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SEX CHANGE AND LIFE HISTORY PATTERN IN THE SHRIMP *THOR MANNINGI* (DECAPODA: CARIDEA): A NOVEL CASE OF PARTIAL PROTANDRIC HERMAPHRODITISM

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ABSTRACT

A population of *Thor manningi* sampled for one year was composed of 50% primary males, 49% protandric hermaphrodites, and 1% primary females. Primary males have prehensile third pereiopods, massive appendices masculinae, and life-long sperm production. Protandric hermaphrodites pass first through a male phase (non-prehensile third pereiopods, small appendices masculinae, sperm production) and a transitional phase (reduction of appendices masculinae and sperm ducts, development of female incubatory flanges, ovarian development) before maturing into breeding (embryo-carrying) females.

Eighty-six to 100% of females (female-phase hermaphrodites and primary females) in monthly samples carried embryos. Breeding females produced new embryo clutches approximately every nine days. Although reproduction was continuous, recruitment chiefly occurred in the summer. Measurements of density, size-specific dry weight, and cohort analysis indicate average life spans of approximately 4–5 months, production of 35 mg dry weight/m^2/year, and a production:biomass ratio of 4.5.

Primary males do not occur in other protandric decapod species. It is hypothesized that *T. manningi* primary males persist at a high frequency in the population because they may be more efficient at fertilizing breeding females than are male-phase hermaphrodites.

INTRODUCTION

Protandric sex change has been reported in relatively few of the approximately 1800 species of caridean shrimps. Carpenter (1978), Subramonian (1981a), and Policansky (1982) have listed decapod crustacean species which have either been shown to be or are purported to be protandric hermaphrodites. Of the 32 decapod species reported as sex changers in these review articles, 26 are caridean shrimps. In the boreal caridean genera *Pandalus* and *Pandalopsis,* nearly all species show varying degrees of protandry (Berkeley, 1930; Butler, 1964, 1980; Hoffman, 1972; Charnov, 1979; Williams, 1984). In some species, all members of a population undergo a protandric sex change, *i.e.,* they reproduce first as males and then, with increasing age and size, become breeding females. In other species, not all individuals are sex changers: a variable proportion (<50%) of the population are primary females, individuals lacking male characters which breed only as females. Primary males, individuals breeding only as males throughout their lifetime, are unknown in protandric pandalid species. Fréchette *et al.* (1970) found a sexual system similar to that of pandalids in the crangonid *Argis dentata* Rathbun. In another well-documented case of protandry in the

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Caridea, Dohrn (1950) found complete protandry in the hippolytid *Lysmata seticaudata* Risso, *i.e.*, all individuals function first as males before changing to females. In protandric carideans, the transformation from male to female is marked externally by loss of the appendices masculinae (shown to be copulatory structures by Bauer, 1976, and Berg and Sandifer, 1984) and by modifications of the endopods of the first pleopods (Dohrn, 1950; Butler, 1964, 1980; Charniaux-Cotton, 1975).

Chace (1972) raised the possibility of protandric hermaphroditism in the hippolytid genus *Thor*. In describing *Thor manningi*, Chace noted that the smaller size classes of a collection (made up of samples from many localities) were composed of males while larger size classes were dominated by mature females. His analysis of the situation was complicated by the occurrence of two types of males: "functional" males, individuals with prehensile third pereiopods and large appendices masculinae; and "nonfunctional" males, those with unmodified third pereiopods and small appendices masculinae. Chace hypothesized that the smaller "nonfunctional" males might represent males which had not yet reached maturity; large "nonfunctional" males might be males in the process of changing sex to female. With the limited museum collection available to him, Chace was unable to make a clear-cut decision on the problem of protandry which he recognized in *T. manningi*.

During a year-long sampling of macroinvertebrate epifauna in *Thalassia testudinum* Koenig seagrass meadows on the north coast of Puerto Rico (Bauer, 1985), several thousand *T. manningi* were collected. Observations and analyses of this material and laboratory studies on live shrimps have revealed the details of *T. manningi's* novel sexual system. The population sampled consists of 50% primary males which never change sex, nearly 50% protandric hermaphrodites which pass through a male phase (Chace's "nonfunctional" males) before maturing as breeding females, and a very small proportion of primary females, females which develop no male characters before reproducing as females. This report analyzes the sexual system of *T. manningi* and describes the changes in external and internal anatomy which support a conclusion of partial protandry in this species. The population structure, reproductive pattern, recruitment, life span, productivity, and other life history characteristics of this species are analyzed and reported.

Materials and Methods

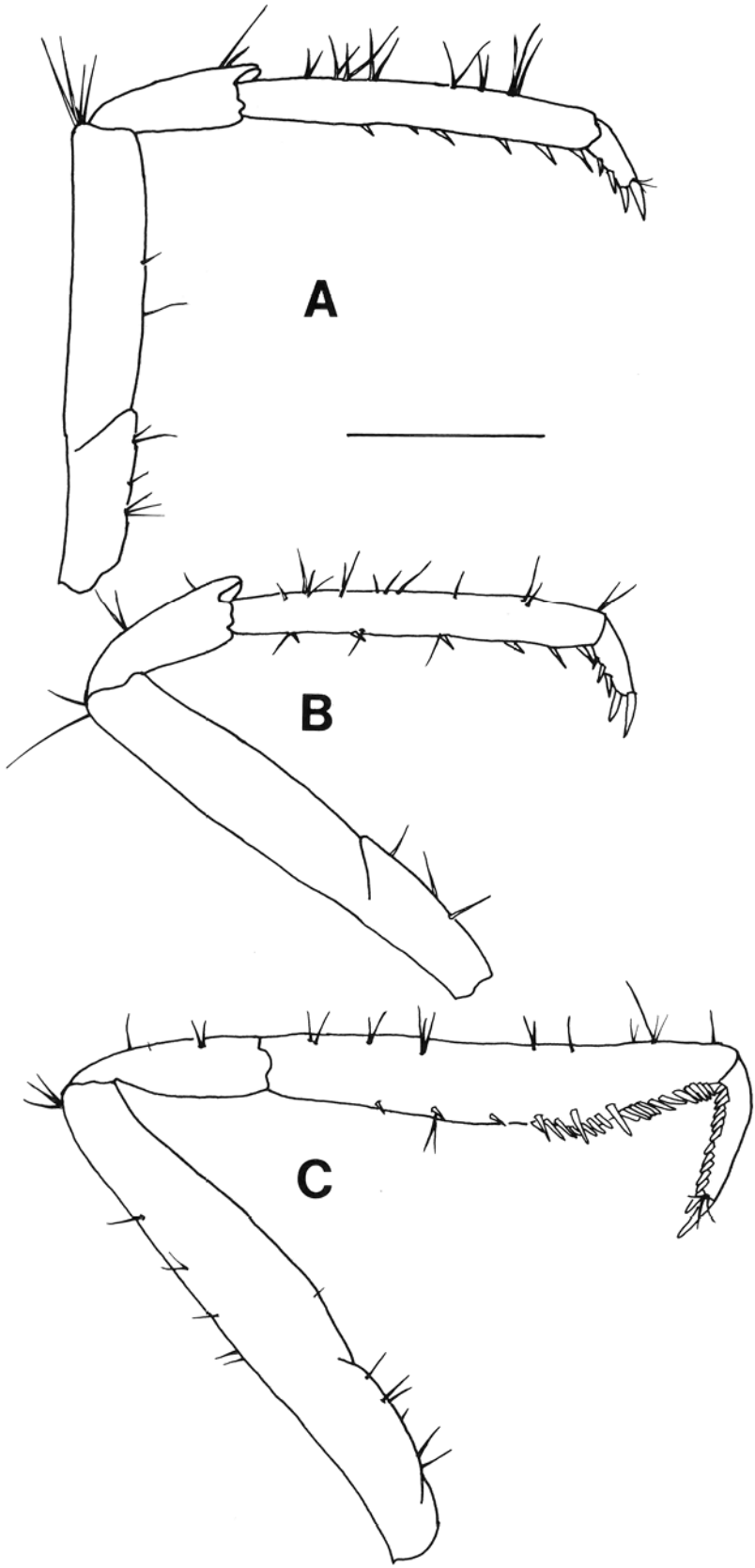
The macroinvertebrate epifauna was sampled monthly from *Thalassia testudinum* meadows at Dorado, Puerto Rico (18° 29'N, 66° 15'W), from March, 1982 to February, 1983 (see Bauer, 1985, for details of habitat and sampling procedures). Samples were immediately preserved in 10% seawater formalin; invertebrates including *T. manningi* were sorted to species and placed in 70% ethanol for permanent storage. Densities of *T. manningi* reported here are based on random samples (n = 20 for 9 months, n = 10 for 3 months) taken at night with a 0.5 m wide pushnet using a 1.0 mm mesh liner. Some workers (Pihl and Rosenberg, 1982; Howard, 1984) have used enclosure trapping in sampling and estimation of shrimp densities in shallow water. In one set of night collections, I compared the efficiency of pushnet *versus* drop-trap (Pihl and Rosenberg, 1982) sampling in the estimation of absolute abundances. For *T. manningi*, there was no statistically significant difference in the mean number of individuals per square meter between pushnet samples (mean = 39.2, n = 10) and drop-trap samples (mean = 22.5, n = 10) (*t*-test, $P > 0.10$). In these seagrass meadows, pushnet sampling is as efficient as enclosure methods in estimating densities. Plankton tows taken at night through the seagrass with a 333 μm mesh net did not yield juveniles smaller

