the northern limits of the distribution of the adult population of *P.homarus* and also the stations occupied by the N.I.W.R. did not extend beyond the edge of the shelf, the furthest being about 25km offshore where the depth was only 200m, so sampling there was not ideal. On alternate months off Durban $(29^{\circ}50'S)$ stations were occupied in the inshore water, the Agulhas current and in some instances beyond the current about 140km offshore. While this was more suitable geographically for sampling *P.homarus*, being towards the centre of distribution of the adult population, adequate physical information particularly on currents was not always available.

During the period from September 1970 to March 1972 ten sampling trips of ten days each were made to Richards Bay virtually every second month, alternating with two day trips off Durban. Sampling continued off Durban until July 1972 and an additional sample was taken in March 1973. In all a total of 368 horizontal tows of 20 minute duration each were made. Their positions and a breakdown of species composition and numbers obtained in each could not be included here due to lack of space, but is available on request from the South African Museum, Cape Town, where the material has been deposited. Positions where some of the rarer species were obtained have, however, been included in the text.

The majority of phyllosomas obtained were scyllarids represented by the genera *Scyllarus* (4 spp.), *Scyllarides* (2 spp.), *Parribacus* (1 sp.) and *Ibacus* (1 sp.). Of the six palinurid species obtained, *P.homarus* predominated and the complete series of developmental stages was present. *P.delagoae* was disappointingly rare and only five stages were identified. Incomplete series of larvae of *?Palinustus mossambicus* Barnard, *Panulirus longipes* (Milne-Edwards), *Panulirus penicillatus* (Olivier) and *Panulirus versicolor* (Latreille) were also obtained. In addition puerulus larvae of *P.homarus*, *Panulirus ornatus* (Fabricius), *Projasus parkeri* George & Grindley and *Palinurellus* sp. Von Martens were collected.

Despite the intensified sampling programme phyllosomas of *P.homarus* were still not particularly abundant and as the current systems off the Natal coast are complex and as yet not fully understood, no more than a tentative explanation of larval distribution in relation to currents has been possible. This paper is therefore largely devoted to descriptions of the palinurid phyllosoma and puerulus larvae and although descriptions of scyllarid phyllosomas are also included they are not treated in as much detail.

Methods

The vessel used was the R.V. Meiring Naudé (31,7m, 360 tons) of the Council for Scientific and Industrial Research (C.S.I.R.). All sampling was done at night between 1900 and 0400hrs. by means of an N100 H net. This net, which has an overall length of about 470cm and 22 meshes per inch, proved to be the largest two men could conveniently operate under the rough, windy conditions common off the Natal coast. It was towed at the surface at a speed of 2 knots measured on the ship's log and each drag lasted for exactly 20 minutes. The mean amount of water sifted in a drag was 930m³, measured by means of a flow meter attached in the mouth of the net. Samples were preserved in 5% neutralized formaldchyde solution. Drawings were made using a *camera lucida* outfit.

Palinurid phyllosomas

Panulirus homarus (Linnaeus, 1758)

A total of 349 phyllosomas was obtained and although eleven arbitrary stages are usually used to describe the development of palinurid phyllosomas, the criteria on which these are based proved to be unreliable in some instances for *P.homarus* in which only nine distinct stages are recognised in the present investigation. These may be identified by means of the key provided below:

Key to Stages

	Company and the second s							
A.	Eye segmented							В
	Eye not segmented							stage 1
B.	Exopod of leg 3 setose							C
	Exopod of leg 3 not setose							stage 2
С.	Leg 4 bifid							Ď
	Leg 4 not bifid							stage 3
D.	Exopod of leg 4 setose							Ē
	Exopod of leg 4 not setose							stage 4
E.	Maxilliped 2 with exopod bud .							Ē
_	Maxilliped 2 without exopod bud							stage 5
F.	Exopod of maxilliped 2 setose .							G
	Exopod of maxilliped 2 not setose							stage 6
G.	Leg 5 fully segmented	•						ĒΗ
	Leg 5 not fully segmented							stage 7
Н.	Pleurobranchs present							stage 9
· · -	Pleurobranchs absent							stage 8

Description

Each stage, which does not necessarily represent a single instar, is illustrated (see Figs. 1-21) and features of each are summarised in Table 1. However, only features used in the key

correspond with any particular stage as the sequence in which other features appear may vary slightly from those shown.

The relative proportions of the cephalic disc are given in Table 2 where it may be seen that in stage 1 it is almost as wide as it is long and it is considerably wider than the thorax. From stages 3 to 9 these body proportions remain fairly constant although the shape of the cephalic disc changes considerably. In stage 1 it is oval but slightly concave antero-laterally (i.e. pear-shaped) with a very obtuse medial point at the posterior end. From stage 2 to stage 4 the antero-lateral margins become progressively more concave just below the insertion of the second antennae and the posterior medial point becomes progressively more pronounced and acute. Thereafter from stages 5 to 9 this situation is reversed and the concavity of the antero-lateral margins becomes progressively reduced and ultimately convex while the posterior medial point becomes progressively more obtuse again, resulting in a sub-ovoid shape in which the anterior end is slightly narrower than the posterior one.

The distance between the mouthparts and the level of the midpoint between the coxae of maxillipeds 2 is relatively small (see Johnson, (1968) for definition of the measurements and comparison with other species). In *P.homarus* the proportions change as may be seen in Table 2, and in stage 1 the distance from the mouthparts to the midpoint between the coxae of maxilliped 2 is slightly greater than the distance between the two coxae, becoming progressively smaller in stages 2 and 3 until the distances are equal in stage 4. From stage 5 to 9 the ratio remains virtually constant with the distance between the coxae being slightly greater.

In stages 1 to 3 the ventral coxal spines are large and conspicuous. Thereafter they become progressively smaller relative to the dorsal coxal spines which enlarge. The ventral coxal spines are replaced in the later stages by sternal spines (positioned adjacent to the proximal ends of the coxae) which are smallest on leg 1 but which become progressivley larger posteriorly and in stages 8 and 9 are hooked.

Conspicuous subexopodal spines (defined as spines which protect the actual articulation of the exopod and endopod in this paper) are present on legs 1 to 3. (The term subexopodal could be confusing as some species have a spine on the opposite side of the merus at the level of the exopod for which the term 'subexopodal' might also be appropriate). In stage 1 there is a conspicuous additional spine on the opposite side of the merus but this becomes reduced and disappears in subsequent stages.

Panulirus longipes (A. Milne-Edwards, 1868). (See Figs. 22, 23)

These larvae almost certainly belong to the spotted-leg subspecies, *P.longipes longipes* which is the only member of the *Panulirus japonicus* group, as definied by George & Holthuis (1965), of which adults have been recorded from the region (Berry 1971a). After P.homarus they were the most abundant of palinurid phyllosomas, a total of thirty-four being obtained. The developmental sequence was classified using the nine arbitrary stages defined by Chittleborough & Thomas (1969) for *P. cygnus* and stages 3 to 7 were found to be represented. The material was compared directly with P.cygnus larvae and found to be indistinguishable. Similarly these larvae conform with the detailed descriptions of *P.longipes* (presumably femoristriga) from New Hebrides given by Michel (1969) and from the South China Sea by Johnson (1971b). They also conform with corresponding stages of larvae of *P.marginatus* up to stage 7 as described by Johnson (1968) from the Hawaiian Archipelago. As these comprehensive descriptions and figures are applicable no detailed description is given here of *P.longipes longipes* which can be distinguished from *P.homarus* on the basis of the following features: The thorax is conspicuously wider than the cephalic disc from stage 4 onwards; the cephalic disc starts pear-shaped and becomes symmetrically oval in the mid and later stages; the mouthparts are situated well forward of the second maxillipeds, the ratio of the distance between the anterior tip of the labrum and the level of the coxae of the second maxillipeds to the distance between the coxac of these maxillipeds (see Johnson, 1968: p77) ranging from 1.5 in stage 3 to 1.1 in the final stage i.e. higher than in *P.homarus* in all stages (see Table 2); the second maxillipeds are long and slender; there are no subexopodal spines; there are no dorsal coxal spines and ventral coxal spines are present at least to stage 6 as defined by Michel (1969) or stage 5 as defined by Chittleborough & Thomas (1969); the tips of the antennae in the gilled stages are not spatulate.

Panulirus penicillatus (Olivier, 1791) (See Figs. 24, 25)

Two specimens conforming in all respects to stages 9 and 10 as described by Johnson (1968) from the Hawaiian Archipelago were obtained at $29^{\circ}48'S$, $32^{\circ}50'E$. One other specimen in stage 9 was obtained at $29^{\circ}38'S$, $31^{\circ}55'E$. Stages 7 to 11 have been described in detail by Johnson so no full description is given here. The specimens of *P.penicillatus* obtained are readily distinguishable from *P.longipes* in that the cephalic disc is equal or almost equal in width to the thorax. Its shape also differs from that of the latter species and instead of being symmetrically oval, the anterior end is more rounded.

