

VARIATION IN SEXUAL SYSTEMS (PROTANDRY,  
GONOCHORISM) AND REPRODUCTIVE BIOLOGY AMONG  
THREE SPECIES OF THE SHRIMP GENUS *THOR*  
(DECAPODA: CARIDEA)

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ABSTRACT

The sexual systems of the caridean shrimp species *Thor dobkini* and *T. floridanus* were investigated by observations on sexual characteristics and population structure from samples in various locations in Florida. Comparison of the sexual systems and reproductive characteristics of these species were made with those of *T. manningi*, whose population structure and breeding was described from samples in various locations in the Caribbean and from a previous study by Bauer (1986). Unlike *T. manningi*, with a sexual system composed of a mix of protandric hermaphrodites, primary males with prehensile third pereopods, and a low percentage of primary (non-hermaphroditic) females, *T. dobkini* and *T. floridanus* are completely gonochoristic, with smaller size classes composed of juvenile primary females and mainly prehensile males. Non-prehensile individuals with male appendices masculinae (NPM's) were abundant in one non-reproductive sample of *T. dobkini* and were rare but present in most samples of *T. floridanus*. In *T. manningi*, such individuals showed, with increasing size, a relative decrease in appendix masculina size, degeneration of the ejaculatory duct, development of the female character of incubatory basipod flanges on the anterior pleopods, and, in many individuals, a maturing ovary filling with vitellogenic oocytes. These individuals are male-phase hermaphrodites in *T. manningi*, and they lose all male characteristics and become breeding females (Bauer, 1986). Detailed morphometric and other direct observations on the third pereopod and sexual characteristics of NPM's in *T. dobkini* and *T. floridanus*, however, showed that such individuals are primary (non-prehensile) males that do not change sex. It is proposed that the NPM's of *T. dobkini* were males, recruited during a non-breeding season, which had not yet developed full scale prehensility. In *T. floridanus*, NPM's were rare but present throughout the year; some showed feminization of the appendix masculina and ejaculatory duct, perhaps due to parasitization by bopyrid isopods. Other NPM's in *T. floridanus* may simply represent a rare male morph with the ancestral condition (non-prehensile) of the male third pereopod. Measures on reproductive condition (% adult females carrying embryos) of samples from this study tentatively supported a hypothesis of increased seasonality (restriction) of breeding with an increase in latitude when comparing different species of *Thor*, ranging from year round in *T. manningi* to definitely seasonal in the most northerly species sampled, *T. dobkini*. Concomitant measures on the stage of ovarian maturation and the stage of embryo development in incubating females showed that many to most females of all three species produced successive broods continuously during the reproductive season.

Sex change is rare in the decapod Crustacea, occurring chiefly in species of caridean shrimps (Subramoniam, 1981; Policansky, 1982). Even in the Caridea, a group of approximately 2,500 spp. (updated from Chace, 1951; F. A. Chace, Jr., pers. comm.), sex change is not common, with documented cases of hermaphroditism in only 32 species (from Suzuki, 1970; Subramoniam, 1981; Policansky, 1982; Bauer, 1986). In caridean shrimps, the form of hermaphroditism is protandric, i.e., sequential sex change from male to female with increasing age and size of the individual. In some protandric caridean species, all individuals change sex, e.g., the hippolytid *Lysmata seticaudata* Risso (Dohrn, 1950) and some pandalid species (Berkeley, 1930; Butler, 1964, 1980; Hoffman, 1972). In other pandalid species (Butler, 1964, 1980; Charnov, 1982) and in the crangonids *Argis dentata*

Rathbun (Fréchet et al., 1970) and *Crangon crangon* (L.) (Boddeke et al., 1991), a variable percentage of the population (<50%) are *primary females* that never pass through a male phase. *Primary males*, individuals that develop only as males and never change sex, were unknown in protandric carideans until the sexual system of the hippolytid *Thor manningi* Chace was described by Bauer (1986). Partial protandry with some primary males has since been described in the alpheid shrimp *Athanas indicus* (Coutière) by Gherardi and Calloni (1993).

Shrimps of the genus *Thor* are characteristic members of the decapod macrofauna of shallow seagrass and reef communities in subtropical and tropical regions. Chace (1972) first suggested the possibility of protandric hermaphroditism in the western Atlantic *Thor manningi*, *T. dobkini* Chace, and *T. floridanus* Kingsley. Bauer (1986) was able to obtain large population samples of *T. manningi* from the north coast of Puerto Rico. With this material, morphological observations on and morphometric analyses of primary and secondary sexual characters were made, along with observations on size-frequency distributions of population samples, which demonstrated a novel sexual system of partial protandric hermaphroditism in *T. manningi* (Bauer, 1986). Smaller size classes were *overwhelmingly composed of individuals with a male copulatory structure, the appendix masculina, on the second abdominal appendages (second pleopods)*. Fifty percent of these individuals, *true or primary males*, were characterized by *third pereopods (first walking legs) that were prehensile and distally spinose; appendices masculinae that remained massive with an increase in body size (isometric with carapace length); and well-developed ejaculatory ducts (filled with sperm) at all body sizes*. The other individuals with appendices masculinae, *male-phase hermaphrodites (MPH)*, had non-prehensile third pereopods, identical in general morphology and setation to those of embryo-carrying females. With increasing size, MPH individuals showed reduction and loss of the appendices masculinae and ejaculatory ducts and, concomitantly, development of primary and secondary female characteristics (ovary with eggs; incubatory basipod flanges on the anterior pleopods, respectively). It was thus demonstrated that most (98%) of breeding females of *T. manningi* from populations from the north coast of Puerto Rico first passed through an apparently functional male phase before transforming into reproductive females. Evidence indicated that primary males (with prehensile third pereopods) functioned as males throughout their lifetime.

In making species descriptions and illustrations of morphological characters in *Thor* spp., Chace (1972) observed no or little overlap in male/female size in *Thor dobkini* and *T. floridanus*, indicating to him protandry and imperfect protandry, respectively. However, the number of specimens available to him was limited and taken from various locales. We have been able to take much larger population samples of these two species, as well as samples from populations of *T. manningi* from other localities besides that sampled in Bauer (1986). The purpose of this study was to analyze and compare the sexual systems of *T. dobkini* and *T. floridanus*, based on examination of population structure and sexual morphology, with that of *T. manningi* described in Bauer (1986). More specifically, we wished to determine the presence or absence of individuals with non-prehensile third pereopods and male appendices masculinae in *T. dobkini* and *T. floridanus* populations and, if present, to make observations to determine if such individuals were male-phase protandric hermaphrodites, as in *T. manningi* (Bauer, 1986). In addition, we made comparative observations on breeding patterns and other aspects of reproductive biology in populations of *T. manningi*, *T. floridanus*, and *T. dobkini* from tropical, subtropical and warm temperate locations, respectively.

## METHODS

**Collections.**—Samples from *Thor* populations were taken in seagrass meadow (*Thalassia testudinum*) habitats: *T. dobkini* from St. Joseph Bay, Florida (29°48'N, 85°18'W) on 22 August and 3 November 1986 and on 5 May 1987; *T. floridanus* from (a) Florida Bay at Cross Bank (25°01'N, 80°35'W) on 16 March 1986 and between Dump and Roscoe Keys (25°06'N, 80°47'W) on 7 November 1986 and 17 May 1987 and (b) the Atlantic side of Windley Key, Florida (24°57'N, 80°36'W) on 17 March and 7 November 1986 and on 17 May 1987; *T. manningi* from Cayo Enrique, southwest coast of Puerto Rico (17°58'N, 67°02'W) on 7 December 1985, and from seagrass meadows on the west side of Little Dipper Key, Twin Cays, Belize (16°48'N, 88°05'W) on 23 May 1986, January 1987, and 11 July 1988.

Populations of all species were sampled in seagrass meadows with a 76 × 38-cm pushnet with a 1 × 2-mm mesh. *Thor manningi* was also obtained by shaking small fire coral colonies (*Millepora*) and associated sessile fauna or rubble with attached *Stoichactis* anemones over a sieve with a 1-mm mesh, when such living structure occurred on or near the seagrass meadow being sampled. *Thor dobkini* had to be sampled at night (when *Thor* spp. are active and more accessible to pushnets; Bauer, 1986) because of generally low abundances at the St. Joseph Bay site. *Thor floridanus* and *T. manningi* were abundant enough in the locations sampled that day samples yielded sufficient material for study. Specimens taken in samples were initially preserved in formalin and later washed in water and transferred to 70% ethyl alcohol for permanent storage.

Species identifications were based on Chace (1972), with verification of the following key characters in specimens from each sample: presence (*Thor dobkini*) or absence (*T. manningi*, *T. floridanus*) of a spine on the distal half of the flexor margin of the first pereopod; in ovigerous females, small (*T. dobkini*, *T. manningi*) or large (*T. floridanus*) eggs; and 4–6, usually 5 (*T. dobkini*, *T. floridanus*) versus 2–4 (*T. manningi*) spines on the flexor margin of the dactyls of pereopods 4–5 proximal to the distal pair of spines.