than the smallest individuals collected with the 1.0 mm pushnet, *i.e.*, the entire size range of the *T. manningi* population was sampled by the pushnet.

Over 1100 females (hermaphrodites and primary females) and 1100 males (primary males) from monthly samples were examined, measured, and sexed in an analysis of monthly population structure. Before beginning routine measurements and sexing of material in monthly collections, extensive observations and dissections were done to understand sexuality in *T. manningi*. In this report, *mature* or *adult females* refers to females which were carrying embryos, or, rarely, those without embryos which showed no male characteristics and which were as large or larger than the smallest embryo-carrying (= ovigerous or brooding) female in that month's sample. Such mature females without embryos usually represent females captured after hatching of one brood but before spawning of the next. *Male-phase hermaphrodites* are individuals with non-prehensile third pereiopods which had appendices masculinae on the second pleopods. *Primary males* are individuals with prehensile third pereiopods. Shrimps in preserved samples sometimes had both third pereiopods missing, but primary males could be distinguished from male-phase hermaphrodites by the former's proportionately larger appendices masculinae, the long curved seta at the tip of the endopod of pleopod 1, and the absence of pleopod flanges (see description of appendage morphology in the Results section). However, only individuals with third pereiopods present were used in the morphometric measurements. Individuals lacking appendices masculinae which were smaller than the smallest ovigerous female but larger than the juvenile size range are termed *primary females*. Only 11 such individuals were observed in the samples. *Juveniles* are small individuals (0.5–1.0 mm carapace length) which could not be reliably sexed. Juveniles comprised from 0–17% (median = 6.5%) of the population in the monthly samples.

Carapace length (CL) is the distance from the posterior edge of the eye orbit to the posterior mid-dorsal edge of the carapace. In hermaphrodites and primary females, the developing ovary with its large yolky eggs can be observed easily through the transparent carapace with a stereomicroscope. Degree of ovarian development was characterized as: stage 1, no noticeable development; stage 2, vitellogenic oocytes distinct but ovary small; stage 3, ovary filling at least half the space above the cardiac stomach; stage 4, ovary completely filling that space. Embryos incubated by brooding females were classified with a system suggested by Allen (1966): stage 1, early embryos with no visible blastoderm; stage 2, blastoderm distinct, no eye development; stage 3, embryos with eyes, abdomen not free from cephalothorax; stage 4, embryos near to hatching, little or no yolk, large eyes, abdomen free from the cephalothorax. Determination of brood or clutch size was made by removing and counting embryos from incubating females. Only broods from females carrying stage 1 or 2 embryos were used; advanced embryos are more easily dislodged from females during sampling and subsequent handling.

Monthly size-frequency distributions with 0.1 mm size classes were constructed for females and primary males. Cohort analysis according to the methods of Harding (1949) and Cassie (1954) was used to identify and to separate overlapping cohorts, to obtain estimates of the mean size of individuals in a cohort, and to calculate the proportion of the total population comprised by a cohort. These are standard methods for analylzing field populations of caridean shrimps (Alon and Stancyk, 1982; Pihl and Rosenberg, 1982; Howard, 1984; Pihl and Pihl, 1984). For production and biomass calculations, the total population density was divided equally between males and females as the sex ratio was never statistically different from 1:1 (Chi-square analysis). The total male or female density was divided up among cohorts according to their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C

proportions in the population. The relationship between dry weight and size (carapace length) was determined from freshly captured individuals which were measured, sexed, oven dried for 2 days at 60°C, and weighed on an analytical balance to the nearest 0.1 mg. The power curve $y = ax^b$ was used as the model for regressions of dry weight on size, where y is dry weight in mg, x is carapace length (mm), a is the y-intercept, and b is the slope. For primary males, the regression constants and explained variance (r^2) are a = 0.89, b = 3.10, and $r^2 = 0.69$ (n = 30); for females, a = 0.69, b = 2.69, and $r^2 = 0.83$ (n = 41). The biomass for males or females at a given sampling period was calculated by summing, for all cohorts, the products of weight of the average-sized individual in a cohort and the density of that cohort. The calculation of net productivity (*P*) of cohorts from one sampling period to the next was based on Crisp's (1971) growth increments method: $P = \sum_{1}^{i} \{(N1 + N2)/2\} (\Delta W)$, where N1 and N2 are density at the beginning and end of the period. W is the average weight of an individual in the cohort, and *i* is the number of cohorts present.

Results

Secondary sexual characteristics of primary males and male-phase hermaphrodites

True or primary males are easily distinguished from male-phase female hermaphrodites by the structure of the third pereiopod (Fig. 1). In males, the distal end of the propodus is expanded and its lateral flexor margin is covered with long spatulate setae (Figs. 1C, 2A). In addition, the dactyl of pereiopod 3 in true males is elongate (compared to male-phase hermaphrodites and mature females) and similarly equipped with spatulate setae (Figs. 1C; 2A, B). The morphology of pereiopod 3 described for *Thor manningi* primary males occurs in males of some other caridean species (Chace, 1972; Butler, 1980) and has been termed "prehensile," and I will use the term in this report. By contrast, the third pereiopod of male-phase hermaphrodites is identical to that of mature females (Figs. 1A, B; 2C, D).

The endopod of pleopod 1 in primary males bears a series of spinulose to serrate setae on its medial edge, and the endopod terminates in a long curved seta (Figs. 3D; 4A, B). Endopods of male-phase hermaphrodites are variable in setation but generally bear medial setae which are more weakly spinulose than in true males. The long terminal endopod seta seen in primary males is much less developed in male-phase hermaphrodites (Fig. 3C). Pleopod 1 endopod structure in the few primary females collected is similar to that of male-phase hermaphrodites of similar size (Fig. 3B, C).

The medial anterior edge of pleopod 2 is the site of a copulatory structure, the appendix masculina (Figs. 4C; 5A, B, C, E). This process is naked proximally and setose distally. There are two basic setal types: (1) an inner group of strong, naked setae set in deep sockets and (2) a group of finely setulate setae which surround the inner stout naked setae (Fig. 4D). In individuals with prehensile third pereiopods, *i.e.*, primary males, the appendices masculinae are always massive in size, nearly as long as the endopods which bear them (Figs. 4C, 5E). In individuals with unmodified third pereiopods, the relative size of the appendices are smaller than in primary males (Figs. 4E; 5A-C). In primary males, the relative length of the appendix masculina appears to remain constant with an increase in male size (carapace length) while in male-phase

FIGURE 1. Third pereiopods of *Thor manningi* sexual types, lateral view. A. Breeding female, 1.3 mm CL; B. Male-phase hermaphrodite, 1.3 mm CL; C. Primary male, 1.2 mm CL. Scale bar represents 0.5 mm.

