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Phyllosoma Larvae and the Ocean Currents off the Hawaiian Islands[1]

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ABSTRACT: A total of 73 phyllosoma larvae of slipper or spiny lobster species and one nisto stage were collected about 20 km off the southwest coast of Oahu between August 1977 and October 1978. Larvae of *Arctides regalis*, *Scyllarus aurora*, *Scyllarides squammosus*, *Panulirus marginatus*, and *Panulirus penicillatus*, all found as adults in the Hawaiian Islands, were present in the samples. In addition, larvae of *Scyllarus demani* and another species tentatively identified as *Panulirus longipes femoristriga*, not recorded as adults in the Hawaiian Islands, were present. The unidentified nisto, possibly of the Hawaiian slipper lobster, *Scyllarus aurora*, is described and illustrated.

CLARKE (1983) EXAMINED the bias due to avoidance and mesh escapement of three sampling devices for the larvae, juveniles, and adults of several species of midwater fishes. One of the three devices was a bongo net 1.25 m in diameter. In addition to fishes, other animals were captured during the sampling program and in this paper the phyllosoma larvae of the Scyllaridae and Palinuridae, the slipper and spiny (rock) lobsters, are reported. Larvae of the important commercial spiny and slipper lobsters are known to be useful as indicators of the origins of the water masses in which they are located (Murano 1957, Johnson and Brinton 1963, McWilliam and Phillips 1983), and the implications of the results are discussed in relation to the oceanography of the Hawaiian Islands.

MATERIALS AND METHODS

The 1.25-m nets for the bongo nets were conical and about 7 m long. The first ca. 5 m was of knotless nylon mesh with openings about 2.5 mm in diameter, and the tail section was of 505-μm nitex plankton netting. TSK flowmeters were mounted inside the frames of the bongo nets and, for purposes of calculating volume filtered, were assumed to have measured the actual flow through the nets.

The nets were towed obliquely and without opening-closing devices. Time-depth recorders were attached. The bongo nets were weighted with about 200 kg of weight. They were launched and towed at ca. 1.75 m/sec for 90 min while cable was paid out at 8 m/min. The ship was then slowed to ca. 1 m/sec and the nets retrieved at ca. 40 m/min. Descent times and wire out were carefully monitored; deviations from the appropriate schedule were rarely more than ± 10 m or ± 1 min. Total retrieval times varied by about 5 min between tows.

All samples were taken about 20 km off the southwest coast of Oahu, Hawaii (21°20–30′ N, 158°20–30′ W), from the R. V. *Kana Keoki* of the University of Hawaii. The water depth at that location was 2000–4000 m. There were 14 cruises between August 1977 and October 1978 (Clarke 1983).

Twenty-eight paired samples were collected from a maximum depth of 425 m (mean, 304 m; range, 175–425 m), and the volume filtered per haul was a mean of 9434 m^3 (range, 7350–13,200 m^3).

Catches were initially preserved in 4% formaldehyde and held in the same solution until sorting and measurement. The samples were

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sorted at 10 × magnification under a dissecting microscope.

RESULTS

A total of 73 phyllosoma larvae, comprising 11 scyllarids and 62 palinurids, and 1 nisto was caught. The phyllosomata were identified using descriptions of the larvae given in the literature, including those of Johnson (1968, 1971*a*,*b*), and by comparison with material in a reference collection held by one of the authors (B.F.P.). However, some palinurid specimens could not be assigned to species known from Hawaii.

Species of the Area

The following species of the Scyllaridae, Synaxidae, and Palinuridae have been recorded as being found as adults in the Hawaiian area.

