



FIRST DESCRIPTION OF A PURE-SEARCH MATING SYSTEM AND PROTANDRY IN THE SHRIMP
RHYNCHOCINETES URITAI (DECAPODA: CARIDEA)

Raymond T. Bauer and Martin Thiel

(RTB, correspondence, rtbauer@louisiana.edu) Department of Biology, University of Louisiana, Lafayette, Louisiana 70504-2451, U.S.A.;

(MT) Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

ABSTRACT

Previous studies on two species of the genus *Rhynchocinetes* (“hingebeak” shrimps) have described mating systems in which large dominant “robustus” males, with hypertrophied cheliped and third maxilliped weaponry, guard and defend smaller females during copulation. The sexual system of these species is gonochoric (separate sexes). In this preliminary study on the sexual biology of *R. uritai*, we report observations indicating a very different sexual and mating system for *Rhynchocinetes*. A sample of *R. uritai* taken off Shimoda, Japan, revealed a population structure with small males and large females with no overlap in size. Two intermediate-sized individuals showed transitional sexual characteristics indicating sex change from male to female (protandrous sequential hermaphroditism). Transitional individuals had male sexual appendices but also were developing female “breeding dress” (incubatory) characters. Furthermore, these individuals had large vitellogenic oocytes in the gonads, typical of maturing ovaries. Mating observations were made on three receptive females to examine whether the smaller males employ the “pure searching” mating strategy. Matings occurred at night after female molting. Mating behavior was brief and simple: males approached and attempted to grasp the newly molted female, followed by a brief (~ 2 sec) copulation, with no evidence of the complex “caging” (guarding) behavior described in two other *Rhynchocinetes* species. These observations on *R. uritai* suggest a “pure searching” mating system, in which mating is brief with little pre- or postcopulatory interaction between male and female and little or no agonistic behavior among males. Such a mating system is characteristic of decapod shrimp species with small males and larger females, i.e., the population structure observed in our sample.

KEY WORDS: hingebeak shrimps, mating system, protandry, *Rhynchocinetes uritai*, sexual dimorphism, sexual system

DOI: 10.1651/10-3378.1

INTRODUCTION

Mating systems, the behavioral strategies employed to obtain mates, include characteristics such as the number of mates, the manner in which they are encountered and obtained, degree of pair bonding, and parental care (Emlen and Oring, 1977). Considerable variation in mating systems may occur within a particular animal group, both within higher (Wilson, 1975; Thornhill and Alcock, 1983; Dunn et al., 2001; Correa and Thiel, 2003) and lower taxonomic categories, i.e., intragenerically [*Ranitomeya* spp. (poison frogs), Brown et al., 2010; *Pan* spp. (bonobo and chimpanzee), Carnahan and Jensen-Seaman, 2008; *Alpheus* spp. (snapping shrimps), Knowlton, 1980; *Lysmata* spp. (cleaner shrimps), Bauer, 2000; Baeza et al., 2009]. Sexual dimorphism in body size, “ornaments,” and weaponry is often due to sexual selection, both intersexual (epigamic) and intrasexual, associated with particular mating systems (Darwin, 1871). The evolution of mating systems and associated sexual dimorphism can often be explained by the ecological milieu and phylogenetic constraints.

Crustaceans are a group in which considerable variation in mating systems occurs (Salmon, 1983; Christy, 1987; Bauer and Martin, 1991; Duffy and Thiel, 2007). Within the decapod crustaceans, the caridean shrimps are a

particularly diverse group, both ecologically and taxonomically (Bauer, 2004). Mating systems and associated sexual dimorphism in Caridea are correspondingly diverse, and four basic categories of mating systems have been documented (Correa and Thiel, 2003; Bauer, 2004). In “pure searching,” small agile males more or less continually search for females that have just undergone a parturial (prespawning) molt. Mating occurs quickly with little or no pre- or post-copulatory behavior. In other carideans, a male may detect and seek out a premolt parturial female, guard her until the molt, when mating occurs, and then quickly abandon her to search for other such females (“search and attend”—Correa and Thiel, 2003; “temporary mate guarding”—Bauer, 2004). In a “neighborhoods of dominance” system, females are attracted to large dominant males and are guarded by them through both the mating molt and subsequent postmating spawning, e.g., *Rhynchocinetes typus* H. Milne-Edwards, 1837 in Correa et al. (2000) and *Macrobrachium rosenbergii* (De Man, 1879) in Karplus et al. (2000). Many caridean species (especially Alpheidae, many pontoniines, some palaemonoideans and hippolytids) cohabit in more or less permanent male-female pairs, which are at least socially monogamous (“monogamy” and “extended mate

guarding” - Correa and Thiel, 2003; Bauer, 2004; Baeza, 2008, 2010).

Sexual dimorphism in body size and cheliped weaponry is usually correlated with mating system in caridean shrimps (Correa and Thiel, 2003; Bauer, 2004). In Caridea, a pure searching mating system is characteristic of species with small males and larger females which have proportionately similar cheliped weaponry. In “neighborhoods of dominance” and “temporary mate guarding” systems, body size is somewhat to considerably larger in some males, whose weaponry (hypertrophied major chelipeds and/or spear-like third maxillipeds) is proportionately greater than in females or other males. Large males with extremely developed major chelipeds and/or third maxillipeds have been reported in Palaemonidae, e.g., *M. rosenbergii* (Kuris et al., 1987; Karplus et al., 2000), Rhynchocinetidae (Okuno, 1994; Okuno and Takeda, 1992a, b; best described in *R. typus*, Correa et al., 2000), and Hippolytidae [*Saron* spp., Kemp, 1914; Tirmizi and Kazmi, 1971; *Heptacarpus palpator* (Owen, 1839) in Bauer (1977)]. In monogamous mating systems, male-female size and weaponry are usually more or less similar. Thus, the sexual dimorphism in body size and weaponry is often a good *a priori* indication of the mating system in shrimps as in many other animal groups, as so well documented by Darwin (1871) and numerous others since (Orians, 1969; Thornhill and Alcock, 1983; Dunn et al., 2001; Shuster and Wade, 2003; Jarman, 2008).

Sexual dimorphism may also suggest a species’ sexual system which, like mating systems, may vary within families and genera of caridean shrimps. Although the majority of carideans studied to date are gonochoristic (separate sexes), there are numerous species with protandric hermaphroditism in which individuals first develop as a male phase (MP) and then change sex to a female phase (FP) (Bauer, 2000; Correa and Thiel, 2003). In at least two genera, *Lysmata* and *Exhippolysmata* (Hippolytidae), this sequential hermaphroditism has evolved one step further. In this group, FP individuals retain elements of the male system after sex change, resulting in simultaneous hermaphrodites which breed readily and successfully as both male or female (protandric simultaneous hermaphroditism or PSH: Bauer and Holt, 1998; Bauer, 2006; Laubenheimer and Rhyn. 2008; Baeza et al., 2009; Braga et al., 2009). Although all *Lysmata* species investigated have PSH, the sexual system of protandrous carideans may vary considerably within a genus, with either gonochoristic or protandric species, e.g., *Pandalus*, *Thor*, possibly *Hippolyte*, *Processa*, and *Crangon* (Bauer, 2000, 2004; Correa and Thiel, 2003).