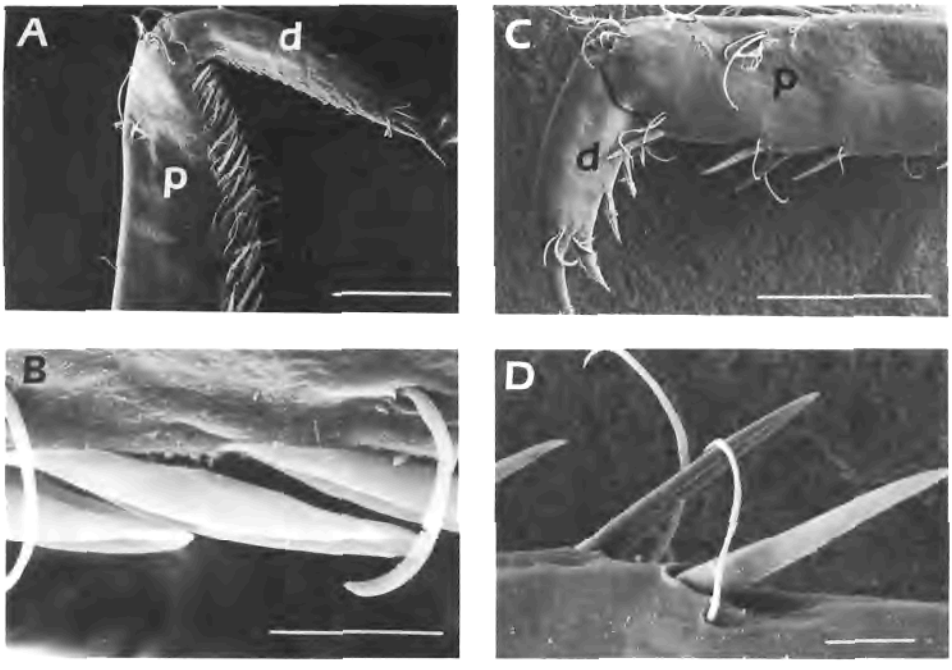

FIGURE 2. Structure of pereiopod 3 propodus and dactyl. A. Propodus and dactyl of primary male; B. Spatulate setae on the flexor margin of the dactyl shown in (A); C. Propodus and dactyl of a male-phase hermaphrodite; D. Setae from the flexor margin of the propodus in (C). p, propodus; d, dactyl; scale bar represents 200 μ.

hermaphrodites, the relative appendix masculina length decreases with increasing size (Fig. 6). This impression is confirmed by regression analysis of log (x + 1) transformed data (both variables in mm) with methods given in Kuris and Carlton (1977). The slope (b) of the regression line $\{P\,(H_0$: no regression) $<0.0001\}$ for primary males is 0.90, indicating appendix masculina growth which is isometric or nearly so (Kuris and Carlton, 1977). For male-phase hermaphrodites, the slope of the regression line $\{P\,(H_0$: no regression) $<0.0001\}$ is 0.20, confirming that appendix masculina growth is negatively allometric in this sexual type.

Another change in pleopod structure which accompanies growth in male-phase hermaphrodites is the development of a posterolateral flange, a thin non-muscular plate, on the basipod of (especially) the anterior three pairs of pleopods. This flange is always well-developed in mature females (Fig. 5D) and is associated with spawning and embryo incubation in many carideans (Hoglund, 1943; Bauer, 1976). In small male-phase hermaphrodites and in primary males of all sizes, the basipod is almost completely filled with muscle and there is no flange (Fig. 5A, E). A plot of flange (defined here as basipod lacking muscular tissue) width on carapace length (Fig. 7) shows that, after male-phase hermaphrodites (unmodified third pereiopod, appendices masculinae) reach 1.3–1.4 mm CL, the development of pleopod flanges is much greater than that of primary males (prehensile third pereiopods, appendices masculinae) in which the flange is virtually non-existent at any size. Again using log (x + 1) transformed variates, with both variables in mm, regression analysis confirms these conclusions. In male-phase hermaphrodites, the slope of the regression line is positive (b = 0.55)

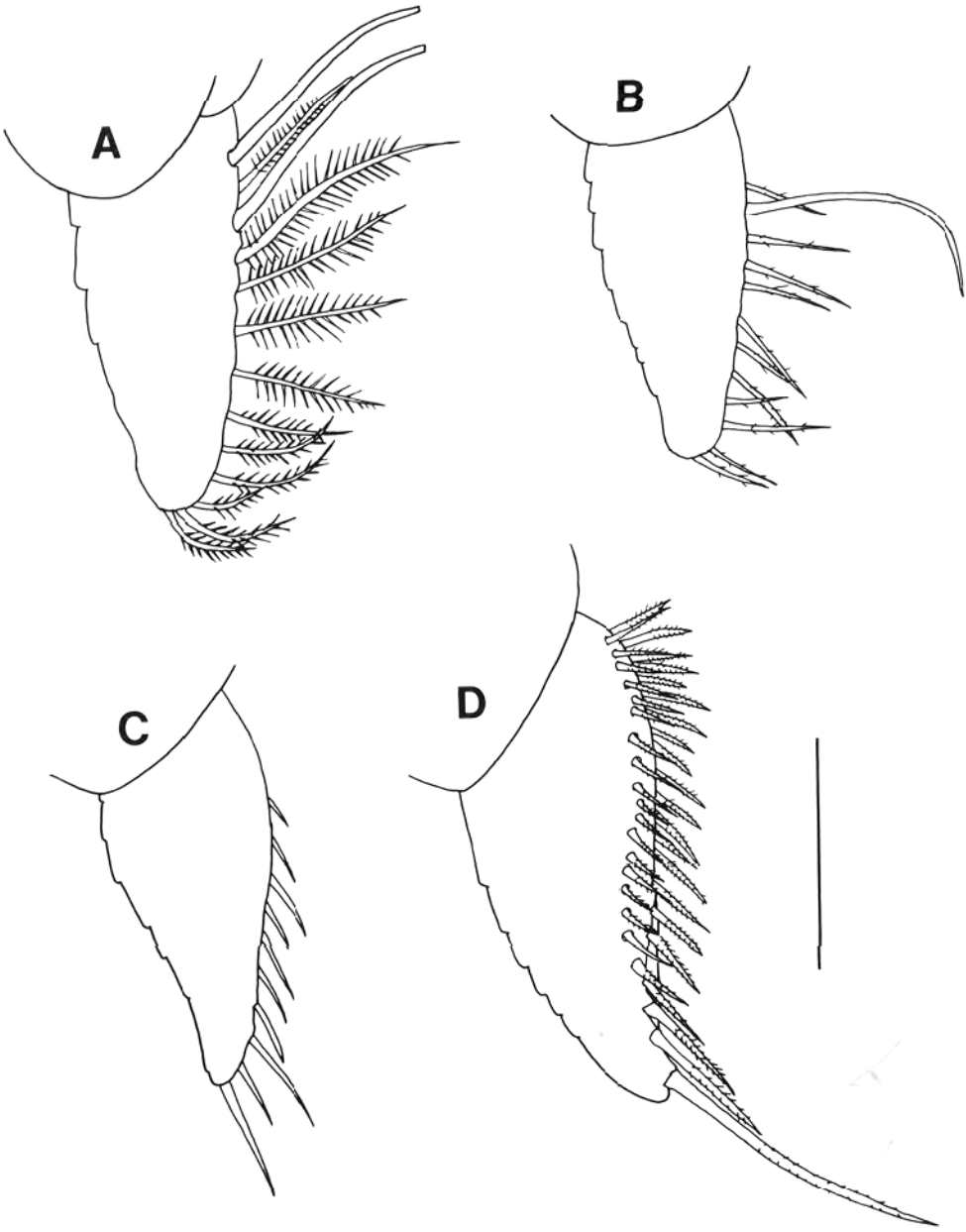

FIGURE 3. Endopods of the right first pleopods of different sexual types, anterior view. A. Breeding female, 1.3 mm CL; B. Primary female, 1.3 mm CL; C. male-phase hermaphrodite, 1.3 mm CL; D. Primary male, 1.2 mm CL. Scale bar represents 0.2 mm.

and the regression is statistically significant $\{P\ (H_0$: no regression) $<0.0001\}$. For primary males, a calculated slope of a regression line is -0.003, *i.e.,* zero, and there is no significant regression $\{P\ (H_0$: no regression) $>0.90\}$.