SCYLLARIDAE:
Scyllarides squamosus (H. Milne Edwards) (Holthuis 1947)
Scyllarides haanii (de Haan) (Morin and MacDonald 1984)
Arctides regalis Holthuis (Holthuis 1963)
Scyllarus modestus Holthuis (Holthuis 1960) [formerly identified as *Scyllarus martensii* Pfeffer by Rathbun (1906) (see Holthuis 1960)]
Scyllarus aurora (Holthuis) (Holthuis 1981) [formerly *Scyllarus timidus* (see Holthuis 1981)]
Parribacus antarcticus (Lund) (Holthuis 1985)

SYNAXIDAE:
Palinurellus wieneckii (de Man) (Titgen and Fielding 1986)

PALINURIDAE:
Justitia mauritiana (Miers) (George and Main 1967)
Panulirus marginatus (Quoy and Gaimard) (George and Holthuis 1965)
Panulirus penicillatus (Olivier) (Edmondson 1925)

Identification and Morphology of the Scyllaridae

No difficulty was encountered in assigning the phyllosoma specimens to described species but the single nisto specimen could not be identified to species.

Description of Nisto of Scyllarus *sp.*

Figure 1

Total length 20.5 mm; carapace length (measured midline from base of rostral tooth) 6.5 mm; carapace width 8.8 mm.

A sharp rostral tooth is present. Anterior and posterior branchial carinae are well developed. The median carina is broad and discontinuous; the gastric section terminating anteriorly in a strong, sharp tooth; the cardiac section blunt anteriorly. The carapace bears a distinctly arched posterior transverse groove, and its posterior margin is incised medially with a small, rounded notch. The lateral margin of carapace is divided into three distinct regions, the anterior one terminating in a strong, sharp anterolateral tooth followed by five or six small, blunt teeth. The mediolateral and posterolateral regions of the margin bear a sharp anterolateral tooth followed by four to five and seven to eight small, blunt teeth, respectively.

The distal squama (= sixth segment) of the antenna is incised with four broad and one narrow lobes, each ending in an acutely angled tip; a smaller sharp sixth lobe is present on the inner margin of this segment. The proximal squama (= fourth segment) of the antenna bears a distinct spinose, dorsal ridge, also two prominent teeth on its anterior margin; its anterolateral corner is produced into a sharp tooth, and the lateral margin has two prominent teeth followed by five to six small teeth posteriorly.

The posterior margin of abdominal terga of somites I–III is incised with a small median notch and rounded lateral notches. Abdominal terga of somites IV and V bear only rounded lateral notches. None of the abdominal somites has a distinct median carina, but the median area of somites II and III is more elevated dorsally than those of the other segments. The

