Gonochoric sexual system in the caridean shrimps *Processa riveroi* and *P. bermudensis* (Decapoda: Processidae) inhabiting a tropical seagrass meadow

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*The sexual system of two caridean shrimps (*Processa riveroi *and* P. bermudensis*) was investigated, stimulated by reports of male to female sex change (protandry) in* Processa edulis *from European waters. Shrimps used in the study were obtained from monthly samples taken from March 1982 to February 1983 in a* Thalassia–Syringodium *seagrass meadow in Puerto Rico. Observations on size, sex, and reproductive condition were used to construct monthly size–frequency distributions and sex-ratios by size-class (SC). Males were smaller than reproductive females, but there was extensive overlap in size between males and immature females. A sex-ratio (SR) analysis by SC of the overall year-long population sample showed an equal or female-biased SR in the smallest SC, a male-biased SR in 1–3 intermediate SC, with larger SC dominated by females incubating embryos. Such a population structure might result from slower growth in males than females and higher mortality in larger males. Observations on and allometric analysis of sexual characters failed to identify transitional individuals (sex-changers) intermediate in reproductive morphology between males and females. Thus, a hypothesis of protandry is rejected, and that of gonochory (separate sexes) is accepted in these two* Processa *species, revealing possible variation in sexual systems among* Processa *species.*

INTRODUCTION

Although the majority of the over 3200 (De Grave *et al.*, 2009) species of caridean shrimps have a sexual system with separate sexes (gonochory), a substantial and growing number of species have been found to be hermaphroditic (Bauer, 2000; Correa & Thiel 2003a; Baeza, 2010; Baeza & Piatoni, 2010; Bauer & Thiel, 2011). Hermaphroditism in carideans is primarily sequential and protandric, in which some or all individuals first develop as functional males ('male phase') and then later change sex to functional females ('female phase') (Bauer, 2000, 2004). Protandry in carideans takes several forms (Bauer, 2000). All individuals change from male to female in some protandric species, e.g. *Pandalopsis dispar* Rathbun, 1902 in Butler (1964), *Paratya curvirostris* (Heller, 1862) in Carpenter (1978) and *Thor amboinensis* (De Man, 1888) in Baeza & Piatoni (2010). In others, e.g. *Pandalus* spp. (Bergström, 2000), most individuals change sex but there are varying proportions of the population that develop directly into females ('primary females'). In the genera *Lysmata* and *Exhippolysmata*, a more advanced form of protandry has evolved ('protandric simultaneous hermaphroditism' (PSH)) in which individuals first develop and function as males but, when changing sex to the female phase, retain

male gonadal structures and sexual ability, i.e. are functionally simultaneous hermaphrodites (Kagwade, 1982; Bauer & Holt, 1998; Bauer, 2006; Baeza, 2006, 2009; Laubenheimer & Rhyne, 2008; Baeza *et al.*, 2009, Braga *et al.*, 2009). Evidence indicating or confirming protandry includes: (1) population size–frequency distributions consisting of small males and larger females, with little to no overlap in size; (2) transitional individuals with a mixture of deteriorating male features and/or development of female primary and secondary sexual characteristics; (3) females with vestiges of male external or internal structures; and (4) direct observation of sex change in individuals maintained in the laboratory (Bauer, 2004; Espinoza-Fuenzalida *et al.*, 2008; Anker *et al.*, 2009).

There is considerable intrageneric variation in sexual systems (gonochory, protandry and PSH) of caridean shrimps (e.g. *Crangon*: Boddeke *et al.*, 1991; Gavio *et al.*, 2006; Schatte & Saborowski, 2006; *Hippolyte*: Zupo, 1994; Cobos *et al.*, 2005; Espinoza-Fuenzalida *et al.*, 2008; Terossi *et al.*, 2008; Zupo *et al.*, 2008; pandalids: reviewed in Bergström, 2000; *Lysmata*: Bauer 2000, 2006; Baeza, 2009; *Thor*: Bauer, 1986; Bauer & VanHoy, 1996; Baeza & Piatoni, 2010; *Rhynchocinetes*; Correa & Thiel, 2003b; Thiel *et al.*, 2010; Bauer & Thiel, 2011). Shrimps of the genus *Processa*, with at least 52 species (De Grave & Fransen, in press), are small, nocturnally active predators that inhabit temperate to tropical shallow-water soft-bottom habitats, and are often important members of the shrimp fauna in seagrass meadows (Manning & Chace, 1971; Bauer, 2004). Previous