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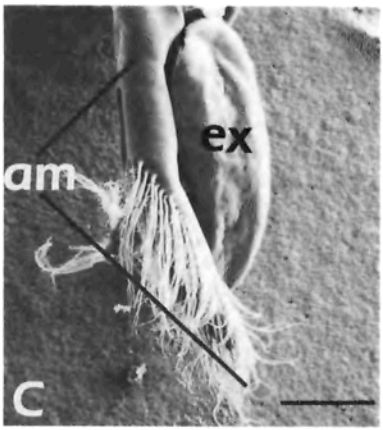
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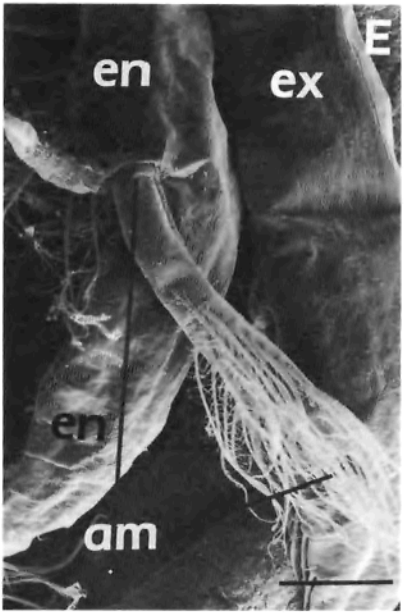
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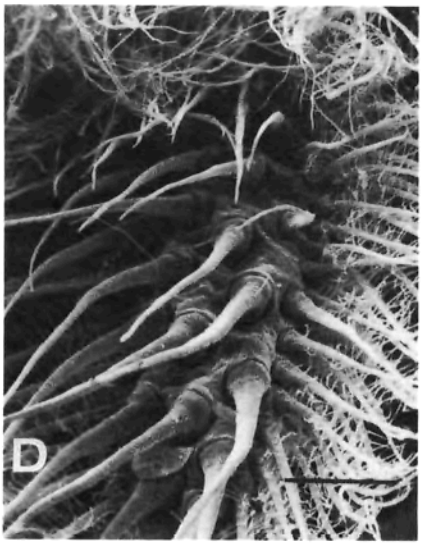
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Changes in primary sexual characteristics in hermaphrodites

Thor manningi males and male-phase hermaphrodites carry sperm in the terminal end of the vas deferens, in structures termed the ejaculatory duct and bulb (Bauer, 1976; Fig. 8A). These latter structures are located in the cephalothorax just dorsal to the coxa of pereiopod 5. In *T. manningi*, a very short canal leads from the ejaculatory bulb to the male genital aperature on the proximal posterior face of the coxa. When the ejaculatory bulb and duct are developed and contain the bullet-shaped sperm of *T. manningi* (Fig. 8D), they can be observed through the body wall just above the pereiopod 5 coxa. From the smallest (0.8 mm CL) to the largest (1.7 mm CL) individuals recognizable as males by pereiopod 3 and pleopod 2 morphology, the ejaculatory bulb and duct are well developed and full of sperm (Fig. 8A, E, H). Dissections of the smallest recognizable male-phase hermaphrodites (0.7–0.9 mm CL) have never revealed sperm production, and sperm ducts, if observed, were rudiments lacking sperm. However, male-phase hermaphrodites larger than 1.0 mm CL always possessed an ejaculatory duct and bulb with some sperm. These structures and the vas deferens degenerate very rapidly with increasing size after 1.2 mm CL. The distal ends of the sperm ducts of three pairs of primary males and male-phase hermaphrodites of increasing size are compared in Figure 8. The sperm ducts of hermaphrodites 1.0–1.1 mm CL are similar in size and fullness of sperm as those of primary males of a similar size (Fig. 8A, B, C), indicating sperm production in the gonad. In hermaphrodites 1.3 mm CL, the vas deferens had degenerated to a narrow cord which lacks sperm (Fig. 8F), evidence of a cessation of sperm production (Fig. 8E, F). The ejaculatory bulb and duct still contain sperm. The gonad is a developing ovary filling with the large yolk-filled oocytes characteristic of carideans (Fig. 8G). There is an obvious relationship between the size of male-phase hermaphrodites and the degree of ovarian development (Table I). There is some vestige of the ejaculatory duct and bulb (with a very few sperm cells) in even the largest male-phase hermaphrodites (2.1 mm CL). In Figure 8I, these structures are shown for a hermaphrodite 1.6 mm CL; the gonad is a well developed ovary full of vitellogenic oocytes in these individuals (Fig. 8J). When hermaphrodites make the final transformation to the female-phase, *i.e.*, carry embryos, all male primary and secondary characteristics are lost. By contrast, with increasing size, the sperm ducts of primary males increase in size (Fig. 8A, E, H), are full of sperm, and the gonad shows testis structure typical of caridean shrimp.

Of over 1100 females (hermaphrodites and primary females) examined, only 11 could be clearly identified as primary females, *i.e.*, non-hermaphroditic females without any sign of primary or secondary male sexual characteristics. These were individuals in the same size range as male-phase hermaphrodites which lacked a prehensile pereiopod 3, showed development of pleopod flanges and/or ovarian development, and which showed no appendix masculina or sperm ducts. The number of primary females is probably underestimated since primary females cannot be distinguished from female-

FIGURE 4. Sexual modifications of the anterior pleopods. A. Endopod and exopod of first pleopod of primary male, anterior view; scale bar, 200 μ; B. Serrate-spinulose setae on medial edge, endopod of pleopod 1, primary male; scale bar, 20 μ; C. Second pleopod of primary male, anterior view; black lines point out the base (upper line) and the setose tip of the massive appendix masculina (am) which completely covers the endopod anteriorly; scale bar in lower right corner, 200 μ; D. Medial view of setose tip of primary male appendix masculina, showing stout naked setae surrounded by finely plumose setae; scale bar, 50 μ; E. Anterior view of endopod and exopod, pleopod 2, of a male-phase hermaphrodite; black lines point out extent of the reduced appendix masculina (am). Note the small relative size of the appendix masculina of this specimen compared to that of the primary male in (C). Scale bar represents 100 μ. am, appendix masculina; b, basipod; en, endopod; ex, exopod.

