Sexual system and sexual dimorphism in the shrimp \textit{Periclimenes brevicarpalis} (Schenkel, 1902) (Caridea: Palaemonidae), symbiotic with the sea anemone \textit{Stichodactyla haddoni} (Saville-Kent, 1893) in the Gulf of Mannar, India

Sanjeevi Prakash\textsuperscript{1,2,3}, Thipramalai T. Ajith Kumar\textsuperscript{3,4}, Thanumalaya Subramoniam\textsuperscript{1} and J. Antonio Baeza\textsuperscript{2,5,6}

\textsuperscript{1}Centre for Climate Change Studies, Sathyabama University, Rajiv Gandhi Salai, Chennai 600 119, Tamil Nadu, India; \textsuperscript{2}Department of Biological Sciences, 132 Lang Hall, Clemson University, Clemson 29634, South Carolina, USA; \textsuperscript{3}Centre of Advanced Study in Marine Biology, Faculty of Marine Sciences, Annamalai University, Portonovo, 608 502, Tamil Nadu, India; \textsuperscript{4}National Bureau of Fish Genetic Resources (ICAR), Canal Ring Road, Dilkusha Post, Lucknow 226 002, Uttar Pradesh, India; \textsuperscript{5}Smithsonian Marine Station at Fort Pierce, 701 Seaway Drive, Fort Pierce, Florida, USA; and \textsuperscript{6}Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

Correspondence: J. A. Baeza; e-mail: baeza.antonio@gmail.com

(Received 12 December 2016; accepted 3 March 2017)

ABSTRACT

Little is known about the biology of Indo-West Pacific ornamental crustaceans, including the peacock-tail shrimp \textit{Periclimenes brevicarpalis} (Schenkel, 1902) (Palaemonidae Rafinesque, 1815), a species that is highly valued by aquarists and marine photographers. We provide information about gender expression and sexual dimorphism in \textit{P. brevicarpalis}. We studied a population inhabiting the Haddon’s carpet sea anemone \textit{Stichodactyla haddoni} in the Gulf of Mannar, Tamil Nadu, India. In the studied population, males attain similar maximum and average body sizes (carapace length) than females. This observation and the absence of transitional individuals exhibiting male (appendices masculinae) and female (eggs underneath the abdomen) reproductive traits, ruled out sequential and simultaneous hermaphroditism in \textit{P. brevicarpalis} and suggest that this species is gonochoric. Minimal differences in claw size (males > females) were observed between the two sexes. The allometric growth of this structure was greater in females than males. The absence of sexual dimorphism in terms of body size concomitantly with the minimal differences in weaponry observed between the two sexes suggest that the species is monogamous, an inference also supported by the common observation of pairs of shrimps inhabiting the same host individual in the field. Additional studies on the behavioral ecology of \textit{P. brevicarpalis} should reveal its mating system.

Key Words: allometry, body size, host use, social monogamy

INTRODUCTION

Caridean shrimps exhibit astonishing diversity in terms of sexual systems (Charnov, 1982; Bauer, 2004). Many species are gonochoric, with populations comprising male and female individuals that never change sex (Bauer, 2001, 2004). Various other species are strict protandric hermaphrodites, with individuals undergoing sex change from male to female with increases in size and/or age (Bergstrom, 2000). Furthermore, several variants of protandry have been reported in caridean shrimps. For instance, a few species exhibit partial protandry, with populations containing a mix of protandric individuals and females that never change sex as in \textit{Processa edulis edulis} (Risso, 1816) (Processidae Ortmann, 1896) (Noel, 1976) and \textit{Crangon crangon} (Linnaeus, 1758) (Crangonidae Haworth, 1825) (Boddeke et al., 1991; Schatte & Saborowski, 2006). Likewise, in the Caribbean shrimp \textit{Thamnallia manningii} Chace 1972, 50% of the individuals in the population are primary males that never change sex, whereas the remaining 50% of the individuals in the population...
are protandric hermaphrodites (Bauer, 1986). Lastly, a few species exhibit protandric simultaneous hermaphroditism, where individuals in the population first mature as males and later in life reproduce as functional simultaneous hermaphrodites. Protandric simultaneous hermaphroditism has been reported to occur in *Lysmata Risso, 1816* (Lysmatidae Dana, 1852) (Bauer, 2004) and also occurs in species of the hippolytoids *Ehhipolytus Stebbing, 1915* (Braga et al., 2009; Baeza et al., 2010) and *Parhippolyte Borradale*, 1900 (Barbouriidae Christoffersen, 1987) (Onaga et al., 2012).