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studies (Noël, 1973, 1976) have suggested protandry in two subspecies of *Processa edulis* (Risso, 1816) from the Atlantic and Mediterrean coasts of France. However, the evidence for protandry in that species is controversial (Labat & Noël, 1987). These reports stimulated our interest in the sexual system of two species, *Processa bermudensis* (Rankin, 1900) and *Processa riveroi* Manning & Chace 1971, whose populations were sampled on a monthly basis in *Thalassia–Syringodium* seagrass meadows on the north coast of Puerto Rico (Bauer, 1985, 1989). In this paper, we test the hypothesis of protandry in these two species with observations on size–frequency distributions, sex-ratio, and morphological data.

MATERIALS AND METHODS

Collection

Seagrass shrimps were taken with a pushnet (1-mm mesh) in day and night sampling of *Thalassia–Syringodium* grass beds just off the public beach (*balneario*) at Dorado, north coast of Puerto Rico (18°28′32″N 66°16′42″W) from March 1982 through to February 1983 (Bauer, 1985). Samples were initially preserved in 10% seawater–formalin, washed, and stored permanently in 70% ethanol. Samples were sorted to species, including *Processa riveroi* and *P. bermudensis*, the subjects of this study.

Population structure and sexual morphology

Individuals (N = 806 in *P. riveroi*; N = 1330 in *P. bermudensis*) were sexed by examination of the second abdominal appendages (pleopods) for the presence (male) or absence (female) of an appendix masculina (AM), a characteristic of males in most caridean shrimp species (Bauer, 2004). The presence or absence of a vitellogenic ovary, easily observed through the thin translucent carapace of this small shrimp, as well as embryos incubated below the abdomen, was recorded (Bauer, 1991). Body size was measured as carapace length (CL), the chordal distance from the posterior edge of the eye orbit to the mid-dorsal posterior edge of the carapace, which was measured with a stereomicroscope equipped with an ocular micrometer. The minimum male size in both species was 1.4 mm CL. The relatively few individuals < 1.4 mm CL lacked an AM and were classified as juveniles; individuals ≥ 1.4 mm CL without an AM and not incubating embryos were termed females without embryos. Individuals incubating embryos were termed females with embryos. Monthly size–frequency distributions were constructed and overall sex-ratios (number of males/number of males +number of females) were calculated using 0.50 mm CL size intervals.

The change from male to female in protandric species can often be recognized by a gradual degeneration of external male characters on the first and second pleopods (Butler, 1964; Bauer, 1986; Bauer & Holt, 1998; Bauer & Newman, 2004). Males of both *Processa* spp. were observed for such changes by measuring the length of the pleopod 2 AM (from base to tip excluding terminal setae) and the number of AM setae as well as the number of cincinnuli (coupling hooks) on the endopod of pleopod 1, another typical male character of carideans (Bauer, 2004). A sample of males were chosen haphazardly from each species, and one of the first and second pleopods from each male were removed and mounted on slides using the slide-mounting medium CMC (trade name of Polysciences Inc. for a mixture of polyvinyl alcohol, lactic acid and phenol in water) for later observation. Additionally, a sample of females incubating embryos was also taken haphazardly and similarly observed for vestiges of these male characters, which remain in some sex-changing species, e.g. *Lysmata wurdemanni* (Gibbes, 1850) in Bauer & Holt (1998) and *L. californica* (Stimpson, 1866) in Bauer & Newman (2004).

Statistics

Allometry of growth in male sexual processes (AM length, number of AM setae, and number of pleopod 1 cincinnuli) was examined with regression analysis, using the log transformation of the allometric growth equation $Y = \alpha X^{\beta}$ [log $(Y) = \beta$ log $(X) +$ log α] where β is the slope and α is the Y-intercept of the regression equation. In this study, $Y =$ AM length (μm) or counts of AM setae or pleopod 1 cincinnuli, and $X =$ CL (mm). Positive allometry, negative allometry, and isometry are indicated by $\beta > 1$, $\beta < 1$, and $\beta = 1$, respectively (Gould, 1966; Kuris *et al.*, 1987). Robust rank regression (SYSTAT, 2007) was used because the assumptions for parametric regressions were not met after log-transformation. For rank regressions, the Spearman correlation coefficient was used to test the hypothesis of a non-significant regression ($\beta = 0$). The slopes (β) of regression lines are reported with lower and upper 95% confidence intervals. For sex-ratios, the hypothesis of no difference from a sex-ratio of 0.50 was tested using Chi-square ($\alpha = 0.05$).