Panulirus ?versicolor (Latreille, 1804)

One stage ?7 was obtained from 30°01.7'S, 31°21.0'E and a single final stage specimen from 29°38.2'S, 31°50.2'E.

Description

These two specimens appear to be identical with *P.homarus* as described in this paper in all respects except that they have subexopodal spines on legs 1 to 4 and not only on legs 1 to 3. (The problem of distinguishing between *P.versicolor* and *P.homarus* is discussed on page 7). The final stage specimen has spatulate antennae.

?Palinustus mossambicus Barnard, 1926

A single damaged and badly distorted palinurid phyllosoma was obtained at 31°28'S, 32°10'E which is provisionally identified as *P.mossambicus*.

Description (see Figs. 26-29)

The cephalic disc is oval, 15.1mm long and 13.6mm wide with a uniformly rounded posterior margin. The thorax is narrower than the cephalic disc and the abdomen is relatively small but fully segmented with bifid pleopods and well formed uropods. The telson does not reach the level of the ends of the uropods. The total length is 20.0mm. Although the specimen conforms basically with *Panulirus*, the antennules are atypical and distinctive, the peduncles being particularly long relative to the peduncles of the antennae. The lengths of the segments from proximal to distal are 1.6mm, 0.5mm and 1.1mm and the middle segment reaches just beyond the level of the distal segment of the antennal peduncle. The antennal peduncles also differ from *Panulirus* in that there are two stout spines on each distal segment. The mouth-parts are very close to the second maxillae. The first maxilliped is trilobed. The exopod of the second maxilliped bears 8 pairs of setae and the third maxilliped has a setose exopod. The terminal segments are only complete on one fourth leg which is subchelate (Fig. 28). Ventral coxal spines are present on maxilliped 3 and legs 1 to 4. There are stout subexopodal spines on legs 1 to 4. The fifth legs are segmented and extend well beyond the end of the telson.

This specimen closely resembles the phyllosoma from the South China Sea which Johnson (1971) refers to as "Panulirus(?) sp.", but his specimen has more spines on the antennal peduncles and has no subexopodal spines. There can be little doubt, however, that the two belong to the same genus.

Palinurus delagoae Barnard, 1926

P.delagoae was tentatively regarded as a variety of Palinurus gilchristi Stebbing, 1900 by

Barnard (1926) but it has now been proposed by Berry & Plante (1973b) that it is a distinct species.

The first four larval stages are described, plus one specimen which is provisionally assigned to stage 6. Only one feral specimen of stage 1 was obtained but others were hatched out in captivity. Stage 2 has not been figured as apart from the jointed eye stalks it is morphologically similar to stage 1.

Description (See Figs. 30-33 and 42-44 and Table 3)

The cephalic disc is rounded; in stage 1 it is as wide as it is long with an almost straight posterior margin, but in the subsequent stages there is a tendency for it to become very slightly longer than wide and for the posterior margin to develop a slight obtuse medial prominence. In all the stages the cephalic disc was more than 1.5 times as wide as the thorax.

There is a projection towards the base of antenna 2, very similar to that found in scyllarids. Antenna 1 has the rudiments of an endopod bud visible even in stage 1. Maxilla 2 is well developed for a first stage larva with setae on both proximal and distal segments. Similarly, the bud of maxilliped 1, which is present in stage 1 bears two terminal setae. The exopod of maxilliped 2 appears as a bud in stage 3 and it is well developed, although not setose, in stage 4. Buds of legs 4 and 5 are present in stage 1. Ventral coxal spines are present but there are no dorsal coxal spines. There is a spine on the postero-ventral side of the merus adjacent to the joints of the exopods in maxilliped 3 and legs 1 to 3 which is conspicuous in stage 1 but becomes progressively reduced in size. (It should be noted that this is not the subexopodal spine as defined on page 5).

Discussion

Identification of the palinurid phyllosomas found off the Natal coast is complicated by the fact that all eight extant genera are represented in the western Indian Ocean so presumably phyllosomas of all these could be present in the samples. Within the genus *Panulirus* alone, adults of *P.homarus*, *P.ornatus*, *P.versicolor*, *P.longipes* and *P.penicillatus* have been recorded from Natal (Berry 1971a). This has led to some uncertainty in separating species of this genus which will be elaborated upon below.

Prasad & Tampi (1959) and Deshmukh (1968) have described tank hatched stage 1 phyllosomas of *P.burgeri* and *P.dasypus* (-P.homarus) from the south and west coasts of India. The S.E. African ones differ from these basically only in that they are slightly larger with a total length range of 1.40–1.70mm as opposed to 1.35–1.40mm. However, as the African sample included both feral and tank hatched specimens their larger size could be due to the presence of later instars. Prasad and Tampi also record the extreme similarity between first stage phyllosomas of *P.ornatus* and *P.homarus* and on the basis of the slight differences they cite between these species it seems doubtful whether reliable separation in this stage would be possible if more than one instar was present.

Johnson (1971b) has described phyllosomas in stages 5? to 9 and 11 from the South China Sea which he provisionally assigned to *P.ornatus*. Up to about his stage 8, which approximates to stage 6 in my *P.homarus* series, these two species appear to be indistinguishable except that dorsal coxal spines appear in stage 3 in *P.homarus* and apparently only in stage 8 in *P.ornatus*. Thereafter the two species may be separated because the cephalic disc of *P.homarus* is evenly rounded posteriorly whereas in *P.ornatus* Johnson shows it to be slightly pointed. In fact the shape of the cephalic disc of late stage *P.homarus* appears to be identical to that of the corresponding stages of *P.versicolor* figured by Johnson in the same publication and by Michel (1969). Unfortunately earlier stage larvae of *P.versicolor* have not been illustrated so a comparison of the shape of the cephalic disc with corresponding early stages of *P.ornatus* and *P.homarus* is not possible. Johnson also described dorsal coxal spines on legs 2 and 3 in stages 4 to 10 and only on legs 3 and 4 in the gilled stage of *P.versicolor*, so in this respect it could be confused with *P.ornatus* from stage 8 onwards and *P.homarus* in the early stages. The only feature where there appears to be a clear distinction is the presence of subexopodal spines on legs 1 to 3 only in both *P. homarus* from Natal and *P. ornatus*, whereas *P. versicolor* as described both by Johnson (1971b) and Michel (1969) has subexopodal spines on legs 1 to 4. If this feature proves to be constant *P.versicolor* should readily be distinguishable from *P*.homarus from S.E. Africa and *P*. ornatus in all but the stages preceding development of the fourth leg. However, some doubt as to its reliability is raised by the fact that Michel (1971) has recorded phyllosomas from the Marquases Islands which he has assigned to *P.homarus* as adults of this species predominate in the region. Unfortunately, apart from a figure of a late stage larva with spatulate antennae he gives no full description nor does he cite the numbers and developmental stages he obtained. The problem is that the specimen he illustrates differs from *P.homarus* from Natal in that it has subexopodal spines on legs 1 to 4 instead of only legs 1 to 3, on the basis of which it conforms with *P.versicolor*. However, this species has not been recorded from the Marquases. It must be pointed out that it has vet to be established whether final stage phyllosomas and pueruli of *P.versicolor* have spatulate antennae or not. If it is subsequently shown that they do, Michel's specimen would appear to be indistinguishable from *P.versicolor*. If in fact it does not belong to the latter species it must be concluded that phyllosomas of *P.homarus* from the Marguases differ from those of the Indian Ocean (which would be in keeping with the view expressed by Dr. R. W. George (pers. comm.) that adults referred to as *P.homarus* from the Marguases belong to a distinct and separate species). Even if this is the case the validity of separation of the phyllosomas assigned to *P.homarus* from Natal and *P.versicolor* on the basis of the presence of absence of a subexopodal spine on the fourth leg is questionable as it is possible that this may prove to be a variable feature in *P.homarus*. If this is the case the problem of separating it from P.versicolor remains unsolved.

The complete absence of subexopodal spines on all legs in both *P.longipes* and *P.penicillatus* readily separates them in all stages from the preceding three species. Late stage specimens of *P.penicillatus* are distinguishable from corresponding stages of *P.longipes* because the cephalic disc is equal or almost equal in width to the thorax instead of being conspicuously narrower and its anterior end is more broadly rounded than the posterior one so that it is not symmetrically oval as it is in *P.longipes*. Johnson (1968) was unable to distinguish between early stage *P.penicillatus* and *P.marginatus* and it seems likely that early stage *P.longipes* and *P.penicillatus* are also indistinguishable in which case some of the early larvae assigned to *P.longipes* in this investigation possibly belong to *P.penicillatus*.

