



The Crustacean Society

Journal of Crustacean Biology

Journal of Crustacean Biology 38(3), 354–366, 2018. doi:10.1093/jcobiol/rux112

Reproduction in the deep-sea penaeoid shrimp *Aristeus alcocki* Ramadan, 1938 (Decapoda: Penaeoidea: Aristeidae) from southwestern India

P. Paramasivam, R. D. Chakraborty, M. Gidda, K. Ganesan, B. Ponnathara Kandankoran, S. Laxmanan and R. Nadakkal

Crustacean Fisheries Division, Central Marine Fisheries Research Institute, Ernakulam North P.O., P.B. No. 1603, Cochin-682018, Kerala, India

Correspondence: R.D. Chakraborty; e-mail: rekhadevi7674@gmail.com

(Received 1 June 2017; accepted 29 November 2017)

ABSTRACT

The Arabian red shrimp, *Aristeus alcocki* Ramadan, 1938, is one of the targets of commercial trawlers operating since 2000 along the Indian coasts at depths of 200–850 m. We report for the first time on the reproductive biology, insemination frequency, ovarian maturation, gonadosomatic index (GSI), size at maturity, and fecundity of *A. alcocki* investigated macroscopically and validated histologically using monthly trawl samples from the southwestern coast of India. Females have an open thelycum with five gonad developmental stages (I to V) and two stages (I and II) in males. A total of 4,170 specimens were examined and 68.6% of the females had been inseminated (carapace length (CL) 22.0–53.0 mm), predominantly during January to May. Females in stage I (immature) measured on average CL 25.5 ± 0.87 mm, those in stages IV and V (mature) CL 41.5 ± 0.62 mm. Immature males were smaller, mean CL 20.5 ± 0.5 mm. Size at first sexual maturity for females was estimated as CL 35.07 mm (total length (TL) 120–170 mm) and the inseminated specimens ($CL_{50\%}$) were mature at CL 31.45 mm using a non-linear method. The smallest mature female was CL 35 mm, whereas the size at maturity ($CL_{50\%}$) of males was estimated as CL 19.6 mm (TL 75–96 mm). We also report synchronous oocyte development and continuous spawning activity with a peak during January to April. Information on the reproduction of this deep-water shrimp will help fishery managers estimate the stock sustainability and develop resource management measures.

Key Words: Arabian red shrimp, gonadosomatic index, insemination, maturity, oocytes

INTRODUCTION

Deep-water shrimps represent an important and valuable fishery resource at the Arabian Sea continental slope of India (Mohamed & Suseelan, 1973; Suseelan, 1974; Suseelan *et al.*, 1989a, b; Radhika, 2011). The major targeting deep-sea shrimps include *Aristeus alcocki* Ramadan, 1938, *Plesionika quasigrandis* Chace, 1985, *Heterocarpus gibbosus* Spence Bate, 1888, *H. woodmasoni* Alcock, 1901, and *Metapenaeopsis andamanensis* (Wood-Mason in Wood-Mason & Alcock, 1891). Landing statistics from 2008 to 2015 reveal that the *A. alcocki* (Aristeidae) is the most important, commercially exploited deep-sea penaeoid along the entire Indian coast (CMFRI, 2008, 2014, 2015), constituting about 36% from the region (CMFRI, 2014, 2015). *Aristeus alcocki*, the Arabian red shrimp, locally known as the ‘red ring’ shrimp (Silas, 1969; Suseelan *et al.*, 1989a; Madhusoodana *et al.*, 2008; CMFRI, 2015),

has been reported from the continental slope of the Gulf of Aden, Arabian Sea, and Bay of Bengal (Pérez Farfante & Kensley, 1997; De Grave & Franssen, 2011). Although the maximum catch of this species occurs between 200 to 850 m, it has been reported as deep as 3,000 m at the upper continental slope (Alcock, 1901).

Aristeid shrimps are more vulnerable to over exploitation than coastal penaeoids because high economic value, low growth rates and longer life spans, complex bathymetric distribution, and aggregation behaviour for reproduction that triggers the seasonal pattern of vulnerable biomass or depletion in the fishing grounds (Ragonese & Bianchini, 1995; Sardà *et al.*, 2003, Tudela *et al.*, 2003; Pezzuto *et al.*, 2006; Dallagnolo *et al.*, 2007; Pezzuto & Dias, 2009). Information about the biology of *A. alcocki* is scarce and only a few reports are available on the bathymetric distribution of the species on the continental slope of the Kerala coast by

Suseelan (1989), Madhusoodana *et al.* (2008), and Radhika (2011). Detailed information on its reproductive biology is lacking.