RESULTS

Population structure

Processa riveroi and *P. bermudensis* showed similar patterns of frequency distribution by sex in which the smaller size-classes (SC) were a mix of males and immature (without embryos) females and the larger SC were dominated by females incubating embryos (Figures 1–2). Intermediate SC were dominated by males. In both species, males showed external chacterisitics of sexually mature males at a very small size (1.4 mm CL) whereas females began incubating embryos at a much larger size (≥ 2.7 mm CL in *P. riveroi*; ≥2.5 mm CL in *P. bermudensis*). Summed over the entire year, the sex-ratio (number of males/number of males + number of females) was female biased (0.42) in *P. riveroi* but was not significantly different (0.48) from 0.50 in *P. bermudensis* (Tables 1–2). Sex-ratios by SC, summed through the year of sampling, clearly show this pattern of smaller SC with immature female-biased or equal SC, male-dominated intermediate SC, and female-dominated large SC (Figure 3; Tables 1–2). Examination of detailed size–frequency distributions (Figure 2) shows the monthly variation from this overall pattern. Females incubating embryos were present throughout the year in this tropical species (Figure 2). Recruitment of individuals into the smallest SC occurred sporadically throughout the year and not on a seasonal basis (Figure 2; Bauer, 1989). Thus, the pattern of recruitment and growth observed in these species appears to be entry of both male and female recruits, with a more rapid growth of females into large size with their
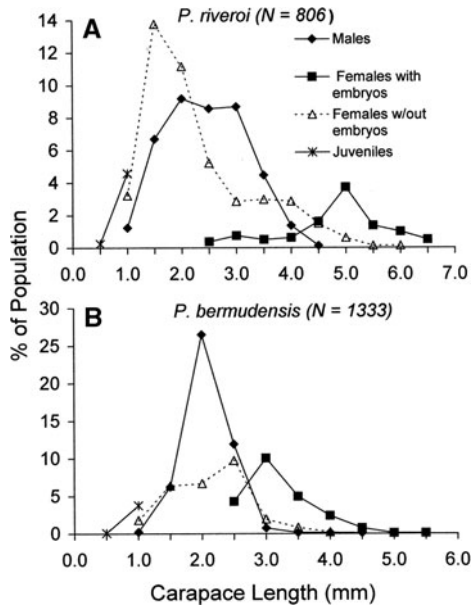
Fig. 1. Frequency distribution of sexual types of *Processa riveroi* and *P. bermudensis*. Percentage frequency of males, females with embryos, females without embryos and juveniles in the total sample of (A) *P. riveroi* and (B) *P. bermudensis* from the seagrass meadows at Dorado, Puerto Rico (sum of monthly samples from March 1982 through to February 1983).

accumulation in and dominance of large SC. Males, on the other hand, grew to a smaller size and accumulated in the intermediate SC.

Variation in sexual characters

To identify negative growth, reduction, or loss of male characters with increasing size, observed in some protandric species, allometric analysis was done on two measures of the AM (length and number of setae) on pleopod 2 and on the number of cincinnuli (coupling hooks) on the endopod of pleopod 1 (Figures 4–5). In both species, the AM length increased isometrically with male size (β not significantly different from 1; Table 3). The number of AM setae was linearly related to body size but the slope (β) was significantly less than 1, indicating negative allometry for both species. Growth in the number of pleopod 1 cincinnuli was isometric in *P. riveroi* and positively allometric in *P. bermudensis* (Table 3).

The anterior pleopods of females from both species (N = 24 in *P. riveroi*; N = 25 in *P. bermudensis*) were examined under high magnification (400 ×) to look for vestiges of a male AM on pleopod 2 and cincinnuli on pleopod 1, an indicator of sex change in some protandric carideans. No such vestiges were observed. During body size measurement and sexing, all individuals were examined for the presence or absence of a developing ovary. None was ever observed in any male, including larger males that might indicate an individual preparing to change sex.

