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A NEW RECORD FOR THE ANCHIALINE SHRIMP LIGUR UVEAE (BORRADAILE, 1899) (DECAPODA, HIPPOLYTIDAE) IN THE PHILIPPINES WITH NOTES ON ITS MORPHOLOGY, BEHAVIOUR AND ECOLOGY

by

ROBERT G. WEAR

Zoology Department, Victoria University, Wellington, New Zealand

and

L. B. HOLTHUIS

Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands With one text-figure and two plates

Introduction

Ligur uveae is generally considered an anchialine species (found in land-locked, generally supralittoral saltwater pools) with the type locality given simply as "Uvea, Loyalty Islands" by Borradaile (1899). The species is widely distributed geographically, although locally evidently confined to a very restricted habitat. Its known range extends from the western Indian Ocean to Polynesia: Aldabra, western Indian Ocean (Borradaile, 1917; Gordon, 1936); Halmahera, northern Moluccas, Indonesia (Holthuis, 1947; 1963); Uvea, Loyalty Islands (Borradaile, 1899; Gordon, 1936); Sayawa Islet near Uvea (Monod, 1968); Vatulele Island, Fiji Archipelago (Gordon, 1936; Derrick, 1957; Marden, 1958; Reed & Hames, 1967); Vanua Vatu and Vanua Levu Islands, Fiji Archipelago (Gordon, 1936; Derrick, 1957); Fangafale Islet, Funafuti Atoll, Ellice Islands (Holthuis, 1973). The species is also thought to occur at the islet of Yanuca, near Bega off the south coast of Viti Levu, Fiji (Clunie, pers. comm.). So far as can be ascertained from these published records and unpublished information, L. wveae is a typical member of the anchialine community. This is supported by the habitat of the present material collected from a small and well sunlit salt-water pool separated from the sea by a sand bar some 40 m wide.

The Philippines specimens are found apparently exclusively on Tini-

guiban, a small islet about one hectare in size lying about 500 m off the island of Guimaras near its southern end. Guimaras Island itself is separated from the larger provincial island of Panay in the central Philippines to the northwest, by about 20 km of open water (fig. 1). Local inhabitants of Igang, the nearby barrio (village) on Guimaras Island, and also those living in Iloilo Province and a large part of the Island of Panay, have known of the existence of *Ligur uveae* for many generations. It is known locally as "pulang pasayan" (red shrimp) after which Tiniguiban Island sometimes takes its name. Close questioning of local people and also others widely travelled within the Republic by one of us (R.G.W.) failed to reveal any suggestion of similar shrimp occurring elsewhere in the Philippines. The possibility cannot be ruled out, however, in view of the many thousands of tiny, uninhabited and rarely visited islands in the area.

Morphological notes on the species (by L.B.H.) are based on 8 preserved specimens from Tiniguiban Islet collected by the first author in June, 1975.

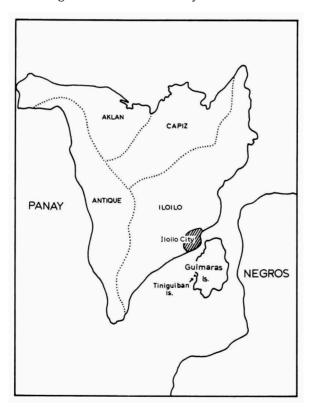


Fig. 1. Map of the island of Panay and the north-western part of the island of Negros, Philippines, showing the position of Tiniguiban Islet.

One of these is an ovigerous female. Information on the habitat and behaviour of the shrimp was obtained during four separate day-trips to the locality by R.G.W. in August 1974, June, and November 1975 and in January 1976. Hydrological observations and notes on breeding and behaviour of juveniles are based on data obtained approximately twice daily between June, 1975 and January, 1976 and more occasional recordings between August, 1974 and the earlier date. These data were collected by staff of the Aquaculture Department of the Southeast Asian Fisheries Development Centre (SEAF-DEC) from their field substation located at Igang, Guimaras Island. The majority of the field work was undertaken by Mr. Alfredo Santiago Jnr. of SEAFDEC, without whose keen interest and assistance, herein gratefully acknowledged, this publication would not have been possible. Feeding studies and laboratory analysis of pond plankton and epibenthos were done in the laboratories of SEAFDEC at their main station at Tigbauan, Iloilo. We wish to acknowledge the use of these facilities.