The form of sexual dimorphism of a species often suggests the possibility of sequential hermaphroditism. Size-frequency distributions composed of small males and larger females, with little overlap in size and a lack of small (juvenile) females, is suggestive, although not conclusive, evidence of protandry (Bauer, 2004). Although numerous “small male, large female” species are protandric in the Caridea, the majority are not (Espinoza-Fuenzalida et al., 2008). Other evidence is needed to test the hypothesis of sequential hermaphroditism, i.e., individuals transitional in internal and/or external morphology between male and

female and/or actual observation of sex change in captive individuals (Butler, 1964; Bauer, 1986; Baeza, 2007; Anker et al., 2008).

The unusual and novel mating system of *R. typus* (“neighborhoods of dominance”) is characterized by alternative mating tactics, where dominant “robustus” males with hypertrophied major chelipeds and third maxillipeds are preferred as mating partners by females over smaller more agile “typus” males with less developed weaponry (Correa et al., 2003). Robustus males compete among themselves (displays, fights) and with subordinate typus males for access to receptive females, which they guard and defend as mating and spawning takes place. In the tropical species *R. brucei* Okuno, 1994, robustus-like males have also been identified, and these guard females during mating interactions (Thiel et al., 2010), similar to those (“caging”) documented for *R. typus* (Correa et al., 2003).

There appears to be considerable variation in the type and degree of sexual dimorphism among the 14 presently known species of *Rhynchocinetes*, a genus with a tropical and subtropical distribution in rocky subtidal habitats worldwide (Okuno, 1997; Chace, 1997). In descriptions of several species of *Rhynchocinetes*, large robustus-like males with hypertrophied weaponry have been observed, but such males apparently do not occur in other species such as *Rhynchocinetes uritai* Kubo, 1942 from the subtropical Pacific (Okuno and Takeda, 1992a, b; Okuno, 1994). Since sexual dimorphism in weaponry and body size is usually correlated with mating system in carideans (Correa and Thiel, 2003; Bauer, 2004), we predicted that *R. uritai* should exhibit the “pure searching” mating system, similar as reported for many other caridean species which lack sexual dimorphism in weaponry and in which males are smaller than females. This difference in male and female body size alerted us that the sexual system of *R. uritai* might be protandric, unlike the gonochory of the better-studied *R. typus*. Therefore, our objectives in this study on *R. uritai* were to test preliminarily the hypotheses that 1) males are smaller than females, 2) this species is a sequential (protandrous) hermaphrodite, and 3) mating is pure search as in other small-male species. Herein we describe the morphometrics of a small sample of *R. uritai*, and we provide a brief description of their mating behavior, sexual system, fecundity, embryo size, developmental time and sperm cell structure.

MATERIALS AND METHODS

Shrimps were sampled in September 2009 near the University of Tsukuba’s Shimoda Marine Research Center (SMRC), Shimoda, Japan (34°35’54”N; 138°56’14”E), on the southern tip of the Izu Peninsula. All shrimps were collected by hand and dipnet during scuba diving and snorkeling at water depths of 3-20 m. *Rhynchocinetes uritai* were taken from among crevices and small spaces of rocky substrata in the shallow subtidal (Fig. 1). Living shrimps were maintained at ~ 23°C in the seawater facilities of the SMRC in aquaria constantly supplied with running seawater. All specimens were preserved initially or after study in 95% ethanol.

Morphometric measurements were made using a stereomicroscope with an ocular micrometer on the 37 individuals collected. The measure of body size, carapace length (CL), was taken as the chordal distance from the posterior edge of the eye orbit to the middorsal posterior edge of the

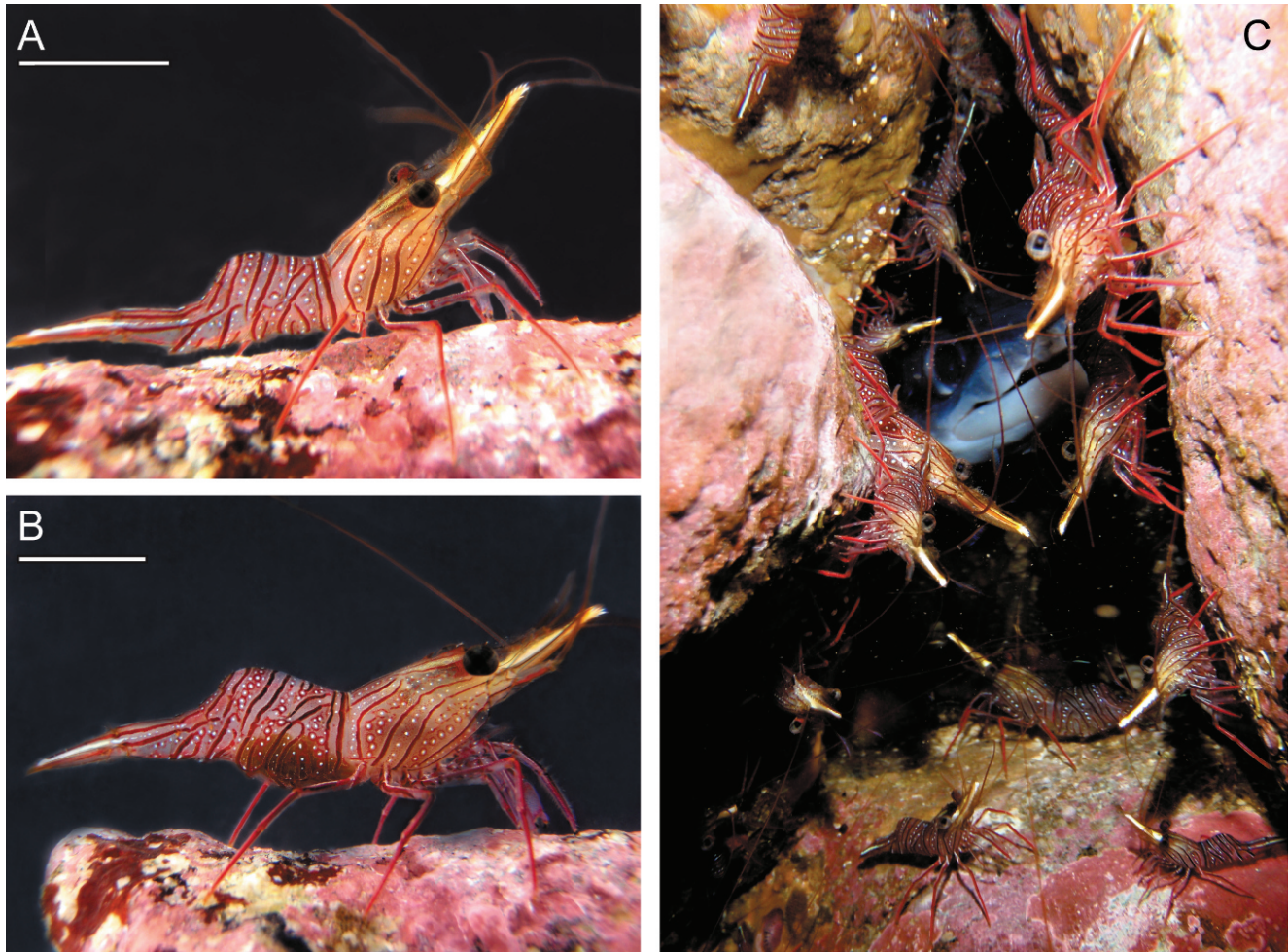


Fig. 1. *Rhynchocinetes uritai*. A, male or nonovigerous female; B, female incubating embryo mass; C, group of individuals sharing crevice in rocky wall along the shore. Scale bars = 10 mm.