Variability in sexual systems varies at different taxonomic levels within the infra-order Caridea. For instance, protandric simultaneous hermaphroditism seems to be a fixed trait in *Lysmata* (Lysmatidae) (Bauer & Holt, 1998; Freddler, 1998; Baeza & Anker, 2008; Baeza, 2008a; Baeza et al., 2007, 2014). In contrast, *Thor* (Thoridae Kingsley, 1879), gender expression varies considerably. *Thor floridanus Kingsley 1878* and *T. dobkinsi Chace, 1972* are gonochoristic species, but the congeneric *T. mansingii* is a partial protandric hermaphrodite and *T. ambonensis De Man, 1883* is a strict protandric hermaphrodite (Bauer, 1986; Bauer & VanHoy, 1996; Baeza & Piantoni, 2010). Similarly, among pandalids (Pandalidae Haworth, 1825), *Alatopandalus propinquus Sars 1870* exhibits a gonochoristic sexual system while *Pandalus eos Makarov, 1935*, *P. gowion Simpson, 1860*, *P. latirostris Rathbun, 1902*, *P. platyurus Brandt, 1831*, and *P. rhathra Brandt, 1851* are sex changers (Butler, 1964, 1980; Komai, 1999; Bergström, 2000). Lastly, most species of *Rynchocinetes H. Milne Edwards, 1837* and *Cheirostylus Holthuis, 1995* (Rynchocinetidae). Ortmann, 1890 are gonochoristic (Correa et al., 2000; Thié et al., 2010; Bauer et al., 2014; Prakash et al., 2016), but recent studies have revealed that the congeneric *R. titon Kubo, 1942* is a strict protandric hermaphrodite (Bauer & Thié, 2011; Osawa et al., 2015).

Our knowledge of gender expression in caridean shrimps has improved substantially during recent decades, but the sexual system of most caridean shrimps is yet to be known (Bauer, 2004). Most studies on gender expression in shrimps have focused in relatively few genera from a limited number of families, including among a few others, Alpheidae Rafinesque, 1815 (*Alpheus spp.* and *Athanas spp.*) (Knowlton, 1980; Gherardi & Caloni, 1993), Grangoniidae Haworth 1825 (*Grangon spp.*) (Boeddeke et al., 1991), Palaemonidae (*Pallangopsis spp.*) (Noel, 1976; Bauer & Conner, 2011), Hippolytidae (*Hippolyte Bate, 1888* (*Charisium Bate, 1888* and *Hippolyte spp.*) (Clarke, 1965; Espinoza-Fuenzaldia et al., 2008; Terossi et al., 2008), and Lysmatidae (*Bauer & Holt, 1998*; Baeza, 2008a, 2010). In Palaemonidae, a species-rich family with considerable ecological disparity, most studies have been conducted in the predominantly freshwater and estuarine genera *Macrobrachium*, *Spence Bate, 1868*, *Palaemon Weber, 1795* and *Exopalaemon Holthuis, 1950* (Ra’anan & Sagit, 1985; Berglund, 1984; Oh et al., 2002; Bauer & Abdalla, 2001). Only a few detailed studies on the sexual system of two symbiotic palamenes, *Odontonia katou Kubo, 1940* (Baeza et al., 2015) and *Pontonia manningi Fransen, 2000* (Baeza et al., 2016a), have been conducted during recent years. The reproductive biology of various species belonging to the commercially important and/or ecologically relevant genera *Macrobrachium* (Ra’anan & Sagit, 1985; Kuris et al., 1987; Miosolin & Bueno, 2002; Mantel & Dudgeon, 2003; Lima et al., 2014) and *Palaemon* (Berglund, 1984; Guerra et al., 1994; Kim & Hong, 2004; Kim et al., 2008; Pascoaal et al., 2013) is known. Still, little is known about the sexual systems of most species in this family.