Навітат

The pool on Tiniguiban is surrounded by land on three sides, and is separated from the open sea by a white coral sand bar about 40 m wide and 6 m in height. There is no apparent connection with the sea, but as the water level in the pool rises and falls with the tides, water must either percolate through the sand bar or there must be subterranean intrusion through the porous rock and deep narrow fissures behind the pool. The pool area reaches a maximum of 200 square metres and is 0.87 metres deep at high spring tides, but at 0.3 metres above chart datum (rarely reached) the pool is completely devoid of water. The three landward sides of the pool are flanked by weathered and cavernicolous coral rock rising at an angle of 45°-60° covered with broadleaf shrubby tropical vegetation. The dominant botanical feature is a small stand of the mangrove *Rhizophora mangle* L. in the centre of the pool.

The substrate is mainly of fine white sand extending from the sand bar on the seaward side, but grades into flocculent black mud near its centre and towards the *Rhizophora* stand. Further landward behind and alongside the mangroves the substrate becomes rocky, leading to the complex of small subterranean fissures in the southwestern corners in which the shrimps take refuge between sundown and sunrise. The water is generally clear at all stages of the tide, but away from the pool fringes the bottom supports a very rich growth of green and blue/green algae. Among the algae, *Chaetomorpha*, *Cladophora*, *Chroococcus*, *Coelosphaerium*, *Lyngbya* and *Oscillatoria* dominate and occur together with *Microcoleus* and *Tolypothrix*. Diatoms

obtained in plankton tows during June, 1975 include an abundance of *Bacillaria, Diploneis, Melosira, Navicula, Nitzschia* spp. and many others, while the dinoflagellates *Ceratium* and *Peridinium* were relatively common. Zooplankton is also marine and includes unidentified Peritricha, Copepoda, nematodes and some chironomid larvae. The sandy parts of the pool support a very large population of small infaunal amphipods which are active on the surface of the sand after the water recedes. Small polychaetes occur in the mud.

Based on twice daily recordings (8.30 a.m. and 4.00 p.m.) between early June 1975 and the end of January 1976, salinities appear to be maintained in the region of 30 0/00. Occasional recordings dating from February 1975 are in agreement. Maximum mean monthly salinity recorded was 34.3 $^{0}/_{00}$ and the minimum 27.1 $^{0}/_{00}$ during the August-September rainy season. Water temperatures are generally around 29°C with a recorded absolute maximum of 40°C and a minimum monthly mean of 26.4°C (October). Dissolved oxygen levels also recorded daily at 8.30 a.m. and 4.00 p.m. are surprisingly high. These range between a maximum average of 19.45 ppm for July just before the onset of the summer monsoon rains when marine algal growth is at its maximum, and fall to a minimum monthly mean of 9.8 ppm in January. Corrected for temperature and salinity, these figures indicate around 300% saturation during daylight hours toward the end of the dry season and a minimum of 170% saturation during the summer rains. It is difficult to envisage how such high figures can be sustained in the pool during daylight hours without serious oxygen depletion occurring at night.

Ligur uveae (Borradaile, 1899)

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Parhippolyte uveae Borradaile, 1899: 414, pl. 38 fig. 11; Holthuis, 1955: 99.

Ligur uveae Kemp, 1914: 123; Borradaile, 1917: 401; Gordon, 1936: 102, fig. 1; Holthuis, 1947: 7, 32; Holthuis, 1963: 271; Monod, 1968: 772, figs. 1-8; Holthuis, 1973: 36.

Ura buta Derrick, 1957: 160, 223.

Long-whiskered Prawn Marden, 1958: 555, 2 figs.

Prawns of Vatulele Reed & Hames, 1967: 163-165.
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Morphology. — The eight specimens upon which these morphological notes are based agree well with the descriptions of this species as given in the literature. They are 42 to 52 mm in total length; the carapace length (including the rostrum) varies from 15 mm to 20 mm. The ovigerous female is 52 mm long with the carapace 18 mm long.