carapace. Specimens were sexed, using the presence (male) or absence (female) of an appendix masculina on the endopod of the second pleopod. Individuals within the male size range which lacked an appendix masculina were considered juveniles. For comparison with other *Rhynchocinetes* species, measurements were taken on the length of the distal segment of the third maxilliped, major chela (propodal length, i.e., the “palm” plus fixed finger), and number of dark corneous spines on the distal end of the third maxilliped. Measures on two characters associated with incubation of embryos (“breeding dress”—Bauer, 2004) were taken: the flange width of the basis of the second pleopod (as in Bauer, 1986) and the height of the second pleonal pleuron, defined as the vertical chordal distance from the ventral edge of the pleuron to the middorsal line of the second pleomere.

The presence or absence of a vitellogenic ovary, visible through the dorsal carapace in preserved specimens, was determined and scored from 1 (no ovarian development) to 4 (ovary full of oocytes, ready for spawning) as in Bauer and Holt (1998). The embryos incubated by two females, which were preserved, were counted and degree of development scored (Bauer and Holt, 1998). The greater (d_2) and lesser (d_1) diameters of 10 embryos, chosen haphazardly from each brood, were taken and measured to calculate embryo volume [oblate spheroid, $V = 1/6 (\pi * d_1^2 * d_2)$] (Turner and Lawrence, 1979). The embryo-incubation period (number of days from spawning to hatching) was recorded for the three females used in mating observations, which successfully spawned after mating and later hatched the embryos.

Sperm cells in the viscous, adhesive spermatid material inside the ejaculatory ducts were prepared for scanning electron microscopy (SEM) as in Bauer and Min (1993). Spermatid material was obtained from a mature male that was squeezed gently on either side of the posterior

cephalothorax where the male gonopores are located (on the coxae of the last walking legs). The material was then spread on a plastic coverslip which had been previously immersed in a polylysine-L solution and then dried before use. The coverslip was then slowly immersed in 10% seawater formalin. It was later gently washed in distilled water and taken through an ethanol series (25%, 35%, 50%, 70%, 80%, 95%) to 100% ethanol, then into an equal mixture of 100% ethanol and 100% HMDS (hexamethyldisilazane) and finally into 100% HMDS (~30 min each solution). The HMDS was drained and the specimen allowed to air dry before sputter-coating with 10 nm of gold. SEM observations were taken with a Hitachi H-3000 thermionic environmental scanning electron microscope.

Observations on precopulatory and mating behavior were conducted in a larger (females 1 and 2: 18 cm × 32 cm surface area, filled to ~20 cm) and a smaller aquarium (female 3: 15 cm × 18.5 cm surface area, filled to ~18 cm) with ambient seawater at 23°C. Molting and mating occurred at night in these nocturnally-active shrimps, and lighting for observations was provided by infrared illumination (IR, 810 nm wavelength) from above the aquarium. Observations were recorded with a Sony Handycam DCR-PCC330 digital video recorder (DVR) set at the “nightshot” option (camera sensitive to IR illumination) and high resolution mode.

For each mating observation ($n = 3$), 3 males (5.2–7.3 mm CL) and a single parturial, premolt female were introduced into the aquarium after dusk (18 h) along with a flat stone on or along which these thigmotactic shrimps preferred to perch. The females used were incubating late-stage embryos when collected but then hatched them and were presumed nearing another parturial molt, which did occur during the mating observations. The DVR and 2 IR lamps were placed above the aquarium on tripods. DVR observations were taken at night, with laboratory lights extinguished.

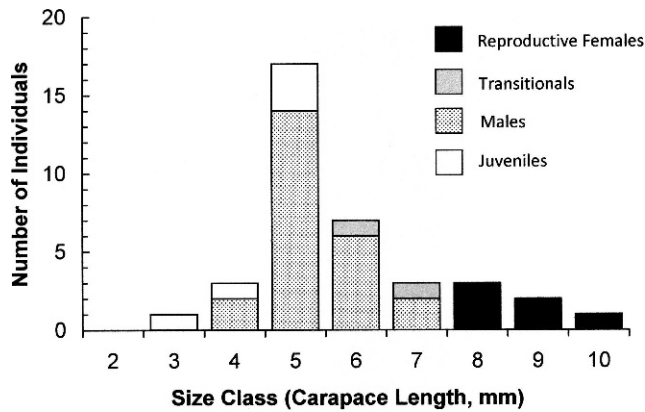


Fig. 2. Size-frequency distribution of *Rhynchocinetes uritai* collected on September 15, 2009, at Shimoda, Japan ($n = 37$).

The following morning, observation of a molt skin in the aquarium indicated that the female had molted. The ovigerous females were removed and returned to isolated containers on running seawater tables to allow them to incubate embryos from the postmolt spawning.

RESULTS

Population Structure and Reproductive Morphology

A total of 24 males, 6 ovigerous females, 5 juveniles, and 2 “transitionals” were collected, sexed and measured. The size-frequency distribution of these 37 individuals shows that males are smaller than reproductive females and that the size distributions of the two groups do not overlap (Fig. 2). All females were reproductive when collected, i.e., incubating a brood of embryos. Juveniles were individuals lacking an appendix masculina and without obvious external female characters. Juveniles occurred in the three smallest body-size groups (3–6 mm CL) along with more numerous males but were not found in the two largest male size groups (Fig. 2). The basipod flange width of the second pleopod was strongly related to CL of male and juvenile shrimp, but that of the female was substantially wider than that of the males (Fig. 3A). Similarly, the pleuron height was linearly related to male and juvenile CL, but females had substantially higher (expanded) pleura (Fig. 3B).