**Sexual Morphs.**—Specimens were assigned to a sexual categories on the basis of presence or absence of appendices masculinae, prehensibility of the third pereopod and, in females, presence or absence of embryos. As in the study on *Thor manningi* by Bauer (1986), observations on these characters were made on most specimens with a stereomicroscope at 25–50×. Sexual categories recognized were: *adult females*, individuals without appendices masculinae which carried embryos or, if without embryos, which were as large or larger than the smallest embryo-bearing female of that species [1.3 mm carapace length (CL) in *T. manningi*, 1.4 mm CL in *T. dobkini*, 1.7 mm CL in *T. floridanus*]; *juvenile females*, individuals without appendices masculinae which were smaller than the smallest embryo-bearing female of that species; *prehensile males*, individuals with appendices masculinae and prehensile third pereopods; *male-phase hermaphrodites*, used only for individuals of *Thor manningi* with appendices masculinae and non-prehensile third pereopods (these individuals were shown to change sex to breeding females by Bauer, 1986); *non-prehensile males*, in *T. dobkini* and *T. floridanus*, individuals with appendices masculinae and non-prehensile third pereopods. Evidence will be presented in this report that these latter individuals do not change sex in *T. floridanus* and *T. dobkini*, but are primary males, and thus for construction of size-frequency diagrams, these relatively rare morphs were classified as males.

**Morphometry.**—to determine if individuals of *Thor dobkini* and *T. floridanus* with appendices masculinae but with third pereopods scored as non-prehensile ("NPM individuals") were primary males or, as in *T. manningi* (Bauer, 1986), male-phase hermaphrodites, morphometry of several secondary sexual characters were done on these individuals for comparison with similar measures in females and prehensile males. Thirty NPM's, 30 prehensile males, and 30 females were chosen at random from the only sample of *T. dobkini* (November 1986) in which NPM's were encountered and from among several samples of *T. floridanus* from Windley Key. In addition, 30 prehensile males and 30 females of *T. dobkini* were chosen from the May 1987 sample, one in which only larger breeding adults but no juveniles nor NPM's were found, for comparison with the November *T. dobkini* sample, composed of non-reproductive individuals. In all individuals with appendices masculinae (prehensile males, NPM's), a third pereopod, second pleopod with the appendix masculina, and an ejaculatory duct (dissected from the base of the last pereopod) were removed and mounted on a slide for viewing with transmitted light at 100×. The maximum width (flexor to extensor margin) of the distal half of the pereopodal propodus, the length of the pereopodal dactyl (minus terminal spines), the number of stout setae on the distal half of the propodus, the length of the appendix masculina (minus spines) and the maximum width of a non-muscular blade (basipod flange) from the second pleopod were measured or counted. The maximum width and length of the ejaculatory duct were measured. Similar counts and measures were made on females except for those concerning the appendices masculinae and ejaculatory ducts, structures not present in females.

Relative growth of various characters was described qualitatively with plots of measures or counts

of characters against carapace length, the measure of body size. Quantitative description of relative growth of characters for different sexual morphs is provided with regression equations of the form:  $\log y = \beta \log x + \log \alpha$  where  $y$  = the dependent variable,  $x$  = the independent variable (carapace length),  $\alpha$  =  $y$ -intercept and  $\beta$  the slope of the regression equation (Kuris et al., 1987), with continuous measures of  $x$  and  $y$  in millimeters. Following Kuris et al. (1987), relative growth of a character was considered isometric when the slope of the regression line was 1 (0.9–1.1). Data transformation was of the form " $\log(y+1)$  and  $\log(x+1)$ " because values of  $y$  were usually less than one, as were some values of  $x$  in each data set. Regressions equations and associated statistics were calculated with the Systat statistical package (Wilkinson, 1988).

*Size Frequency Distributions and Reproductive Data.*—Observations were taken on size, sexual characteristics and reproductive condition in specimens from samples in order to construct size-frequency distributions and to characterize reproductive status of populations from which the samples were taken. Each sample was poured into a dissecting pan with a numbered grid on its bottom; subsamples were chosen using a random numbers table until the total subsample reached or exceeded 300. Observations were taken on all specimens of samples in which  $N < 300$ . Size was measured as carapace length (CL), the distance from the posterior edge of the eye orbit to the posterior mid-dorsal edge of the carapace. As in Bauer (1986), observations were taken with a stereomicroscope on the third pereopod (scored as prehensile, as in Fig. 1D, E, or non-prehensile, as in Fig. 1A–C) and on the presence or absence of appendices masculinae (a male secondary sexual character in caridean shrimps) on the second pleopods. Presence or absence of bopyrid isopod parasites was recorded for all specimens.

The presence or absence of embryos was recorded in females (individuals without appendices masculinae). The stage of development of embryos carried by gravid females was recorded, as in Bauer (1986): 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 hatching, little yolk, large eyes. Degree of ovarian development was recorded. Maturing ovaries could be recognized by the presence of large yolky oocytes which were easily observed through the thin transparent cuticle of the dorsal carapace in these shrimps. Since maturing ovaries were observed and recorded in this way in male-phase hermaphrodites of *Thor manningi* (Bauer, 1986) and since an objective of this study was to determine if protandry occurs in other *Thor* species, observations on possible ovarian development were made and recorded on all specimens of all sexual morphs in the three species. Degree of ovarian development was characterized as Stage 1 (no noticeable ovarian development); Stage 2, vitellogenic oocytes distinct but ovary small, filling less than half the space above the cardiac stomach; Stage 3, ovary with vitellogenic oocytes filling more than half but not all the space above the cardiac stomach; Stage 4, ovary completely filling that space.

## RESULTS

*Comparison of Sexual Characters of Non-Prehensile "Males," Prehensile Males, and Females in Thor dobkini and T. floridanus.*—The third pereopods of a breeding female, a non-ovigerous female, a NPM (non-prehensile male), and prehensile males from a non-reproductive and a reproductive population of *Thor dobkini* are shown in Figure 1. The third pereopods of the same morphs in *T. floridanus* were qualitatively similar. Detailed measures of characters contributing to prehensility of the third pereopod (width of the distal half of the propodus, length of the dactyl, number of spines on the distal half of the propodus) are compared among different sexual morphs in Figure 2A–F in *T. dobkini* and in Figure 3A–C for *T. floridanus*. In a *T. dobkini* population in which large breeding females and prehensile males but no NPM's were collected (May 1987), the differences in relative propodal width, dactylar length, and number of propodal spines between adult females and prehensile males are obvious (Fig. 2A, C, E), with males showing relatively wider propodi, longer dactyls, and a much greater number of propodal spines. In the November 1986 population, in which NPM's were collected along with juvenile and non-breeding females and prehensile males, the propodus width of females is clearly less than that of prehensile males at a given size (Fig. 2B, Table 1). The propodus width of the NPM's appears intermediate between that of prehensile males and females in the size range in which NPM's, prehensile males and smaller females overlap (Fig. 2B). Dactylar length and number of propodal spines of the sexual morphs show similar trends, although the slopes of the re-

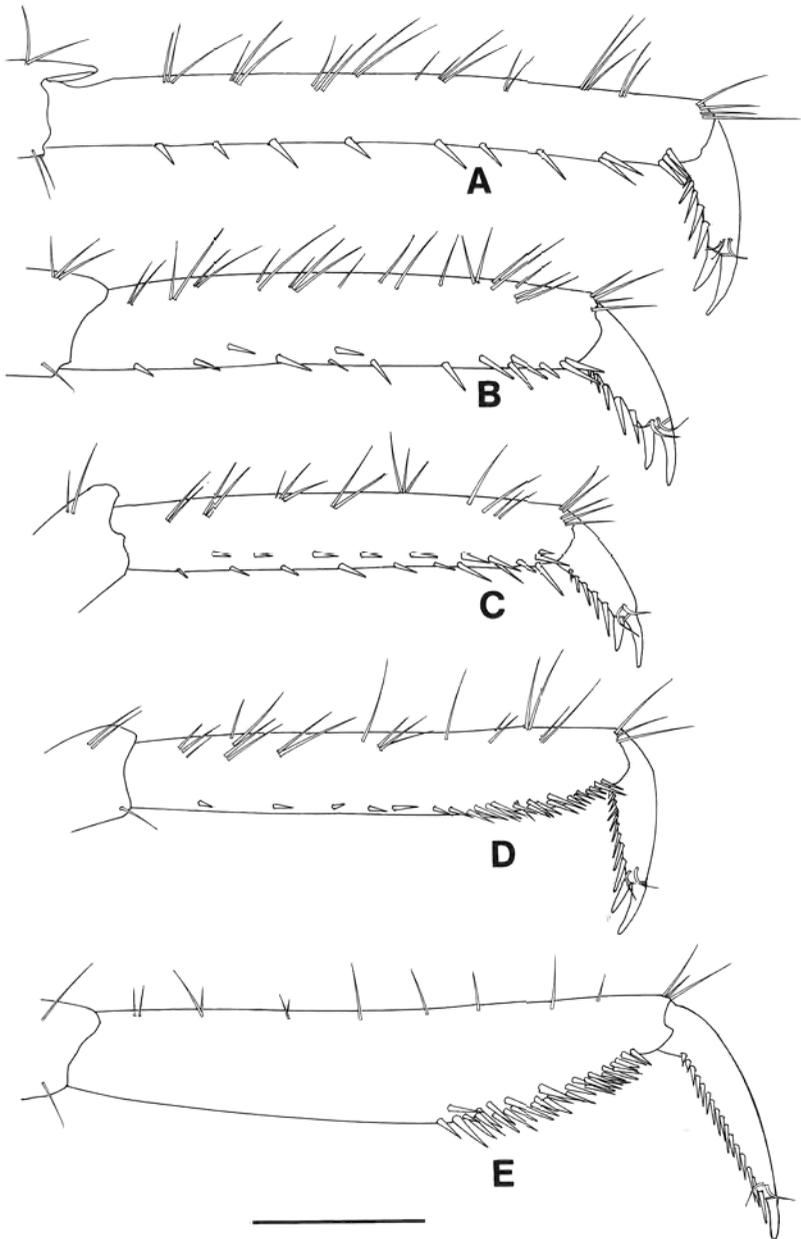


Figure 1. Third pereopods (right side, lateral view) of different sexual morphs of *Thor dobkini*: A, ovigerous female, 2.0 mm carapace length (CL) (May sample, reproductive population); B, non-ovigerous female, 1.6 mm CL (November sample, non-reproductive population); C, non-prehensile male, 1.3 mm CL (November sample); D, prehensile male, 1.3 mm CL (November sample); E, prehensile male, 1.4 mm CL (May sample). Scale bar = 0.5 mm.