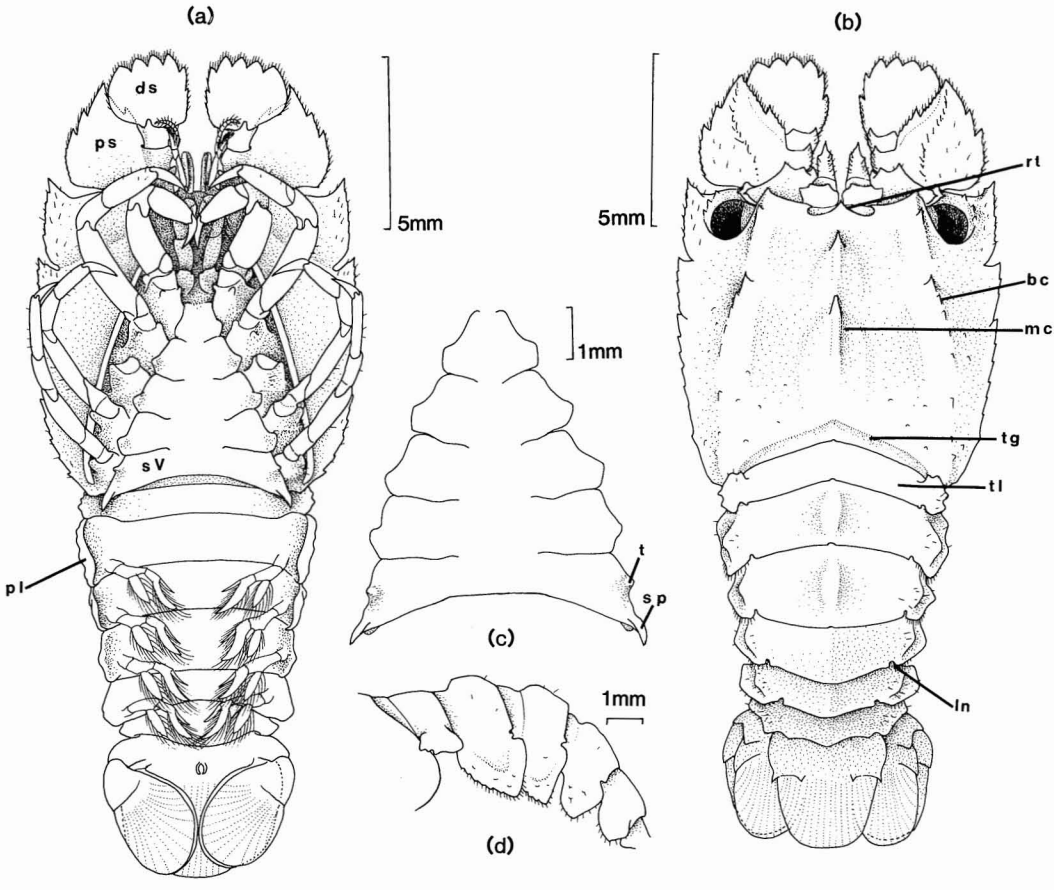

FIGURE 1. Nisto of *Scyllarus* sp.: (*a*) Ventral surface; (*b*) dorsal surface; (*c*) enlarged view of sternal plates; (*d*) lateral view of abdomen. (bc = posterior section of branchial carina, ds = distal squama of antenna, ln = lateral notch, mc = cardiac section of median carina, pl = pleuron, ps = proximal squama, rt = rostral tooth, sp = sternal spine, sV = fifth thoracic sternite, t = tubercle, tl = tergum of abdominal somite I, tg = transverse groove.)

pleura of somites II and III end in a posteriorly directed point; those of somites IV and V are more rounded distally.

The posterolateral margins of the fifth thoracic sternite are produced as a long spinous process with a distinct lateral tubercle on each anterolateral margin. No tubercles are apparent on the other sternites.

In many features, this nisto closely resembles those of adult *Scyllarus aurora* described by Holthuis (1981), and of the few members of this genus recorded from Hawaiian waters, this species seems to be the most likely candidate for its identity.

Indentification and Morphology of the Palinuridae

Only *Panulirus marginatus* and *P. penicillatus* are recorded from the Hawaiian Islands, and it is possible to separate *P. marginatus* and *P. penicillatus* phyllosoma specimens by differences in the shape of the cephalic shield. The length/width measurements of the cephalic shield are normally greater in *P. marginatus* than in *P. penicillatus*. However, these ratios in some of the material originally assigned to these species did not fit the data of Johnson (1968). Other characteristics examined in-

cluded the special arrangement of the mouthparts in relation to the maxillipeds and the number of pairs of swimming setae on the exopods of the third maxilliped and the first four pairs of walking legs (pereiopods).

A summary of the data for some of the specimens difficult to identify is given in Table 1, and one of these specimens is illustrated in Figure 2.

None of these characteristics is useful alone because relationships change as the larvae develop. A particularly useful characteristic used by Johnson (1968) to examine *P. marginatus* and *P. penicillatus* was the distance from the midpoint between the coxal segments of the second maxillipeds to the mouthparts (labrum–first maxillae). This distance is expressed as a proportion of the distance between the attachment of the coxae to the thorax. To make measurements comparable and to allow for changes due to larval growth, the distance (a) between the coxae is always considered 1.0 and the proportional distance (b) extends from the midpoint between the coxae to the anterior margin of the labrum (see Figure 2).