We were particularly interested in examining the sexual system of the marine palaemonid *Periclimenes brevicarpalis* (Schmekel 1902), widely distributed across the Indo-West Pacific, which engages in symbiotic interactions with various tropical sea anemones (*Bruce & Svoboda, 1983*; Fautin & Allen 1992). Detailed studies on the social structure of *P. brevicarpalis* are lacking. However, this species is presumed to inhabit sea anemones as adult pairs that might share ‘their’ host individuals with a few conspecific juveniles (i.e., in contrast to that reported for the assoail congeneric *Anylomenes pedersoni* (Chace, 1956) (Nizinski, 1989). Female shrimps most often hide under the sea anemone’s tentacles, whereas males most frequently are found on top of the sea anemone’s oral surface (*Bruce & Svoboda, 1983*). The symbiotic interrelationship between *P. brevicarpalis* and sea anemones seems to be parasitic because shrimps feed upon the tentacles of the host (*Suzuki & Hayashi, 1977; Bruce & Svoboda, 1983*). In turn, growth rate, molting interval, and larval production increases in *P. brevicarpalis* when in association with sea anemones (*Fautin et al., 1995*).

In India, *P. brevicarpalis* is widely distributed in the Gulf of Mannar and Lakshadweep (*Kemp, 1922*; Prakash et al., 2015), Andaman and Nicobar Islands (*Tikader et al., 1986*), and Gulf of Kutch (*Unmesh & Prakash, 2011*). The species is collected and traded along with sea anemones by the ornamental industry (*Prakash et al., 2017*).

We examined the size-frequency distribution of males and female shrimps, the presence of secondary sexual characters in the population, sexual dimorphism, and the morphometry of different body parts (e.g., second pair of chelipeds and flap of the second pleopod) to reveal the sexual system of *P. brevicarpalis*.

### MATERIALS AND METHODS

#### Collection of shrimps and hosts

The sexual system of the peacock-tail shrimp *Periclimenes brevicarpalis* was examined using individuals collected in the shallow coastal waters of the Gulf of Mannar (GOM) (08°30’N, 78°12’E to 09°15’N, 79°30’E), Tamil Nadu, India, from April to September 2013. The Gulf of Mannar lies on the southeast coast of India between the cities of Rameswaram and Tuticorin, covering an area of approximately 10,500 km² (Fig. 1A). Twenty-one islands run parallel to the coast with fringing reefs adjacent to the islands (*SAC, 2012*). The Gulf of Mannar is exceptionally rich in marine biodiversity (*Venkataraman & Wafar, 2005*) and was recognized as the first marine biosphere reserve in south Asia.

Specimens of *P. brevicarpalis* were collected from Haddon’s carpet sea anemone *Stichodactyla haddoni* Saville-Kent, 1893 during day hours while scuba diving at depths ranging between 2 and 10 m. Shrimps were collected using mesh nets (pore size = 1 mm) after gently disturbing the sea anemone tentacles and column (Fig. 1B–C). After collection, most of the specimens were preserved in 5–10% seawater formalin and transported to the wet laboratory in the Centre of Advanced Study in Marine Biology, Annamalai University, Portonovo, Tamil Nadu, India. Preserved shrimps were rinsed with freshwater and transferred to 70% ethanol for permanent storage until further study.

#### Sexual system in *Periclimenes brevicarpalis*

We conducted observations on the reproductive morphology in a total of 78 individuals: carapace length (CL in mm, distance from the posterior edge of the eye orbit to the mid-dorsal posterior edge of the carapace), propodus length (PL) of the second (larger) pair of chelipeds, and basipod flap width (FW) of the second pleopod. All measurements were made under a stereomicroscope (Motic-MS20) using a graduated ocular micrometer to the nearest 0.1 mm. The sex of each shrimp was determined based on the presence (in males) or absence (in females) of appendices masculines on the endopod of the second pleopods (see *Bauer, 2000, 2004*). Females were classified as ovigerous and non-ovigerous depending upon the presence or absence of developing embryos under the abdomen, respectively. Four different embryo stages were recognized: Stage 1, newly spawned embryos bright green in color with no visible blastoderm; Stage 2, blastoderm distinct with no eye development; Stage 3, embryos containing 2/3 of the original yolk with visible eye spots and appendages with small orange spots; Stage 4, completely developed embryos, translucent white in color, yolk nearly depleted, eyes prominent and abdomen free from the cephalothorax (see *Allen, 1966*).
We focused in identifying individuals exhibiting a mixture of male (presence of appendix masculina in the second pleopods) and female (embryos under the abdomen) reproductive traits. These ‘transitional’ individuals have been reported in other species of caridean shrimps that exhibit sex change and represent a reliable indication of protandry in the same clade (Butler, 1964, 1980; Bauer & VanHoy, 1996; Bauer & Holt, 1998; Baeza et al., 2007, 2014; Baeza, 2008a; Baeza & Piantoni, 2010; Bauer & Thiel, 2011).