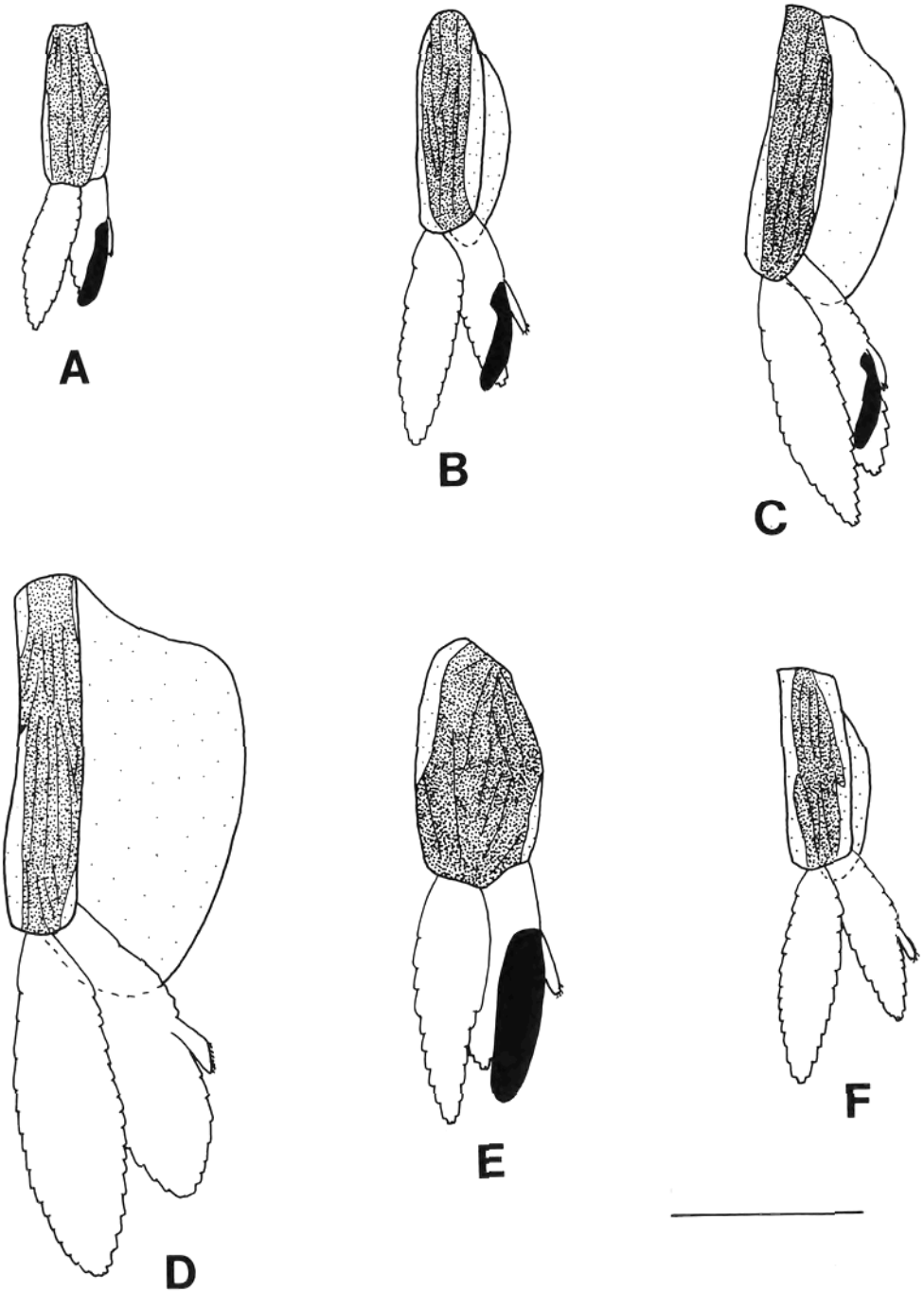


FIGURE 5. Diagrams of second pleopods of different sexual types, anterior view. A, B, C. From male-phase hermaphrodites of 1.0, 1.3, and 1.7 mm CL, respectively; D. Breeding female, 2.0 mm CL; E. Primary male, 1.3 mm CL, F. Primary female, 1.3 mm CL. The appendix masculina is shaded entirely black; heavy stippling represents basipod musculature; light stippling represents basipod free of musculature (basipod flange in B, C, D, and F). Scale bar represents 0.5 mm.

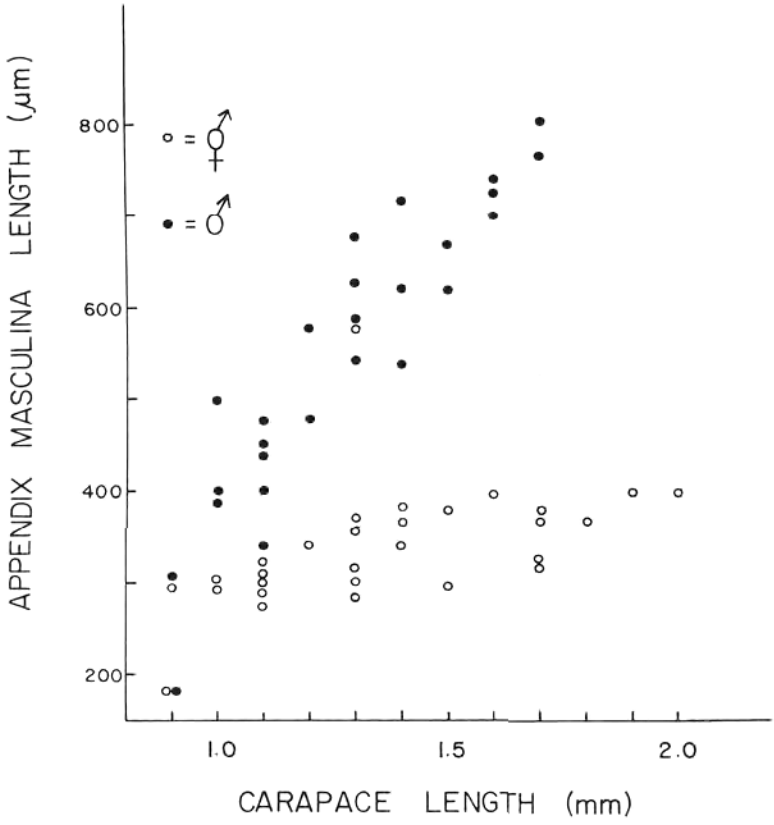


FIGURE 6. Variation of appendix masculina length with increasing size (carapace length) in primary males (dots) and male-phase hermaphrodites (circles).

phase hermaphrodites after the latter make the final change from male-phase hermaphrodite to ovigerous female. The low frequency of primary females in larger size groups may be inferred from their frequency in the smaller size groups (where they can be distinguished) assuming there is no differential mortality between male-phase hermaphrodites and immature primary females.

Size at sex change in hermaphrodites

The size of transformation from male-phase to embryo-carrying female-phase hermaphrodite was quite variable (Fig. 9). The size of the smallest ovigerous female varied in monthly samples 1.3–1.9 mm CL (median = 1.5 mm CL). On the other hand, the size of the largest male-phase hermaphrodite varied from 1.6–2.1 mm CL (median = 2.0). In some months of the study, there was considerable overlap between the male-phase hermaphrodite and mature female size-frequency distributions (Fig. 9). The fact that some male-phase hermaphrodites mature into mature females much more rapidly than most can be seen in Table I, where a small percentage of individuals in the smaller size classes do show distinct ovarian development. At the other extreme, a small percentage of the largest male-phase hermaphrodites show little or no ovarian

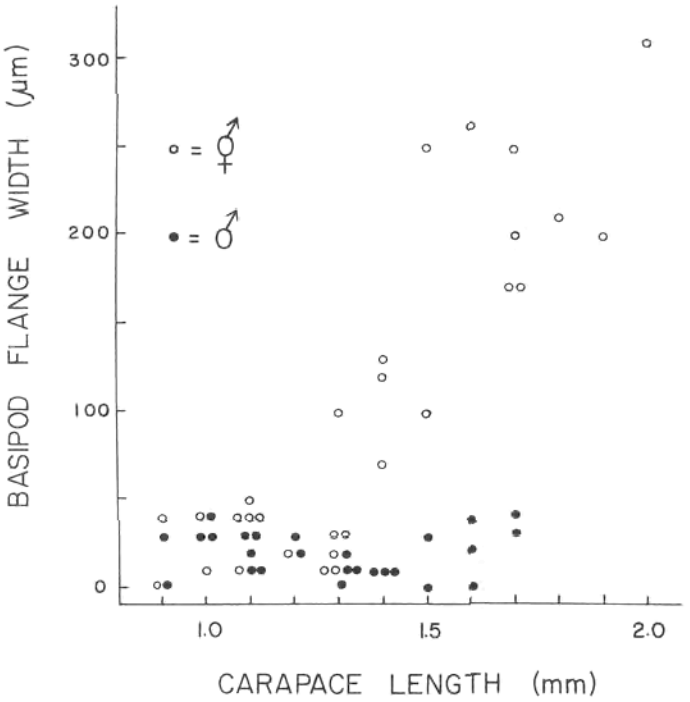


FIGURE 7. Variation of pleopod 2 basipod flange width with increasing size (carapace length) in primary males (black dots) and male phase hermaphrodites (open circles).

development, indicating a slow change in gonadal maturation to breeding female for some individuals.