Prasad and Tampi (1959) have described a series of larvae from off S.W. India in Laccadive waters which they tentatively assigned to *P. penicillatus*. However, the identity of *P. penicillatus* has subsequently been established with certainty by Johnson (1968) and as Prasad & Tampi's species is obviously different, Michel (1969) and Johnson (1971b) suggested that it is *P. versicolor*. However, if the presence of a subexopodal spine on the fourth leg is a diagnostic characteristic of the latter species, this cannot be correct as Prasad & Tampi's species has subexopodal spines on legs 1 to 3 only. In view of the shape of the cephalic disc in the latter stages this series is considered almost certainly to belong to the same species as has been called *P.homarus* from Natal, with the possible exception of the first stage. This is not shown to have subexopodal spines by Prasad & Tampi and as the mouthparts are situated well forward on the cephalic disc it probably belongs to *P. longipes* or *P. penicillatus*.

Murano (1971) has described five species of palinurid phyllosomas from Japan and the South China Sea which he designated forms A to E, and has given a useful figure showing all five together. On the basis of present evidence it is suggested that his species A, B and C, which have no subexopodal spines, belong to *P.longipes*, *P.japonicus* and *P.penicillatus* respectively. The others all have subexopodal spines on legs 1 to 3 and, as noted by Murano, his species D is identical with Prasad & Tampi's '*P.penicillatus*' which is therefore considered

to be *P.homarus*, as described in this investigation, while his species E undoubtedly conforms with *P.ornatus* as described by Johnson (1971b).

In conclusion, the problem of identification of the phyllosomas of the Indian Ocean *Panulirus* species appears to be approaching solution although certain species still appear to be indistinguishable for part and others for the entire developmental sequence. Least is known about *P.polyphagus* of which only the first stage appears to have been described (Deshmukh 1968), but as subexopodal spines are clearly shown in that author's figure it obviously falls into the *P.homarus* — *P.ornatus* — *P.versicolor* complex and its separation within it remains to be resolved.

A provisional key for separation of the Indian Ocean *Panulirus* species on the basis of available evidence is given below.

1	Subexopodal spines on some legs
	Subexopodal spines absent on all legs
*2	Subexopodal spines on legs 1-3
	Subexopodal spines on legs 1-4
3	Dorsal coxal spines appear in stage 3; late stage with cephalic disc rounded
	posteriorly
-	Dorsal coxal spines appear approximately at stage when exopod of maxil-
	liped 2 becomes setose; late stage with cephalic disc slightly pointed P.ornatus
†4	Cephalic disc symmetrically oval in late stages and conspicuously narrower
	than thorax
	Cephalic disc wider anteriorly than posteriorly and as wide or nearly as
	wide as thorax in late stages
*It	is not known whether <i>P. polyphagus</i> has subexopodal spines on leg 4 or not and on present
inf	formation it cannot be separated from <i>P.versicolor</i> , <i>P.ornatus</i> and <i>P.homarus</i> .
$+\Gamma_{a}$	ulu stope longe on moon to be indictinguishable

†Early stage larvae appear to be indistinguishable.

The identification of the specimen provisionally referred to as Palinustus mossambicus was arrived at largely by a process of elimination. It seems unlikely to belong to Panulirus as phyllosomas can be linked with all the species of this genus known from the south western Indian Ocean with reasonable certainty, viz: P.homarus, P.ornatus, P.versicolor, P.longipes and *P. penicillatus*. As it certainly does not belong to *Palinurus* the only other possible genera are Puerulus, Linuparus, Justitia and Palinurellus. Of these Justitia, the identity of which has been established by Johnson & Robertson (1970), can be eliminated. I believe that the clue to its identity may lie in its unusually long antennules and the relative proportions of their peduncular segments. In photographs of adult Palinustus mossambicus by Barnard (1926) the antennules are strikingly long with the proximal segment of the peduncles extending beyond the level of the distal antennal peduncle segment. Relative proportions of the segments from proximal to distal (from the photographs) are 3:1:2 which compares well with 3.2:1:2.2 in the larva. In adults of *Linuparus* and *Puerulus* the antennules are not unusually elongate and in specimens of L.somniosus Berry & George, and P.angulatus (Bate) the proportions of the segments were found to be the same in both, i.e. 3.1:1:1.3. Johnson (1968a and 1971b) has described "phyllamphion" type larvae which in the later paper he suggests might be Linuparus and Puerulus. If length of the peduncles of the antennules and the relative proportions of the segments is a valid diagnostic character his identification seems justified as in the specimens he figures this conforms with the arrangement in adult *Linuparus* and Puerulus and not with Palinustus.

Figures of *Synaxes* (= *Palinurellus*) given by Bate (1881) show even less conformity with that of the larva in question in regard to the antennules which are not unusually long and have relative proportions of the peduncular segments of 2.4:1:1.2. It thus seems justified to provisionally assign this phyllosoma to *Palinustus mossambicus*.

Compared with members of the genera Panulirus and Jasus, the stage 1 larva of P.delagoae

hatches in a considerably more advanced state of development with features present such as the buds of legs 4 and 5, and the inner flagellum of the antennule. It is also somewhat larger, with a total length of 2.8mm as opposed to 1.5mm in *P.homarus*, for example, which is possibly associated with a relatively large egg size and long incubatory period of five to six months in *P.delagoae* (Berry 1973a).

The scarcity of *P.delagoae* larvae in the samples compared with *P.homarus* indicates that they either occur at greater depth or perhaps further offshore. The former seems more likely as ovigerous females occur on the edge of the continental slope (Berry 1973a) and several of the larvae obtained were in inshore water (i.e. inside the Agulhas current). No late stage larvae were obtained but Von Bonde (1930), Gurney (1936) and Lazarus (1967) figure what appear to be late to final stage larvae from the Cape (presumably of *P.gilchristi*) with total lengths of only 15.6mm, 23.0mm and 11.5mm respectively. This is considerably smaller than the equivalent *Panulirus* stages and in view of the fact that the larvae of *P.delagoae* hatch in an advanced stage of development it seems reasonable to suppose that they might have a relatively short life.

Palinurid puerulus larvae

As noted by Deshmukh (1966) the palinurid puerulus is a definite planktonic larval stage and the term 'post-larva' which has been applied to it by some authors is confusing. In this paper the term 'puerulus' is used for the stage with natatory pleopods (even if the larvae have settled and are no longer planktonic) whereas the term 'post-larva' is applied to the early stages in which the adult morphology has been assumed and in which the pleopods are no longer natatory. Transformation from puerulus to post-larva appears to take place in a single moult, at least in the genus *Panulirus*. In the present investigation puerulus larvae were never captured in the surface plankton tows in which phyllosomas were obtained. However, large numbers belonging to *P.homarus* and *P.ornatus* were sporadically found clinging to the protective shark nets off the Durban beaches when these were serviced and one specimen of *Palinurellus* sp. was also obtained from this source. A further four pueruli belonging to *Projasus parkeri* were obtained from the net of a trawler.

On page 8 it was stated that the late stage phyllosomas of *P.homarus* and *P.ornatus* were very similar. Likewise the pueruli of these two species were found to be extremely difficult to separate on morphological grounds and apart from some rather unreliable morphological differences they could only be distinguished with certainty on the basis of pigmentation patterns. Pigmentation starts to be deposited in the puerulus stage soon after settlement on some substratum and is fully developed just prior to the moult into the first postlarva. The description below of the puerulus larvae of *P.homarus* and *P.ornatus* is based on pigmented specimens only in which their identity could be established with absolute certainty. Unfortunately this has meant that the identity of the majority of pueruli collected could not be determined and the numbers in which a positive identification was possible are small, particularly as preserved specimens lose their pigmentation after a few months.

P.homarus pueruli obtained from Natal conform basically to the description and figures given by Gordon (1953) for this species from the Marquesas (although it now seems likely that this is closely related to but distinct from *P.homarus* in the Indo-West Pacific). Moreover, her description of a specimen from Kenya fits the *P.ornatus* pueruli from Natal. The brief description given below applies to both *P.homarus* and *P.ornatus* from Natal and is supplementary to Gordon's comprehensive ones.

Panulirus homarus and Panulirus ornatus

Description (See Fig. 34 and Table 4)

The intact antennae are about 2 x the total body length and broadly spatulate distally. Those of *P.ornatus* tend to be slightly longer than in *P.homarus*. The peduncular segments of the antennule, particularly the proximal segments containing the statoliths tend to be slightly

shorter and stouter in *P.homarus* than in *P.ornatus*. Statoliths were present in all specimens examined of both species.

The spination of the dorsal surface of the carapace is illustrated in Fig. 34 and conforms to that described by Gordon except that in *P.ornatus* the number of spines on the lateral keel is variable and one or two may be present. Two were invariably present in *P.homarus*. In the precervical region a group of four minute spinules (the 'incipient' spines described by Gordon) are frequently but not always present in both species. Sometimes there are no actual spines present on the exoskeleton but they are visible on the underlying exoskeleton, giving the impression that they are present.

The dorsal surface of the abdominal segments is smooth in both species but transverse grooves can sometimes be made out in the pigmented underlying exoskeleton in *P.homarus* just prior to the moult into the first postlarva.