Allometric growth of body parts in *Periclimenes brevicarpalis*

In order to determine whether or not a linear (proportional) relationship exists between the measured traits (length of the propodus of the major cheliped in the second pair of pereopods (PL), basipod flange width of the second pleopod (FW)) and body size (CL), we used the allometric model \( y = ax^b \) (Hartnoll, 1978, 1982). The slope \( b \) of the log-log least-squares linear regression characterizes the degree of exponential increase \( (b > 1) \) or decrease \( (b < 1) \) of the length of PL, DL, and FW with a unit of increase in body size (CL). For example, if the cheliped or the basipod flange grow more or less than proportionately with a unit increase in body size in *P. brevicarpalis*, then the slope should be greater or smaller than the unity, respectively (Hartnoll, 1978, 1982). Different t-tests were conducted to determine whether the different calculated slopes \( b \) diverge from an expected slope of unity (Hartnoll, 1978, 1982; SAS, 2004).

We investigated whether or not each measured body dimension differed between the sexes using independent analyses of covariance (ANCOVA) (Sokal & Rohlf, 1981). In each of these ANCOVAS, we used CL as the covariate, sex as the independent variable, and one of the measured body traits (PL and FW) as dependent variables.

RESULTS

Sexual system in *Periclimenes brevicarpalis*

A total of 78 specimens of *P. brevicarpalis* were retrieved from the sea anemone *Stichodactyla haddoni*. Thirty-eight out of 78 shrimps (48.7%) were classified as females based on the absence of appendices masculinae on the endopods of the second pair of pleopods. Appendices internae with numerous cincinnuli were present in the endopods of the second pair of pleopods in these females (Fig. 2A, B). Nineteen out of the 38 females (50%) carried eggs underneath the abdomen in different stages of development (Stage 1 = 6, Stage 2 = 5, Stage 3 = 3, and Stage 4 = 5).

Forty out of 78 shrimps (51.3%) were considered males given the presence of both appendices masculinae and appendices internae on the endopods of the second pair of pleopods (Fig. 2C, D). The appendices internae showed numerous distal cincinnuli (coupling hook-like structures) in all male specimens. The appendices masculinae exhibited numerous, long distal spines, especially among the largest males in our sample (Fig. 2C, D). In all males, the endopods were between two and three times shorter than the exopods of the first pair of pleopods and did lack appendices internae and cincinnuli. We did not observe any transitional individuals.

Sexual dimorphism and allometry in *Periclimenes brevicarpalis*

The carapace length of male and female shrimps ranged from 1.5 to 10 mm (mean ± SE, 4.59 ± 0.33 mm) (\( N = 40 \)) and 1.3 to 9.0 mm (5.18 ± 0.34 mm) (\( N = 38 \)), respectively. No statistical differences were observed between the mean carapace length
SEXUAL SYSTEM AND DIMORPHISM IN *PERICLIMENES BREVICARPAIS*

A total of 40 males and 38 females were used for the analysis of allometric growth. A positive correlation was found between propodus length (PL) of the major chelipeds and carapace length (CL) and between basipod flange width (FW) of the second pleopods and carapace length (CL) in males and females ($P < 0.0001$ in all cases). The status and degree of allometry differed among various body parts as well as between the sexes. The propodus length of the major cheliped showed negative allometry with regards to carapace length in the two sexes; the slope depicting the relationship between PL and CL was less than unity in males ($b = 0.69, t(1,38) = 2.024, P < 0.0001$) and females ($b = 0.82, t(1,36) = 2.028, P < 0.0001$) (Table 1; Fig. 3B). An analysis of covariance (ANCOVA) demonstrated a significant effect of sex ($F = 59.5776, df = 3, 74, P < 0.0001$) and PL ($F = 991.6355, df = 3, 74, P < 0.0001$) on CL. The interaction term in the ANCOVA was significant ($F = 7.2973, df = 3, 74, P = 0.0086$). This indicates that the propodus length of the major cheliped was larger in males than in females. The difference in major propodus length between males and females was nevertheless much greater in small than in large shrimps. The major cheliped was quite similar in size among the largest males and females in the population indicating that the major propodus grows faster in females than males during ontogeny (Fig. 3B).