Data of specimens marked with an asterisk in Table 1 do not fit the data for *P. marginatus* or *P. penicillatus* given by Johnson (1968). In addition, from stage VI onward the ratio of the cephalic shield width to thorax width is about 1:1 in *P. penicillatus*, and in most cases the specimens treated in Table 1 have a ratio of 1:1.13 or higher. Also, the size of all stage VI or older stages is less than the minimum size given by Johnson (1968) for equivalent stages of *P. marginatus* and *P. penicillatus*.

After examination of the data and advice from Johnson (pers. comm.), it was concluded that at least one *Panulirus* species other than *P. marginatus* or *P. penicillatus* was present in the samples. Positive identification of single specimens is always difficult, and most specimens were damaged. Hence, it is possible that some of the specimens could be the larvae of *Panulirus longipes* or of a species for which the larvae are not yet described, but they are definitely neither *P. marginatus* nor *P. penicillatus*. It was eventually decided that at least 11 of the specimens were the larvae of *Panulirus longipes femoristriga* (von Martens).

The list of species and the total number in

TABLE 1

MORPHOMETRICS OF SELECTED *Panulirus* SPECIMENS OF DOUBTFUL IDENTITY

SPECIES	DATE	STAGE	TOTAL LENGTH (mm)	CEPHALIC SHIELD (CS) LENGTH (mm)	CEPHALIC SHIELD (CS) WIDTH (mm)	RATIO SHIELD W:L	a (mm)	b (mm)	RATIO a:b	THORAX WIDTH AT PEREIPOD 2 (mm)	RATIO CS WIDTH: THORAX WIDTH	FIG.
P. longipes femoristriga?	Oct. 1977	III	3.10	2.10	1.35	1:1.60	0.30	0.6	1:2.0	1.20	1:1.12	
P. longipes femoristriga?	Sept. 1977	V	6.20	4.45	2.50	1:1.78	0.70	0.95	1:1.36	3.05	1:1.22	
P. longipes femoristriga?	Nov. 1977	VI	7.30	5.50	3.50	1:1.55	0.95	1.40	1:1.47*	4.00	1:1.12	2c
P. marginatus?	Sept. 1978	VI	7.50	5.65	3.30	1:1.70	0.90	1.10	1:1.22*	3.70	1:1.13	
P. marginatus?	Feb. 1978	VII	11.30	9.00	5.00	1:1.80	1.45	1.80	1:1.24*	6.50	1:1.30	
P. marginatus?	Sept. 1977	VII	11.30	8.80	5.90	1:1.49	1.90	2.20	1:1.16*	6.40	1:1.08	
P. longipes femoristriga?	Aug. 1978	VII	12.80	9.80	5.90	1:1.66	1.50	2.00	1:1.33	6.90	1:1.20	
P. longipes femoristriga?	Feb. 1978	VIII	16.10	11.90	7.20	1:1.65	1.90	2.50	1:1.32	8.80	1:1.20	

NOTE: a = distance between coxae of second maxillipeds (always considered as 1.0); b = length of the perpendicular from the anterior edge of labrum to this line.
* Do not fit *Panulirus marginatus* or *Panulirus pencillatus* data of Johnson (1968).