DISCUSSION

Analysis of population size–frequency distribution and sex-ratio by SC does not support a hypothesis of protandry in
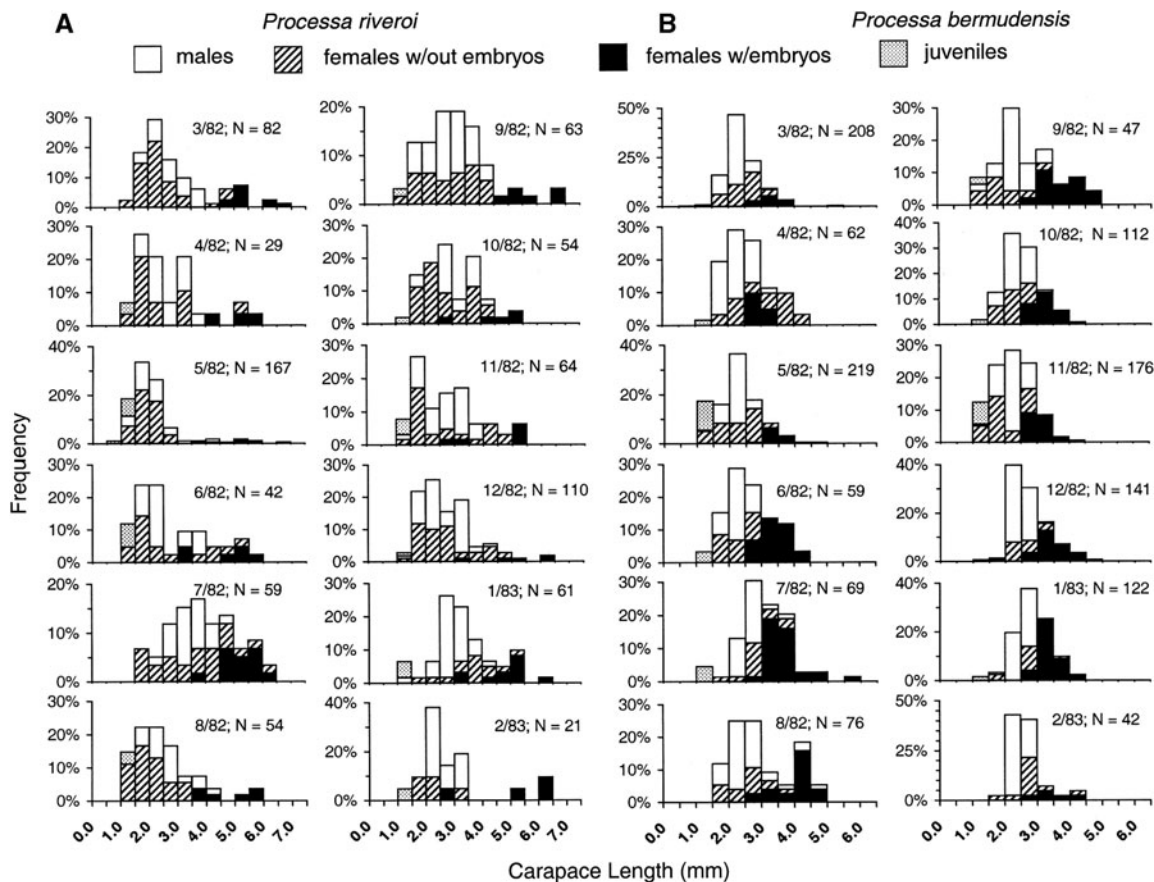

Fig. 2. Monthly size–frequency distributions of *Processa riveroi* and *P. bermudensis* from March 1982 to February 1983. The frequency of males, females with embryos, females without embryos and juveniles from monthly population samples is given for (A) *P. riveroi* and (B) *P. bermudensis*.