The rostrum in most specimens is rather shorter than in the specimens reported from other localities. It reaches to or slightly beyond the base of the second segment of the antennular peduncle. Gordon (1936: 103) reported the rostrum as reaching "approximately to the distal end of the penultimate

segment of the antennular peduncle", while Borradaile (1899, pl. 38 fig. 11a) shows it almost reaching the end of the peduncle. Monod's (1968) fig. 1, however, shows the rostrum about as long as in the present material. The dorsal teeth of the carapace are three in number, the posterior standing at about 1/6 of the length of the carapace (rostrum excluded) behind the orbit. The ventral rostral teeth are 1 to 5 in number, often irregularly placed and greatly different in size. The rostrum in most specimens is quite high, sometimes 2/3 as high as long. Behind the last dorsal tooth there is a middorsal carina, which extends posteriorly about halfway the distance to the posterior margin of the carapace. The carapace is somewhat swollen, and in the posteromedian area curves rather abruptly down to the posterior margin.

The antennal and branchiostegal spines are as described by Gordon. The spinule on the antennal lobe is often quite distinct, but is not always present. If present, its place is not always the same: sometimes it is situated on the upper margin of the lobe; sometimes it stands more in the middle of the lobe.

The third abdominal somite is clearly produced in the posteromedian area and forms there a broad blunt triangular projection over the anterior part of the fourth somite. The pleura of the first three abdominal somites are broadly rounded; those of the fifth and sixth somite end in a distinct spine, as indicated by Monod (1968).

Of the three pairs of posterior spines on the telson, the outer are shortest and are situated on the same level as the acute tip of the telson. The two other pairs are placed on a lower level. The outer of these consists of strong straight spines, which are about three times as long as the outer upper spines. The inner spines are slender and distinctly curved up; they are about half as long as the strong spines, or shorter.

As indicated by Monod (1968) the ischium and merus of the second pereiopod are annulated, although less distinctly than the carpus. In the following legs the annulation of the propodus is also distinct.

Size. — As stated before, the present specimens are 42 to 52 mm long. The species may, however, grow to a much greater length: a specimen from Aldabra sent by Dr. H. W. Fricke (Seewiesen) was 77 mm long (carapace length 27 mm), while the type was said to be 110 mm in length. Gordon's specimens were 76 and 106 mm; Holthuis's (1947, 1963) Halmahera specimens measured 45 to 51 mm, and Monod's (1968) Loyalty Islands specimens 72 and 73 mm. The eggs in the ovigerous female now examined are 0.6 to 0.7 mm in diameter after preservation in 10% formalin, and are quite numerous.

In the Aldabra male of 77 mm two sperm masses protruded from the male openings.

Colour. — The first colour description ever published of this species was Gordon's (1936: 107) statement: "Being in nature of a rose-red colour the Fijians refer to it as "ura damudamu" (lit. = prawn red)". According to Derrick (1957: 160) an alternative name is "ura buta" (lit. = cooked prawns). Marden (1958: 555, figs) published excellent coloured photographs of the species showing them to be orange red, the anterior half of the abdominal somites being lighter than the posterior and with an irregular lighter spot in the centre of the carapace; the legs also show some irregular lighter parts, while the antennal and antennular flagella are white except for their basal part which is orange red. A 16 mm colour cine film of the Vatulele population kindly provided by Professor W. R. Geddes of the University of Sydney, and personal observations at Vatulele by Mr. Fergus Clunie of the Fiji Museum, confirm the overall colouration of the Fijian material as orange red.

The specimens from the Philippines are generally more red than orange, this presumably accounting for the name "pulang pasayan" (lit. = red shrimp). After exposure to strong sunlight living animals quite rapidly become practically carmine red (pl. 1 fig. 3) resembling the deep sea shrimps of the genus Acanthephyra. Other specimens photographed are paler, the lightest being a dark pink (pl. 1 fig. 2). Not only is the intensity of the red colour somewhat variable, but also the extent of it. In the dark red specimen just referred to, the entire body, including the full length of the antennal and antennular flagella, is red. Also the pereiopods are uniformly dark red, perhaps with the exception of the dactyli, which may be paler. The difference in colour between the anterior and posterior parts of the abdominal somites is hardly noticeable, the anterior parts may be slightly paler. In other shrimps from the Philippines the carapace is uniformly red or slightly mottled, the internal organs usually shining through as a dark, often purplish, mass. The abdominal somites have a wide dark band along the posterior margin. The tailfan has the basal part lightest, the distal part of the exopod being darkest. The scaphocerite sometimes has a light spot in the outer half of the basal part. The antennal and antennular flagella may be colourless for a greater or smaller distal part of their length. The third maxillipeds are uniformly red, and the first pereiopods also are red with the chelae perhaps slightly more orange. Of the walking legs the basal part is dark red, the rest is red or pink, with the articulations between ischium, merus, carpus and propodus light or almost white. The merus and carpus may show a darker band over the middle, the propodus and dactylus may be uncoloured.