In both species there is a large posteriorly directed pair of spines on the last somite of the thoracic sternum.

Other than the slight difference in size and proportions which are unreliable as diagnostic criteria due to variability and overlap, no other means of separating the two species morphologically could be found.

While still planktonic and for a few days after settlement on some substratum the puerulus of both species is transparent and the only pigmentation present (apart from transient red chromatophores) is in the spatulate tips of the antennae, which range from being opaquewhite to chocolate-brown, and just over half the way along the flagella from the tips where there is a brown band. However, pigment is gradually laid down in the underlying exoskeleton prior to moulting into the first postlarval stage. First the antennae develop alternate white and brown transverse bands while the body is still transparent, then pigment is gradually deposited in the cephalothorax and abdomen and it is only at this stage that the pueruli of *P.homarus* and *P.ornatus* become distinguishable. In both species the cephalothorax is speckled with brown but laterally in the pre- and postcervical regions there is a denser area of pigmentation which is darker brown in *P. homarus* and almost black in *P. ornatus*. Similarly on the dorsum in the postcervical region there is a dense patch of pigmentation on either side of the midline which shows the same difference in colour between the species. Although it is only the intensity of pigmentation and not the pattern which differs between the two species on the cephalothorax the patterns on the abdomens are completely different. In *P.homarus*, the entire dorsal surface of the abdomen is mottled with irregular pale brown patches which are darkest and more dense towards the pleura and somewhat less evident, though still present, medially. In *P.ornatus* there is a distinct rectangular white 'saddle' medially in segments 1-4 with dense, chocolate-brown pigment laterally. Deshmukh (1966) figures the pigment pattern of *P. polyphagus* which is somewhat similar on the abdomen to *P. ornatus* except that the white saddle is present on all abdominal segments and is triangular.

Projasus parkeri George & Grindley

In April 1972, two pueruli were obtained from the net of a trawler operating S.E. of the Bluff, Durban at a depth of 414m. Later the same month a further two specimens were obtained from virtually the same locality. Adults had previously been obtained in this vicinity (Berry 1971a).

Description

As can be seen from Table 4 these specimens are large to be pueruli and it was first thought that they were post-larvae. However, examination of the pleopods showed them all to be natatory with the endo- and exopodites equally developed and the endopodites each bearing an *appendix interna*, complete with coupling hooks. Thus by definition these specimens are pueruli. However, unlike the *Panulirus* pueruli examined the spination of the *Projasus* specimens conformed to the adult situation as described and figured by Stebbing (1902). Thus in this aspect the specimens resemble post-larvae although it must be remembered that the

dorsal cephalothorax of adult *Projasus* bears only a few large spines as opposed to the numerous small spines in *Panulirus*. Postero-lateral spines are present on the sternum but are not enlarged as in pueruli of some *Panulirus* spp. None of the specimens had intact antennae but in one, which still had some of one antennal flagellum, there was a single band of brown pigment midway along its length. Two of the specimens were completely transparent when obtained but the other two had had a slight pinkish tinge to the cephalothorax and abdomen.

Palinurellus sp.

In May 1971 a single specimen was obtained with numerous *P.homarus* pueruli from the protective shark nets at Durban.

Description (See Fig. 35)

There is a well-developed trifurcate rostrum. Each side of the carapace in the precervical region is produced into a large tooth which is slightly crenulate along its outer margin. On either side on the dorsal precervical carapace is a short ridge. The eyes are well recessed and only the cornea is visible dorsally. In the postcervical region the carapace is slightly distorted in this specimen but it is obviously angular with two lateral keels and a median keel. There is a slight concavity in the cervical region which is probably an artifact caused by the distortion. The entire dorsal surface of the carapace is smooth and devoid of spines. The carapace length is 12.1mm and the total length is 28.0mm. The antennae and antennules are shorter than in *Panulirus* and bear numerous plumose setae. The dorsal surface of the abdomen is smooth and there are biramous natatory pleopods with coupling *appendices interna* on segments 2-5.

Palinurellus has not previously been recorded from the east coast of southern Africa although Barnard (1950) mentions that it occurs at Mauritius. The Natal specimen is very similar to *P.wieneckii* described by Michel (1971) from the Pacific but appears to differ from it slightly in the morphology of the antennae and, according to Michel, the sternal spines are as in *P.homarus*, *P.ornatus* and *P.polyphagus*.

Discussion

As far as is known the puerulus stages of the following Indo-pacific *Panulirus* species have been previously described: *P.homarus* (Bouvier 1913, Von Bonde 1930, Gordon 1953, Michel 1971); *P. japonicus* (Nakazawa 1917 and Kinoshita 1934); *P.cygnus* (George 1962); *P.longipes femoristriga* (Michel 1971); *P.polyphagus* (Deshmukh 1966); *P.penicillatus* (Michel 1971); *P.versicolor* (Calman 1909, Kubo 1950, Gordon 1953 and Michel 1971). On the basis of observations made on *P.ornatus* in Natal I concur with the deduction by Deshmukh (1966) that the single specimen described by Gordon (1953) from the Kenyan coast probably belongs to *P.ornatus*.

The striking feature about the puerulus larvae of the Indo-pacific *Panulirus* species is the extreme morphological similarity between them. Although more information is needed it appears that it might be possible to divide them into two basic groups on the basis of the relative length of the antennae, the presence or absence of a spatulate tip and the shape and degree of development of the spines on the posterior segment of the sternum. In *P.homarus, P.ornatus* and *P.polyphagus* the antennae are relatively long being approximately 2.0, 2.5 and 4.0 x the total body length respectively and all have spatulate tips. These species all have well developed posteriorly directed (hooked) spines on the last thoracic sternal somite. In contrast *P.japonicus, P.cygnus, P.longipes* and also *P.penicillatus* have relatively short antennae (just over 1 x the body length) with tapering tips and the sternal spines are feebly developed (see Michel 1971). The situation in *P.versicolor* is not certain as according to Gordon (1953) there is some doubt as to the validity of the specimens assigned to this species by Kubo (1950). On the basis of Gordon's description it appears that the antennal length is at least

2.5 x the total length, but whether or not the tips are spatulate is not clear. Certainly *P. versi*color might be expected to be likely to conform to the same pattern as the closely similar *P.ornatus*, and according to Michel (1971) the sternal spines are as in *P.homarus*, *P.ornatus* and *P. polyphagus*. Unfortunately the morphology of the antennae seems of limited value for identification purposes as the majority of pueruli collected do not have them intact. In a key for identification of all the Indo-Pacific species of *Panulirus* (excluding *P.longipes* and *P.cygnus*) Deshmukh (1966) has used the presence or absence of the expodite on the third maxilliped as a diagnostic criterion. Although this may well prove to be a reliable feature it appears that he has assumed it to be present in the puerulus of *P. penicillatus* and totally absent in *P.versicolor* on the basis of adult morphology, and ratification of the validity of this is required as the specimens assigned to *P.versicolor* by Michel (1971) did have a small exopodite on the third maxilliped. Deshmukh also separates P. japonicus on the basis of there being "no posterolateral" thoracic spine. I have only had specimens of *P. cygnus* as representative of the "P. japonicus group" available for examination and in these this spine is certainly present although much smaller and not hooked and directed posteriorly as in P. homarus and P.ornatus, for example. Michel (1971) reports that it is poorly developed and not directed posteriorly in *P.longipes femoristriga* and this is therefore almost certainly the case in *P.longipes longipes*. More information on pigmentation patterns in *P.penicillatus*, *P.versicolor* and *P.longipes* would substantially help to solve the problem of identification of puerulus larvae in the Indo-Pacific Panulirus species.

The common occurrence of *P.ornatus* pueruli on the Durban shark nets is surprising as the Natal coast is environmentally unsuitable for the adults and a small, non-breeding population is only known to occur in Durban Harbour (Berry 1971a). It seems probable that late stage phyllosoma larvae, emanating from lower latitudes on the East African and Malagasy coasts, must be swept southwards in the Moçambique-Agulhas current and metamorphose into the puerulus stage which is then capable of reaching the shore of Natal.

It is not known whether the specimens of *Projasus parkeri* were captured on or near the bottom or in midwater. However on the basis of the morphology of the pleopods and slight pigmentation in some it seems probable that they had recently settled on the bottom. Unless the sequence of morphological change of the pleopods from being adapted to a natatory function to a non-natatory one is gradual and takes place over several moults as opposed to sudden change completed in one moult as in *Panulirus*, it seems reasonable to regard these specimens as being true pueruli. In this case final stage phyllosomas would be expected to attain a large size, possibly even comparable with the so-called giant scyllarid larvae.