The two individuals with both male and female sexual characters (“transitionals”) had, as do males of *R. uritai* and other caridean species, an appendix masculina on the endopod of the second pleopods (male: Fig. 4A, D; transitional: B, E). The first pleopods of these two specimens are male-like, with an appendix interna (male: Fig. 5A, D; transitional: Fig. 5B, E), which is lacking on the first pleopods in females of most caridean species. In *R. uritai*, the endopod of the first pleopod of males has a prominent lateral lobe which the females lack (Fig. 5A, arrow) (Chace, 1997). The transitional individuals show less development of this feature (Fig. 5B, arrow). The transitionals also showed elements of the female “breeding dress” (Bauer, 2004), i.e., expanded flanges on the basipods of the first three pleopods (Figs. 4C, F) and expanded pleura (side plates) of the first three pleomeres, a character associated with spawning eggs and brooding

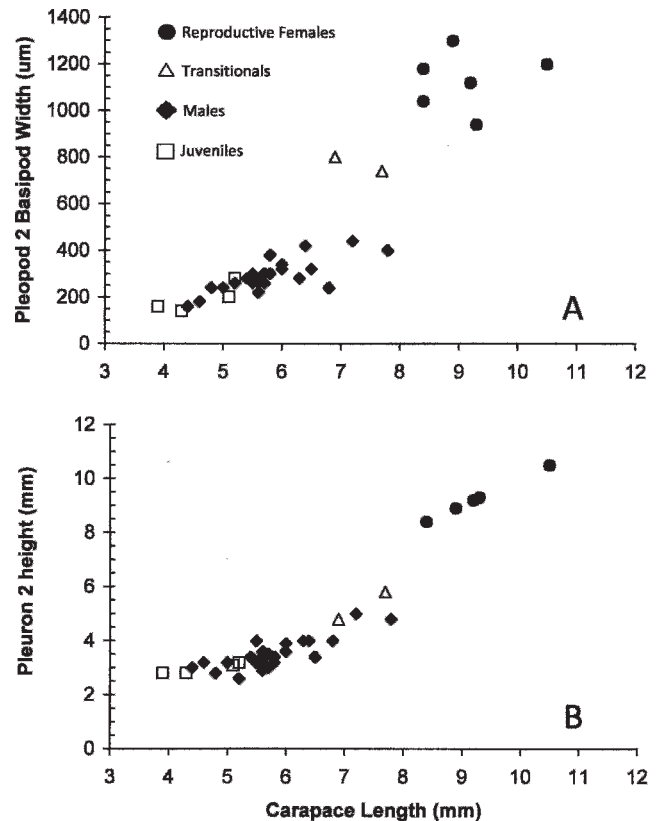


Fig. 3. Incubatory characters (“breeding dress”) of *Rhynchocinetes uritai*. A, variation in pleopod 2 basipod-flange width with body size (CL); B, variation in pleomere 2 pleuron height with body size (CL).

embryos (Höglund, 1943). Measurements on the pleopod 2 basipod-flange width and the height of pleonal pleuron 2 show the intermediate nature of transitional secondary sexual characters (Fig. 3A, B). Gonads with maturing ovarian tissue could be observed by external examination of these two specimens. A bright yellow color in ethanol-preserved material is characteristic for the large vitellogenic oöcytes (Fig. 5C, F) in the gonads. The two transitionals were 6.9 and 7.7 mm CL, which places them in the largest two male size classes and just below the size classes of reproductive females (Fig. 2).

The relative size of the major chelipeds and third maxillipeds (terminal article), as well as the number of corneous spines on the latter, differs among females, small subordinate (“typus”) and large dominant (“robustus”) males in *R. typus* (Correa et al., 2000). In the *R. uritai* sample, the relative size of these characters does not appear to vary with sexual type (Fig. 6A–C).

Measurements on two important parameters of fecundity, brood and embryo size, were taken on the two reproductive females incubating stage-2 embryos. The two broods contained 2,076 and 1,676 embryos from a 8.4 mm CL and a 9.3 mm CL female, respectively. The means of the greater and lesser diameters of 10 embryos carried by the 8.4 mm CL female were 0.24 mm and 0.19 mm; those of the 9.3 mm CL female measured 0.21 and 0.22 mm, with a mean volume of individual embryos for both females of 0.005 mm^3 .

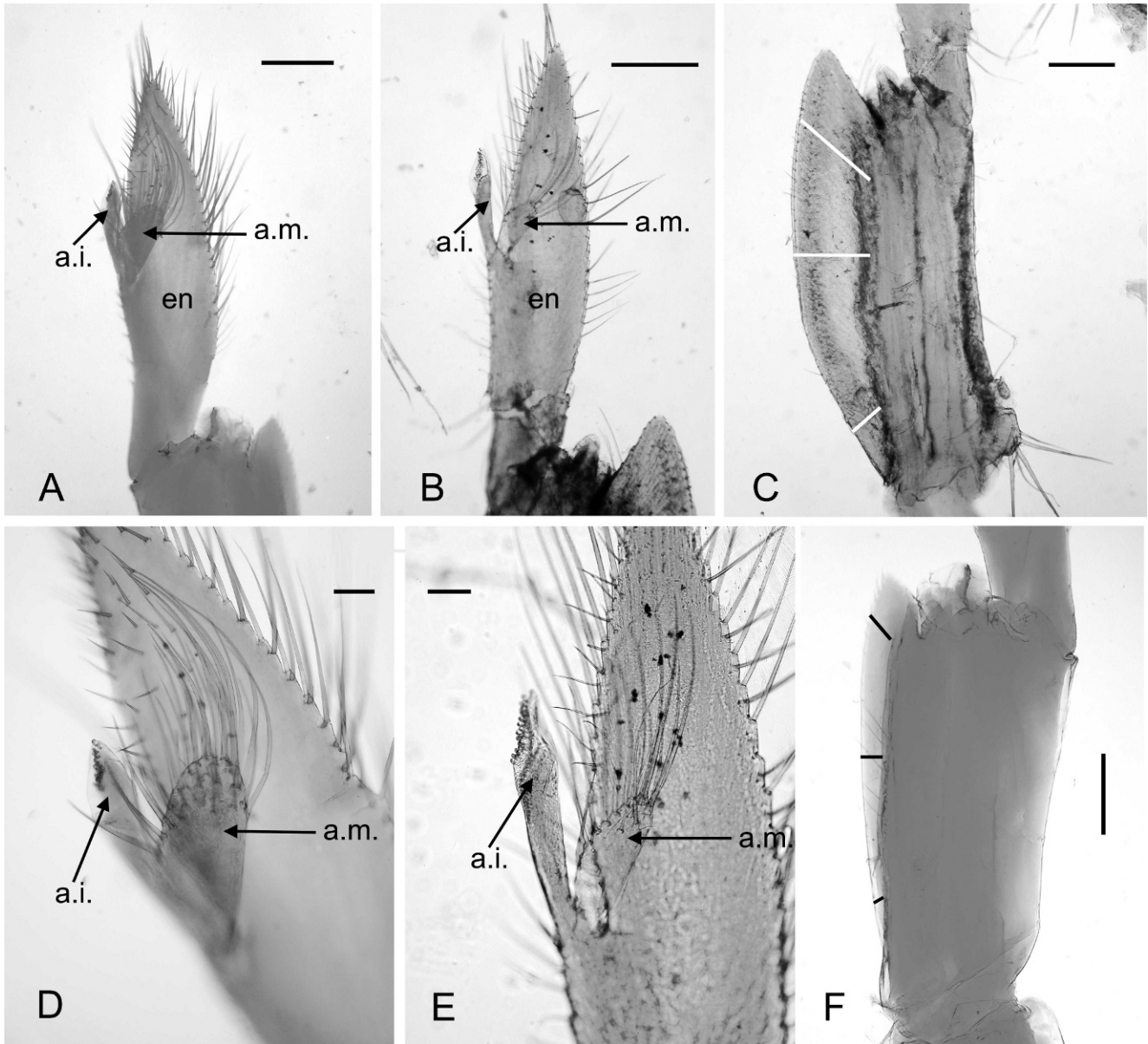


Fig. 4. Pleopod 2 characters of males and transitionals. A, pleopod 2 endopod of a male 6.8 mm CL with appendix masculina; B, pleopod 2 endopod of transitional (6.9 mm CL with developing ovary) with appendix masculina; C, pleopod 2 basis of same transitional showing width (white lines) of expanded incubatory flange; D, higher magnification of appendices interna and masculina in the 6.8 mm CL male. E, higher magnification of appendices interna and masculina in the 6.9 mm CL transitional individual; F, pleopod 2 basis of 6.8 mm male with very narrow flange (width indicated with black lines). a.i., appendix interna; a.m., appendix masculina; en, endopod. Scale bars: A, B, C, F = 400 μ m; D, E = 100 μ m.