Table 1. Sex-ratios (number of males/number of males + number of females) in 0.5 mm carapace length (CL) size-classes in *Processa riveroi* in seagrass meadows at Dorado, Puerto Rico, March 1982 to February 1983. N = total number of males + females in a size-class. The hypothesis of a 0.5 sex-ratio was tested using Chi-square (1 df) for all size-classes with both males and females. An asterisk next to the sex-ratio indicates that the null hypothesis of a 0.5 sex-ratio was rejected ($P \leq 0.05$). The conclusion column indicates whether the number of males in the size-class was equal, less than or greater than the number of females.

Size-class (CL, mm)	Sex-ratio	N	X_1^2 value	P value	Conclusion
1.0 – 1.49	0.28*	36	7.11	0.005 < P < 0.01	F > M
1.5 – 1.99	0.33*	165	19.7	<< 0.005	F > M
2.0 – 2.49	0.45	164	1.6	0.1 < P < 0.25	M = F
2.5 – 2.99	0.60*	114	5.0	0.01 < P < 0.025	M > F
3.0 – 3.49	0.71*	99	17.0	<< 0.005	M > F
3.5 – 3.99	0.56	64	1.0	0.5 < P < 0.75	M = F
4.0 – 4.49	0.28*	39	7.4	0.005 < P < 0.01	F > M
4.5 – 4.99	0.04*	26	22.1	<< 0.005	F > M
5.0 – 5.49	0	35	—	—	F > M
5.5 – 5.99	0	12	—	—	F > M
6.0 – 6.49	0	9	—	—	F > M
6.5 – 6.99	0	4	—	—	F > M
All size-classes	0.42*	767	17.8	<< 0.005	F > M

either of the two *Processa* species investigated. A population structure composed of small males and larger females with little or no overlap in size is often used to initally suggest protandric sex change in caridean shrimps (e.g. Butler, 1964; Carpenter, 1978; Bauer, 1986, 2004; Baeza, 2010; Baeza & Piatoni, 2010; Bauer & Thiel, 2011). This was the most important evidence used by Noël (1973, 1976) to conclude that Atlantic and Mediterranean subspecies of *P. edulis* were protandric. Monthly size–frequency distributions in the Caribbean *P. riveroi* and *P. bermudensis* examined in this study did show that females reached larger size than males. However, smaller SC contained both males and immature females throughout the year, although there were some months when there were more males than females in some of these SC. A sex-ratio (SR) analysis by SC of the overall year-long population sample showed an equal or female-biased SR in the smallest SC, a male-biased SR in 1–3 intermediate SC, with larger SC dominated by females incubating embryos. Such a population structure may result from differential growth and mortality in males and females (Wenner, 1972; Labat & Noël, 1987). Indeed, a size–frequency distribution with only small males and only larger females, with little overlap in male and size, may occur in completely gonochoric

species at certain seasons of the year (*Heptacarpus sitchensis* (Brandt, 1851) in Bauer (1976); *Thor dobkini* Chace, 1972 in Bauer & VanHoy (1996); reviewed in Bauer (2004)). In *P. riveroi* and *P. bermudensis*, slower growth to smaller male body size together with a higher mortality on large males may have caused the observed accumulation of males in intermediate SC, resulting in an 'anomalous pattern' (Wenner, 1972) in size–frequency distributions.

Observation of transitional individuals with sexual characters intermediate between male and female has been important in identification of protandry or protandric simultaneous hermaphroditism in caridean shrimps (e.g. pandalids: Berkeley, 1930; Butler, 1964; Bergström, 2000; hippolytids: Kagwade, 1982; Bauer, 1986; Bauer & Holt, 1998; Braga *et al.*, 2009; Baeza, 2010; Baeza & Piatoni, 2010) even when population sample sizes are small (Baeza, 2010; Baeza & Piatoni, 2010; Bauer & Thiel, 2011). In some species, such as the hippolytid *Thor manningi* Chace, 1972, the size of male characters such as the relative size of the AM and ejaculatory ducts diminish in size (Bauer, 1986). In the same transitional individuals, female 'breeding dress' characters associated with spawning and embryo incubation, such as the width of pleopod flanges and abdominal pleura, increase

Table 2. Sex-ratios (number of males/number of males + number of females) in 0.5 mm carapace length (CL) size-classes in *Processa bermudensis* from seagrass meadows at Dorado, Puerto Rico, March 1982 to February 1983. See Table 1 for symbol legend used below.