Scyllarid phyllosomas

Scyllarid larvae, believed to belong to the following genera were obtained:

Scyllarus (4 species), Scyllarides (2 species), Ibacus (1 species) and Parribacus (1 species). Barnard (1950) recorded adults of Scyllarus cultrifer (Ortm.), S.martensii (Pfr.), S.tuberculosus (Bate) (=S.rugosus H. Milne-Edwards), Scyllarides elizabethi (Ortm.), Scyllarides squammosus (H. Milne-Edwards) (from Mauritius), Parribacus ursus major (Herbst) (=P.antarcticus (Lund)), Thenus orientalis (Lund) and Ibacus incisus (Peron) (=I.novemdentatus Gibbes) from the east coast of southern Africa. Subsequently another species, Scyllarus ornatus Holthuis has been added and thus Thenus is the only genus not represented among the larvae obtained.

Scyllarus sp.A

This species was by far the most abundant of both palinurid and scyllarid phyllosomas and a total of 1862 were obtained. Although a complete developmental series is represented in the material collected the morphology and changes which take place are described but no attempt has been made to classify the larvae into definite stages as this study was chiefly concerned with palinurids.

Description (see Figs. 36, 38 and 45-47)

The newly hatched larvae with unstalked eyes are particularly small; the mean length of the cephalic disc is 0.8mm, the width 1.0mm and the total body length is 1.2mm. The anterolateral margins of the cephalic disc are slightly concave while the posterior half is almost perfectly semi-circular. There are large ventral coxal spines on legs 1-3 and on maxilliped 3. There are no dorsal coxal spines but there is a large dorsal spine on the proximal end of the merus of legs 1-3. Large subexopodal spines are present on legs 1 and 2 but on legs 3, in which the exopodite is only a bud, the spine is small and more ventral in position. Leg 4 is not present. The telson bears conspicuous lateral spines.

In the first stage in which the eyes are stalked (see Fig. 36) the mean length of the cephalic disc is 1.1mm, the width is 1.3mm and the total length is 1.9mm. The eye stalks are long and reach the level of the base of the second antennae. The antero-lateral margins of the cephalic disc are now straight and the posterior half has a slight point postero-medially. The spination is as in the previous stage with well developed ventral coxal spines, but the dorsal spines on the meri are somewhat reduced in size relative to them. The subexopodal spine on leg 3 is as in the other legs; the fourth is present as a uniramous bud.

In subsequent stages the usual sequence of development of appendages follows; the eye stalks become progressively more elongated and after the second stage always reach laterally beyond the level of the base of antennae 2. The first antennae are always considerably longer than the second antennae. The antero-lateral margins of the cephalic disc become progressively more convex, making it almost round except for the postero-medial point which persists until the gilled stage. Ventral coxal spines persist on legs 1-3 and develop on the fourth leg. Subsequently short stout spines even develop on the coxae of the fifth leg at the stage when it is first becoming segmented. The dorsal spines on the merus become progressively more insignificant and at a cephalic disc length of about 5.5mm they are usually only visible on legs 3 and 4, those on legs 1 and 2 being minute or absent. The uropods are only ever slightly pointed in the earlier stages and they become progressively more rounded.

At the gilled stage (Fig. 38) the cephalic disc has a mean length of 9.1mm; breadth of 9.7mm and the total length is 15.3mm. The eye stalks extend laterally well beyond the level of the base of the second antennae. The cephalic disc is almost perfectly rounded except along its posterior margin where it is slightly concave on either side of a slight median pro-truberance. Ventral coxal spines persist on maxilliped 3 and legs 1-5. The dorsal spines of the meri are minute if present at all. The uropods and telson are definitely rounded but sharp, conspicuous lateral spines persist on the telson (hidden by the uropods when viewed ventrally).

Remarks

The gilled stage has been figured and described by von Bonde (1932) who incorrectly assigned it to *Scyllarides elizabethi*. This species is very similar to Johnson's (1971b) "Species C" from the South China Sea and is only readily distinguishable from it by the length of the eyestalks which are shorter in Johnson's species and do not extend beyond the level of the base of the antennae.

Judging by the size attained by species A larvae relative to the larvae of the other three *Scyllarus* species obtained, and the relative sizes of the four adult species recorded from the region it is tentatively suggested that it is *Scyllarus rugosus*.

Scyllarus sp.B

This was the second most abundant *Scyllarus* species and a total of 85 phyllosomas, representing all stages of development, were obtained.

Description (See Fig. 41)

This species is very similar to S.martensii Pfeffer, from the South China Sea, as described

and figured by Johnson (1971b) but differs from it in that the telson has no lateral spines, the expanded portion of maxilla 2 is more pointed anteriorly, the ventral coxal spines of the fifth legs are more robust and the overall size is slightly larger. In respect of the absence of lateral spines on the telson, species B therefore agrees with the description of *S.modestus* Holthuis from Hawaii, described and figured in detail by Johnson (1971). In fact species B conforms in all respects with his description of the early stages of *S.modestus* and only in late and final stages larvae do the following differences become evident: In species B the ventral coxal spine of the fifth leg is considerably stouter and longer than on the other legs, the expanded portion of maxilla 2 is more pointed anteriorly and the peduncle also has a distinct enlargement on the anterior margin which is absent on *S.modestus* according to Johnson's (1971) Fig. 20; the overall size appears to be slightly smaller than in *S.modestus*.

Remarks

This species was incorrectly assigned to *Scyllarides elizabethi* by von Bonde (1932). As it is the only species of *Scyllarus* recorded with distinctly pointed uropods it is readily distinguishable from the other members of this genus from the region.

Adults of *S.modestus* have not been recorded from the southern African coast, whereas Barnard (1950) has recorded *S.martensii*. In view of the close similarity between the larvae of *S.martensii* as described by Johnson (1971b) and the species B larvae there can be little doubt that the latter belong to the species described as *S.martensii* by Barnard (1950). However, because slight differences exist between the larvae the identity of the adults from the two regions requires re-examination.

Scyllarus sp.C

This species comprised less than 1% of the total *Scyllarus* larvae and only five specimens were obtained. However, only late stage specimens could be distinguished from species A and early stage specimens were possibly present in the material.

Description (see Figs. 39, 40)

Even the late and final stage larvae closely resemble species A, particularly in the shape of the cephalic disc, although the overall size of species C is somewhat smaller. In three final stage larvae the mean length of the cephalic disc is 6.9mm, the width 7.0mm and the total length is 11.3mm. The only features distinguishable species C from A are the short eye stalks which do not extend laterally beyond the level of the base of the antennae, the slightly shorter antennules and the more pointed uropods.

Remarks

Species C is almost identical with "Scyllarus sp. C" described by Johnson (1971b; Fig. 65) from the South China Sea, except that in Johnson's figure the carapace is slightly wider relative to the length and the antennules are a little shorter. This is the smallest *Scyllarus* larva recorded and it is therefore tentatively assigned to *S.ornatus*, the smallest adult species of the four known to occur in the region.

Scyllarus sp.D

A single specimen was obtained by the South African Sea Fisheries Branch on 26 January 1973 at 30°26.2'S, 30°50.3'E.

Description (See Fig. 49)

The measurements of this gilled and presumably final stage larva are: cephalic disc length 19.5mm, width 23.8mm and total length 32.4mm.

The antennules are longer than the antennae. The eye stalks extend laterally to just beyond the level of the bases of the antennae. The cephalic disc is rounded but concave posteriorly where it overlaps the thorax. Maxilliped 2 bears a swelling representing the exopod. Maxilliped 3 and all the legs have ventral coxal spines. The distal end of the merus of leg 5 is armed with a conspicuous spine. Subexopodal spines are present on legs 1-4. The posterior margins of the meri of legs 3 and 4 each bear a row of large spines. The abdomen has well developed pleopods. The uropods are slightly pointed.

Remarks

This large *Scyllarus* larva is similar in many respects to "*Scyllarus* sp. B" described by Johnson (1971b; Fig. 57) from the South China Sea. It is by far the largest of the larvae obtained belonging to *Scyllarus* and as *S.cultrifer* adults attain the largest size among the *Scyllarus* species recorded from the region it seems most likely to belong to that species.

Ibacus novemdentatus Gibbes

Two rather badly damaged specimens in the same stage of development were obtained from $28^{\circ}53.6'$ S, $32^{\circ}08.9'$ E and $29^{\circ}52'$ S, $31^{\circ}14.0'$ E.

Description (See Fig. 37)

Their respective measurements are as follows: cephalic disc lengths 2.4mm and 3.2mm, widths 4.0mm and 4.7mm and total lengths 4.8mm and 4.6mm. The cephalic disc is much wider than long and has almost a bilobed appearance. The antennules are not fully segmented and are much longer than the antennae. Maxilla 1 has two stout spines on the anterior branch. Maxilla 2 has a large proximal segment with two setae on the anterior margin and a much smaller distal segment bearing four long setae. Maxilliped 1 is present as a rudimentary bud. Small ventral coxal spines are present on all five legs and maxilliped 3. The endopod of the fifth leg is fully formed and bears an unsegmented, non-setose exopod bud. All the legs have a small subexopodal spine. The abdomen is narrow and parallel sided with biramous uropod buds. The telson terminates in two blunt lateral points each bearing a single seta.