Spermatophore material from a male used in breeding experiments was full of sperm cells (Fig. 7A, B). Spermatozooids were composed of the usual caridean cap and spike (Fig. 7C) but, unlike most other caridean sperm cells, the cap was extended into at least 9 rays connected at their bases by a thin membrane (Fig. 7F), similar to those described in *R. typus* by Dupré and Barros (1983). The rays are folded above the spike in the spermatophore (Fig. 7C) but upon exposure to seawater, the rays unfold (Fig. 7D-F).

Mating Behavior

A total of 3 complete matings of females that had hatched their brood within the previous 24 hours were arranged and

recorded. All matings occurred during hours of darkness (night) and were first preceded by the female's molt. Males often appeared to recognize the upcoming molting event up to 5 min in advance, occasionally approaching or touching the female, which reacted to such advances by jumping away using tail flips (backward escape response) and/or by vigorous swimming. The males approached and touched the female during the molting process. In all three matings, at least one male started to cling to the female as soon as she initiated molting, i.e., once the female had shed the anterior part but not the posterior part of the exoskeleton. After the female completed the molt, she began a series of vigorous tail flips and/or forward swimming with males in pursuit. During these movements she often bumped into the

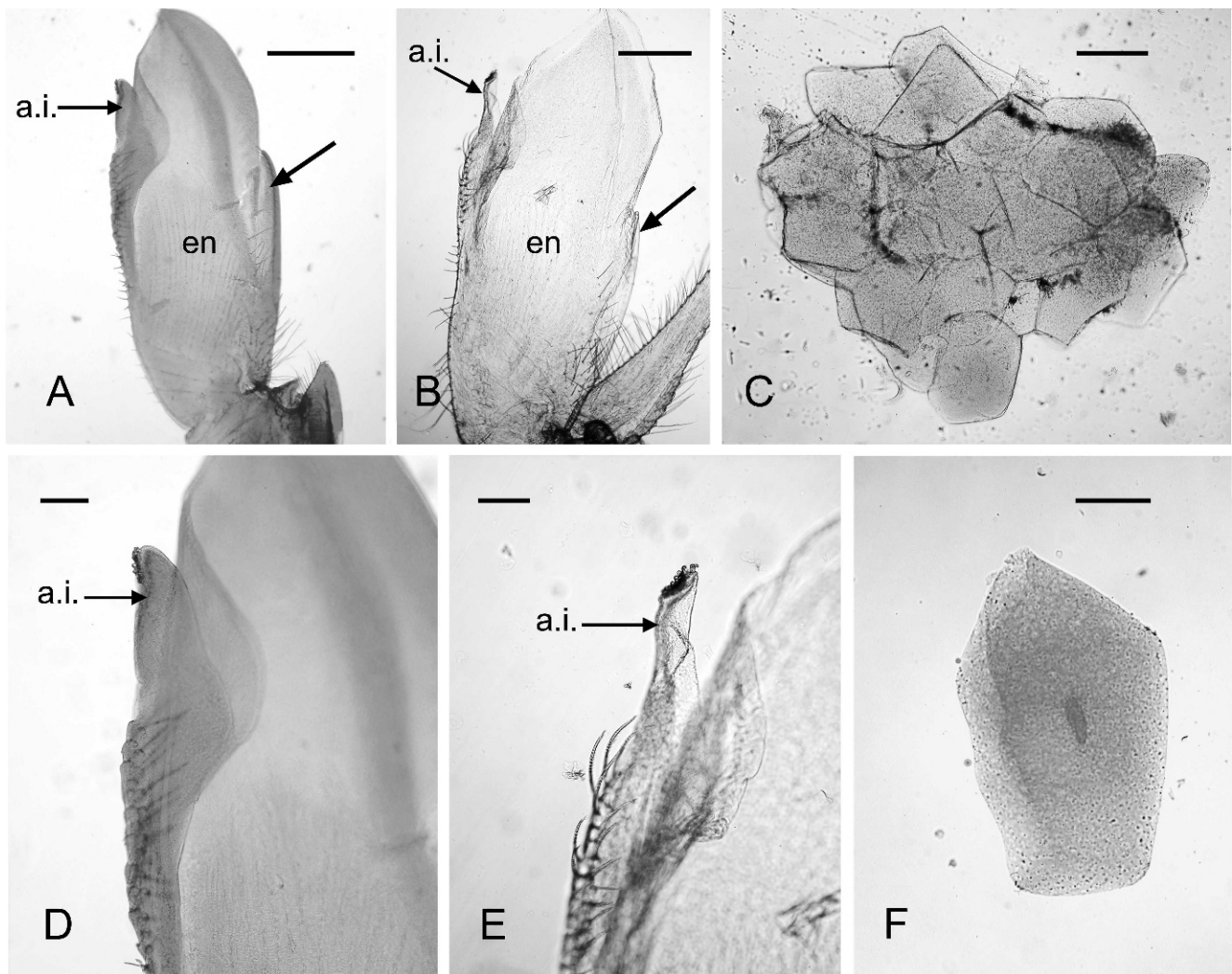


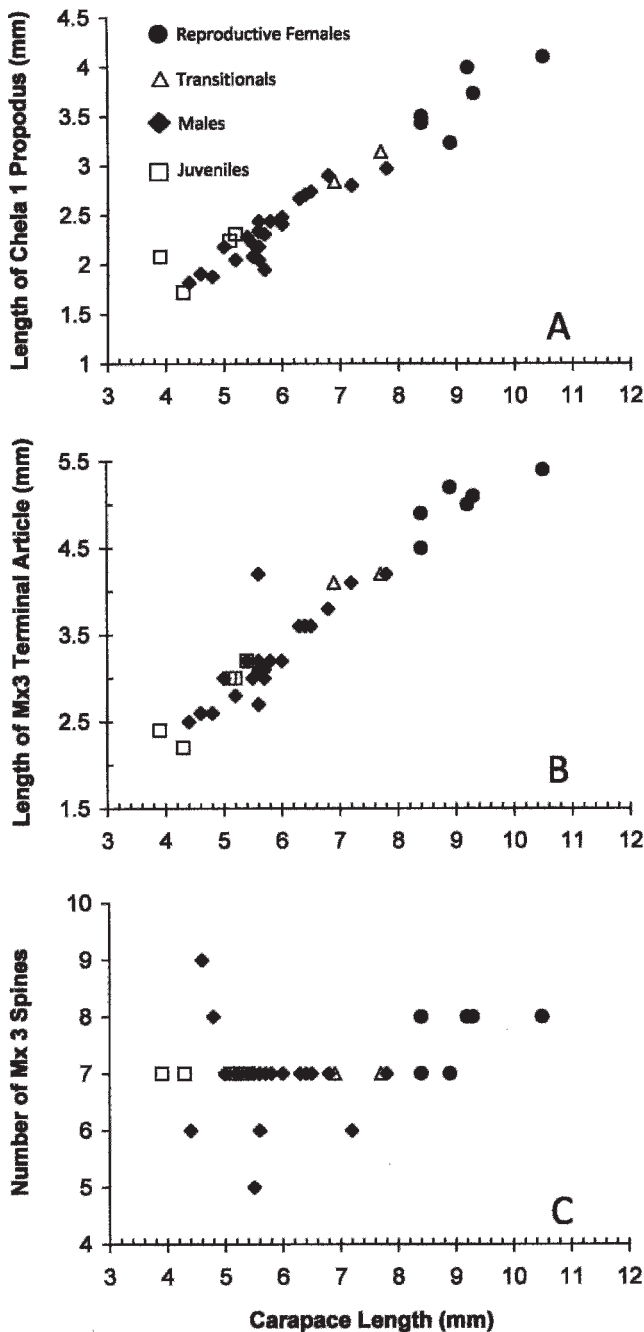
Fig. 5. Appendices internae of pleopod 1, male and transitional individuals, and developing ovary of the latter. A, pleopod 1 of 6.8 mm male, showing appendix interna and lateral lobe (arrow); B, pleopod 1 of 7.7 mm CL transitional individual with appendix interna and reduced lateral lobe (arrow); C, developing ovarian tissue with vitellogenic oocytes from the 6.9 mm transitional individual; D, higher magnification of appendix interna shown in A (6.8 mm male); E, higher magnification of appendix interna shown in B (7.7 mm transitional); F, vitellogenic oocyte from the developing ovary of the 7.7 mm CL transitional. a.i., appendix interna; en, endopod. Scale bars: A, B, C = 400 μ m; D, E = 100 μ m, and F = 235 μ m.