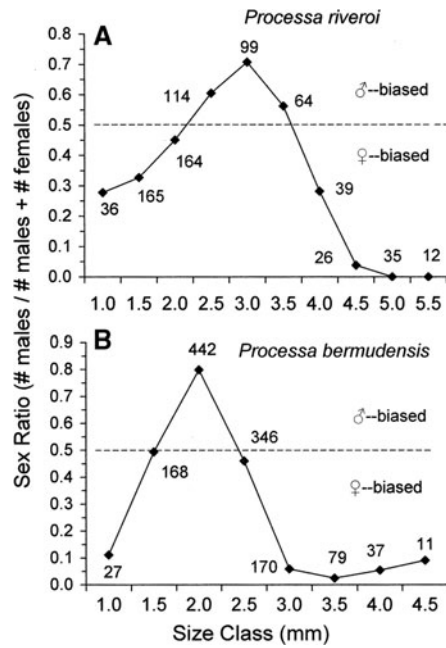| Size-class (CL, mm)	Sex-ratio	N	X_1^2 value	P value	Conclusion
1.0 – 1.49	0.111*	27	16.3	<< 0.005	F > M
1.5 – 1.99	0.49	168	0.02	0.90 < P < 0.95	M = F
2.0 – 2.49	0.80*	442	175.7	<< 0.005	M > F
2.5 – 2.99	0.46	346	2.3	0.10 < P < 0.25	M = F
3.0 – 3.49	0.06*	170	132.3	<< 0.005	F > M
3.5 – 3.99	0.02*	79	71.2	<< 0.005	F > M
4.0 – 4.49	0.05*	37	29.4	<< 0.005	F > M
4.5 – 4.99	0.09*	11	7.4	0.005 < P < 0.01	F > M
5.0 – 5.49	0	1	—	—	F > M
5.5 – 5.99	0	1	—	—	F > M
All size-classes	0.478	1282	2.4	0.10 < P < 0.25	M = F

Fig. 3. Sex-ratios by size-class from the total sample of (A) *Processa riveroi* and (B) *P. bermudensis*.

and become more female-like. Prior to sex change, individuals with male external characters can be observed with macroscopically visible vitellogenic ovaries in various stages of development (e.g. Bauer, 1986; Bauer & Holt, 1998; Baeza, 2010; Baeza & Piatoni, 2010). In this study, careful measures of two male characters, the AM (length; number of setae) and pleopod 1 cincinnuli, showed no or little reduction with increasing body size. No vestiges of external male structures
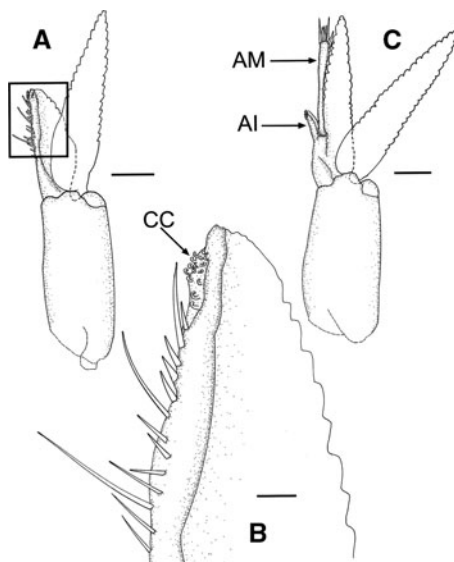

Fig. 4. Male external sexual characters from a *Processa riveroi* male, 3.3. mm carapace length (A) pleopod 1 showing portion (box) of endopod magnified in (B); (B) distal half of endopod, pleopod 1, showing setae and cincinnuli (coupling hooks, CC) characteristic of males and lacking in females; (C) pleopod 2 of same male, showing the appendix masculina (AM) and appendix interna (AI) with cincinnuli. Scale bars = 250 μm in A and C, 50 μm in B.

were observed in females whose anterior pleopods were examined microscopically. Likewise, no male individuals of the many examined in this study during sexing showed any development of gonads with vitellogenic oocytes.