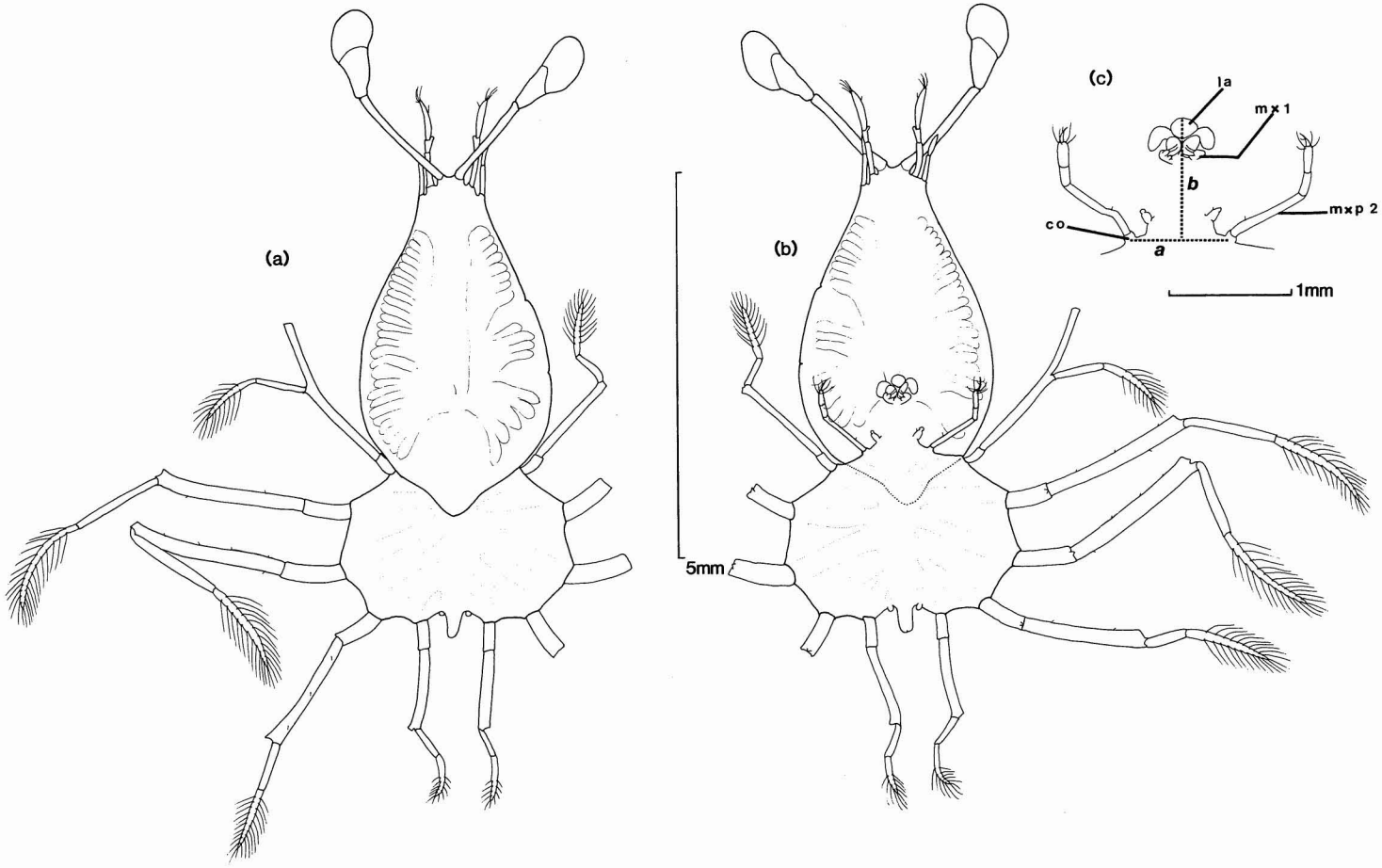

FIGURE 2. *Panulirus longipes femoristriga* stage V: (*a*) dorsal surface; (*b*) ventral surface; (*c*) mouthparts. The method of measuring the distance between the coxae (a) and from the midpoint between the coxal segments of the second maxillipeds to the mouthparts (labrum–first maxillae) (b) is indicated. (co = coxa, la = labrum, mxl = first maxilla, mxp 2 = second maxilliped.)

TABLE 2

PHYLLOSOMA LARVAE AND NISTOS COLLECTED IN TRAWLS OFF THE SOUTHWEST COAST OF OAHU BETWEEN AUGUST 1977 AND OCTOBER 1978

SPECIES	NO. OF PHYLLOSOMATA	NO. OF NISTOS
Scyllaridae		
Arctides regalis	4	
Scyllarus aurora	3	
Scyllarus demani	1	
Scyllarus sp.	0	1
Scyllarides squammosus	3	
Total	11	1
Palinuridae		
Panulirus marginatus	10	
Panulirus marginatus?	26	
Panulirus penicillatus	6	
Panulirus penicillatus?	4	
Panulirus penicillatus/marginatus?	5	
Panulirus longipes femoristriga?	11	
Total	62	

the samples is given in Table 2. The data were too few for seasonal analysis.