A knowledge of the reproductive biology of *A. alcocki* is necessary for monitoring programs on the conservation of its stocks and thus for the development of adequate fisheries policies in India. The main goal of this study was to describe the developmental stages of the gonads of female and male *A. alcocki* by macroscopic and microscopic analysis. The study aimed to show the relationship between fecundity and length and gonad weight (GW) and spawning season which will help fishery managers to estimate the stock sustainability and to develop management strategies of the resource.

MATERIAL AND METHODS

Samples of *A. alcocki* were collected every two weeks between January 2013 and May 2015 using deep-sea bottom trawlers with a mesh size of 20–26 mm in its cod-end and, operated off the southwestern coast of India at depths of 200–900 m (Fig. 1). Date, time, depth (m), trawling speed (2 nm h⁻¹), and fishing duration (1–2 h haul⁻¹), catch composition (kg), and species composition

were recorded for each trawl. Data were collected from January to December except for June to August, the monsoon ban. In total, 4,060 specimens of *A. alcocki* were collected and transported in fresh condition in an insulated icebox to the laboratory for further analysis. Male individuals were identified using the presence of petasma; a thelycum in females. The presence of spermatophores in the thelycum was also recorded in all the specimens (Fig. 2) (Dall *et al.*, 1990). The size of specimens (carapace length (CL) from the posterior edge of the eye orbit to the outer edge of the carapace; total length (TL) from the anterior edge of the rostrum to the tip of the telson) were measured to the nearest 0.01 mm using calipers. The body weight (BW) was measured (with 0.0001 g accuracy) using a Mettler Toledo, ME203E (Mettler, Greifensee, Switzerland) weighing balance. Morphological identification of *A. alcocki* followed the taxonomic keys of Alcock (1901) and Suseelan *et al.* (1989b).

Development of the gonads

The developmental stages of the ovary and testes were determined by both macroscopic and microscopic analysis.



Figure 1. Location of sampling areas of *Aristeus alcocki* along the southwestern coast of India.

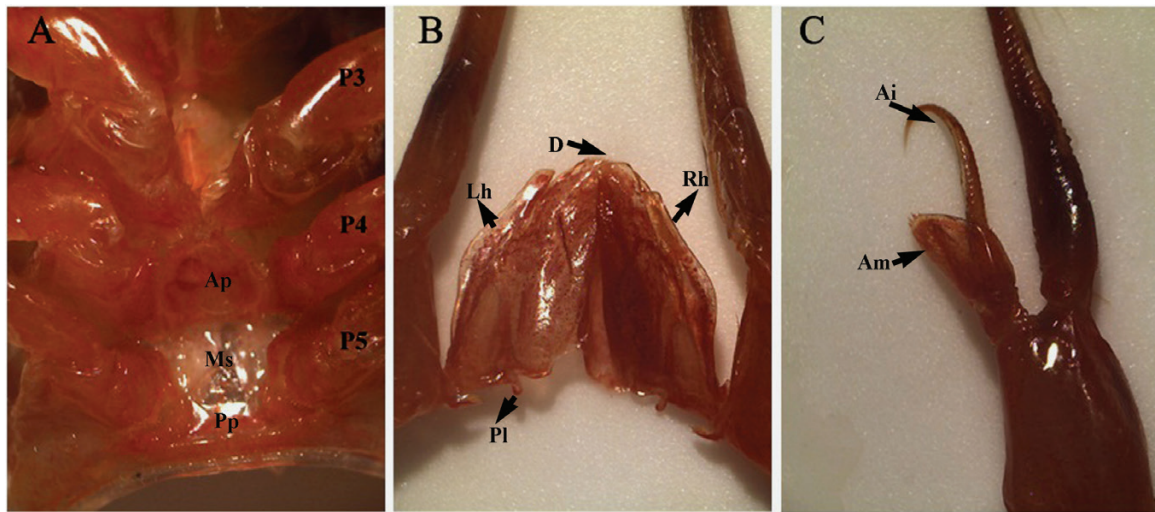


Figure 2. Reproductive morphology of *Aristeus alcocki*: ventral view of thelycum (A); P3, third pereopods; P4, fourth pereopods; P5, fifth pereopod; Ap, anterior portion; Pp, posterior portion; Ms, median surface; petasma (B): Lh, left half; Rh, right half; D, distal end; Pl, papilla; Secondary sexual organs (C): Am, appendix masculina; Ai, appendix interna. Magnification = 4–10×