Thus, evidence presented here does not suggest protandry in *P. riveroi* and *P. bermudensis*. In a very thorough study on the population biology of *P. nouveli holthuisi* Al-Adhub & Williamson, 1975 by Gros (1979), no evidence of protandry in size–frequency distributions and no intersexes was found. In the larger SC during the reproductive season, males were significantly smaller than females with low overlap, but in smaller SC, both males and juvenile females occurred in similar numbers. In *P. edulis*, the size–frequency distribution was strongly suggestive of protandry, particularly partial protandry, a sexual system in which most indviduals go through sex change ('secondary females') but with some individuals that develop directly into females without a male phase ('primary females') (Noël 1973, 1976). Partial protandry is quite common in North Pacific pandalids (review in Bergström, 2000), with sometimes numerous primary females. However, morphological evidence for protandry in these pandalids is quite convincing, with sexually transitional individuals intermediate in size between smaller males and larger reproductive females.

There is little direct morphological evidence for protandry in *P. edulis*. Only 4 of approximately 3500 individuals examined (0.11%) showing striking intersex characters (Noël, 1976), although Noël (1976: 86) does state that some unspecified number ('plusieurs'; i.e. some or several) showed an apparently less striking mix of male and female characters. Other clearly gonochoristic species may have a much higher rate of intersex individuals, e.g. 1–2% reported by Blackless *et al.* (2000) for *Homo sapiens* Linnaeus, 1758. However, Noël (1976) suggested that sex change occurs in a single moult in *P. edulis*, accounting for the relative lack of individuals with either external or internal (gonadal) transitional characters.

Other similar controversial cases of protandry occur in the caridean genera *Hippolyte* and *Crangon*. *Hippolyte inermis* Leach, 1815 was intially described as protandric by Reverberi (1950) in a short descriptive paper, a conclusion supported by Zupo (1994) with extensive size–frequency analysis. However, Cobos *et al.* (2005) performed careful histological work which showed no evidence of a transitional gonad. Zupo *et al.* (2008) observed growth and external sexual morphology in males in the laboratory; in several instances, males lost the male appendices masculinae in a single moult. Furthermore, one such individual did show, upon histological examination, development of an active ovary. Likewise, protandry in *Crangon crangon* (Linnaeus, 1758) has been disputed for some time. For example, Bodekke *et al.* (1991), based on size–frequency and morphological observations including purported transitional individuals, concluded that a significant proportion of the population studied underwent sex change. On the other hand, Schatte & Saborowski (2006) observed sex change in one individual directly but suggested that sex change in this species may be facultative. Gavio *et al.* (2006), using a variety of evidence including transitional individuals and direct observation of sex change in 2 captive individuals, showed more convincingly that the sexual system of *C. franciscorum* Stimpson, 1856 is partial protandry. In species where protandry is strongly suggested on the basis of population structure, but where
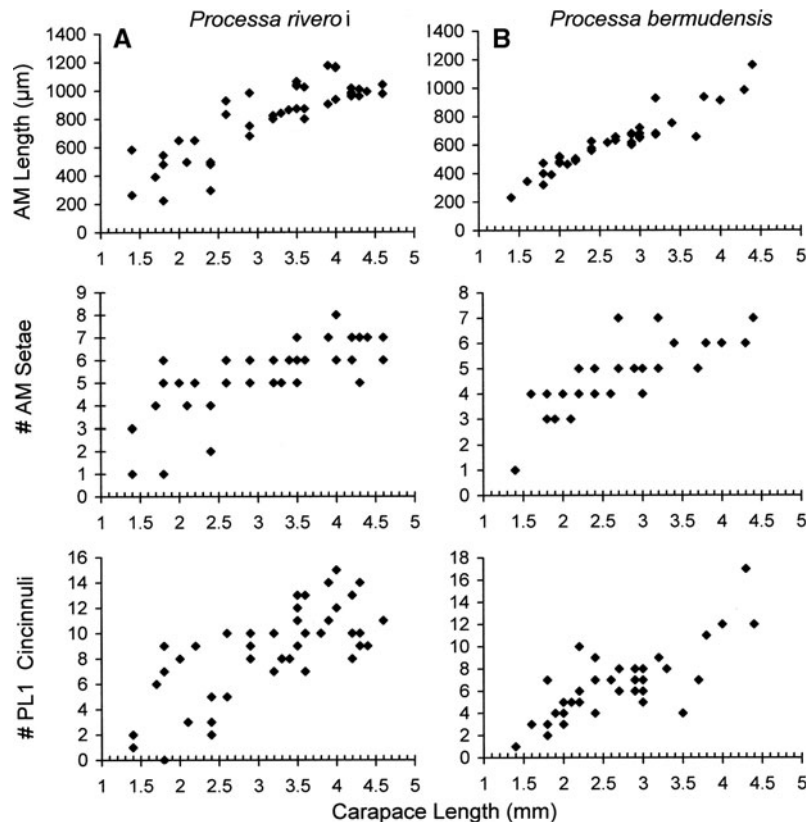
Fig. 5. Morphometric measures of male external sexual characters of *Processa riveroi* and *P. bermudensis*. Appendix masculina (AM) length, number of AM setae, and number of pleopod 1 cincinnuli are plotted against size (carapace length) in (A) *Processa riveroi* and (B) *P. bermudensis*. See Table 3 for regression coefficients and statistics.