DISCUSSION

The specimen referred, after comparison with reference material, to *Scyllarus demani* Holthuis was a final (gilled) stage. *S. demani* has not previously been reported from Hawaii. However it is reported from Australia (Ritz 1977) and Indonesia (Holthuis 1947). The specimen strongly resembles the specimen described by Johnson (1971*b*) as *Scyllarus* sp. C. from the South China Sea.

Of the 11 specimens provisionally identified as *Panulirus longipes femoristriga*, 8 (stages IV–VII) were caught between August and November, 1 (stage V) in January, 1 (stage VIII) in February, and 1 (stage VII) in March. Johnson (1971*a*) stressed the local origin of the Hawaiian species described in that paper, but *P. longipes femoristriga* is not known from Oahu or any other island in the chain. This species is widespread in the Indo-Pacific and is known from Amboina, Banda, Moluccas, Papua New Guinea, Japan, Queensland, New South Wales, New Caledonia, New Hebrides, Fiji (George and Holthuis 1965, Pyne 1970), Guam and the Northern Mariana Islands (R. Uchida, pers. comm.), and as far east as the Tuvalu and the Tuamotu islands (Michel 1969).

The late stages of development of both species of these larvae suggest that they could have been transported over a considerable distance from their point of hatching (Phillips and McWilliam 1986). Furthermore, their time of capture around Hawaii is consistent with the timing of certain broad features of the oceanographic circulation of the region.

The oceanographic model of the Hawaiian region proposed by Seckel (1962:407–408) was an "envelope" of North Pacific Central Water moving up and down the chain of islands in association with the seasonal variation in the intensity and position of surface boundary currents. This movement brings water from the northern part of the Hawaiian chain to the southern islands such as Oahu during the period of September or October through April or May. Studies by Robinson (1969) and Hasunuma and Yoshida (1978) have revealed that the surface flow from west to east across the North Pacific gyre is a countercurrent, now called the Subtropical Countercurrent, which flows in the opposite direction to the major current system in the Hawaiian Archipelago, the North Pacific Equatorial Current. The Subtropical Counter-

current extends from the western boundary of the Pacific to the Hawaiian Archipelago and consists of a train of anticyclonic eddies about 300–600 km across that travel east at variable speed but occasionally accelerate to over 50 cm/s. Hence, phyllosoma larvae that were carried out by the Subtropical Countercurrent from the western Pacific into the circulation system of the Hawaiian region could eventually become distributed around Oahu.

Edmondson (1940), in reviewing the relation of the marine fauna of Hawaii to that of the other sections of the Pacific area, reported that the shoal-water crustacean fauna of Hawaii is chiefly of Indo-Pacific origin. Many of the common shore species range all the way from the Red Sea to Hawaii. A preponderance of Indo-West-Pacific elements in the Hawaiian marine fauna is evident in more recent data that indicate a relatively low percentage of endemic species in most of the coastal, benthic invertebrate taxa of central Pacific islands (Scheltema 1986) and especially of the Hawaiian Archipelago (Kay and Palumbi 1987). This also applies to the Palinuroidea (palinurid, synaxid, and scyllarid lobsters) recorded to date. *Arctides regalis*, *Scyllarus modestus*, *S. aurora*, and *Panulirus marginatus* are the only Hawaiian endemics of the 10 species listed here. The remaining species have West Pacific, Indian Ocean, or Indo-West-Pacific distributions (Phillips et al. 1980), and *Parribacus antarticus* also has an Atlantic distribution (Holthuis 1985). Two of the species listed, *Scyllarides haanii* and *Palinurellus wieneckii*, are very recent first records (Morin and MacDonald 1984, Titgen and Fielding 1986). Therefore, it is possible that adults of *Scyllarus demani* and *Panulirus longipes femoristriga* already inhabit the Hawaiian region. They may be found eventually in further field surveys, or reported after taxonomic revisions of lobster material held in earlier collections from the Hawaiian Archipelago.