A colour photograph of a specimen from Aldabra provided by Dr. Fricke shows the same general colour pattern. The animal is dark red, with a slight colour differentiation in the abdomen (posterior parts of the somites somewhat darker than the anterior). The scaphocerite shows a pale external basal spot; the distal parts of the antennal and antennular flagella are whitish. The third maxillipeds and first pereiopods are entirely red, the second leg is red in the basal part (including the merus and basal part of the carpus) and pink in the distal part of the carpus and the chela. The last three pereiopods have the basal segments up to and including the merus red, the carpus is red or pink, with the articulation between merus and carpus white. The propodus and dactylus, and perhaps also the extreme distal part of the carpus, are very pale pink, almost white. See also Addenda, on p. 139.

Shrimp population and associated fauna. — The number of adult shrimp observed in the body of the pool approximates 3,000 individuals for most of the year (based on a single count by the first author in August 1974 and a monthly census between June 1975 and January 1976). During the months of September, October and November the observed adult population lies between 1,000 and 1,500 individuals but many thousands of juveniles are present in addition. During the period of study, Ligur uveae were the only large animals present in the pool apart from one large specimen of Scylla serrata (Forskål) occupying the mangrove patch, and a very small population of Grapsus tenuicrustatus (Herbst) and large numbers of the ubiquitous isopod *Liqia* occupying rock crevices above the waterline. Deep burrows up to 10 cm in diameter in the sand bar indicate the presence of large tropical ocypodid crabs. These other decapods are assumed to have little influence on the shrimp and apparently do not breed in the pool, as their larvae have not been found in the pool plankton. Observations do not suggest that the red shrimps have any natural predators or competitors at the present time. There are no wading birds, and the only possible predators seen in the area are kingfishers but at no time have these been seen fishing for the shrimp.

Conversations with older folk from the nearby barrio of Igang revealed that until around 20 years ago, a population of similarly red-coloured fish about the size of the palm of one's hand also lived in the pool with the pulang pasayan, but these have not survived.

Behaviour. — The behaviour of the shrimp is most remarkable. The animals are essentially "sun lovers" and few are seen on cloudy days. They are totally absent between the hours of sunset and sunrise and also on sunny days during lowest tides when there is insufficient water to provide direct connection with the subterranean fissures in which they take refuge. As soon as the sun strikes the water, the animals emerge cautiously from these rock crevices and move off slowly toward the centre of the pool by way

of a shallow channel some 2 metres wide between the *Rhizophora* stand and the southwest corner of the pool. The animals travel just three or four abreast in almost military fashion over a distance of about 8 metres to the body of the pool, where they disperse and thereafter rarely approach to within 20 cm of each other unless disturbed. They maintain a very even distribution over the sunlit part of the pool and among the mangroves, and are constantly on the move — all the while scratching and scraping the surface of the substrate with their third maxillipeds and anterior two pairs of pereiopods presumably in search of food. Near sundown, or as soon as the sun leaves the water, as if by some signal, the population re-assembles and the procession moves in the reverse direction as the shrimp file back into the rocks from whence they came. This unique ritual involving up to 3,000 individuals on fine bright days is made even more spectacular by their brilliant red colour.

Breeding and feeding. — Ovigerous females occurred between mid-June and mid-August 1975 and records suggest that there is only this short breeding period each year. Eggs are dull orange-yellow in colour, and measure about 0.80 mm × 0.60 mm when fresh. Large females of 60 mm to 70 mm total length carry a maximum of around 400 eggs. Hatching occurs from late June and larvae are abundant in the pool plankton until late August. Juveniles are gregarious and spend most of their time lining the rock walls and crevices leading to the subterranean fissures, congregating there in vast numbers and showing little inclination to move. At about 20 mm total length, juveniles assume the daily migrating behaviour of the adults, and by October many thousands of these new recruits accompany the much larger adults in the daily procession to and from the body of the pool.

The adult shrimps are extremely hardy, and apparently omnivorous as indicated by laboratory experiments. Two successive generations have now been reared in the laboratory indicating that they breed readily and survive well under laboratory aquarium conditions. In their natural environment they probably feed on unicellular and filamentous green algae, diatoms, copepods, amphipods and polychaetes. Early larval stages reared in the laboratory consumed *Artemia* nauplii, and later larval stages and juveniles thrived on a diet of algae and zooplankton collected from the pond supplemented with finely chopped fish, mussel meat and fish pellets.

