

THE SEXUALITY OF TROPICAL DEEPWATER SHRIMPS (DECAPODA: PANDALIDAE)

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ABSTRACT

Morphometric studies were carried out as part of resource assessment surveys on deepwater pandalid shrimps in both the northern and southern tropical Pacific Ocean.

Previous works have suggested that pandalid shrimps, including those of some tropical species, are typically protandrous hermaphrodites. In this study, however, measurements of certain male secondary sexual characteristics were positively correlated with shrimp size. There was no evidence of degeneration of these characteristics in larger individuals as would be expected with protandrous hermaphrodites. We conclude that shrimps of the tropical pandalid species examined are dioecious and that sex reversal does not occur.

Sex reversal in pandalid shrimps was first noted in *Pandalus danae* (Berkeley, 1929) and, since that time, has been reported for a large number of exploited pandalids from northern temperate waters including *P. jordani* and *P. borealis* (Butler, 1964). Butler stated that, with "one or two known exceptions," all pandalid shrimps so far investigated were protandrous hermaphrodites.

The usual pattern in hermaphroditic pandalid shrimps is for individuals to mature and function first as males and, at two or three years of age, to change sex and function as females. During the change in sex, the appendices masculinae on the endopods of the second pair of pleopods of the male degenerate during a series of intersex or transitional stages, until these structures are entirely lacking in females.

Deepwater pandalid shrimps are also widely distributed in the tropical Pacific Ocean, including Hawaii (Clarke, 1972; Struhsaker and Aasted, 1974), Guam (Wilder, 1977), New Caledonia (Intès, 1978), Fiji (King, in press), Tahiti (Anonymous, 1979), Western Samoa (King, 1980), Vanuatu, west of Fiji (King, 1981a), Tonga (King, 1981b), Papua New Guinea (King, 1982), and the Northern Marianas (Moffitt, 1983). Some species, particularly of the genus *Heterocarpus*, are found in sufficient abundance to stimulate interest in commercial exploitation (King, 1981c). Shrimps of several of these species including *H. ensifer* (Clarke, 1972), *H. ensifer* and *H. laevigatus* (Wilder, 1977), and *H. sibogae* and *H. laevigatus* (King, 1981a) were thought to be protandrous hermaphrodites similar to temperate pandalid species.

During studies on the biology and commercial potential of deepwater shrimps in Fiji and the Marianas, at least thirteen different species have been found (Table 1). This paper examines the morphometry and the sexuality of five species which were obtained in sufficient numbers and over a wide size range. The species examined were *Plesionika longirostris*, *H. ensifer*, *H. sibogae*, *H. gibbosus*, and *H. laevigatus* in Fiji and *P. longirostris*, *H. ensifer*, and *H. laevigatus* in the Marianas.

METHODS

All shrimps examined were caught in baited traps similar to those described in previous resource surveys (e.g., King, 1981a).

The size of all shrimps was recorded as carapace length (the distance between the posterior margin of the orbit and the posterior median edge of the cephalothorax) measured to the nearest 0.1 mm.

Shrimps were sexed by an examination of the endopods of the first two pairs of pleopods and the

Table 1. Pandalid shrimps caught during deepwater trapping surveys in Fiji and the Marianas. The trap abundance of each species in each of the two locations is indicated as C (common), O (occasional), R (rare), or no letter (not found). The depth or depth range at which each species was caught is given in metres.

Species		Fiji	Marianas	Depth (m)
<i>Parapandalus serratifrons</i>	Pyjama shrimp	C	—	<380
<i>Parapandalus serratifrons</i> **		O	—	<380
<i>Plesionika longirostris</i>	Stars and stripes shrimp	C	C	120–540
<i>Plesionika rostricrescentis</i>		R	—	240–290
<i>Plesionika sindoi</i>		—	R	375
<i>Plesionika ensis</i>	Striped gladiator shrimp*	O	R	450–640
<i>Plesionika martia</i>	Golden shrimp*	O	R	360–600
<i>Heterocarpus ensifer</i>	Armed nylon shrimp*	O	C	240–580
<i>Heterocarpus sibogae</i>	Mino nylon shrimp*	C	R	250–750
<i>Heterocarpus gibbosus</i>	Humpback nylon shrimp*	C	R	280–750
<i>Heterocarpus lepidus</i>		—	O	630–740
<i>Heterocarpus laevigatus</i>	Smooth nylon shrimp*	C	C	400–825
<i>Heterocarpus longirostris</i>		—	C	<825
<i>Heterocarpus dorsalis</i>	Madagascar nylon shrimp*	—	C	630–920

* Standard FAO name (Holthuis, 1980).