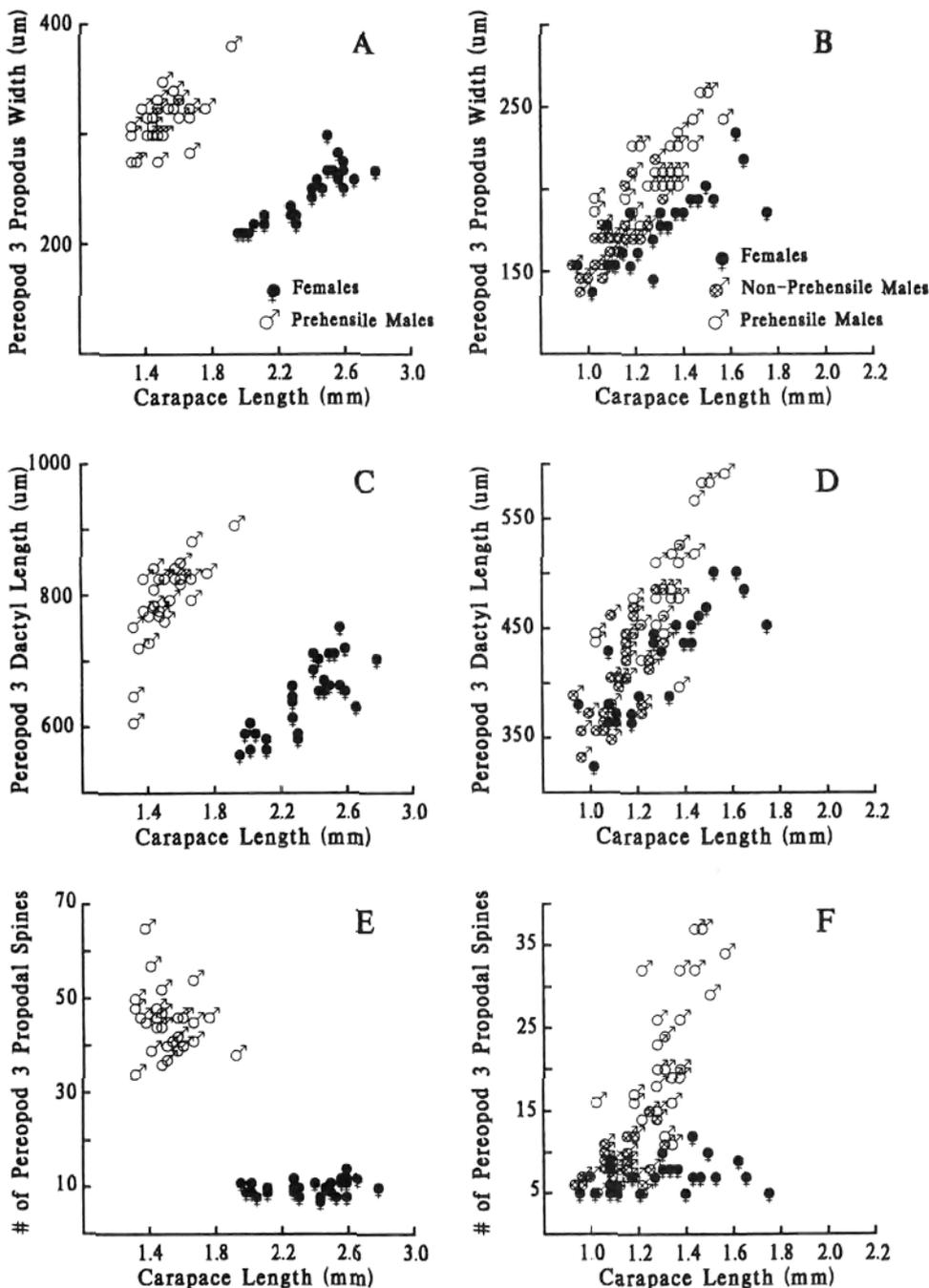


Figure 2. Comparison of pereopod 3 characters in sexual morphs of *Thor dobkini*. Propodal width ( $\mu\text{m}$ ), dactylar length ( $\mu\text{m}$ ), and number of propodal spines are plotted against carapace length (mm) for prehensile males and females from the May (reproductive) population in A, C, E, and for prehensile males, females, and non-prehensile females from the November (non-reproductive) population in B, D, F.

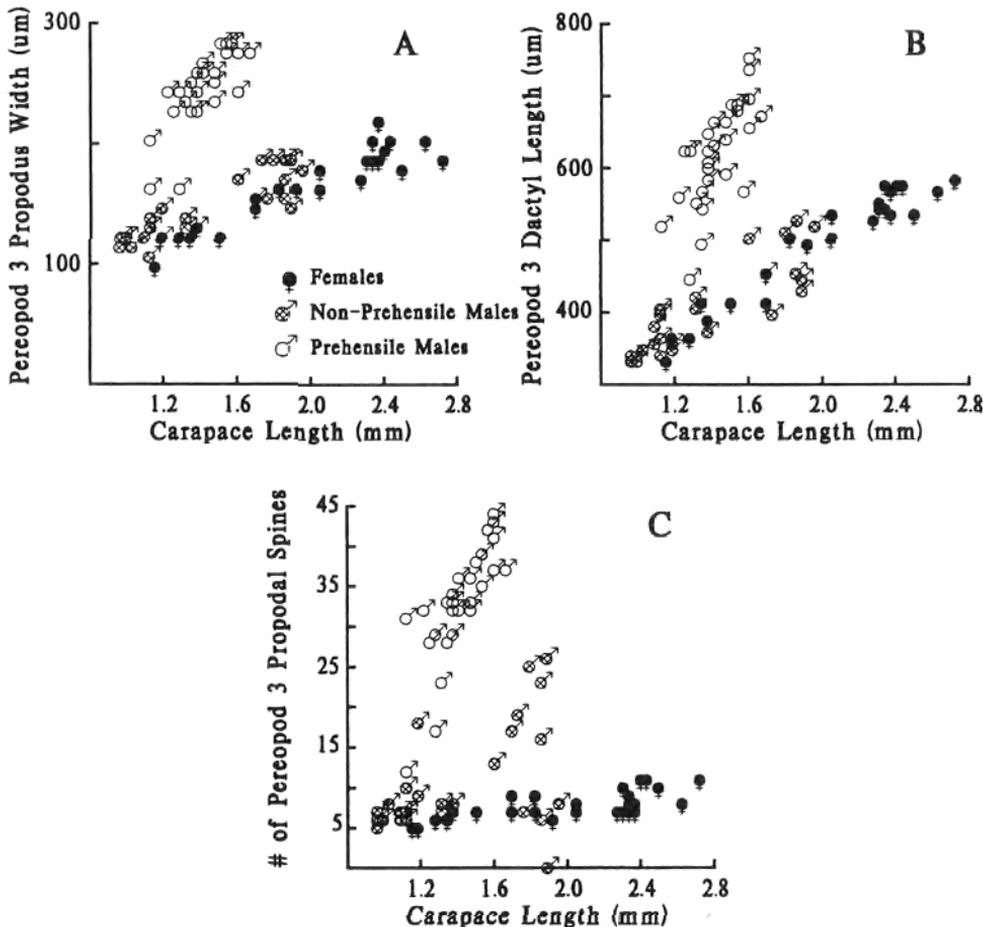


Figure 3. Comparison of pereopod 3 characters in sexual morphs (prehensile males, non-prehensile males, and females) of *Thor floridanus*. Propodal width ( $\mu\text{m}$ ), dactylar length ( $\mu\text{m}$ ), and number of propodal spines are plotted against carapace length (mm) in A, B, and C, respectively.

gression lines for these characters in NPM's are more similar to that of prehensile males than females (Fig. 2D, F, Table 1). In *T. floridanus*, the non-prehensile nature of the third pereopod of specimens classified as NPM's is clearly shown in the similarity with females and differences from prehensile males in propodus width and dactylar length (Fig. 3A, B; slopes of regression lines, Table 1). Propodal spine number was quite variable in NPM's in *T. floridanus*, similar to that of females in smaller specimens, intermediate between that of prehensile males and females in larger specimens (Fig. 3C). This variability is apparent in the non-significant regression for NPM's in this character (Table 1).