Reproduction

Reproductive activity was high throughout the year (Fig. 9). The percentage of individuals with adult or mature female morphological characters which carried embryos varied between 86–100% in the monthly samples (median = 96%). Breeding females were iteroparous. At the same time incubated embryos were developing, the ovary filled again with vitellogenic oocytes. Figure 10 shows the positive correlation between stage of embryo development and stage of ovarian development. Females carrying recently spawned and fertilized embryos showed little ovarian development, while females with embryos near hatching had enlarged ovaries packed with yolk-filled egg cells. Laboratory observations indicate that within a day of embryo hatching, the female's post-hatch molt, mating, and spawning take place. Estimates of the duration of embryo incubation range from 6–10 days (median = 8 days, n = 20). These estimates are based on maintenance of captured females carrying recently spawned and fertilized embryos. The few females successfully mated in the laboratory showed incubation times within the range given above. Thus, the average adult female produces a new clutch of embryos approximately every nine days.

Clutch size varied from 22–147 embryos (median = 65) (Fig. 11). The regression line $Y = -95.3 + 83X$ describes the relationship between number of embryos per

clutch (Y) and female carapace length (X). There is considerable variation ($r^2 = .33$; $n = 54$) in clutch size with increasing female size, *i.e.*, some large females had lower than expected broods (Fig. 11). In studies on the caridean *Heptacarpus pictus* Stimpson (Bauer, 1976), I observed that females breeding for the first time had small broods for their size (unpub. obs.). The large *T. manningi* females with low clutch sizes might be those females which completed sex change at a large size and thus were producing their first brood.

Recruitment and life span

Episodes of recruitment, *i.e.*, the appearance of a cohort of individuals in the smaller size classes, occurred several times throughout the year (Fig. 9). However, the strength of recruitment fluctuated greatly among these episodes. The monthly abundance of *T. manningi* varied seasonally, with highs from May–September (Fig. 12). These higher abundances were due to heavy recruitment in May, June, and August (male and female cohorts b, c; Fig. 9). A high proportion of individuals in samples from these months were in the smallest size classes; individuals too immature to sex accurately comprised large percentages (15–18%) of the samples. Thus, the high densities of *T. manningi* from July–September resulted from the strong pulses of recruitment in May, June, and August.

The life span of the "average" individual in a cohort on the seagrass meadows was estimated as the number of months the cohort was recognizable in the size-frequency distributions. Since separation of cohorts by the probability paper methods used is not precise, the following estimates of longevity should be viewed as approximations. Cohorts b and c (Fig. 9) were clearly recruited and subsequently disappeared during the sampling period. In females (hermaphrodites and primary females), both these cohorts survived 5 months; in males, cohorts b and c had apparent longevities of 4 and 3 months, respectively. Cohort a, occupying the smallest size classes in March, probably was recruited that month and thus females survived at least 5 months and males at least three months. Cohort d was recruited in October and had nearly died out by February, *i.e.*, a probable life span of 5 months. In summary, the median cohort longevity was 5 months for females and 3.5 months for males. The discrepancy between males and females might reflect a true difference in length of life. However, the size range of primary males is less than that of females, and a lower resolution of overlapping cohorts in males might be responsible for a lower estimate of their life span.

Maturation

When female cohorts were first sampled, the average-sized individual was near or at the size (1.0 mm CL) at which most individuals are male-phase hermaphrodites (Fig. 9). Approximately two months later, the "average" individual in the cohort reached mature female size (larger than the smallest ovigerous female in a particular month). In female cohorts a and d, the average-sized female was then breeding as a female for three months; in cohorts b and c, this period was about 2 months. Thus, breeding females were capable of producing 6–10 clutches of embryos during their lifetime, given the constant iteroparous reproduction discussed earlier and 9 days between spawnings. The mean size of individuals in male cohorts was always equal to or greater than the minimum size (0.8–0.9 mm CL) at which primary males have copulatory appendices and sperm in the sperm ducts. Primary males were thus reproductively mature by the time they were first sampled after recruitment, *i.e.*, within a month or less after settling from the plankton.

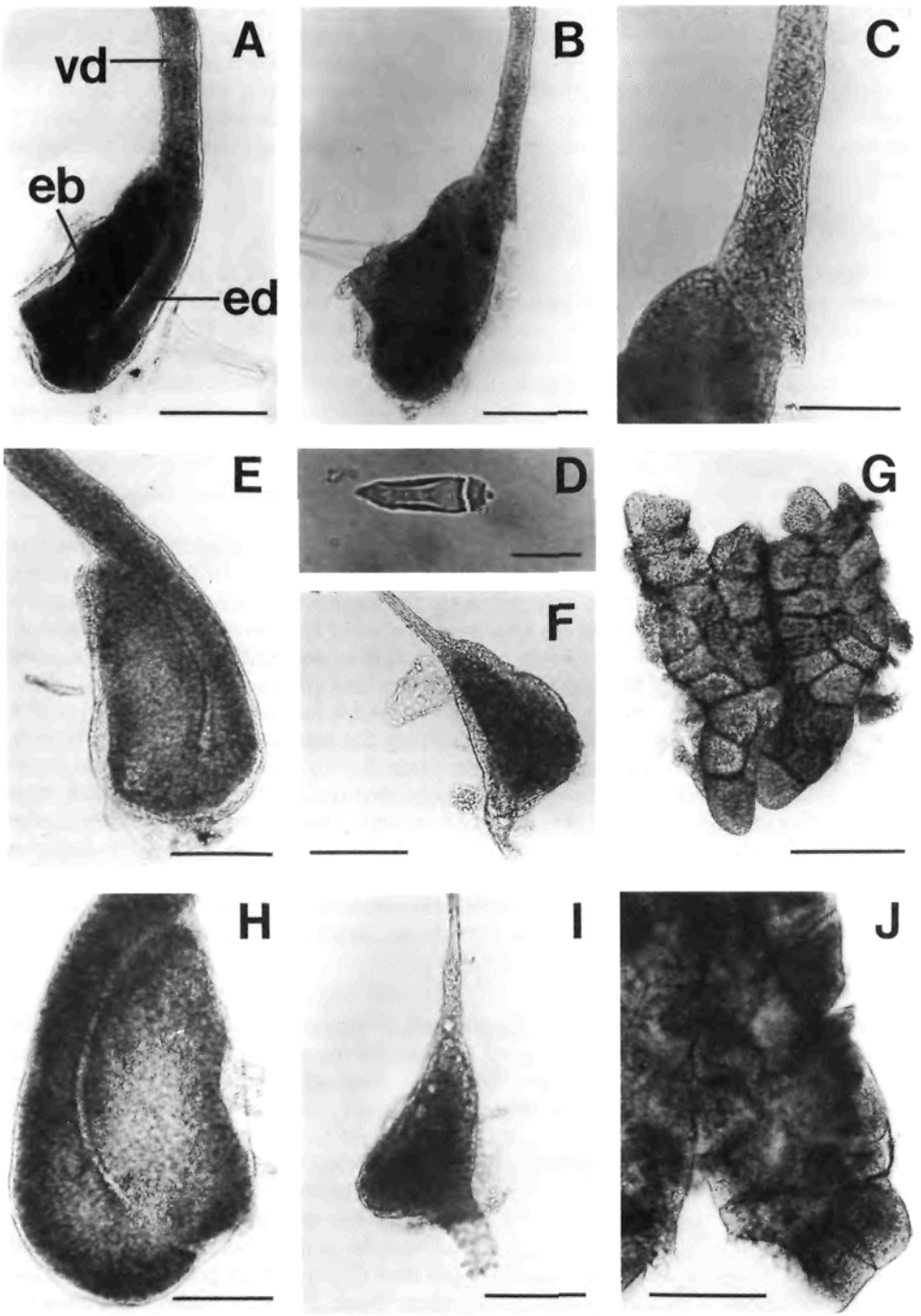


FIGURE 8. Primary sexual characteristics of *Thor manningi* sexual types. A. Terminal end of sperm duct, primary male, 1.1 mm CL; scale bar, 200 μ. B. End of sperm duct in male-phase hermaphrodite, 1.1 mm CL; scale bar, 200 μ. C. Vas deferens full of rod-like sperm cells; scale bar, 100 μ. D. Sperm cell; scale