The larval life-history of *L. uveae* will be described in a later paper by the first author and Mr. Santiago of SEAFDEC.

Local beliefs and superstitions. — The pulang pasayan are a local legend in themselves, not only because of their great beauty, but because of their extreme tameness and curiosity (as witnessed by their marked interest in the unshod feet of human intruders) — tribute indeed to the generations of Filipinos who have left these animals undisturbed. They are furthermore considered a "forbidden" animal by way of superstition passed down through generations. They are not eaten for fear of illness (though not considered poisonous), and the most moderate view we could obtain was that they tasted very bitter and were not therefore eaten. One of us (R.G.W.) tested these theories by eating one specimen ungarnished and after very light steaming, and found it to be almost tasteless. Certainly no ill effects were suffered. Notwithstanding these varying opinions, the shrimps are regarded as protected by unwritten law and are not interfered with in any way in spite of their obvious attractiveness and the fact that their presence is widely known. Apparently the red fish which allegedly lived with the pulang pasayan up till 20 years ago have not been so fortunate.

Discussion

Ligur uveae, as it occurs in the Philippines, is a typical member of the anchialine community. Neither Borradaile (1917) nor Gordon (1936), who re-examined Borradaile's material, gave any information on the habitat of the species at Aldabra, but Dr. H. W. Fricke of the Max-Planck-Institut für Verhaltenphysiologie, Seewiesen, Germany, who visited Aldabra in September 1975 and collected Ligur uveae there, described the pool in a letter to us as landlocked, about 50 m long and 30 m wide, and drained through a deep opening or hole in the bottom near its centre. See also Addendum I, on p. 139.

Although we (L.B.H.) have thoroughly perused Dr. Heinrich Agathon Bernstein's correspondence present in the archives of the Rijksmuseum van Natuurlijke Historie at Leiden, no reference to the present species or its habitat at Halmahera has been found.

The type locality is just indicated "Uvea, Loyalty Islands", without any further details. It is possible that the types originated from the same locality as the specimens described later by Monod (1968: 792) from "l'îlot de Sayawa, voisin d'Ouvea, Iles Loyalty". Monod described the habitat as "une mare d'eau saumâtre dont le niveau est apparemment un peu au-dessus de celui de la mer et où il tombe des feuilles de palétuvier qui y pourissent". This might be a pool similar to the one from which the present material originates.

Pl. 2. I, View from Guimaras Island; Tiniguiban Islet in the background.
2, Tiniguiban Islet, seaward side; the sand bar separating the pool from the sea is visible as a white line between two rock outcroppings.

^{3,} Tiniguiban Islet, sand bar, overgrown with *Ipomoea pes-caprae* and other plants, behind which the pool is situated. The higher vegetation of trees and shrubs is on the landward side of the pool.

Much more is known about the habitat of the locality at Vatulele, Fiji Islands. Gordon (1936: 107) described the habitat as follows: "it is found in land-locked pools of salt water shut off from the sea by coral rocks, through which, however, there is sufficiently rapid seepage to render the water level in the pools influenced by the rise and fall of tides". This habitat, known as Korolamalama, near the north end of the island of Vatulele, was similarly described by Derrick (1957: 223). A coloured figure of the pool at Vatulele was published by Marden (1958: 555) showing it to be rather deep with outcrops of coral rock and, at least at one side, bordered by trees or shrubs; the bottom, judging by Marden's second figure, consists of coral sand and stones.

A rather more complete picture of the Vatulele habitat has been obtained through Professor Geddes's coloured film and personal discussion with Mr. Clunie who camped there for one week during a National Museum of New Zealand/Fiji Museum joint ornithological expedition during 12-18 July 1973.