The relative sizes of two male characters, appendix masculina length and ejaculatory duct "size" (length  $\times$  width), are compared in NPM's and prehensile males in *Thor dobkini* and *T. floridanus* in Fig. 4A–D. Relative growth of the appendix masculina of prehensile males from a reproductive (May 1987) population was similar to that of smaller prehensile males from a non-reproductive (November 1986) population (Fig. 4A) as shown by a similarity in regression constants (Table 1). There was considerable overlap in the size of appendices

Table 1. Values for the y-intercept ( $\alpha$ ), slope ( $\beta$ ), square of Pearson correlation coefficient ( $r^2$ ), and probability ( $P$ ) from a t-test of the null hypothesis:  $\beta = 0$ , from regression equations of various dependent variables (in mm or as counts) on the independent size variable, carapace length in mm, in the form of  $\{\log(y + 1) = \beta \log(x + 1) + \log \alpha\}$ . Values of  $P > 0.05$  (marked with an asterisk) are considered non-significant, i.e., the null hypothesis is accepted; Species codes: dn, *Thor dobkini* (November sample, non-reproductive population); dm, *T. dobkini* (May sample, reproductive population); fl, *T. floridanus*. Sex codes: f, female; npm, non-prehensile males; pm, prehensile males. P3, pereopod 3.

Dependent variable	Species	Sex	$\alpha$	$\beta$	$r^2$	$P$	Figure (no.)	
P3 propodus width	dm	f	0.920	0.252	0.769	<0.001	2A	
P3 propodus width	dm	pm	1.119	0.175	0.308	0.001	2A	
P3 propodus width	dn	f	1.014	0.181	0.693	<0.001	2B	
P3 propodus width	dn	npm	0.962	0.264	0.530	<0.001	2B	
P3 propodus width	dn	pm	1.012	0.219	0.529	<0.001	2B	
P3 propodus width	fl	f	0.986	0.156	0.885	<0.001	3A	
P3 propodus width	fl	npm	1.023	0.129	0.773	<0.001	3A	
P3 propodus width	fl	pm	0.933	0.328	0.603	<0.001	3A	
P3 Dactyl length	dm	f	1.042	0.381	0.622	<0.001	2C	
P3 Dactyl length	dm	pm	1.159	0.475	0.546	<0.001	2C	
P3 Dactyl length	dn	f	1.102	0.311	0.720	<0.001	2D	
P3 Dactyl length	dn	npm	1.035	0.404	0.424	<0.001	2D	
P3 Dactyl length	dn	pm	1.023	0.447	0.528	<0.001	2D	
P3 Dactyl length	fl	f	1.079	0.302	0.937	<0.001	3B	
P3 Dactyl length	fl	npm	1.130	0.252	0.739	<0.001	3B	
P3 Dactyl length	fl	pm	1.099	0.648	0.583	<0.001	3B	
P3 Propodal spines	dm	f	6.209	0.470	0.049	0.238*	2E	
P3 Propodal spines	dm	pm	72.277	-0.504	0.041	0.284*	2E	
P3 Propodal spines	dn	f	4.169	0.788	0.108	0.100*	2F	
P3 Propodal spines	dn	npm	1.400	3.512	0.206	0.013	2F	
P3 Propodal spines	dn	pm	0.883	3.801	0.324	0.001	2F	
P3 Propodal spines	fl	f	3.475	0.846	0.524	<0.001	3C	
P3 Propodal spines	fl	npm	3.520	1.168	0.077	0.154*	3C	
P3 Propodal spines	fl	pm	2.167	3.101	0.530	<0.001	3C	
Apdx. Masculina length	dn	npm	0.815	0.693	0.541	<0.001	4A	
Apdx. Masculina length	dn	pm	1.026	0.441	0.525	<0.001	4A	
Apdx. Masculina length	dm	pm	1.172	0.444	0.499	<0.001	4A	
Apdx. Masculina length	fl	npm	1.040	0.294	0.549	<0.001	4B	
Apdx. Masculina length	fl	pm	0.839	0.762	0.554	<0.001	4B	
Ejac. Duct "size"	dn	npm	0.847	0.367	0.278	0.007	4C	
Ejac. Duct "size"	dn	pm	0.800	0.479	0.397	<0.001	4C	
Ejac. Duct "size"	dm	pm	0.993	0.312	0.077	0.138*	4C	
Ejac. Duct "size"	fl	npm	1.138	-0.043	0.026	0.462*	4D	
Ejac. Duct "size"	fl	pm	0.661	0.780	0.427	<0.001	4D	
Basipod flange width	dm	f	1.094	0.455	0.256	0.004	5A	
Basipod flange width	dm	pm	0.995	0.013	0.004	0.750*	5A	
Basipod flange width	dn	f	1.253	0.332	0.277	0.003	5B	
Basipod flange width	dn	npm	0.982	0.037	0.032	0.344*	5B	
Basipod flange width	dn	pm	0.923	-0.071	0.036	0.318*	5B	
Basipod flange width	fl	f	0.423	0.982	0.765	<0.001	5C	
Basipod flange width	fl	npm	0.993	0.011	0.040	0.307*	5C	
Basipod flange width	fl	pm	no variation in data (all "0" values)					

masculinae in the NPM's and prehensile males from the same sample (Fig. 4A). On the other hand, in *T. floridanus* the relative size of the appendix masculina clearly decreased with an increase in body size in the NPM's while that of the prehensile males was more nearly isometric (Fig. 4B, Table 1). In *T. dobkini*, relative size of the ejaculatory duct of various male morphs followed similar trends to that of the appendices masculinae, with a great deal of overlap between

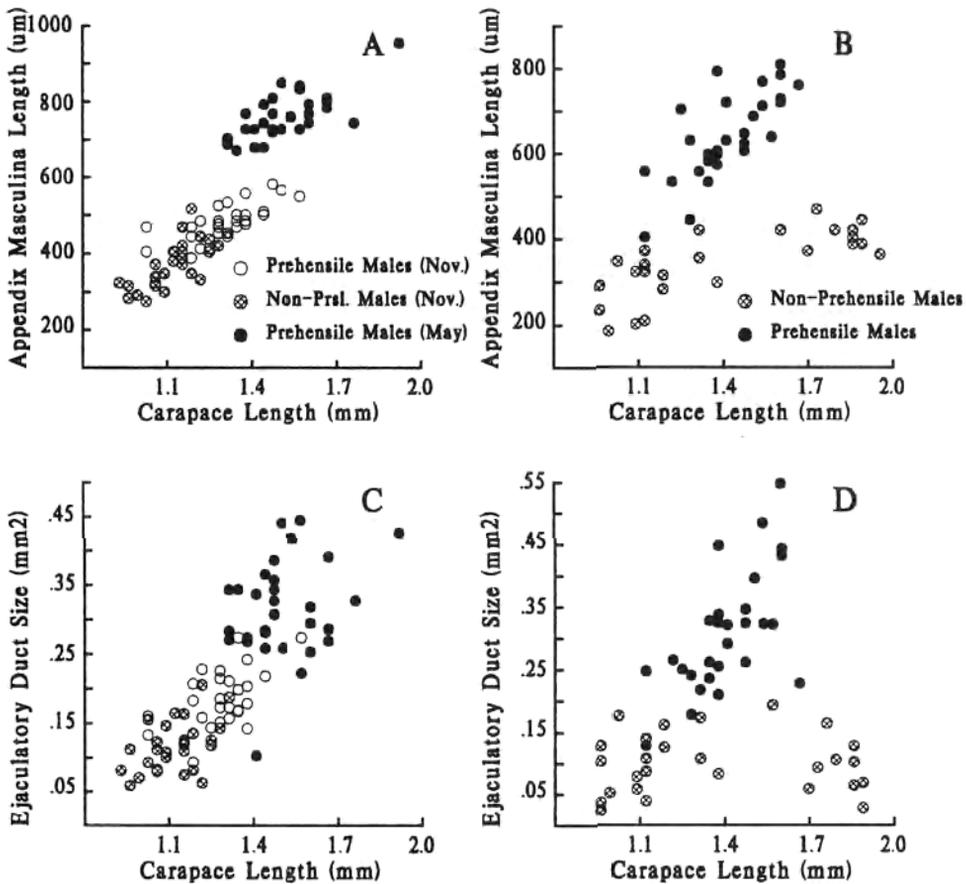


Figure 4. Comparison of male sexual characters (appendix masculina length, ejaculatory duct "size") among male morphs in *Thor dobkini* and *T. floridanus*. The appendix masculina length ( $\mu\text{m}$ ) and ejaculatory duct "size" (length  $\times$  width,  $\text{mm}^2$ ) are plotted against carapace length (mm) in A and C, respectively, for prehensile males (from May and November samples) and non-prehensile males (November sample) of *T. dobkini*, and in B and D for prehensile and non-prehensile males of *T. floridanus*.

prehensile males and NPM's of similar size (Fig. 4C). However, in *T. floridanus*, the size of the ejaculatory duct showed a strong positive correlation with body size in prehensile males while that of NPM's did not, with all NPM's showing small ejaculatory ducts even at larger body sizes (Fig. 4D, Table 1).