The width of the flange belonging to the second abdominal segment (FW) exhibited positive allometry with respect to carapace length (CL) in the two sexes; the slope of the line depicting the relationship between basipod (FW) of the second pleopod and carapace length (CL) was greater than unity in males ($t(1,26) = 2.056, b = 1.88, P < 0.0001$) and females ($t(1,34) = 2.032, b = 1.80, P < 0.0001$) (Table 1, 3C). An ANCOVA demonstrated a significant effect of sex ($F = 113.7130, df = 3, 60, P < 0.0001$) and carapace length (CL) ($F = 224.8990, df = 3, 60, P < 0.0001$) on FW. The interaction term in this ANCOVA was not significant ($F = 0.1006, df = 3, 60, P = 0.7522$). This indicates that the basipod flange width of the second pleopod of females is always larger than that of males at any given body size and that the growth rate of this structure is similar between males and females during ontogeny (Fig. 3C).

**DISCUSSION**

**Sexual system in *Periclimenes brevicarpalis***

The average and maximum body size attained by males was not different from that attained by females. The absence of this difference in body size between the sexes agrees with that reported for other gonochoric species of caridean shrimps (Baeza 2008b; Espinoza-Fuenzalida et al., 2008; Baeza et al., 2013, 2015, 2016a, b). Furthermore, we never observed transitional individuals.
having characteristics of both males and females, which demonstrates the absence of individuals in the process of changing sex in natural populations of *P. brevicarpalis* and rules out sequential and simultaneous hermaphroditism as the sexual system of this species. Transitional individuals have been reported before for various other shrimp species that undergo shifts in sex allocation during their lifetime and do represent a reliable indication of sex change in other crustaceans, including caridean shrimps (Butler, 1964, 1980; Bauer & VanHoy, 1996; Bauer & Holt, 1998; Baeza et al., 2007, 2014; Baeza, 2008a; Baeza & Piantoni, 2010; Bauer & Thiel, 2011). Our results indicate that *P. brevicarpalis* is a gonochoric species, and as such individuals settle in the benthos, grow, mature, reproduce, and remain as either males or females during their entire lifetime.

Individuals of a few species of caridean shrimps have been observed to change sex occasionally and at low frequency. For instance, laboratory experiments and morphological studies have demonstrated sex change only in 2 out of 40 experimental males in *Crangon franciscorum franciscorum* Stimpson 1856 (Gavio et al., 2006). Laboratory observations over a period of time extending for about 8 months have similarly demonstrated that less than 2% of the males in a population of another protandric shrimp, *Crangon crangon* (Linnaeus, 1758), change sex to females (Schatte & Saborowski, 2006). It could therefore be argued that *P. brevicarpalis* does change sex, but that the transition from males to females in this species is facultative and that it occurs rarely, as reported before for the above species. If sex change in *P. brevicarpalis* is non-obligatory and the probability of sex change in males is considerably low, then our low sample size (78) would allow sex change in this species to go undetected. Future studies could track individual shrimps to test for facultative sex change in this species. Nonetheless, all presently available information suggests that *P. brevicarpalis* is gonochoric.

### Table 1. The relative growth of different body structures in males and females of *Periclimenes brevicarpalis*. Indicated are the regression equations, correlation coefficients ($r^2$ adjusted for df), standard errors (SE) of the slopes, and the allometric status of each selected variable: carapace length (CL), propodus length (PL) of the major chelipeds and basipod flange width (FW) of the second pleopods respectively.

<table>
<thead>
<tr>
<th></th>
<th>x</th>
<th>Regression</th>
<th>$r^2$</th>
<th>SE</th>
<th>t</th>
<th>P</th>
<th>Allometry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>PL CL</td>
<td>$y = 0.6545x + 0.3221$</td>
<td>0.93</td>
<td>0.0295</td>
<td>-10.50</td>
<td>&lt; 0.0001</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>FW CL</td>
<td>$y = 1.8833x – 1.8319$</td>
<td>0.80</td>
<td>0.1835</td>
<td>-4.66</td>
<td>&lt; 0.0001</td>
<td>+</td>
</tr>
<tr>
<td>Females</td>
<td>PL CL</td>
<td>$y = 0.8249x + 0.1605$</td>
<td>0.93</td>
<td>0.0386</td>
<td>4.79</td>
<td>&lt; 0.0001</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>FW CL</td>
<td>$y = 1.8053x – 1.3989$</td>
<td>0.83</td>
<td>0.1432</td>
<td>5.59</td>
<td>&lt; 0.0001</td>
<td>+</td>
</tr>
</tbody>
</table>