The Parribacus — Scyllarides — Arctides Group

Three species of larvae belonging to this group were obtained.

Species X

Five late stage larvae were obtained from the following localities: 28°07.8'S, 32°07.8'E, one specimen of c.l. 22.0mm, c.w. 15.8mm and t.l. 26.8mm, one specimen of c.l. 21.9mm, c.w. 15.1mm and t.l. 26.5mm and one of c.l. 22.0mm, c.w. 16.8mm and t.l. 26.8mm; 29°06.8'S, 32°08.2'E, one specimen of c.l. 16.3mm, c.w. 12.0mm and t.l. 20.9mm; 29°53.0'S, 31°44.0'E one specimen of c.l. 18.1mm, c.w. 13.0mm and t.l. 22.6mm.

Description (See Figs. 50-53)

These specimens conform with Scyllarides squammosus as described by Johnson (1971).

The cephalic disc is subelliptical. The thorax is almost as wide as the cephalic disc and is angular with the legs originating from the angles. It has a deep emargination posteriorly containing the fifth legs and abdomen. In the smaller two specimens the antennules are about twice the length of the antennae and have well developed internal and external flagella. The antennae have only a single segment in these two specimens and small lateral processes are evident. In the larger specimens the antennac reach the level of the base of the inner flagella of the antennules, they have an extra segment and the lateral processes are well developed. The eye stalks are long and the eyes reach the level of the lateral margins of the cephalic disc. In the smaller two specimens maxilla 2 is a non-setose bilobed bud. In the larger specimens it is not much more developed, being only more expanded terminally. Maxilliped 1 is a small bud. Maxilliped 2 has a stout serrated lower spine opposing the dactyl and is therefore virtually chelate. There are no coxal spines or subexopodal spines. Legs 1-4 bear exopods but the endopods have been lost in these specimens. The fifth legs, which are rudimentary and situated within the posterior emargination of the thorax, do not extend to the level of the base of the fourth leg in the two smaller specimens. In the larger two they do and there is also the first trace of segmentation. The abdomen is short and narrow with no pleopods, biramous uropod buds and no terminal setae, and extends to the level of the base of the fifth legs in the smaller specimens. In the larger specimens it extends just beyond the level of the base of the fifth legs. There are uniramous pleopod buds and the uropods and telson have rounded margins.

Species Y

One specimen from 29°40.5'S, 31°53.0'E, c.l. 19.4 mm, c.w. 14.2 mm and t.l. 23.0mm. Another extremely large one from 30°09.3'S, 31°21.2'E, c.l. 44mm, c.w. 36mm and t.l. 54mm.

Description (See Figs. 60-66)

These two specimens conform with stages 8 and 11 of *Parribacus antarcticus* as described by Johnson (1971).

The antennules are fully segmented in both specimens; in the larger of the two one antennule is considerably longer than the other. The antennae are unsegmented in the smaller specimen, but in the larger one the first signs of segmentation are evident and there is a conspicuous outer process. The cephalic disc is subelliptical and in the smaller specimen is virtually identical with that of species X; in the larger specimen it is more rounded. Maxilla 2 is poorly developed in both specimens but in the larger one it consists of a single segment bearing one minute seta. Maxilliped 1 is a rudimentary bud in the smaller specimen and is only slightly enlarged and still unsegmented in the larger one. The most obvious difference between this species and species X is that all the legs, including the fifth, are fully developed with natatory exopods. The fourth leg has an elongate scythe-like dactylus as figured by Johnson (1971). There are no coxal or subexopodal spines. The thorax is angular, as in species X, and deeply emarginated posteriorly. The abdomen of the smaller specimen is unsegmented and without pleopods or uropods; in the larger one it is fully segmented with biramous but unsegmented pleopods and biramous uropods. The abdomen does not project beyond the level of the bases of the fifth legs.

Species Z

Three specimens were obtained from the following localities: 29°43.2'S, 31°16.2'E, one of c.l. 2.7mm, c.w. 2.1mm and t.l. 3.8mm; 28°52.8'S, 32°12.0'E, of one c.l. 4.1mm, c.w. 3.0mm and t.l. 5.2mm; 29°35.0'S, 32°19.2'E, one badly crushed specimen of c.l. 18.0mm, c.w. 12.0mm and t.l. 22.0mm (measurements approximate).

Description (See Figs. 54-59)

In the small specimens (which are tentatively assigned to this species but might equally well belong to species Y) the cephalic disc is pear-shaped. The thorax is angular but there is no emargination posteriorly, the posterior margin being virtually straight. Antenna 1 is unsegmented but has rudiments of the internal flagellum. It is much longer than antenna 2 which is unsegmented and divide into two subequal branches. Maxilla 2 is narrow and elongate and bears four setae on the distal segment. Maxilliped 1 is absent. Maxillipeds 2 and 3 have no exopods. Legs 1-3 are fully formed with natatory exopods and each bears a ventral coxal spine. The endopod of leg 4 is not yet fully developed in the smallest specimen and the exopod is a non-setose bud. The fifth legs are represented as uniramous buds. The abdomen is narrow and without appendages.

In the larger specimen the cephalic disc is subelliptical and virtually indistinguishable from the preceding two species. Antenna 1 is fully segmented. Antenna 2 is fully segmented with a well developed lateral process (see Fig. 55) and extends beyond the level of the base of the flagella of the first antennae. Maxilla 2 and maxillipeds 1-3 are more advanced than in species Y and similar to those of species X. There are no coxal or subexopodal spines. As in both species X and Y the thorax is angular with a leg originating from each angle. Posteriorly it is deeply emarginated and as in species Y the fifth leg is fully formed with a natatory exopod. The abdomen is well developed, reaching beyond the level of the bases of the fifth legs and is fully segmented with biramous pleopods and well formed uropods.

Remarks

Within the *Parribacus* — *Scyllarides* — *Arctides* group adults of *Scyllarides elizabethi*, and *Parribacus antarcticus* have been recorded from the Natal coast (Barnard 1950). In the same publication Barnard also cites records of *Scyllarides squammosus* from Mauritius and according to Holthuis (*pers. comm.*) it occurs in East Africa, so larvae of these three species, at least, might be expected in the samples.

All three species described above agree with the larval characteristics of the genus Scyllarides defined by Robertson (1969), However, Johnson (1971) reviewed the literature on Parribacus, Scyllarides and Arctides and concluded that this revealed no clearcut diagnostic features separating these three genera. Both Robertson (1969) and Johnson (1971) point out that the presence of either well developed or else rudimentary fifth less appears to be only a specific feature and not a generic one as within the genus Scyllarides S.aequinoctialis (Lund) and S.astori Holthuis have well developed fifth legs from an early stage, whereas S.nodifer (Stimpson), S. latus (Latrielle), S. herklotsii (Herklots), S. delfosi (Holthuis), S. squammosus (H. Milne-Edwards) and S.deceptor Holthuis belong to the second category with fifth legs remaining rudimentary throughout development. In reviewing the literature on larvae referred to Parribacus I found that all were reported to have well developed fifth legs except the series described from Florida and Yucatan Straits by Sims (1965), but as pointed out by Johnson (1970a) this series appears to involve separate species or genera. Assuming that *S.elizabethi*, S.squammosus and P.antarcticus are the only three species occurring in the S.E. African region, it would therefore seem more likely that either species Y or Z with normal fifth legs belong to Parribacus. Of these two species Z is rather small (t.l. 23mm) for the stage of development it has attained to belong to *Parribacus* and anyway species Y conforms in all respects with Johnson's (1971) description of *P.antarcticus*, to which it is therefore provisionally assigned. This means that species X and Z probably belong to Scyllarides and as X, with rudimentary fifth legs, agrees with Johnson's (1971) description of S. sauanimosus its identity seems reasonably certain, thus leaving species Z as probably being *S.elizabethi*.

Notes and discussion on ecology and distribution, particularly of *P.homarus*

A most important factor to be established was the length of the planktonic larval life of *P.homarus*. However, this species breeds repetitively throughout the year (Berry 1971b) with the result that there is no clear picture of progression through the various stages of development in phyllosomas and widely differing stages were recorded during much of the year (See Table 5).

From 1969-72 the men servicing the protective shark nets off Durban collected settled pueruli whenever they noticed them to be abundant on the nets. In 1973 a regular record of the presence or absence of pueruli was kept and although a complete record is only available for this year it may be seen in Table 6 that puerulus settlement is predominantly in the late summer and early winter months. Considering then that the first evidence of substantial hatchings of larvae from eggs was in August (Berry 1971b, Figs. 11 and 12), the first final stage phyllosoma larva was recorded in January and the first puerulus larvae in February, a six month larval life seems possible. Although breeding occurs throughout the year there is a distinct peak of egg-bearing from November to February after which there is a sharp drop off in March due to large scale hatching of eggs. It therefore seems reasonable to assume that the last settlement of pueruli recorded in July hatched in March. This would indicate a shorter larval life of four months, which in fact seems likely to be the more accurate of the two estimates. However, the length of larval life is almost certainly affected by water temperature as a drop is known to considerably prolong the incubation of eggs (Berry 1971b) and also to prolong the length of the intermoult period in phyllosomas of Scyllarides aequinoctialis (Robertson 1969).