In *Thor manningi*, non-prehensile individuals with appendices masculinae develop a female character associated with incubation of embryos, a pronounced basipod flange, on anterior pleopods with an increase in size (Bauer, 1986 and qualitative observations on such individuals in the collections from this study). This character was measured and is compared among different sexual morphs of *T. dobkini* and *T. floridanus* in Fig. 5A-C. In *T. dobkini*, the basipod flange was little or not developed on the second pleopods of prehensile males in the reproductive population used for morphometry while in adult females the flange was quite large (Fig. 5A). In the non-reproductive population of *T. dobkini* in which NPM's were collected, females generally showed greater flange development than that of prehensile males or NPM's (Fig. 5B). In *T. floridanus*, there was no or little development of a basipod flange in prehensile males, NPM's and smaller

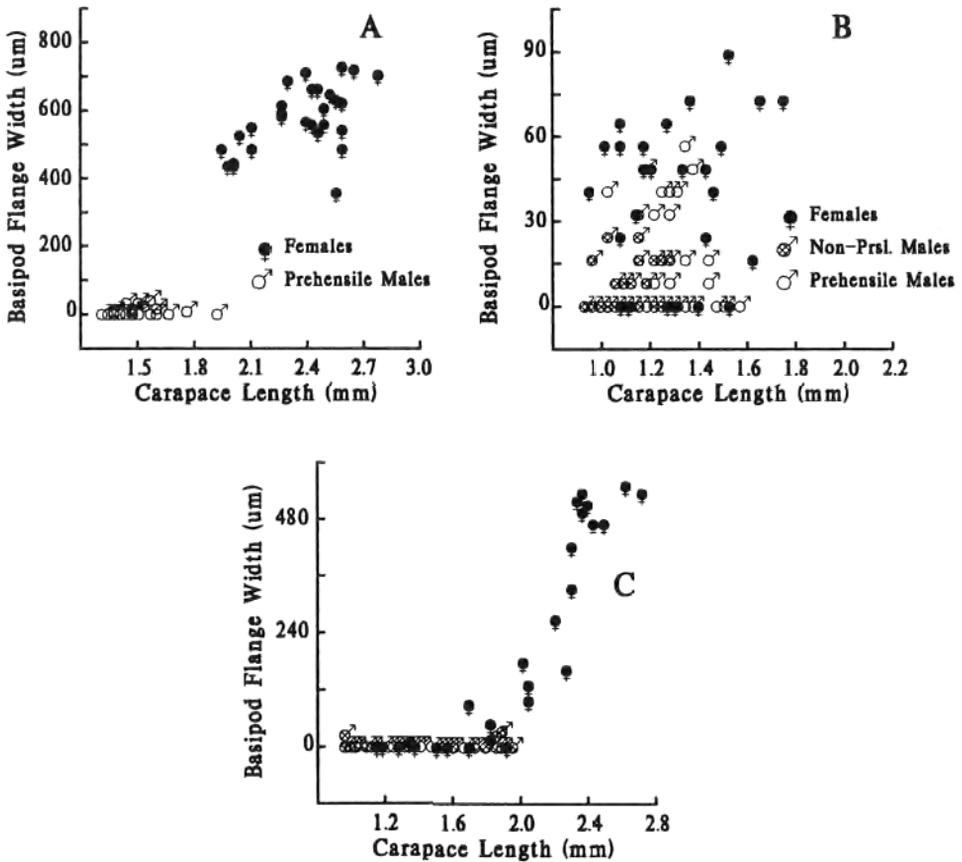


Figure 5. Comparison of basipod flange width ( $\mu\text{m}$ ) plotted against carapace length (mm) in prehensile males and females from the May sample of *Thor dobkini* (A) and from prehensile males, non-prehensile males, and females from the November samples of *T. dobkini* (B) and from samples of *T. floridanus* (C). Symbols legends in B and C are the same.

(juvenile) females, while larger (adult) females showed pronounced development of the flange (Fig. 5C).

The non-prehensile individuals with appendices masculinae of *T. manningi* collected in this study, classified as in Bauer (1986) as male-phase hermaphrodites, were examined for the presence of ovarian maturation, as were the NPM's of *T. dobkini* and *T. floridanus*. In *T. manningi*, ovarian development (Stages 2–4) could be recognized in 65% of these individuals ( $N = 116$ ) (Table 2). In contrast, none of the NPM individuals showed any signs of ovarian development ( $N = 99$  in *T. dobkini*,  $N = 31$  in *T. floridanus*). Accordingly, the non-prehensile individuals with appendices masculinae were classified with the females (male-phase hermaphrodites, as in Bauer, 1986) in the size frequency distributions of *T. manningi* given in this paper, whereas, given all the evidence presented above, such individuals were classified with the males (as non-prehensile males) in the following size frequency distributions of *T. dobkini* and *T. floridanus*.

*Population Structure and Breeding.*—Size frequency distributions for *Thor manningi*, *T. dobkini*, and *T. floridanus* populations are given in Figures 6–9. In *T. manningi*, smaller size classes were dominated by prehensile (primary) males and

Table 2. Degree of ovarian development in male-phase hermaphrodites from Caribbean *Thor manningi* populations sampled in this study

Size class	% Individuals with ovarian development at:				N
	Stage 1	Stage 2	Stage 3	Stage 4	
0.70-0.79	100	0	0	0	2
0.80-0.89	60	20	20	0	5
0.90-0.99	67	33	0	0	6
1.00-1.09	60	40	0	0	10
1.10-1.19	56	11	33	0	9
1.20-1.29	39	44	11	6	18
1.30-1.39	29	29	29	12	17
1.40-1.49	17	17	33	33	12
1.50-1.59	20	60	20	0	5
1.60-1.69	23	8	23	46	13
1.70-1.79	20	33	22	44	9
1.80-1.89	20	0	20	60	5
1.90-1.99	33	33	17	17	6

male-phase hermaphrodites (Fig. 6). Some primary (non-hermaphroditic) juvenile females were present as well, composing 5.8%, 5.2%, 16.4% and 16.6% of the combined juvenile female + male-phase hermaphrodite portion of the population in the December 1985, May 1986, July 1988 and January 1987 samples, respectively. In contrast, the smaller size classes of *T. dobkini* and both populations of *T. floridanus* were dominated by prehensile males and juvenile (non-hermaphroditic) females (Figs. 7-9). Adult females dominated larger size classes in all populations observed. Non-prehensile males were observed only in the November 1986 sample of *T. dobkini*, a sample in which they were also more abundant than prehensile males (Fig. 7). In *T. floridanus*, non-prehensile males were observed in samples from both locations, but their frequency was always low (Figs. 8, 9).

Ovigerous (breeding) females were observed in all time periods sampled in *Thor manningi*, with the percentage of adult females carrying embryos at 82.3, 95.3, 83.7, 97.2 in the December 1985, May 1986, January 1987 and July 1988 samples, respectively. In *T. dobkini*, breeding females were found in the August 1986 (61.5% adult females ovigerous) and May 1987 samples (84.6% adult females ovigerous) while no breeding females were found in the November 1986 samples (Fig. 7). Breeding females were present in all samples of *T. floridanus* from Windley Key, with percent adult females carrying embryos at 47.8, 50.6, and 40 in the March 1986, November 1986, and May 1987 samples, respectively (Fig. 8). In contrast, only a few breeding females (2.4% of adult females) were found in the March 1986 population of *T. floridanus* from Florida Bay, with higher values in the November 1986 (43.8%) and May 1987 (72%) samples (Fig. 9).

The relationship of the stage of ovarian development with the stage of embryo development indicates the degree to which females in a population are producing successive broods. In all species, most breeding females carrying advanced embryos had ovaries in advanced stages of maturation, while females which had more recently spawned (embryos at Stage 1) had little ovarian development (Fig. 10). The hypothesis of no relationship between stage of ovarian development and stage of embryo development in incubating females was tested with chi-square analysis of  $4 \times 4$  two-way tables. Values of chi-square (9 degrees of freedom) were 354.2 (N = 455 females), 129.0 (N = 150), and 224.5 (N = 268) for *T.*