transitional individuals are not routinely observed, direct observation of sex change in individuals followed through time may provide key evidence of protandry.

In carideans, there is considerable intrageneric variation in sexual systems (gonochory; protandry; protandric simultaneous hermaphroditism or PSH). In some genera, such as *Pandalus*, nearly all species are protandric (Bergström, 2000); likewise, all of the several *Lysmata* and the two *Exhippolysmata* spp. examined to date have a PSH sexual system (Kagwade, 1982; Bauer & Holt, 1998; Bauer, 2006; Baeza, 2006, 2009; Laubenheimer & Rhyne, 2008; Baeza *et al.*, 2009; Braga *et al.*, 2009). On the other hand, of the

four *Thor* species examined, one species has a mix of protandric and primary male individuals (Bauer, 1986), another is purely protandric (Baeza & Piatoni, 2010), and two others are definitely gonochoristic (Bauer & VanHoy, 1996). These four *Thor* spp. are tropical or subtropical seagrass species, and three are very similar in size and habitat requirements (Bauer & VanHoy, 1996). In this study, we found no strong or convincing evidence for protandry in *P. riveroi* and *P. bermudensis*, small tropical seagrass-meadow species with continuous reproduction, episodic recruitment, and a probable short life span of less than one year (Figure 2; and see Bauer, 1989). On the other hand, *P. edulis*, a temperate-zone

Table 3. Allometry of male secondary sexual characters in *Processa riveroi* (above) and *P. bermudensis* (below). The slope (β) (with lower and upper 95% confidence limits) is given for rank regressions of appendix masculina length, the number of appendix masculina setae, and the number of pleopod 1 cincinnuli regressed on carapace length of the form $(Y) = \beta (\log X) + y$-intercept. The Spearman correlation coefficient (r_s) tests the null hypothesis of no significant regression ($\beta = 0$) which was rejected for all regressions ($P <<< 0.001$).

Sexual character	β	r_s	Allometry
Processa riveroi			
Appendix masculina length (N = 45)	0.921 (0.739; 1.104)	0.772	Isometric
Number of appendix masculina setae (N = 45)	0.629 (0.470; 0.789)	0.697	Negative
Number of pleopod 1 cincinnuli (N = 42)	0.970 (0.615; 1.325)	0.665	Isometric
Processa bermudensis			
Appendix masculina length (N = 38)	1.038 (0.924; 1.151)	0.947	Isometric
Number of appendix masculina setae (N = 38)	0.709 (0.526; 0.892)	0.801	Negative
Number of pleopod 1 cincinnuli (N = 39)	1.453 (1.130; 1.777)	0.717	Positive

species with highly seasonal reproduction and a 2–2.5 year life span, is considered protandric (Noël, 1973, 1976), although such a conclusion is controversial and needs to be resolved. The mating system of these species has not been studied in detail, but most likely is a promiscuous 'pure searching' typical of caridean species with small males and larger females (Wickler & Seibt, 1981; Bauer, 2004) (e.g. mating observations on *P. edulis* by Noël, 1976). The interesting and important question that must be asked and resolved about sexual systems in carideans is: what are the selective pressures which favour one sexual system (gonochory, protandry or PSH) over another among closely related species? To answer this question, the true variation in sexual systems among caridean species must be known, which will require careful examination and testing of sexuality in caridean species suspected of protandric hermaphroditism or PSH.

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