aquarium wall, suggesting that in a natural environment she would have moved appreciable distances from the molting site. More than one male would follow and contact the female, and within 1 min of molting one male grabbed the female and engaged in copulation. The male swung its body underneath the female, forming the typical mating cross observed in many caridean shrimps (see illustrations in Bauer, 1976; Berg and Sandifer, 1984). The copulation, during which the male most likely transferred the spermatophore, was brief (~ 2 sec). In one mating all three males clung to the female, and we could not clearly identify whether only one or possibly more males transferred a spermatophore. As soon as copulation had occurred the female jumped away and males refrained from clinging to it any further. After mating, one of the three males in each of three replicates maintained intermittent body contact with the female (touching it with the antennae) for times ranging from 40 sec to 187 sec (Table 1). Spawning occurred consistently between

74.3 min and 98.5 min after molting (Table 1). All 3 females incubated and hatched the embryos after 13 d (at 23°C).

DISCUSSION

Our results indicate that the sexual system of *R. uritai* is protandrous, i.e., individuals first mature sexually as males and then later (when older and larger) change sex to females. The size-frequency distribution of our limited sample displays the classic portrait of a purely protandrous species (Bauer, 2004). Males are smaller than females and the size distributions of the two do not overlap. We could not determine if the few juveniles observed were male or female, but, if the latter, primary females would be a small percentage of the population. Most individuals between 4 and 8 mm carapace length were males, suggesting that *R. uritai* mature first as males and then become secondary females. In support of this suggestion, we observed two



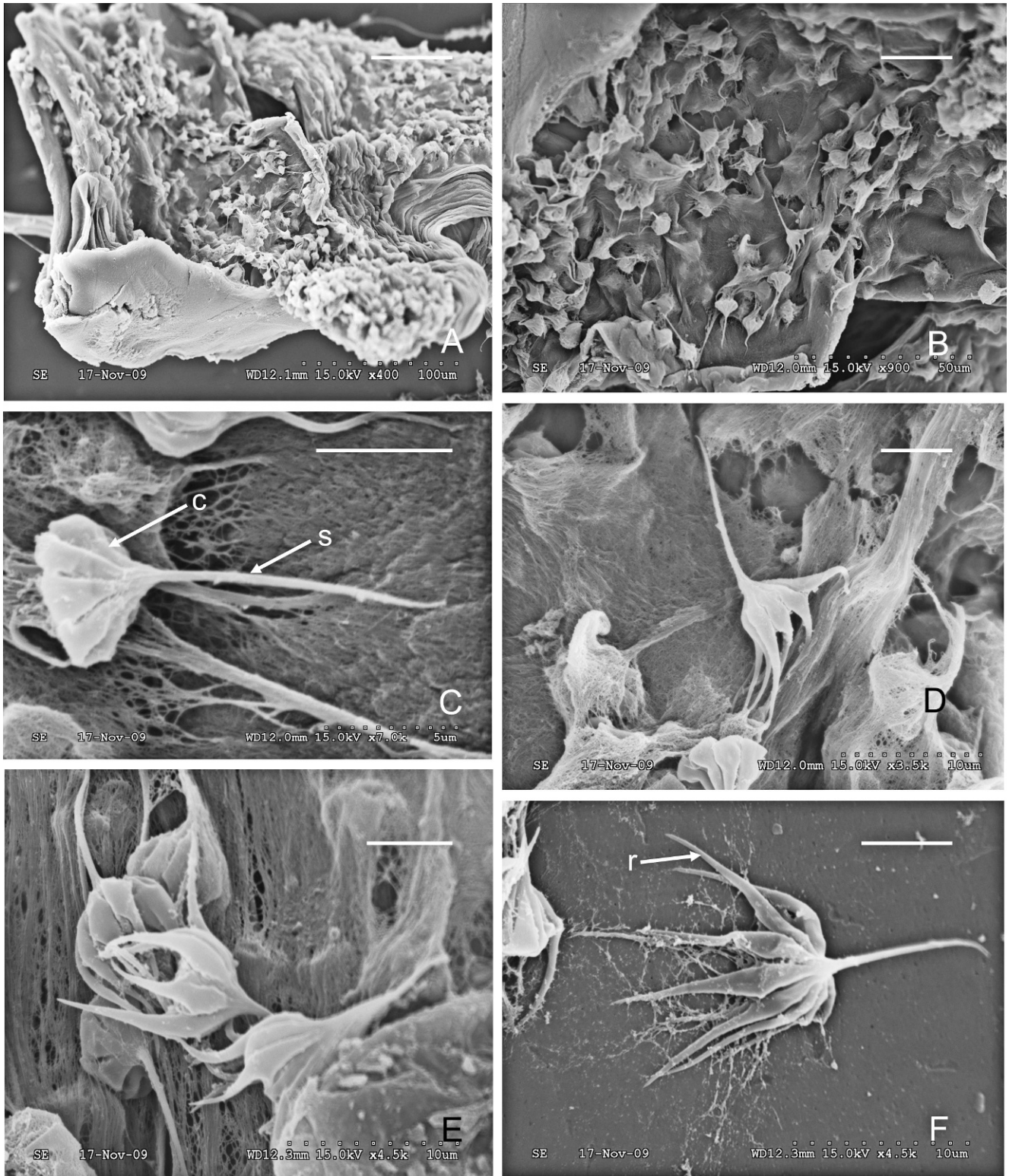


Fig. 7. Spermatozooids of *Rhynchocinetes typus*. A, freshly emitted spermatoaphore material; B, spermatozoid surrounded by seminal material; C, unfolded spermatozoid; D, E, unfolding spermatozooids; F, single spermatozooids. c, cap; s, spike. Scale bars: A = 50 μ m; B = 20 μ m; C, D, E, F = 5 μ m.