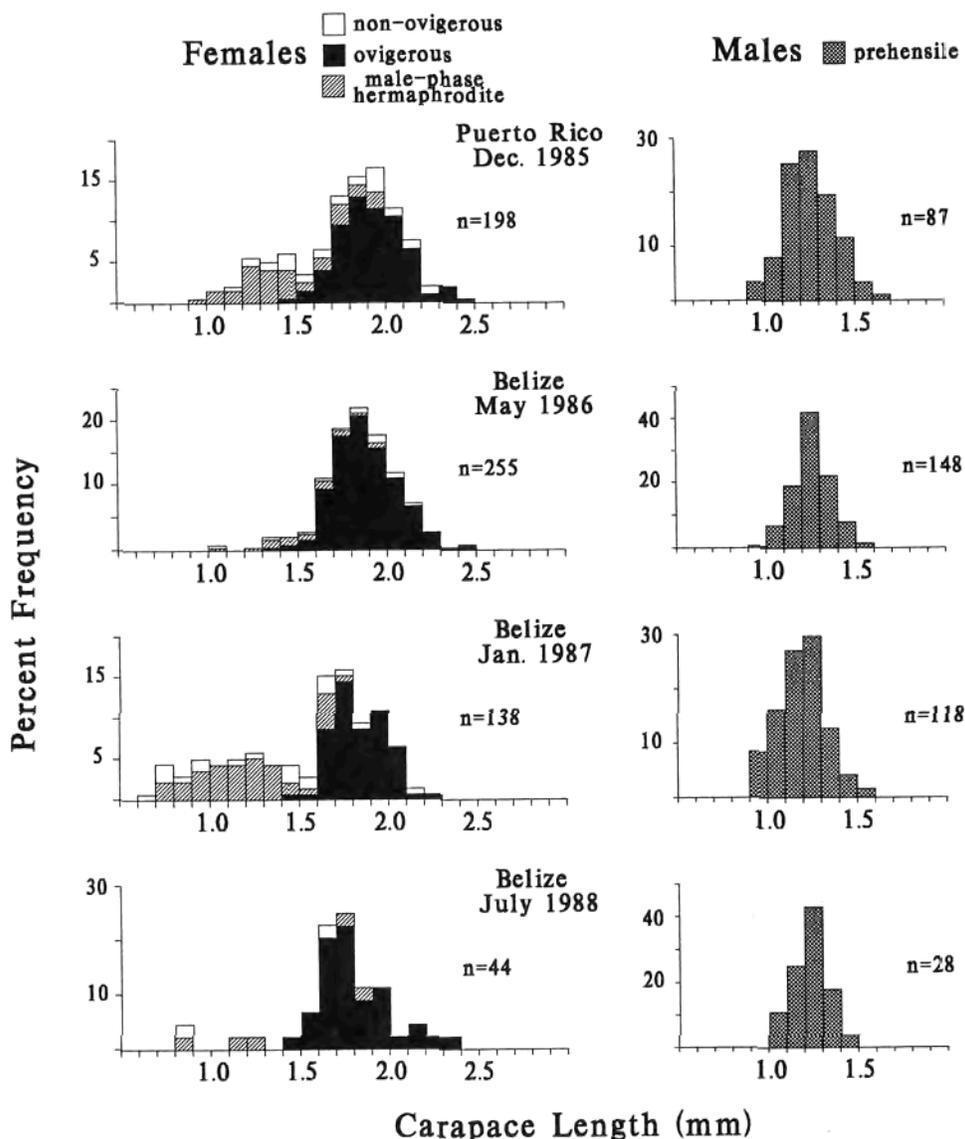


Figure 6. Size frequency distributions of *Thor manningi* from southern Puerto Rico and from Belize.

*manningi*, *T. dobkini* and *T. floridanus*, respectively. The null hypothesis of no relationship was rejected in all cases ( $P \ll 0.001$ ).

#### DISCUSSION

Analysis of sexual types and population structure of *Thor dobkini* and *T. floridanus* shows that the sexual system is gonochory, not partial protandry as described for *T. manningi* (Bauer, 1986). In most samples of both *T. dobkini* and *T. floridanus*, smaller size classes contained, in addition to prehensile males, juvenile females, i.e., individuals without the male appendices masculinae and with non-prehensile third pereopods. In one sample of *T. dobkini* (May 1987), there

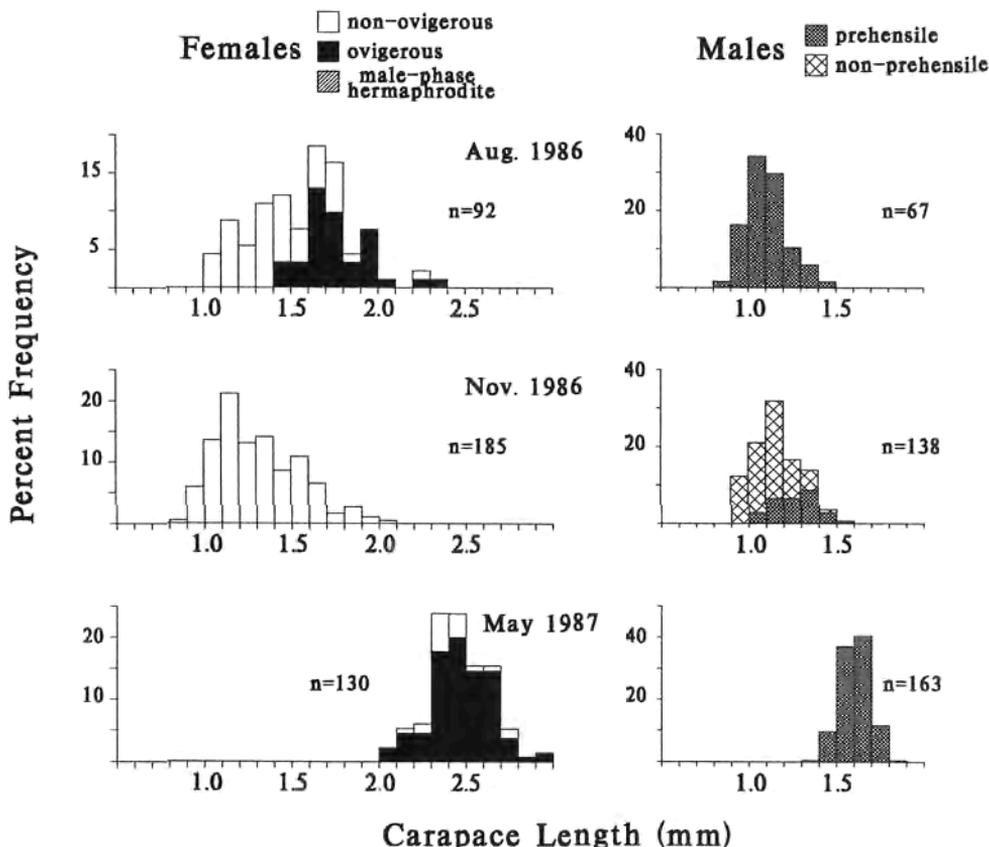


Figure 7. Size frequency distributions of *Thor dobkini* from St. Joseph Bay, Florida.

were no juvenile females nor small prehensile males, only large prehensile males and adult breeding females. In that sample, there was no overlap in size between males and females. Observations of this type of size frequency distribution suggest protandry and account for suggestions of protandry in *T. dobkini* (Chace, 1972) and other species with sexual dimorphism in size. However, the other two samples of *T. dobkini* from an August and a November sample clearly showed an abundance of juvenile females completely overlapping in size with males. Bauer (1976) also found a similar phenomenon in the hippolytid caridean *Heptacarpus pictus* (Stimpson). A non-reproductive population with complete overlap in male and female size changed with time to a reproductive population in which females had outgrown the males, giving rise to an non-overlap of male and female size.

Populations of *Thor manningi* from two different sites in the Caribbean were sampled for comparison with those in which the unusual system of protandry of this species was first described and studied in detail (Bauer, 1986). As in those populations from the north coast of Puerto Rico, smaller size classes contained both prehensile males and non-prehensile male-phase hermaphrodites. Sex change in the latter group was verified directly by observation of ovarian development in many individuals and by qualitative observations indicating reduction of appendices masculinae and development of basipod flanges with an increase in size, similar to that shown with quantitative observations by Bauer (1986). The inci-

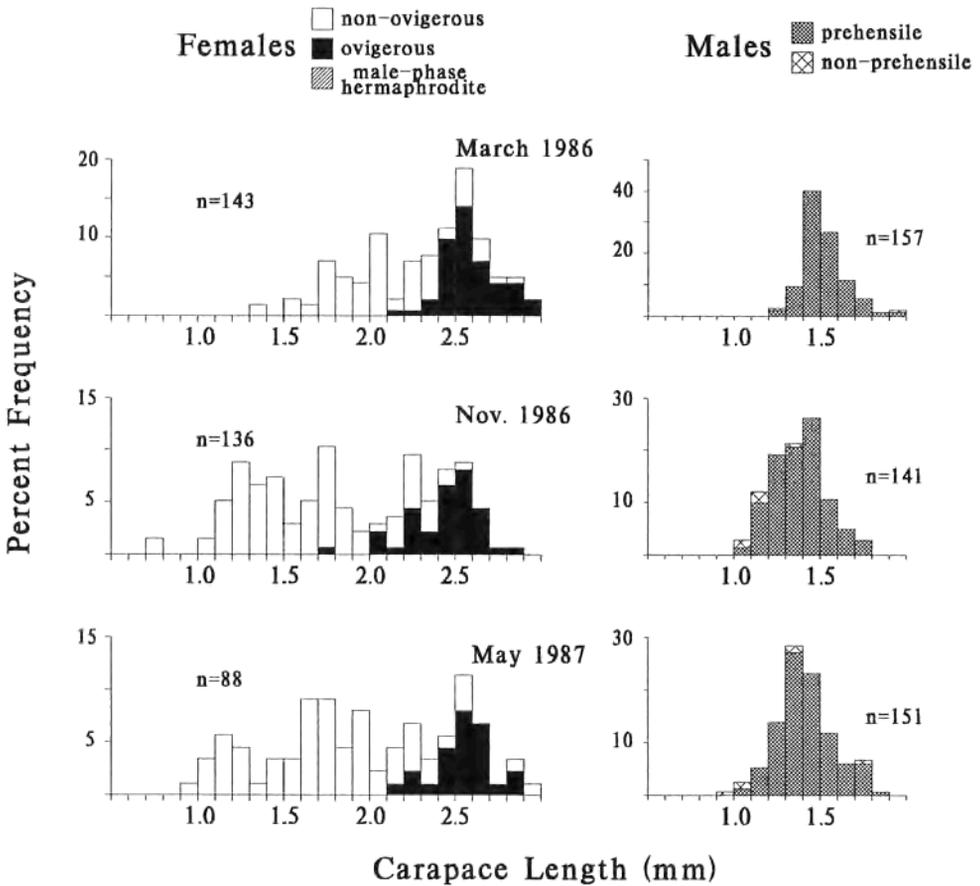


Figure 8. Size frequency distributions of *Thor floridanus* from the eastern (Atlantic) side of Windley Key, Florida.

dence of primary females, estimated from the percentage of juvenile females in the combined juvenile female + male-phase hermaphrodite segment of a sample, was somewhat higher (5.2–16.6%) in the Caribbean populations from this study than that (2.4%) of the population from the north (Atlantic) coast of Puerto Rico (Bauer, 1986). Our conclusion is that the unusual system of protandry in *T. manningi*, i.e., with prehensile primary males, protandric hermaphrodites, and a low percentage of primary females is qualitatively similar in populations sampled throughout its range.