TABLE I

Degree of ovarian development in Thor manningi *male-phase hermaphrodites**

Size Class	% Individuals with ovary in developmental stage:				
	Stage 1	Stage 2	Stage 3	Stage 4	n
0.70–0.79	100	0	0	0	2
0.80–0.89	94	6	0	0	33
0.90–0.99	96	2	2	0	72
1.00–1.09	97	3	0	0	59
1.10–1.19	98	0	2	0	48
1.20–1.29	98	2	0	0	54
1.30–1.39	80	11	7	2	45
1.40–1.49	86	5	9	0	21
1.50–1.59	50	21	29	0	34
1.60–1.69	27	30	30	13	30
1.70–1.79	25	50	21	4	24
1.80–1.89	20	10	0	70	10
1.90–1.99	18	18	45	18	11
2.00–2.10	0	50	25	25	4

* Stage 1, no noticeable development; Stage 2, vitellogenic oocytes distinct but ovary small; Stage 3, ovary filling at least one-half the space above the caridac stomach; Stage 4, ovary completely filling space above the caridac stomach. Male-phase hermaphrodites are grouped in 0.1 mm CL size classes. n, number of individuals examined in each size class.

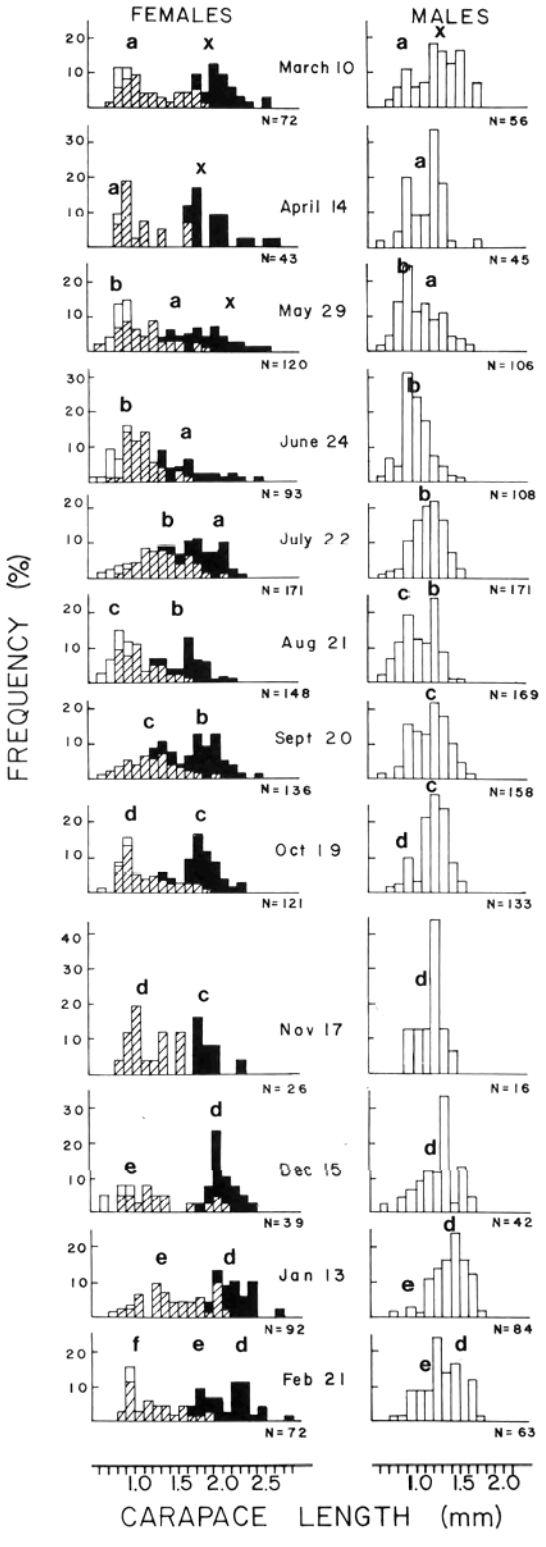
Productivity

The net secondary productivity, estimated by the growth increments method (Crisp, 1971), was 34.7 mg dry weight/m^2 for the 11.6 month period for which it could be calculated. Females (hermaphrodites and primary females) accounted for 63% of this production as opposed to 37% by the smaller males. The average annual biomass of the *T. manningi* population at the Dorado meadows was 8.4 mg dry weight/m^2. Using a value for production extrapolated to 12 months from the 11.6 month period covered in sampling, the production to average annual biomass ratio for this population is estimated to be 4.5. This population was thus replacing its average biomass every 2.7 months (turnover time).

DISCUSSION

Ghiselin (1969) proposed a size advantage model as one explanation for the evolution of protandric hermaphroditism. This model was further amplified by Warner (1979), Charnov (1982), and discussed in various reviews such as Policansky (1982). According to this hypothesis, protandry is favored in a species in which reproductive fitness is positively correlated with size in females but not in males. There is a positive correlation between clutch size and body size in *T. manningi* females (however, this is generally true of gonochoristic caridean shrimp species as well). *Thor manningi*

bar, 10 μ. E. End of sperm duct, primary male, 1.3 mm CL; scale bar, 200 μ. F. End of sperm duct of male-phase hermaphrodite, 1.3 mm CL; scale bar, 200 μ. G. Ovary of the male-phase hermaphrodite whose reduced sperm duct is shown in (F); note vitellogenic oocytes; scale bar, 500 μ. H. End of sperm duct of a primary male, 1.5 mm CL; scale bar, 200 μ. I. End of sperm duct of male-phase hermaphrodite 1.6 mm CL; scale bar, 200 μ. J. Ovary of male-phase hermaphrodite whose reduced sperm duct is shown in (I); eb, ejaculatory bulb; ed, ejaculatory duct; vd, was deferens, scale bar, 500 μ.


FEMALES
MALES
March 10
April 14
May 29
June 24
July 22
Aug 21
Sept 20
Oct 19
Nov 17
Dec 15
Jan 13
Feb 21
N=72
N=56
N=43
N=45
N=120
N=106
N=93
N=108
N=171
N=171
N=148
N=169
N=136
N=158
N=121
N=133
N=26
N=16
N=39
N=42
N=92
N=84
N=72
N=63
FREQUENCY (%)
1.0 1.5 2.0 2.5
1.0 1.5 2.0
CARAPACE LENGTH (mm)

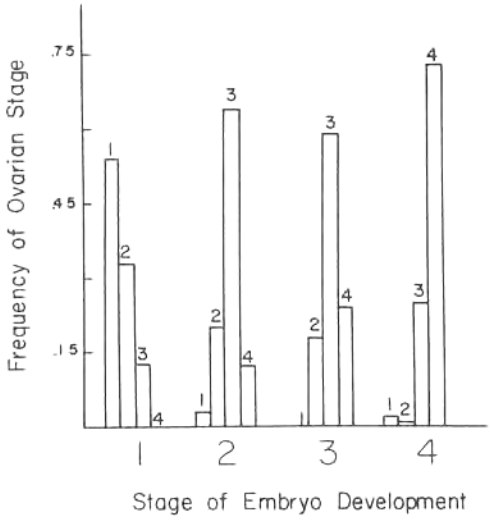


FIGURE 10. Degree of ovarian development in females carrying embryos at early (no noticeable blastodisc, stage 1) to late (nearly hatching, stage 4) stages of development. Stages of ovarian development are written above their histogram bars and range from stage 1 (no noticeable ovarian development) to stage 4 (maximum ovarian fullness). Numbers of females examined with embryos at stage 1, 213; stage 2, 64; stage 3, 34; stage 4, 95.

primary males are smaller than mature females and the evidence available indicates that male reproductive success is not correlated with size. Sufficient sperm production for insemination of the largest female clutches begins at a very small size in primary males. Observations on *T. manningi* in laboratory aquaria give no indication of male-female pair formation, male defense of a territory, fighting between males or other conditions which would favor large male size. This species is very similar in overall morphology and behavior to other hippolytids such as *Heptacarpus pictus* and *H. paludicola*, and mating in these species (Bauer, 1976; 1979), as in many carideans with disparate male-female size, is a brief encounter without complex precopulatory behavior (in which a larger male size could be an advantage).