The best known pool is located 70 m to 80 m from the sea in a heavily forested coral rock platform at the foot of a limestone cliff some 25 m in height. A similarly forested bar of coral upraised to 4 m or 5 m isolates the pool from the sea. The pool is roughly pear-shaped and tapers from a maximum width of about 6 m into a narrow, deep and almost straight channel around 2 m wide which connects the pool with the sea diagonally over a distance of 80 or 90 m. There is, however, no direct connection with the sea, as the seaward entrance to the channel is completely blocked by a large limestone block some 5 m in height, probably originating from the nearby escarpment and deposited in Recent times. The channel is more or less completely overhung with dense vegetation, and extends laterally beneath the coralline crust as suggested by the presence of scattered, small water-filled and tidal holes along its lower and more seaward side. The pool itself is deep and completely shaded by the canopy for most of its area and by high limestone cliff faces along two sides, thus creating an awesome, silent atmosphere — perhaps as one would experience in any ancient and empty Gothic cathedral. Away from the narrower channel end the pool shelves upward steeply as it widens, to become quite shallow with a substrate of coral sand and small stones. This shallow end is relatively well sunlit and carpeted with patches of rotting leaves and detritus. Subterranean connections are apparently quite extensive, as several other pools, some quite large, occur in the vicinity.

With the help of Professor Geddes's film and Mr. Clunie's personal observations of the Vatulele population it has also been possible to note some

interesting points concerning the biology of these animals. A few small brown fish coexist with the shrimp, and the reef heron, Egretta sacra (Gmelin), is a natural predator and has been observed feeding on Ligur uveae. The most interesting observations concern the behaviour of the species at Vatulele. They appear to shelter in the deeper parts of the pool and a few have been seen swimming in the channel. In the early mornings groups of five up to ten individuals are seen swimming from deeper and shaded areas to the shallow and sunlit part of the pool where they remain during most of the day among the detritus and on the coral sand in full view, industriously scraping the substrate as observed in the Tiniguiban population. Toward the end of the day, these groups of individuals return to shelter. On the one rainy day during Mr. Clunie's visitation, none were seen. The only apparent difference between this behavioural pattern and that observed for the species at Tiniguiban, is that at Vatulele the animals migrate in groups rather than in a continuing stream. This can be simply explained by the fact that the Tiniguiban population has only one shallow access channel between the subterranean fissures and the shallow body of the pool; at Vatulele their 'home territory' is more widely scattered and it is possible for them to move from various points along the sides of the pool and from deeper water.

Nothing is known about the habitat of the species at Vanua Vatu and Vanua Levu islands, or at the islet of Yanuca, but Derrick (1957: 160) notes that at Vanua Vatu the shrimps occur in "limestone grottoes" in flowing water.

The habitat at Fangafale Islet, Funafuti, was described as follows: "The pool in Funafuti is rather large and is located on the north end of Fangafale Islet; on the east side it is bordered by the coral of the island, but on the west by what appears to be a boulder ridge thrown up possibly by previous hurricanes; both sides are somewhat porous and the water rises and falls with the tides outside" (Holthuis, 1973: 7).

In all cases, thus, when the habitat is known, the same general picture is shown.

At Vatulele, the apparently natural daily migrating behaviour of *L. wveae* is exploited by the Fijians. Derrick (1957: 223) noted that the ura buta are "regarded with superstitious awe by the local people, who refuse to eat them, and when suitably encouraged call them from their hiding places by traditional chants and incantations". This is obviously still practised for the benefit of tourists and during important ceremonies at least, as Professor Geddes's film very vividly shows groups of red shrimps swimming around the shallow part of the pool and being "encouraged" to do so by the Head of the Mataqali (the group of related families owning the land on which the pool is located)

loudly chanting and gesticulating in a most energetic manner. No doubt the shrimp would perform similarly without such human persuasion.

Apparently all unusual phenomena were attributed to supernatural agency by the early Fijians, and because of their colour the ura buta have long been "tabu" (Derrick, 1957). Gordon (1936: 107) stated about the species in Vatulele "It is regarded by the natives as a "tevora" (devil) and the capture or eating of it is strictly "tabu". — The reluctance of the Fijians to touch it accounts for the fact that, although it has been known in the group for many years, very few specimens have been procured by collectors from the relatively inaccessable localities in which it is known to occur". Also, Marden (1958: 555) referred to this in the caption of his figure (the only place where the shrimps are mentioned in this paper): "No One May Harm Vatulele's Long-whiskered Prawns — Taboo! Possibly because of their bright color, these salt-water crustaceans are held sacred. A paramount chief raised the taboo long enough for pictures to be taken. The goggled diver caught four prawns in the pool, then freed them".