is considerable variation in sexual dimorphism and mating system among species of Rhynchocinetidae. In *R. typus*, large older “robustus” males with hypertrophied chelipeds and third maxillipeds attract the smaller females, which

prefer them to the smaller, “weapons-poor” males (Correa et al., 2003; Díaz and Thiel, 2004 and references cited therein). Mating behavior in *R. typus* is complex and unusual compared to that of most other carideans, with

Table 1. Timing of the three main events (female molting, spermatophore transfers, and female spawning), duration of male attendance and number of males interacting with females during mating interactions with receptive females of *Rhynchocinetes uritai* in the laboratory. STE—Spermatophore Transfer Event, FOV—moment when female was first identified as fully ovigerous. Time of low tide in the field is also provided.

	Low tide (time)	Molt (time)	STE (s after molting)	FOV (min after molting)	Male attendance of female after STE (s)	Males contacting female
Female 1	21:27	19:50	+39	+91.5	50+	3
Female 2	22:02	22:07	+49	+74.3	40+	3
Female 3	23:44	00:28 (+1)	+45	+98.5	187	3

prolonged “caging” (mate guarding) of postmolt females by males. Moderately developed “robustus” males and somewhat less complex mating interactions with postcopulatory mate guarding have been reported for *R. brucei* (Thiel et al., 2010). In contrast, our observations on *R. uritai* indicate that males are smaller than females and have, proportionately, similar-sized weaponry.

Observed matings did not involve caging or prolonged interaction of any kind. Rather, our observations suggest that males attend females less than a minute before the latter’s pre-mating molt. Copulation was very short in duration, a few seconds at most, apparently with only one spermatophore transfer. Females rapidly became unattractive to males after copulation, and they avoid further male contact after copulation while preparing for spawning, which occurs within a few hours of mating. This type of sexual dimorphism and mating behavior is typical of caridean shrimps with a “pure search” mating system (Wickler and Seibt, 1981) in which males constantly search for receptive females, mate quickly, and abandon the female shortly thereafter, without any precopulatory guarding or complex behavior (Correa and Thiel, 2003; Bauer, 2004). In such species, where males defend neither females nor resources, there is no selection for large male size and weaponry but instead for large female size correlated with increased fecundity.

The ultimate causes of the apparent variation in rhynchocinetid sexual dimorphism, mating systems, and sexual systems can only be speculated at this time. Comparative as well as experimental studies have indicated that, independent of phylogeny, factors such as predation pressure, food and spatial resources, trophic ecology, and social organization may cause such variation (alpheid shrimps: Knowlton, 1980; *Lysmata* spp.: Bauer, 2000; insects: Thornhill and Alcock, 1983; mammals: Emlen and Oring, 1977; birds: Dunn et al., 2001; poison frogs: Brown et al., 2010). Such ecological factors then may or may not favor sexual selection, both by intersexual (epigamic) and intrasexual selection, resulting in the extremes of pure search mating systems with small males and larger females, e.g., in *R. uritai*, compared to smaller females and large robustus males with hypertrophied weaponry in neighborhoods of dominance systems, e.g., in *R. typus* and *R. brucei*.

ACKNOWLEDGEMENTS

We are indebted to Masakazu Aoki and his graduate students at the University of Tsukuba’s Shimoda Marine Research Center, Japan, for their hospitality and invaluable help with this study. We thank Junji Okuno for his valuable information on *Rhynchocinetes* taxonomy and distribution,

and Ivan A. Hinojosa for his help in preparing Figure 1. Publication was supported by the Louisiana Sea Grant College Program with funds from the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under the grant No. NA06OAR4170022, Project No. R/SA-04 to RTB. MT acknowledges the support of UCN during his sabbatical stay in Asia. This is Contribution No. 141 of the University of Louisiana’s Laboratory for Crustacean Biology.

REFERENCES

- Anker, A., J. A. Baeza, and S. De Grave. 2009. A new species of *Lysmata* (Crustacea, Decapoda, Hippolytidae) from the Pacific coast of Panama, with observations of its reproductive biology. *Zoological Studies* 48: 682-692.
- Baeza, J. A. 2007. No effect of group size on sex allocation in a protandric-simultaneous hermaphroditic shrimp. *Journal of the Marine Biological Association United Kingdom* 87: 1169-1174.
- . 2008. Social monogamy in the shrimp *Pontonia margarita*, a symbiont of *Pinctada mazatlanica*, off the Pacific coast of Panama. *Marine Biology* 153: 387-395.
- . 2010. The symbiotic lifestyle and its evolutionary consequences: social monogamy and sex allocation in the hermaphroditic shrimp *Lysmata pedersenii*. *Naturwissenschaften* 97: 729-741.
- , C. D. Schubart, P. Zillner, S. Fuentes, and R. T. Bauer. 2009. Molecular phylogeny of shrimps from the genus *Lysmata* (Caridea: Hippolytidae): the evolutionary origins of protandric simultaneous hermaphroditism and social monogamy. *Biological Journal of the Linnean Society* 96: 415-424.
- Bauer, R. T. 1976. Mating behaviour and spermatophore transfer in the shrimp *Heptacarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae). *Journal of Natural History* 10: 315-440.
- . 1977. Antifouling adaptations of marine shrimp (Decapoda: Caridea): functional morphology and adaptive significance of antennular preening by the third maxillipeds. *Marine Biology* 40: 260-276.
- . 1986. Sex change and life history pattern in the shrimp *Thor manningi* (Decapoda: Caridea): a novel case of partial protandric hermaphroditism. *Biological Bulletin* 170: 11-31.
- . 1991. Analysis of embryo production in a caridean shrimp guild inhabiting tropical seagrass meadows, pp. 181-191. In, A. Wenner and A. Kuris (eds.), *Crustacean Egg Production*. A. A. Balkema, Rotterdam.
- . 2000. Simultaneous hermaphroditism in caridean shrimps: a unique and puzzling sexual system in the Decapoda. *Journal of Crustacean Biology* 20 (Special No. 2): 116-128.
- . 2004. Remarkable Shrimps: Adaptations and Natural History of the Carideans. University of Oklahoma Press, Norman.
- , and G. J. Holt. 1998. Simultaneous hermaphroditism in the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae): an undescribed sexual system in the decapod Crustacea. *Marine Biology* 132: 223-235.
- , and J. W. Martin (eds.). 1991. *Crustacean Sexual Biology*. Columbia University Press, New York.
- , and L. J. Min. 1993. Spermatophores and plug substance of the marine shrimp *Trachypenaeus similis* (Crustacea: Decapoda: Penaeidae): formation in the male reproductive tract and disposition in the inseminated female. *Biological Bulletin* 185: 174-185.
- Berg, A. B., and P. A. Sandifer. 1984. Mating behavior of the grass shrimp *Palaemonetes pugio* Holthuis (Decapod: Caridea). *Journal of Crustacean Biology* 4: 417-424.
- Brown, J. L., V. Morales, and K. Summers. 2010. A key ecological trait drove the evolution of parental care and monogamy in an amphibian. *American Naturalist* 175: 436-446.