Because the larvae referred to *P. longipes femoristriga* included some mid- as well as late stages of development, the presence of a fairly local (though undetected) parental stock, coupled with the seasonality of the Hawaiian circulation pattern, seems the more likely explanation for both their temporal and spatial occurrence off Oahu. However, the possibility that some of their late-stage larvae in the catch represent sporadic recruitment from a western source such as Johnston Island (some 687 km to the southwest) or the more westerly Wake Island cannot be dismissed.

Grigg (1981), in his discussion of possible sources of larval recruitment for *Acropora*, has estimated possible transport time by the Subtropical Countercurrent from Johnston Island to French Frigate Shoals of 50 days and from Wake Island of 187 days. Both of these timespans are within the larval life span of most palinurid species (Phillips and Sastry 1980), and both Johnston and Wake Islands are possible sources of larval recruitment.

A timespan of 50 days from Johnston Island may be well within the normal larval life span of *Scyllarus demani* also. Laboratory-reared phyllosomata of this species averaged about 48 days from hatching to metamorphosis (M. Ito, James Cook University of North Queensland, pers. comm.). This single final phyllosoma of *S. demani* collected off Oahu may be an "expatriate" (Johnson and Brinton 1963) from a more westerly stock. If it did not hatch somewhere along the Hawaiian chain, then its occurence here suggests that settlement on the archipelago by additional West Pacific lobster species transported in the Subtropical Countercurrent is still possible. Johnson (1977) described a final-stage larva of another *Scyllarus* species unknown from the Hawaiian area that he believed was of local origin.

Amerson and Shelton (1976) did not report either *Scyllarus demani* or *Panulirus longipes femoristriga* as present at Johnston Atoll (Island) (although *P. marginatus* and *P. penicillatus* were collected). However, no extensive systematic sampling was carried out, and, as pointed out by the authors, further collecting would probably result in the location of additional species.

In general, the larvae of the Palinuridae (of which *P. longipes femoristriga* is a member) have a more oceanic character and are the numerically dominant phyllosomata in plankton samples taken in midocean (George 1974, Phillips and McWilliam 1986). Larvae of the smaller members of the Scyllaridae, particu-

larly those of the genus *Scyllarus*, have a more coastal character and outnumber palinurid larvae in samples taken in shelf waters (Johnson 1971*b*, Maigret 1978, McWilliam and Phillips 1983). Even the limited data of this study conform to the general pattern. The total catch numbered 11 scyllarid larvae (including only 1 *Scyllarus* phyllosoma) compared with 62 palinurid larvae. All were collected in oceanic waters.

The oceanic larvae of Indo-West-Pacific species, therefore, seem to have a greater chance of settling on oceanic islands and atolls of the central Pacific than larvae of more coastal character. This is evident in the species composition of lobsters with an Indo-West-Pacific distribution recorded from the Hawaiian region to date. The more coastal lobster larvae typically belong to the smaller scyllarid species, which have a relatively short pelagic larval phase, with fewer larval stages. The larval life span of some *Scyllarus* species is short (25 days to 3–4 months) compared with that reported for *Panulirus*, *Palinurellus* (12 months), and the few *Scyllarides* (8–9 months) investigated (Phillips and Sastry 1980: table IV). But oceanic larvae are not confined to the Palinuridae and Synaxidae. The larger scyllarids, such as species of *Scyllarides* and *Arctides* as well as *P. antarcticus*, have as many larval stages as the palinurids (Johnson 1971*a*, Robertson 1969*a*,*b*) and, by inference, a long pelagic larval phase.

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