The legend of "The Prawns of Vatulele" as retold by A. W. Reed in Reed & Hames (1967: 163-165) may be paraphrased as follows:

From the larger islands of Viti Levu and Vanua Levu, and from a hundred smaller islands, eager suitors hurried to Vatulele to pay court to Yalewa-nicagi-bula, the beautiful daughter of the chief. All were spurned, and to appease her exasperated father. Yalewa agreed that she would marry the first suitor who flew to Vatulele or who travelled there by means other than canoe. At that moment an enterprising chief of noble birth, too impatient to travel slowly by canoe, expedited the journey by first rolling huge stones down the mountains to the beach. He then picked them up one by one and threw them into the sea as stepping stones in advance of his progress to Vatulele. Such was his haste, that instead of prepared food and valuable gifts he carried with him a basket of cooked prawns. Upon his arrival, Yalewa's scorn was so great that she snatched the basket out of his hands and banged him with it repeatedly until it burst apart scattering the prawns far and wide. Some of them fell into a pool beside the path, where they came to life again. The young suitor was now so frightened of Yalewa-ni-cagi-bula that he ran back to his home never again to return to the little island to brave her anger and scorn. As he did so, the stepping stones sank behind him to the bed of the sea. The prawns are still to be found there, darting among the stones and gleaming redly in the sunshine. The inhabitants of Vatulele regard them as sacred and say that if anyone catches them and takes them away, he will never reach the mainland because his canoe will be wrecked.

As far as is known, no such legend is associated with Ligur uveae at

Tiniguiban, but one of the most remarkable facts is that the superstition and tabu relating to these animals in the Fiji Islands is practically duplicated in the Philippines.

Correspondence from Dr. H. W. Fricke to the second author contains some very valuable observations on the Aldabra population of Ligur uveae which we are grateful for his permission to publish. There are apparently some distinct differences in the behaviour of L. uveae in Aldabra compared with our observations on the species in the Philippines and Fiji. In Aldabra the shrimps are active in the daytime, and also at night when they change colour from red to become almost transparent. During daylight, shortly after the high tide, the animals retreated from the level part of the pool into the deep hole in the centre. At night they stayed much longer in the pool until the water level reached as low as 10 cm depth. Dr. Fricke suggests that these tide-linked migrations, differing between day and night, are influenced by predator pressure in the environment. He has observed a few species of herons in the pool, hunting industriously during the day, and presented to us the theory that in daytime the shrimps could evade their enemies by leaving the level part of the pool in this critical period when the water level fell to 40 cm depth or less allowing the herons to enter. See also Addendum I, on p. 139.

Assuming this theory to be correct, pressure from predators has not had the same influence in either Tiniguiban or Vatulele. Here there is evidence indicating that L. uveae is active in the open water only during daylight, that the species prefers sunlit and shallow areas during this time, and that many fewer shrimps (or none) are seen on cloudy or rainy days. In Tiniguiban the only factor related to tides is that during low spring tides there may not be sufficient depth of water to provide access between the subterranean fissures and the body of the pool. We suggest that this may be the basic or unmodified behavioural pattern, and that predators such as Egretta sacra observed in Vatulele or possibly kingfishers seen in the vicinity of the pool at Tiniguiban have not been sufficiently active to force the shrimps to evolve nocturnal habits. In Aldabra the herons, which feed by day and roost by night, have presumably had this effect. Whether or not the Vatulele and Tiniguiban shrimps become transparent at night is not known, although the fact that strong sunlight intensifies their red colouration suggests that the reverse may occur in the absence of light. See also Addendum II, on p. 139.

The apparent preference of *Ligur uveae* for incident sunlight is difficult of explain, but one reasonable suggestion is that in Tiniguiban at least, there may be some correlation with dissolved oxygen levels. Although it has not been possible to obtain meaningful readings from the Tiniguiban pool during

the hours of darkness, it is likely that oxygen depletion occurs overnight in view of the high algal and diatom populations in the shallow water which lift dissolved oxygen levels to supersaturation during daylight hours. The shrimps may respond to this cycle by moving back into the fissures with subterranean marine connections after sundown simply to attend to their oxygen requirements.

In personal correspondence, Dr. Fricke writes of a further significant observation in homing behaviour in *L. wveae* at Aldabra translated from German as follows: ... "the red species has a home range to which it always returns daily". Marked individuals moved from the drainage opening to a definite area within the pool which "is occupied by them for at least a period covered by 8 high tides (which is the time during which the paint stayed on the carapace).