Given that individuals with non-prehensile third pereopods and with appendices masculinae represent a male phase of protandric sex change in *Thor manningi*, careful search and special scrutiny was made for and given to individuals with these characters from *T. dobkini* and *T. floridanus* populations sampled. Such individuals were fairly abundant in only one sample of *T. dobkini*, that from a non-reproductive population, but were quite rare but present in most samples of *T. floridanus* from the Atlantic side of the Florida Keys and from Florida Bay. All individuals were subjectively scored as prehensile or non-prehensile when viewed with a stereomicroscope. This distinction was always quite clear in *T. manningi* in Bauer (1986) and in the present study. Morphometry was conducted

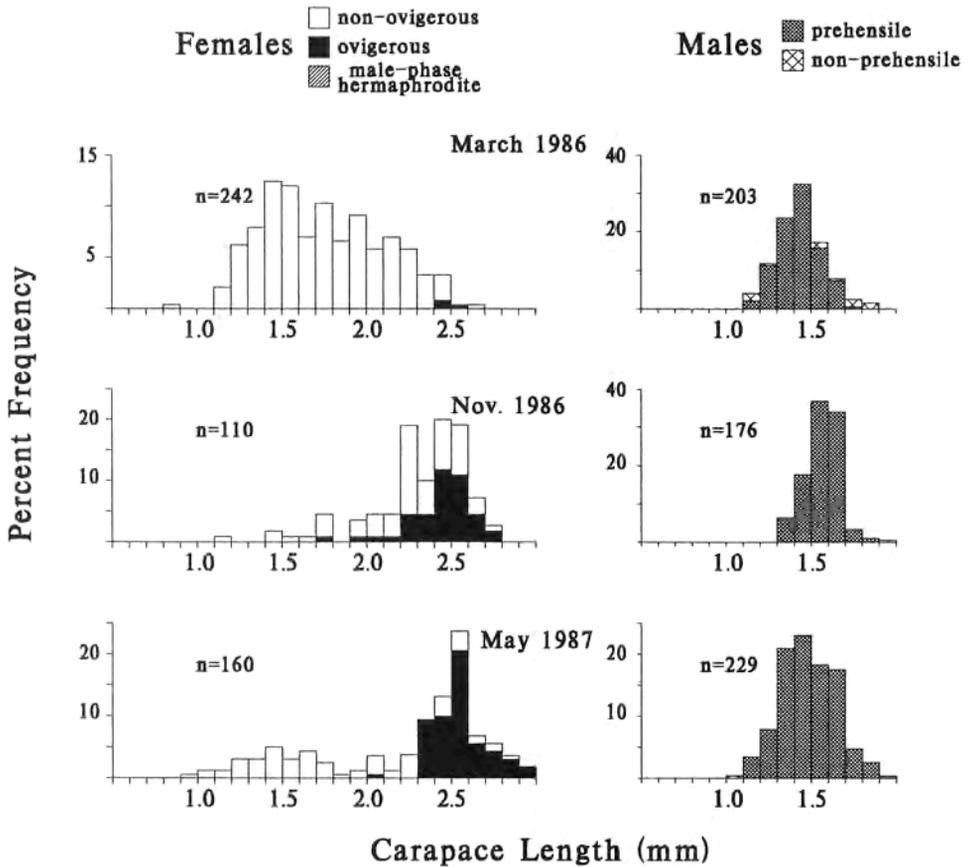


Figure 9. Size frequency distributions of *Thor floridanus* from Florida Bay, Florida.

on the third pereopods of the non-prehensile individuals with appendices masculinae ("NPM's") in *T. dobkini* and *T. floridanus* from this study in order to determine if the subjective scoring was adequate to distinguish prehensile from non-prehensile, i.e., were these individuals really non-prehensile? Comparisons of pereopod 3 characters distinguishing prehensile from non-prehensile, i.e., the width of the distal propodus, length of the dactyl, number of spines on the distal propodus (wider, longer, more numerous, respectively, in prehensile males) were made among NPM's, prehensile males and females in *T. dobkini* and *T. floridanus*. These analyses showed the clear separation in these characters between prehensile males and (non-prehensile) females, and demonstrated that in general the structure of the NPM's pereopod 3 was similar to that of females, i.e., non-prehensile, but with some tendency, both quantitatively and qualitatively, towards prehensileness in NPM specimens of *T. dobkini* but not *T. floridanus*.

Study of relative growth of key sexual characters of NPM individuals of *Thor dobkini* and *T. floridanus* was made for comparison with those done on similar individuals of *T. manningi* in Bauer (1986). The relative growth of the appendix masculina and ejaculatory ducts of NPM's of *T. dobkini* appeared similar to that of prehensile males. In *T. manningi*, such individuals (male-phase hermaphrodites) showed a marked relative decrease in size of the appendix masculina with increase

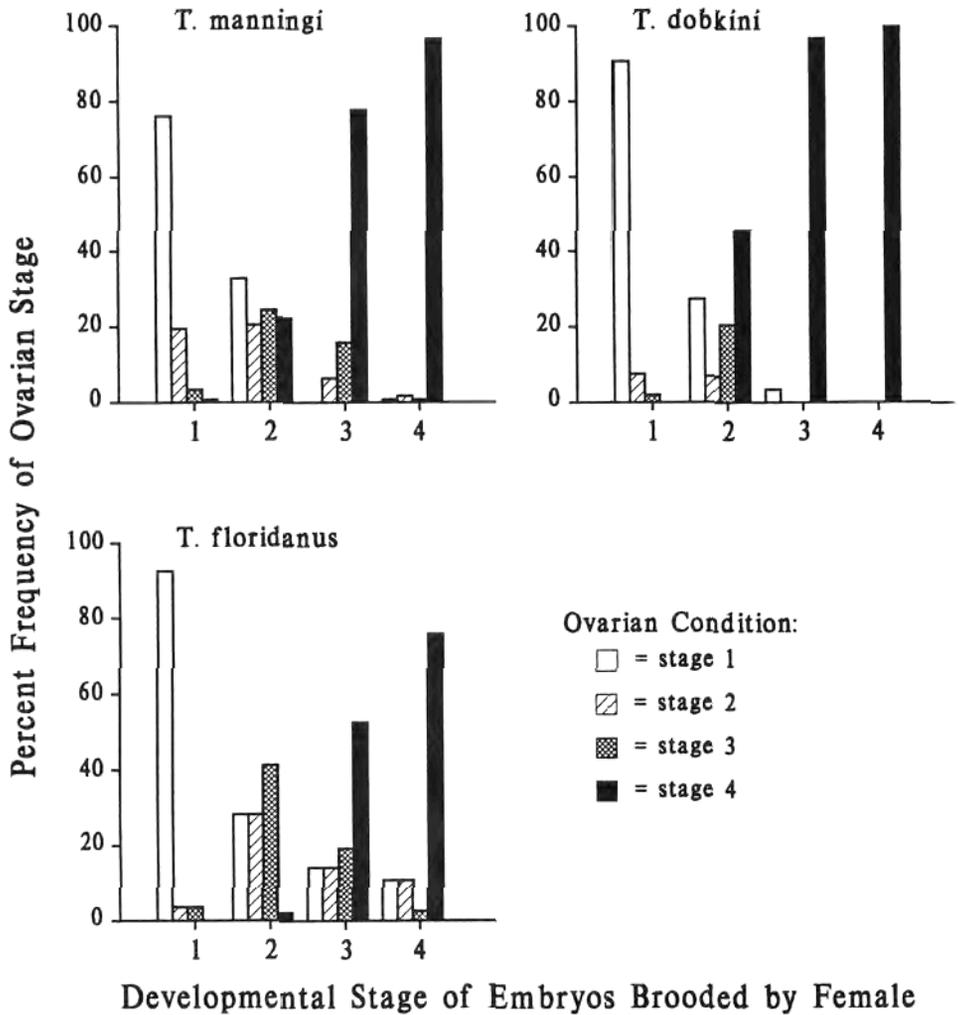


Figure 10. Histograms showing the relationship in embryo-bearing females between stage of development of their ovaries (stage 1 = no development, to stage 4 = ripe, full of vitellogenic oocytes) with the stage of development of their brooded embryos (stage 1 = recently spawned, to stage 4 = near hatching) in *Thor manningi* (N = 455 females), *T. dobkini* (N = 150) and *T. floridanus* (N = 268).

in body size (negative allometry) while relative growth of appendices masculinae was isometric in prehensile males (Bauer, 1986). On the other hand, the basipod flange of the pleopods, a female character associated with incubation of embryos, was never developed to any degree in prehensile males, but did develop in the male-phase hermaphrodites of *T. manningi* with an increase in size, in conjunction with degeneration of the male system (ejaculatory duct) and concomitant appearance of maturing ovaries. In *T. dobkini*, NPM's showed no significant development of the basipod flange, no degeneration of ejaculatory ducts, and no sign of gonadal maturation, so easily observed in male-phase hermaphrodites of *T. manningi*.