As all larvae were taken in surface hauls no information on vertical distribution was obtained and investigation of the extent of the geographical distribution of *P.homarus* in the south-west Indian Ocean was beyond the scope of this project. However, from the transects done off Durban the distance of all palinurid larvae offshore and, in the case of *P.homarus*, each developmental stage was determined. This is recorded in Fig. 67 which shows each transect separately as the distance of the Agulhas current from the coast was not necessarily the same in each. In Fig. 68 the data from the transects have, however, been combined and additional stations which were not part of transects were included. Both from the transects and the composite data it is evident that the majority of *P.homarus* larvae are not distributed much further offshore than about 65km in Natal waters north of Durban. The furthest record offshore was 117km and this was off the Tugela Bank where the continental shelf is widest and the Agulhas current is evident.

Too few *P.delagoae* larvae were obtained to gain any meaningful impression of their distribution but a similar pattern to that of *P.homarus* is suggested. This is not the case in *P.longipes*, *P.penicillatus* and *P.versicolor*, the other *Panulirus* species recorded, which tended to be distributed further off the coast than *P.homarus*.

The shoreward edge of the Agulhas current can usually be detected by a sharp rise in temperature of up to 2°C from that of the inshore water. On the basis of this difference in temperature and also direction of ship's drift it was possible in some, although by no means all cases, to establish with a fair degree of certainty whether stations were in inshore or Agulhas water. Despite the obvious shortcomings an attempt has been made to separate stations into those from inshore water and those from the Agulhas current (omitting thirty-one obviously indeterminate ones out of a total of 368).

In Table 7 the numbers of each developmental stage of *P.homarus* phyllosomas per 1000m³ of water obtained from inshore and Agulhas water are presented and relative abundance in each water mass is expressed as a ratio in each case. While it is considered that these data are inadequate for any reliable inferences to be made regarding the proportions of each developmental stage recorded in Agulhas and inshore water, they do suggest a tendency for stage 1 larvae to predominate in inshore water and all later stages to be more abundant in Agulhas water. Despite this, however, all stages were recorded in both water masses, the possible significance of which will be elaborated upon below.

Berry (in press) has presented evidence to show that adult *P.homarus* from the S.E. Coasts of Madagascar and Africa are morphologically similar and suggests that they should be regarded as a subspecies (*P.homarus rubellus*), distinct from two other proposed subspecies *P.homarus megasculptus* from the north-western Indian Ocean and *P.homarus homarus homarus* which is concentrated in the eastern Indian Ocean.

The Malagasy population of *P.homarus rubellus* (which appears to be fairly substantial as it supports a small commercial fishery) must be regarded as a potential source of larval recruits to the south-east African population, particularly as according to Duncan (1970) the East Madagascar current flows directly from that coast to form an important component of the Agulhas current off Natal. However, the presence of larvae of *P.homarus* in all stages of development in inshore water off Natal provides evidence that local repopulation occurs there and although the Malagasy population may make a contribution of unknown magnitude to recruitment on the south-east African coast it is considered likely that the population of this region is largely self-perpetuating. It is also conceivable that the south-east African population could contribute a gene flow to the Malagasy population by means of the Agulhas return current described by Duncan, but there is no evidence to substantiate this as yet. The problem is to explain how the larvae could affect repopulation on the south-east African coast without being carried away in the Agulhas current which is so close inshore. Oliff (1969), summarising recent knowledge of water movements off the Natal coast described how the inshore water mass between the Agulhas current and the shore exhibits a system of short

term reversals at fairly regular intervals associated with the appearance of low pressure systems. The speed of flow of these inshore currents is between 0.1 and 0.4 m/sec. (as opposed to between 1 and 2 m/sec of the Agulhas) and despite reversals there appears to be a slow nett movement northwards. It is therefore considered that possible bleeding off of water from the western edge of the Agulhas, the prevalence of northward going currents in the inshore water and presumably re-entry of inshore water to the Agulhas could provide a palpable mechanism by which phyllosomas could circulate, which would account for the presence of all larval stages of development in both inshore and Agulhas water. In view of the indicated length of larval life of four to six months in *P.homarus* it would nevertheless seem likely that a high proportion would be swept away in the Agulhas, which is indeed in accord with the presence of larvae in all stages of development in it and the extended subtraction margin of adults found along the Transkeian coast. Moreover, *P.homarus*, is considerably more fecund than any other member of *Panulirus* recorded so far (Berry 1971b) which could well be a mechanism to compensate for such a high mortality.

Puerulus larvae of *P.homarus* and *P.ornatus* collected from offshore protective shark nets were kept in tanks, thus enabling their behaviour to be observed. All specimens displayed a strongly negative phototrophic response. When first placed in a tank or if detached from the substratum they exhibited the typical escape response of the adults, propelling themselves backwards by means of the abdomen and tail fan. However they then stopped and swam off extremely swiftly forwards, propelled by their pleopods with the abdomen held straight and the antennae held straight out in front. They were never observed to swim upside-down as has been recorded in *P.polyphagus* by Deshmukh (1966). It seems probable that the spatulate tips to the antennae have a planing function and in addition to giving "lift", small movements of them relative to the plane of the body would control rising or descending. Considering the powerful swimming ability of the puerulus stage larva it is likely that movement towards the shore for settlement is active and pueruli are probably capable of swimming out of the Agulhas current.

It is interesting to note that 84% of the total number of phyllosomas obtained were scyllarids, a situation similar to that in the South China Sea where Johnson (1971b) recorded 95% scyllarids. Moreover, of the scyllarid phyllosomas a single species, *Scyllarus* sp. A (possibly *S.rugosus*) comprised about 96% of the total and the next most abundant species, *Scyllarus* sp. B (possibly *S.martensii*) only 4%.

The hypothesis proposed above of possible repopulation of the south-east African region by *P.homarus* by means of circulation between inshore water and the Agulhas current can also be applied to *Scyllarus* sp. A and *Scyllarus* sp. B as in both these, larvae in all stages of development were also found in both inshore and Agulhas water. However, whereas in *P.homarus* about 59% of all phyllosoma were in Agulhas water the situation was reversed in *Scyllarus* sp. A in which only 6% were in the Agulhas and 94% in inshore water: (Numbers of *Scyllarus* sp. B were inadequate for a similar determination). It seems unlikely, however, that the comparatively higher proportion of *P.homarus* larvae in Agulhas water gives any indication of rate of recruitment of larvae of this species from S.E. Madagascar, as might be supposed, as it could also be the result of behavioural differences between the two species or a shorter larval life in *Scyllarus* sp. A (it attains a much smaller size than *P.homarus*), thus possibly enabling a high proportion to metamorphose without ever entering the Agulhas.

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Figures

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Figs. 9, 10. Panulirus homarus stages 8 and 9 respectively (scales=5mm).

















Figs. 11-21. *Panulirus homarus*; 11-19, maxilla 2 and maxillipeds 1 and 2 in stages 1-9 respectively (scales 0.5mm); 20, end of abdomen of stage 1 (scale -0.15mm); 21, spatulate tip of antenna in stage 9 (scale = 0.5mm).



















Figs. 45-47. Species A (? *Scyllarus rugosus*); 45 and 46, maxilla 2 and maxillipeds 1 and 2, in specimens of t.l 6.7mm, 14.7mm respectively; 47, abdomen of specimen of t.l. 6.7mm (scales - 0.25mm).

Fig. 48. Species D (? Scyllarus cultrifer), maxilla 2 and maxillipeds 1 and 2 (scale = 0.5mm).



Figs. 50-53. Species X (? Scyllarides squammosus); 50 (scale=5mm); 51, abdomen (scale=0.5mm); 52, antenna 1 and 2 (scale=1mm); 53, maxilla 2 and maxillipeds 1 and 2 (scale=0.5mm).







No. of P. homarus.	12	8	43	7	26	6	11	1	4	0	0	0	1	0	0	0	0
No. of P. longipes.	0	0	0	1	0	0	2	2	3	8	0	2	0	0	1	0	0
No. of Drags.	23	8	23	23	22	14	22	8	16	8	4	6	1	0	6	2	0
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Fig. 68. Distance offshore that each developmental stage of the different species of palinurid phyllosomas was obtained in combined samples taken between latitudes $20^{\circ}30'S$ and $30^{\circ}00'S$.