We wondered how the shrimps got orientated. Therefore we made three experimental groups of individuals. These we released in the posterior-most part of the pool and noted the time they needed to reach the drainage opening" (some 45 m distant). "In the individuals of one group the antennae were removed, those of the second group had the eyes covered with black lacquer, while the third group consisted of intact animals. The result was that the intact and blind animals needed the same time to reach the exit opening; the individuals without antennae needed much more time or did not reach the exit at all. It is clear that the antennae are used for orientation". See also Addendum I, on p. 139.

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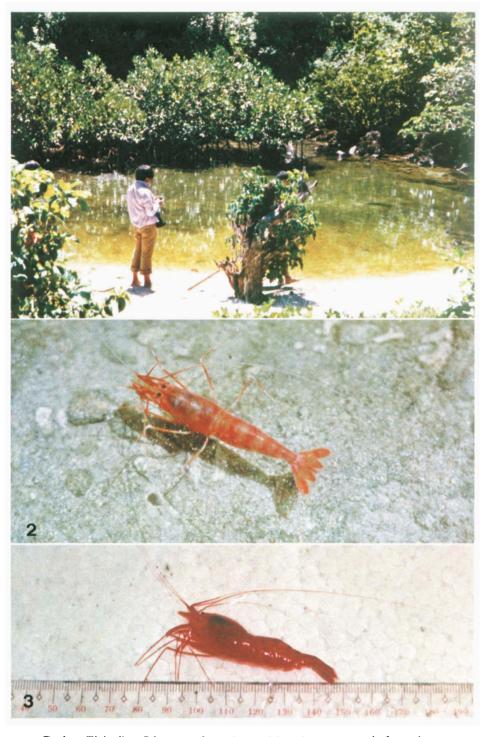
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ADDENDA

I. Since the present note was set up in type, we received Dr. H. W. Fricke's (1976) book "Bericht aus dem Riff. Ein Verhaltensforscher experimentiert im Meer": 1-254, figs. 1-87 (R. Piper & Co., München). In this book, on pp. 129-133, figs. 50, 51, the Aldabra shrimp pool and the shrimps are extensively discussed. The pool is shown in the coloured figures 50a (pool being drained by the outgoing tide), b (the dried and cracked bottom of the pool at low tide), and c (dried algae hanging from the sharp edges of coral rock of the pool's margin at low tide). The coloured figure 51 shows a beautiful shot of Liqur uveae. Dr. Fricke described the pool in detail, showing it to be typically anchialine. The behaviour of Ligur also is extensively discussed. Apart from Ligur the pool houses two more species of shrimp: numerous Palaemon debilis Dana (family Palaemonidae, subfamily Palaemoninae), which rather passively drift into and out of the pool with the incoming and outgoing tides, and Periclimenes pholeter Holthuis (family Palaemonidae, subfamily Pontoniinae), which does not venture out of the drainage opening Palaemon debilis is a species with a wide range throughout the Indo-West Pacific area, where it inhabits a great variety of habitats, while Periclimenes pholeter so far is only known from Aldabra and from the Sinai Peninsula, in both localities inhabiting anchialine habitats.

II. Recently (November 1976), during a new visit to the Philippines, the senior author had the opportunity to observe *Ligur uveae* at night in the aquarium. The colour of the animals at night was very light pink to translucent white, with chalky white patches and red bands. The somatic red pigment condenses into very well defined bands located posteriorly across the carapace, across the pre-cardiac area and a patch in the branchiostegal region of each side and frontally at the base of the rostrum. There is also a red band across the posterior part of each abdominal somite. On the antennae and pleopods the pigment condenses to the base of the appendage. In the tailfan the colour contracts to small patches: one on the telson near its base

with a second patch centrally; and three on each uropod (one on the protopodite, and one centrally on the exo- and endopodites). In the walking legs the red colour condenses toward the middle of each segment, occupying 2/3 to 3/4 of the segment away from the joints, which are often chalky white. Chalky white pigment patches are located at almost all movable joints of all appendages. Such white patches are also found in the following places: particularly strong in the cardiac region, otherwise irregular in the carapace; immediately anterior to each of the red bands of the abdominal somites, but not extending down to the ventrolateral parts of the pleura; and marginally on the telson and uropods.



1, Pool at Tiniguiban Islet, seen from the sand bar that separates it from the sea. 2, 3, Ligur uveae (Borradaile) from Tiniguiban Islet, pink and red stages respectively.