- Carnahan, S. J., and M. I. Jehnson-Seaman. 2008. Hominoid seminal protein evolution and ancestral mating behavior. *American Journal of Primatology* 70: 939-948.
- Chace, F. A., Jr. 1997. The caridean shrimps (Crustacea, Decapoda) of the Albatross Expedition, 1907-1910, Part 7: Families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae. *Smithsonian Contributions to Zoology* Number 587: 1-106.
- Christy, J. H. 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. *Bulletin of Marine Science* 41:177-191.
- Correa, C., and M. Thiel. 2003. Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Revista Chilena de Historia Natural* 76: 187-203.
- , J. A. Baeza, I. Hinojosa, and M. Thiel. 2003. Male dominance hierarchy and mating tactics in the rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *Journal of Crustacean Biology* 23: 33-45.
- , ———, E. Dupré, I. A. Hinojosa, and M. Thiel. 2000. Mating behavior and fertilization success of three ontogenetic stages of male rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *Journal of Crustacean Biology* 20: 628-641.
- Corey, S., and D. M. Reid. 1991. Comparative fecundity of decapod crustaceans. I. The fecundity of thirty-three species of nine families of caridean shrimps. *Crustaceana* 60: 270-294.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. Murray, London.
- De Man, J. G. 1879. On some species of the genus *Palaemon* Fabr. with descriptions of two new forms. *Notes from the Royal Zoological Museum of the Netherlands at Leyden* 1: 165-184.
- Díaz, E. R., and M. Thiel. 2004. Chemical and visual communication during mate searching in rock shrimp. *Biological Bulletin* 206: 134-143.
- Duffy, J. E., and ———. 2007. *Evolutionary Ecology of Social and Sexual Systems*. Oxford University Press, New York.
- Dunn, P. O., L. A. Whittingham, and T. E. Pitcher. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55:161-175.
- Dupré, E., and C. Barros. 1983. Fine structure of the mature spermatozoon of *Rhynchocinetes typus*, Crustacea Decapoda. *Gamete Research* 7: 1-18.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-233.
- Espinoza-Fuenzalida, N. L., M. Thiel, E. Dupre, and J. A. Baeza, 2008. Is *Hippolyte williamsi* gonochoric or hermaphroditic? A multi-approach study and a review of sexual systems in *Hippolyte* shrimps. *Marine Biology* 155: 623-635.
- Höglund, H. 1943. On the biology and larval development of *Leander squilla* (L.) forma typica De Man. *Svenska Hydrografisk-Biologiska Kommissiones Skrifter Stockholm N.S.* 2: 1-44.
- Jarman, P. 2008. Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biological Reviews* 58: 485-520.
- Karplus, I., S. R. Malecha, and A. Sagi. 2000. The biology and management of size variation, pp. 259-289. In, M. B. New and W. C. Valenti (eds.), *Freshwater Prawn Culture: the Farming of *Macrobrachium rosenbergii**. Blackwell Science, Malden, Massachusetts.
- Kemp, S. 1914. Notes on Crustacea Decapoda in the Indian Museum. V. Hippolytidae. *Records of the Indian Museum* 10, 2: 81-129.
- Knowlton, N. 1980. Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp. *Evolution* 34: 161-173.
- Kuris, A. M., Z. Ra'anan, A. Sagi, and D. Cohen. 1987. Morphotypic differentiation of male Malaysian giant prawns, *Macrobrachium rosenbergii*. *Journal of Crustacean Biology* 7: 219-237.
- Kubo, I. 1942. On two new species of Decapoda Macrura. *Annotationes Zoologicae Japonenses* 21: 30-38.
- Milne Edwards, H. 1837. *Histoire naturelle des Crustacés. Comrenant l'Anatomie, la Physiologie et la Classification de ces Animaux.* 2: 1-532.
- Okuno, J. 1994. A new species of hinge-beak shrimp from the Western Pacific (Crustacea, Decapoda, Rhynchocinetidae). *The Beagle, Records of the Museums and Arts Galleries of the Northern Territory* 11: 29-37.
- . 1997. A new shrimp of the genus *Rhynchocinetes* from the Great Australian Bight (Crustacea: Decapoda: Rhynchocinetidae). *Records of the South Australian Bight* 30: 13-18.
- , and M. Takeda. 1992a. Description of a new hinge-beak shrimp, *Rhynchocinetes conspicuocellus*, from southern Japan, with designation of the lectotype of *R. uritai* Kubo, 1942. *Bulletin of the National Science Magazine, Tokyo, Series A* 18: 63-72.
- , and ———. 1992b. Distinction between two hinge-beak shrimps, *Rhynchocinetes durbanensis* Gordon and *R. uritai* Kubo (Family Rhynchocinetidae). *Revue Française d'Aquariologie y Herpétologie* 19: 85-90.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* 109: 589-603.
- Owen, R. 1839. Crustacea, pp. 77-97. In, F. W. Beechey (ed.), *The Zoology of Captain Beechey's Voyage*. Henry G. Bohn, London.
- Salmon, M. 1983. Courtship, mating systems, and sexual selection in decapods, pp. 143-169. In, S. Rebach and D. W. Dunham (eds.), *Studies in Adaptation: the Behavior of Higher Crustacea*. J. Wiley and Sons, New York.
- Shuster, S. M., and M. J. Wade. 2003. *Mating Systems and Strategies*. Princeton University Press, Princeton, New Jersey.
- Thiel, M., S. T. C. Chak, and C. P. Dumont. 2010. Mating behavior of the dancing shrimp *Rhynchocinetes brucei* (Decapoda: Caridea). *Journal of Crustacean Biology* 30: 580-588.
- Thornhill, R., and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, Massachusetts.
- Tirmizi, N. M. and M. A. Kazmi. 1971. Sexual Dimorphism in *Saron marmoratus* (Olivier) (Decapoda, Hippolytidae). *Crustaceana* 21: 283-293.
- Turner, R. L. and J. M. Lawrence. 1979. Volume and composition of echinoderm eggs: implications for use of egg size in life-history models, pp. 25-40. In, S. E. Stancyk (ed.), *Reproductive Ecology and of Marine Invertebrates*. University of South Carolina Press, Columbia.
- Wilson, E. O. 1975. *Sociobiology. The New Synthesis*. Belknap Press, Cambridge, Massachusetts.
- Wickler, W., and U. Seibt. 1981. Monogamy in Crustacea and Man. *Zeitschrift für Tierpsychologie* 57: 215-234.

RECEIVED: 17 July 2010.

ACCEPTED: 28 September 2010.