Our conclusion is that the NPM's of *T. dobkini* are primary males which had

not yet developed full prehensility of the third pereopod. Such non-prehensile males were not observed in the other two samples, both from reproductive periods, including one from August in which the size of the males (all prehensile) overlapped completely with those of the November sample in which a majority of males were non-prehensile. Our interpretation is that the non-prehensile males of the sample without breeding females (non-reproductive) were individuals recruited into the population as it was entering a non-reproductive period. The male character of prehensility had not yet developed in these mostly smaller individuals as it had in other prehensile males perhaps surviving from an earlier reproductive period (the preceding summer). A similar mixture of males, with varying degrees of development in some male characters, was observed during the fall non-reproductive period in *Heptacarpus pictus* from southern California (Bauer, 1976).

In *T. floridanus*, NPM's were rare but encountered in samples from all time periods either in the Windley Key or Florida Bay location. As in *T. dobkini*, NPM's did not develop a basipod flange and none were observed with ripening ovaries as would be expected in some if they were protandric. However, in the relative growth of both the appendix masculina and in that of the ejaculatory duct, the NPM's were similar to the male-phase hermaphrodites of *T. manningi* (Bauer, 1986), i.e., the absolute size of these characters did not increase significantly with an increase in body size. We checked our records on the *T. floridanus* NPM's used for morphometry, and we found that 6 of the 10 largest individuals were parasitized by bopyrid isopods. The infestation rate of all *T. floridanus* by these bopyrids, *Bopyrinella thorii* (Richardson) and *Loki circumsaltanus* Markham, was 1.8% (N = 1824) while that of the NPM's (N = 29) was much higher at 31.3%. For some NPM's, female characteristics such as non-prehensile third pereopods and reduced size of appendices masculinae and ejaculatory ducts might have been due to a feminization effect of the bopyrid isopods, which castrate females and have been reported to feminize secondary sexual characters in some carideans and other decapods (Reinhard, 1956). No *T. dobkini* were parasitized and the rate of infestation by bopyrids in the *T. manningi* observed in this study was 0.7% in N = 1,016 (only adult females).

Our conclusion is that the rare NPM's of *T. floridanus* are primary males which have not developed or have retarded development of various male characters because of parasitization, developmental anomalies, or other unknown factors. Perhaps some of these NPM's are simply male morphs with the primitive genotype for the third pereopod. In carideans, prehensility in males is relatively rare, known only in a few groups, e.g., some *Hippolyte* spp. (Chace, 1972), *Pandalus danae* Stimpson among *Pandalus* spp. (Butler, 1980). Most male carideans have non-prehensile third pereopods, and it is reasonable to assume that the group from which *Thor* descended was non-prehensile. Whatever the case may be, there is no indication that the NPM's observed in this study in *T. dobkini* nor in *T. floridanus* were sex-changers as observed and analysed in detail in *T. manningi* (Bauer, 1986).

The results of this study show that two species of *Thor* from the Western Atlantic, *T. dobkini* and *T. floridanus* are gonochoristic, without sex changers in their populations, while in another species, *T. manningi*, most females go through a male phase before breeding as females (Bauer, 1986; this study). Policansky (1982), in his review of sex change in plants and animals, posed the question: why do relatively few species change sex when many or most of their relatives do not? This question must now be posed about *Thor*, as well as other caridean groups, such as the pandalids, in which some species are completely gonochoristic

(Hoffman, 1972; King and Moffitt, 1984) while others are completely or partially (with some primary females) protandric (Butler, 1980).

The usual explanation for the evolution of protandry in carideans in the "Size Advantage Model" (Ghiselin, 1969; Warner, 1975; Charnov, 1982; Policansky, 1982) which proposes that sex change is adaptive in species in which reproductive success is correlated with increasing body size in females but not in males. As Bauer (1986) pointed out, many caridean species have small males and large females. The mating system of such species is most likely "pure searching" (Wickler and Seibt, 1981), in which males test as many females as possible for receptivity, mate with any receptive ones that are encountered, and quickly abandon the female after mating in order to search for other receptive females. In such a mating system, there is no selection for large male size associated with defense or guarding of a female. Small males have sufficient sperm to fertilize the largest females in *Heptacarpus pictus* (Bauer, 1976; pers. obs.) which has sexual dimorphism similar to that of *Thor* spp. On the other hand, females of such species have increased fecundity with larger body size, a relationship well known in the Caridea (Bauer, 1986, 1991).

Bauer (1986) supported the view of Hoffman (1972) that sex changers in protandric Caridea, at least in pandalids and in *Thor*, evolved from females and not males, as some previous workers (Charniaux-Cotton, 1975) had suggested. The evolutionary scenario for *Thor manningi* proposed by Bauer (1986) can be summarized in the following fashion. In the group that gave rise to *T. manningi*, there would be increased reproductive fitness in females which, at relatively little energetic cost, produced sperm and developed relatively small appendices masculinae as they grew through the same size range as the smaller primary males in the process of reaching adult female size. Such "females" (protandric hermaphrodites) would reproduce both as males and females and thus largely replace the primary (non-hermaphroditic) females in *T. manningi* because of this reproductive advantage. It was proposed that primary males, unknown in other protandric carideans, remained in *T. manningi* with the evolution of a prehensile third pereopod and (relative to male-phase hermaphrodites) massive appendices masculinae, features suggested as advantageous enough in mating interactions to maintain primary males in the population.

However, this scenario no longer seems tenable since it is now been shown that other species of *Thor* (*T. floridanus*, *T. dobkini*) are completely gonochoristic but most males are prehensile and have massive appendices masculinae like primary males of *T. manningi*. Clearly, the character of prehensility did not evolve in response to the evolution of protandry in females of the ancestor of *T. manningi*, but instead might be viewed as a presumed mating adaptation (clasping) which allowed primary males to be maintained in *T. manningi* as protandry was evolving in a novel female morph. The question of why protandry occurs in *T. manningi* and not in the other two *Thor* spp. which are similar in general morphology, size, and habitat remains unanswered. Perhaps comparative studies on mating behavior of male-phase hermaphrodites and prehensile males in *T. manningi*, and study and description the sexual systems of the other 8 *Thor* spp., along with detailed studies on demography and life history, will reveal the answer to questions posed above about the evolution of sex change in caridean species.

Measures of breeding activity (percentage of adult females carrying embryos) in these three *Thor* species from tropical (*T. manningi*, this study; Bauer, 1986), subtropical (*T. floridanus*) and warm temperate (*T. dobkini*) seagrass habitats support a hypothesis that breeding is more seasonal with an increase in latitude in this group, as in many caridean and penaeoidean shrimps (Bauer, 1992; Bauer

and Lin, 1994). All samples of *T. manningi* populations from four different time periods in this study and monthly samples along the north coast of Puerto Rico (Bauer, 1986) showed that females of this species produced embryos throughout the year. In *T. floridanus*, a high percentage of females from the Windley Key (Atlantic Side) population were reproductively active in November, March, and May, while in Florida Bay, the *T. floridanus* populations sampled showed high breeding activity in the November and May but *not* in the March sample. These differences in breeding activity of the same species at nearby locations might be explained by environmental differences. Water temperatures of seagrass-covered banks of Florida Bay, with its shallow water and restricted circulation, were much more affected by cold air temperatures, especially during strong winter cold fronts, than the coastal waters of the Atlantic side of the Florida Keys (Holmquist et al., 1989a). These habitat differences are reflected in marine faunal differences between Florida Bay and the Atlantic side of the keys, primarily Gulf-Carolinean (temperate) in Florida Bay but somewhat more Antillean (tropical) on the Atlantic side of the Keys (Holmquist et al., 1989b). Reproduction in *T. dobkini*, occurring in the most northerly of the locations sampled, showed indications of strong seasonality, with a high percentage of gravid females in August and May, but with a non-breeding population in November. Sampling at more frequent time periods during the year in *T. floridanus* and *T. dobkini* is needed to confirm these indications of increasing seasonality of breeding with an increase in latitude in *Thor* spp. This might prove difficult for the *T. floridanus* populations in Florida Bay, given the recent mass mortality of the seagrass (*Thalassia testudinum*) (Robblee et al., 1991) which it primarily inhabits.

Successive broods of embryos are produced by breeding females in the three *Thor* spp. studied. In many caridean species of small body size, maturation of a new group of oocytes begins in the ovary at the same time the incubated embryos are developing below the abdomen of the female (Bauer, 1976, 1989). Within a few days after hatching of the embryos, the female with a now mature ovary molts, mates, and spawns a new brood, and the cycle of embryo development and ovarian maturation begins again. This pattern is indicated in breeding females from all three *Thor* spp. sampled here, as in *T. manningi* (1986), by the high positive correlation between the stage of ovarian maturation and stage of embryo development. In *T. manningi*, analysis of cohorts in monthly size frequency distributions indicated that the life span of females on the seagrass beds was approximately 4–5 months (Bauer, 1986), and it was proposed that the intense reproductive effort of this short-lived species was adaptive given the short life span available for reproduction. It appears that a similar intensity of reproduction (continuous production of successive broods) may be characteristic of *T. dobkini* and *T. floridanus* as well.

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