** Possibly a second form of *P. serratifrons* or a distinct species (King, in press).

basal segments of the last pair of pereiopods. The former structures are shown for *H. sibogae* in Fig. 1 and were similar in the other species studied.

The endopod of the second pleopod in males in particular was examined by using a low power microscope to measure the size of the appendix masculina as a percentage of the size of the appendix interna. Thus, scores ranged from zero (no visible appendix masculina) to close to 100 (when the appendix interna and the appendix masculina were of a similar size). This quantity was called the "relative length" of the appendix masculina.

Data from a wide size range of males were used to determine the relation between shrimp size (carapace length) and the relative length of the appendix masculina and to test the alternative hypotheses that this organ was either, (a) decreasing in size with shrimp growth (suggesting that male characteristics were degenerating and individuals were changing to female form), or, (b) increasing in size with shrimp growth (suggesting that male characteristics were developing and that individuals with reduced appendices masculinae were immature males).

RESULTS

The sex of even the smallest individuals examined in this study was easily determined by examination of the endopod of the first pleopod and the coxa of the fifth pereiopod. The shape of the endopod of the first pleopod varied somewhat with species and shrimp size (carapace length), but were always of either distinctly male or distinctly female form. Also, the male gonopores located on the coxal segments of the fifth pair of pereiopods were always present in males, though minute in the very small males, and absent in females of all sizes. These characters were consistent. The appendix masculina on the endopod of the second pleopod of males, however, underwent considerable change with shrimp growth. In very small males, the appendix masculina was absent, making the second pleopod essentially indistinguishable from that of females of the same size. These structures first appeared in developing males as small rounded buds and increased in relative length with increasing shrimp size. The distal end of the organ also became covered with an increasing number of setae in larger individuals.

The relationship between shrimp carapace length and the relative length of the appendix masculina is shown in Fig. 2 for *P. longirostris*, *H. ensifer*, *H. sibogae*, *H. gibbosus*, and *H. laevigatus* from Fiji and *P. longirostris*, *H. ensifer*, and *H. laevigatus* from the Marianas.

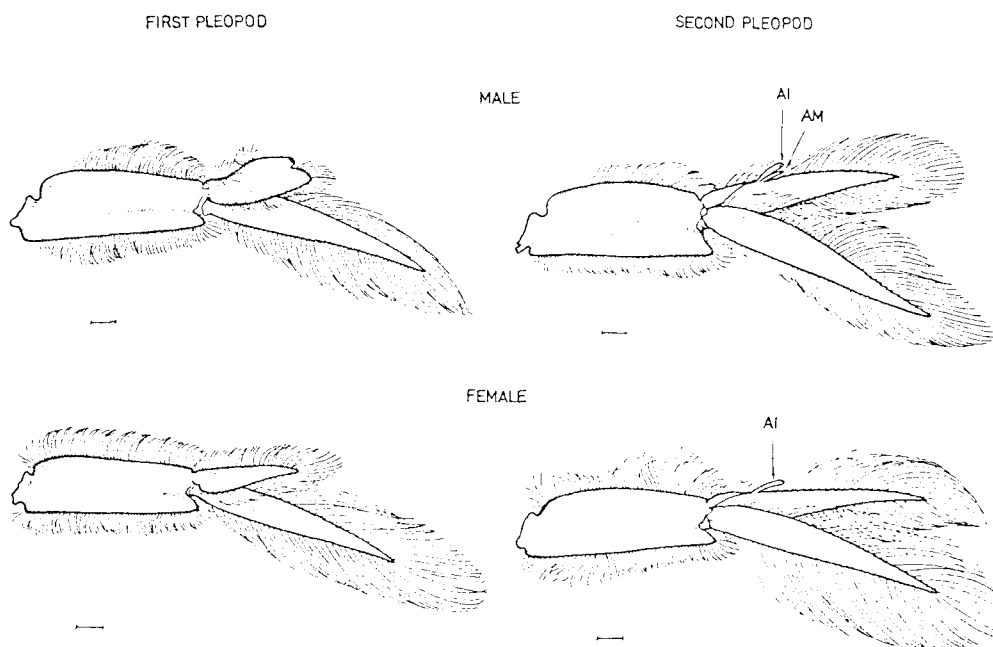


Fig. 1. *Heterocarpus sibogae*. Left: first pleopod showing male (top) and female endopod (bottom). Right: second pleopod with appendix masculina (AM) and appendix interna (AI) of male (top) and latter organ only in female (bottom). Pleopods illustrated from a 26.0-mm (carapace length) male and a 26.3-mm female. Horizontal scales indicate 1 mm.