Given the above, protandry in *T. manningi* and similar species should be advantageous. Females have to pass through a size range at which they are not large enough to produce embryos. It is the same size range at which primary males can produce sperm and fertilize females. It appears that in *T. manningi* females there has been selection for development of male characteristics during their growth (juvenile stage) to minimum breeding female size. Such females, now protandric hermaphrodites as a result of this selection, have increased their total reproductive output, even if they mate just once (as a male) with an adult female (female-phase hermaphrodite or primary

FIGURE 9. Monthly size-frequency distributions of *Thor manningi* females (= male-phase hermaphrodites, female-phase hermaphrodites, and primary females) and males (= primary males). In the female distributions, histogram bars with diagonal lines represent male-phase hermaphrodites; shaded bars mature females; primary females which could be identified as such (n = 11) were too few to represent separately from male-phase hermaphrodites in the figure; unshaded bars, juveniles. Juveniles are not separated from mature males in the male histograms. Juveniles were individuals which could not be reliably sexed and were distributed between males and females at random (see Materials and Methods). Lower case letters represent cohorts, and are placed to show the mean size of individuals in that cohort for a particular month.

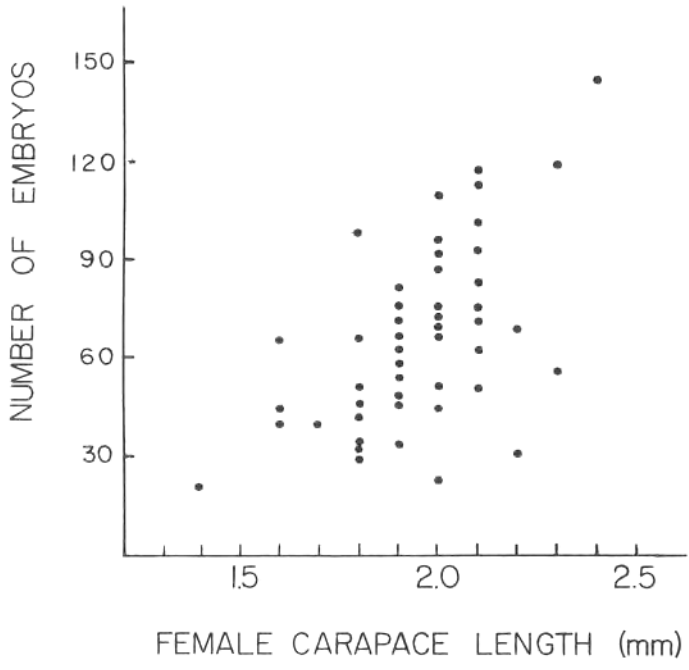


FIGURE 11. Variation of clutch size (number of embryos carried) with female size (carapace length).

female). It is easy to propose this scenario but the disturbing question (*cf.*, Policansky, 1982) is: why have not more caridean species with similar small male:large female size-frequency distributions evolved protandry as in *T. manningi?* There are many hippolytid species with small males and large females. The size-frequency distributions of males and females in the hippolytid *Heptacarpus pictus* showed no overlap at the beginning of the winter breeding season (Bauer, 1976) but sampling throughout the year and examination of sexual characters demonstrated that this was due to differential growth, not protandry. The only well-studied case of protandry described in the Hippolytidae is that of *Lysmata seticaudata* (Dohrn, 1950; Charniaux-Cotton, 1975).

Although protandry is not common in the Hippolytidae, it is usual in the pandalid genera *Pandalus* and *Pandalopsis* (Butler, 1980; Williams, 1984). In these genera, some species are completely protandric *i.e.*, all individuals in the population function first as males, then as females. In other pandalid species, the majority of individuals are protandric while the rest of the population are primary females which do not pass through a male phase. The proportion of primary females in these pandalids varies from a few percent to nearly (but always less than) 50% of the population (Charnov, 1979, 1982). There are *never* primary males in pandalid species with protandry. However, there are some pandalids, *e.g., Pandalus bonnieri* (Hoffman, 1972) and *P. propinquus* (Williams, 1984) which are completely dioecious with primary males and primary females. Fréchette *et al* (1970) reported a protandric system with primary females in the crangonid *Argis dentata,* while Noel (1973) described an apparently similar situation in the processid *Procesa edulis.* In the hippolytid *Lysmata seticaudata,* all individuals are protandric (Dohrn, 1950). Subramoniam (1981b) described the sexual system of the sand crab *Emerita asiatica* as one in which the population is 50%

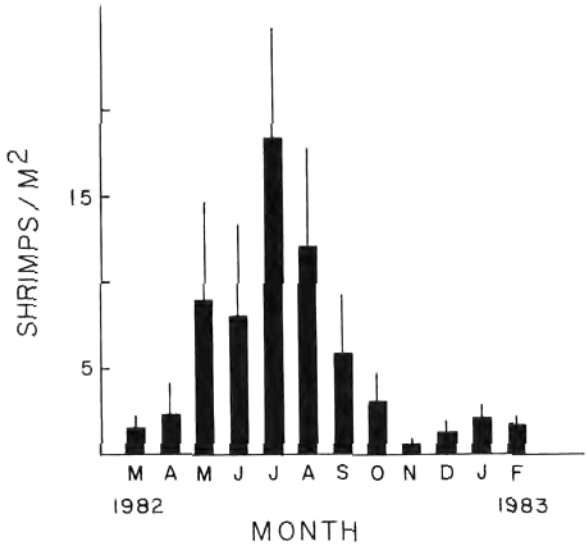


FIGURE 12. Monthly abundances (densities) of *Thor manningi* at Dorado, Puerto Rico, seagrass meadows. Bars are mean number of individuals per square meter, vertical lines above the bars are the upper 95% confidence intervals.

protandric, 50% primary female. *Thor manningi* appears to be unique among decapod crustaceans exhibiting protandric hermaphroditism in that there are primary males; in fact, 50% of the population studied were primary males.

An intriguing question arises: why are there primary males in *T. manningi* populations? Permanent males do not exist in other protandric decapod species. Based on the size advantage model and Charnov's (1982) hypotheses on sex allocation, one might predict that sexual systems with only protandric hermaphrodites or a mix of hermaphrodites and primary females would supplant those with primary males. However, in the *T. manningi* sexual system, primary males may be maintaining themselves genetically in the population by being more efficient inseminators of breeding females than the male-phase hermaphrodites. There is evidence that this is true in *T. manningi*. Primary males produce sperm very soon after arriving on the seagrass meadows and continue to do so throughout their lives. In contrast, male-phase hermaphrodites actively produce sperm only for a brief period, when they are between 1.0–1.2 mm CL. Although larger male-phase hermaphrodites no longer produce sperm, they invariably have a small packet of sperm in the persisting ejaculatory duct. This may indicate that they do not mate as males after gonadal sperm production stops. If they did, one would expect to find some of these larger male-phase hermaphrodites with empty ejaculatory ducts, *i.e.*, sperm has been discharged in mating. In addition, these large male-phase hermaphrodites have copulatory structures (appendices masculinae) which are reduced in size. Primary males, on the other hand, have enlarged appendices masculinae and the third pereiopod is prehensile, perhaps an adaptation for mating (seizing the female). In summary, I hypothesize that primary males fertilize a higher percentage of embryo clutches (produced by the iteoparous females) than do male-phase hermaphrodites and, for that reason, primary males continue to persist so successfully in *T. manningi* populations. Experiments on the mating success of primary

males and male-phase hermaphrodites (of various sizes) must be done in order to test this hypothesis.

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