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Fig. 67. Distance offshore that each developmental stage of phyllosomas of *P.homarus* (solid dots) and *P.longipes* was recorded in transects off Durban. The arrows indicate the distance offshore covered in each

able	el. Sun	nmary or i	the dev	/elopm/	entai :	sequen	ce III	pnyilos	soma i	arvae	UD Fan	uiirus	потаг	us.			
Stage	Mean Length (mm) and No.	Length range (mm)	Ant. 1	Ant. 2	Eye	mx. 2	mxd. 1	mxd. 2	mxd. 3	leg 1	leg 2	leg 3	leg 4	leg 5	pleo.	uro.	gills
-	1.5 M=20	1.4-1.7	1 seg.	1 seg. ≺ ant. 1	un- statked	2 seg. distal +4 setae	0	no exo.	exo. setose V.C.S.	exo. setose V.C.S. S.E.S.	exo. setose V.C.S. S.E.S.	exo. bud V.C.S. S.E.S.	0	0	0	0	0
2	2.5 N=15	2.2-2.9	1 seg.	1 seg. ≺ ant. 1	stalked	distal seg. + 4 setae	0	no exo.	V.C.S.	V.C.S. S.E.S.	V.C.S. S.E.S.	exo. bud V.C.S. S.E.S.	0	0	0	0	0
er o	3.3 N=20	2.9-3.9	1 seg.	1 seg. ≺ant. 1	stalked	distal seg. + 4 setae	0	по ехо.	V.C.S.	V.C.S. S.E.S.	V.C.S. S.E.S. D.C.S.	V.C.S. S.E.S. D.C.S. exo. + setae	pnq	0	0	0	0
4	5.1 N=21	3.6-6.7	1 seg.	1 seg. = = ant. 1	stalked	distal seg. + 4-5 setae	0	no exo.	V.C.S.	V.C.S. S.E.S.	V.C.S. S.E.S. D.C.S.	V.C.S. S.E.S. D.C.S.	biramous bud	0	0	0	0
5	6.8 N=20	5.6-8.4	end.	1 seg. V ant. 1	stalked	distal seg. + 5-7 setae	0	no exo.	V.C.S.	V.C.S. S.E.S.	S.E.S. D.C.S.	S.E.S. D.C.S.	end. bud exo. + setae D.C.S.	pnq	low bud	low bud	0
9	9.2 N=20	6.2-11.3	± 4 seg. end. enlarged	2 seg.	stalked	distal seg. + numerous setae	low bud	exo, bud	V.C.S.	V.C.S. S.E.S.	S.E.S. D.C.S. S.S.	S.E.S. D.C.S. S.S.	end. 3 seg. D.C.S.	pnq	pnq	pud	0
7	15.4 N=10	12.5–18.6	4 seg. end. en- larged	=4 seg.	stalked	distal seg. en- larged flat	pnq	exo. setose	V.C.S.	V.C.S. S.E.S. S.S.	S.E.S. D.C.S. S.S.	S.E.S. D.C.S. S.S.	епd. 5 seg. V.C.S. S.S.	1 seg.	biramous bud	biramous bud	0
8	21.3 N=8	15.8-25.2	end. en- larged	4 seg.	stalked	enlarged flat	÷ bifid	exo. setose	V.C.S.	V.C.S. S.S.	S.E.S. D.C.S. S.S.	S.E.S. D.C.S. S.S.	D.C.S. S.S.	5 seg. S.S.	biramous enlarged	biramous enlarged	podo., arthro.
6	29.6 N=6	25.4-32.0	end. exo.	4 seg. may be spatu- late distally	stalked	enlarged, flat	bifid	exo. setose	V.C.S.	V.C.S. S.S.	S.E.S. D.C.S. S.S.	S.E.S. D.C.S. S.S.	D.C.S. S.S.	5 seg. S.S.	func- tional	func- tional	podo., arthro, pleuro,
ant.l=ani S.Sste	tennule, ant. rnal spine, e)	2-antenna, rr xo.=exopodite	ıx. = maxill , endo. = e	a, mxd. ≕r ndopodite	naxillipec . (Only f∈	i, seg.≕se ∋atures usι	gment, \ ed in key	/.C.S. = ve correspor	ntral coxe	al spine, l jes).	D.C.S. = d	orsal co	kal spine, S	S.E.S.=s	ub-exopo	dal spine,	

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Table 2. Ratio of cephalic disc length/width, cephalic disc width/thorax width and distance between the mouthparts and the midline between the coxae of maxillipeds 2 in *Panulirus homarus*.

Stage	Cephalic disc length/width	Cephalic disc width/thorax width	Mouthparts to coxae level distance between coxae
1	1.1	1.5	1.3
2	1.2	1.3	1.3
3	1.4	1.2	1.2
4	1.4	1.1	1.0
5	1.5	1.0	0.9
6	1.5	1.0	0.9
7	1.4	1.0	0.8
8	1.4	1.1	0.8
9	1.4	1.1	0.8

Stage	Mean Length (mm)	Length Range (mm)	ant. 1	ant, 2	Eye	mx. 2	mxd. 1	mxd. 2	mxd. 3	leg 1	leg 2	leg 3	leg 4	leg 5	pieo.	uro,
-	2.83 N=10	2.80-2.87	end. bud	1 seg. +process, < ant. 1	unstalked	distal seg. – 7 setae	pnq	no exo.	exo. setose V.C.S.	exo. setose V.C.S.	exo. setose V.C.S.	V.C.S. exo. bud.	pnq	pnq	0	0
5	2.93 N=1		end. bud	1 seg. +process. ≺ant.1	stalked	distal seg. + 7 setae	pnq	NO 6 X0.	exo. setose V.C.S.	exo. setose V.C.S.	exo. setose V.C.S.	exo. bud V.C.S.	pnq	pnq	0	0
m	3.45 N=2	3.01-3.89	end. exo.	1 seg. +process, ≺ant. 1	stalked	distal seg. flat +9 setae	enlarged bud	exo. bud	exo. setose V.C.S.	exo. setose V.C.S.	exo. setose V.C.S.	exo. setose V.C.S.	en- larged bud	pnq	0	0
4	5.00 N=3	4.1-6.4	end. exo.	2 seg. +process, =ant. 1	stalked	distal seg. flat +15 setae	enlarged bud	elongate bud	exo. setose V.C.S.	exo. setose V.C.S.	exo. setose V.C.S.	exo. setose V.C.S.	bifid bud V.C.S.	elongate bud	pnq	bifid bud
5			NOT RE	PRESENT	ED											
9	9.2 N=1		end. exo.	4 seg. +process. V ant. 1	stalked	distal seg. enlarged, flat many setae	bifid	exo. setose	exo. setose V.C.S.	exo. setose V.C.S.	exo. setose V.C.S.	exo. setcse V.C.S.	bifid. exo. setose endo.+ 5 seg.	2 seg.	bifid	bifid

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		carapace length	total length	antenna Iength	ratio of length/ width of the proximal segment of the antennule <u>I</u> w	No. of spines on lateral keel
si Si		10	10		10	10
natı		7.4	10	1	15	
ori	X	1.4	21.8	43.4	3.1	1=40%, 2=-04%
ď.	range	7.1-8.2	20.0–23.8	36.0-47.5	2.9–3.4	
arus	n	14	10	5	13	13
ŝmo	x	7.0	20.9	36.0	2.6	1 0%, 2=100%
Р. ћ	range	6.2-7.7	18.8–22.5	30.3-38.7	2.2-3.0	
eri	n	4	4			
ark	x	24.3	59.0			
Р. р	range	21.6-26.8	56.7-61.4			

Table 4. Measurements of pueruli of *Panulirus homarus*, *Panulirus ornatus* and *Projasus parkeri* (mm).

Table 5.	Numbers of Pa	anulirus homaru	s phyllosomas	in each	stage in	Richa	ards
Bay and	Durban samples	combined over	the period Sep	tember	1970—Ma	arch 1	973.

Stage Month	1	2	3	4	5	6	7	8	9
September	87								
October									
November	6					1			
December	1								
January	29	9	11	18	15	3		1	1
February	17	6	8	27	7	6		1	5
March			3	3	2	7	9	8	2
April	6	4	5	10	1	4	2	1	
May			1	3	3	1	4		
June						2	1		
July	2			1	1		1	3	
August									

	1969	1970	1971	1972	1973	
January						
February					+	
March			+		+	
April			÷-	+	+	
May	-+-	+		+	+	
June	+		+	+	+-	
July					+	
August						
September	+					
October						
November						
December						

Table 6. Months in which puerulus larvae of *Panulirus homarus* were obtained from the Durban shark nets.

Table 7.Occurrence of each developmental stage of Panulirus homarus phyllo-
somas in inshore and Agulhas water.

	Stage	1	2	3	4	5	6	7	8	9
ore er	No. of Iarvae	100	4	2	12	6	9	2	2	1
lnsh wat	No. per 1000m³(A)	0.55	0.02	0.01	0.07	0.03	0.05	0.01	0.01	0.005
has er	No. of Iarvae	49	15	23	48	22	14	11	10	4
Agul wat	No. per 1000m³(B)	0.32	0.10	0.15	0.31	0.14	0.090	0.071	0.065	0.023
	Ratio <u>A</u> B	1.72	0.20	0.07	0.23	0.21	0.51	0.14	0.15	0.22

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