### Figure 3. Sexual dimorphism in *Periclimenes brevicarpalis*. A, Size frequency distribution of body size (carapace length, CL, in mm) in males and females; B, Relative growth propodus length (Log PL, mm) of major cheliped as a function of carapace length (Log CL in mm) in males and females; C, Relative growth of basipod flange width (Log FW, mm) of second pleopod in males and females as a function of carapace length (Log CL, mm).
SEXUAL SYSTEM AND DIMORPHISM IN PERICLIMENES BREVICARPALIS

Sagi, 1983; Kuris et al., 1987; Mossolin & Bueno, 2002; Mantel & Dudgeon, 2005; Lima et al., 2014) and Rhynchocinetes sp. (Correa et al., 2000; Thiel et al., 2010; Prakash et al., 2016), mating systems in which sexual dimorphism is remarkable. Either males may attain body sizes larger than females displaying classic sexual dimorphism (in polygamous species; see Thiel et al., 2010) or instances where sexual dimorphism is reverse (females > males, in promiscuous species; see Bauer, 1976). The conditions explaining the absence of sexual dimorphism in terms of body size in P. brevicarpalis are so far unknown. This species has been observed in the field inhabiting sea anemones in male-female pairs (SP & JAB, personal observations). These pairs are occasionally accompanied by conspecific juveniles (Bruce & Svoboda, 1983). Such host-use pattern is indicative of monogamy. Male-male competition is rather weak in monogamous mating systems (Baesa, 2008b) and therefore there are no selective pressures for males to develop large body size to increase opportunities for access to receptive females (Baesa & Thiel, 2007). Whether P. brevicarpalis is a socially monogamous species remains to be experimentally addressed.

The infraorder Caridea, to which P. brevicarpalis belongs, is the most diverse in terms of sexual systems among decapod crustaceans (Bauer, 2004). In addition to gonochorism, other species are reported to exhibit social sequential hermaphroditism such as protandry in Thor amboinensis (Baesa & Piantoni, 2010) and Sergia rhizophorae Rathbun, 1900 (Baesa, 2010), or mixed protandry where individuals that undergo sex change coexist with other conspecifics that mature either as pure males or females and that do not change sex as in Thor manningi (Bauer, 1986). Protandric simultaneous hermaphroditism has been demonstrated in other carideans such as Lysmata, Echiptypolynemata, and Parathelphus (Bauer, 2004; Braga et al., 2009; Baesa et al., 2010; Onaga et al., 2012). Similarly, mating systems vary considerably in carideans. Some species, such as Pontonia marginata (Baesa, 2008b) and Pontonia sp. (Aucoin & Himmelman, 2010) are monogamous, whereas others such as Macrobrachium sp. (Ra’anan & Sagi, 1985) and Rhynchocinetes sp. (Thiel et al., 2010; Prakash et al., 2016), are polygamous. Other species exhibit even more complex sexual behaviors such as alternative mating tactics in species of Macrobrachium and Rhynchocinetes (Bauer, 2004). Further detailed studies on the lifestyle, sexual, and mating system of additional species of caridean shrimps and the development of a comprehensive molecular phylogeny in this clade (see Li et al., 2011; Baesa, 2013; De Grave et al., 2014) are necessary to elucidate the fascinating evolutionary history of gender expression and mating behavior in Caridea.

ACKNOWLEDGEMENTS

SP and TTAK are grateful to former Director & Dean K. Kathiresan, Faculty of Marine Sciences, Annamalai University, Portonovo, India for encouragement, the authorities of Annamalai University for the facilities provided and the Chancellor, Pro Chancellor, Vice President, and Pro Vice Chancellor of Sathyabama University, Chennai, India for their constant support to the Centre for Climate Change Studies. TTAK is thankful to the Director of the National Bureau of Fish Genetic Resources (ICAR), Lucknow. SP acknowledges The Rufford Foundation, London for the award of a Rufford Small Grant project (no. 15679-1) and United States-India Educational Foundation for the award of a Fulbright-Nehru Post-Doctoral Research Fellowship (no. 2162/FNPDPR/2016) where most of this manuscript has been developed. The authors are also thankful to three anonymous reviewers whose constructive criticism greatly improved the manuscript.

REFERENCES