DISCUSSION

Morphometric evidence presented here strongly suggested that the pandalid species examined were dioecious. In previous work on tropical deepwater pandalids, authors appear to have incorrectly concluded that some of these same species were protandrous hermaphrodites. This may be because of one or several reasons including, (a) unreliable characteristics being used to determine sex, (b) the presence of a high ratio of females to males in the largest size classes, and (c) the presence of small males with reduced appendices masculinae.

Wilder (1977), in particular, stated that small females were not evident in his large samples of *H. ensifer* and *H. laevigatus* from Guam. During our investigations of shrimps from Guam and the northern Marianas Islands, however, we found that small females were common in these species and that sex ratios in small size classes were close to 1:1.

Sex ratios favouring females in larger size classes have traditionally been used as evidence for sex reversal (Wenner, 1972). Although such sex ratios were evident in some samples of shrimps obtained in our study, it should be noted that similar variations in sex ratios can occur in dioecious organisms where there are sex related differences in growth, mortality, migration, and habitat preference. In the case of animals caught by trapping, it is also possible that susceptibility to traps may differ between sexes. Sex ratios appear to have been incorrectly used to support sex reversal hypotheses in at least some other crustaceans (see Wenner and Haley, 1981).

Sex reversal is known to be common in temperate deepwater pandalids (Rasmussen, 1953; Butler, 1964). In our studies, small males with reduced appendices

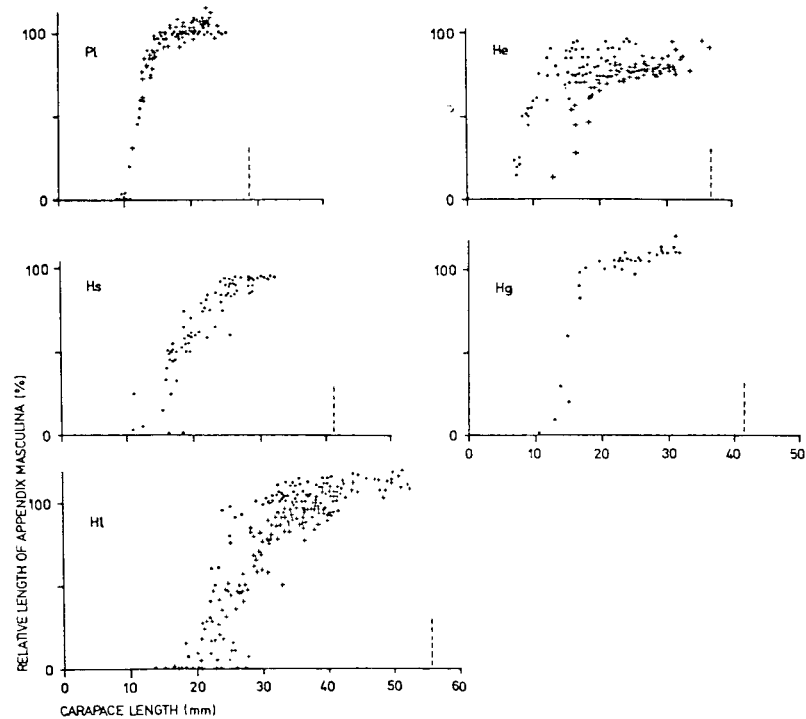


Fig. 2. Relation of relative size (%) of appendix masculina to shrimp carapace length (mm) in samples collected from Fiji (dots) and Guam (crosses). Species are Pl (*Plesionika longirostris*), He (*Heterocarpus ensifer*), Hs (*H. sibogae*), Hg (*H. gibbosus*) and Hl (*H. laevigatus*). Maximum carapace length of each species indicated by vertical broken line.

masculinae were similar, with respect to the appearance of the second pleopods, to the intersex, or transitional, individuals of these temperate species. They were, however, clearly males, based on the morphology of the previously described organs. This indicates that these individuals, in tropical pandalids, were not transitionals, but were immature and developing males. Although not all shrimp species caught during our surveys (Table 1) were analysed due to the lack of small individuals in our collections of some species, dioecy may be widespread in tropical deepwater pandalids.

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