Macroscopic analysis was used to categorize the developmental stages based on the shape, structural dimensions, and color of the gonads (Dall *et al.*, 1990; Kao *et al.*, 1999). Five stages were distinguished in females: immature (stage I), early mature (stage II), late mature (stage III), mature (stage IV), and spent (stage V); two stages in males (immature: stage I; mature: stage II). Microscopic analysis in male and female gonads were carried out by selecting 8–10 specimens from each developmental stage; gonadal tissue was dissected and stored in Davidson's fixative for 24 h for further histological analysis (Bell & Lightner, 1988). Fixed tissues were dehydrated with ascending grades of alcohol, cleared in xylene, embedded in paraffin using an automatic tissue processor (Leica TP 1020, Leica, Heerbrugg, Switzerland) and sectioned at 5–6 μm (semi-automatic rotary microtome; Leica RM 2145). Gonadal tissue sections were stained with haematoxylin and eosin (Bell & Lightner, 1988) and mounted in DPX for microscopic analysis. A compound microscope (Leica DM 750) at a magnification of 4–10 \times was used to observe the developmental changes in oocytes. These changes were photographed, and images were recorded using tpsDig2 (Rohlf, 2006).

Gonadosomatic index and fecundity

The gonadosomatic index (GSI) was calculated as $\text{GSI} = \text{GW} / \text{BW} \times 100$ (Bagenal & Branum, 1978), where GW is the total gonad weight and BW body weight. In addition, 110 fresh females in stage IV were collected to determine the fecundity. Mature specimens were sorted and the dorsal surface of the specimen was cut open to collect the ovary from the cephalic, thoracic, and abdominal regions; pooled oocyte data were used for fecundity analysis. Body weight and ovary weight of the specimens were recorded separately. Pre-weighed subsamples were used to count the number of oocytes using NaClO^- method (Kapiris & Thessalou-Legaki, 2006) except that 2–4% NaClO^- was diluted with seawater. Each subsample was transferred to a beaker and 5–10 ml of NaClO^- solution was added and shaken gently (250 rpm) for 5–10 min for the separation of oocytes from follicular tissue. The number of oocytes was counted under a compound microscope (10–40 \times ; Leica D750); the length and width of the oocytes were also measured. Absolute fecundity (AF) and relative fecundity (RF) were estimated using the standard formula $\text{AF} = \text{no. of eggs} \times \text{GW weight sample}^{-1}$; $\text{RF} = (\text{AF} \times 100) / \text{BW}$ (Bagenal & Bram, 1978) to establish the relationship between fecundity and the size of the specimens.

Analysis of data

The Kolmogorov-Smirnov two-sample test was used to detect possible differences between the size frequency of specimens of inseminated and non-inseminated females. The Mann-Whitney test was used to compare the medians. Size at maturity (CL_{50}) was estimated by non-linear method (WinBUGS 3.0.3; Lunn *et al.*, 2009). Females were segregated into three CL classes to understand the insemination differentiation with CL. Smaller ($\text{CL} < 30$ mm), medium ($\text{CL} 30\text{--}40$ mm) and large specimens ($\text{CL} > 40$ mm), using pooled data collected during 2013–2015. The relationship between absolute, relative fecundity/CL, BW, GW and GW/CL, BW were assessed by linear regression using the formula: fecundity (F) = $a + b \text{Log } x$ where F = fecundity, x = CL, a = constant, and b = slope (Rhode & Ross, 1987). The data were transformed to logarithmic form to derive the linear relationship and normality of fecundity distribution.

RESULTS

Morphology of the reproductive system

Females have an open thelycum, which consists of anterior and posterior portions without seminal receptacles (Fig. 2A). The anterior portion has a transverse plate with broad and pointed apex projecting anteriorly lying between the fourth pereopods; it has concave and smooth surface posteriorly while its anterior surface is covered with setae. The posterior portion of the thelycum contains two lateral plates located between the fifth pereopods. These plates are bordered by oblique ridges on either side and are covered with setae that enabled attachment of the spermatophores. The median surface appears smooth, quadrangular, and conspicuously depressed, which allows the settling of spermatophores.

The petasma is a simple, heart-shaped, membranous structure formed as a laminar modification of the endopods of the first pleopods and consisting of a right and left half (Fig. 2B). Both halves are glabrous on the dorsal and ventral surfaces, which join at the internal level; each half has a papilla-like projection at the basal side. The distal part of the petasma is blunt and rounded, the margins are convex.

The appendix masculina (Fig. 2C) is a modification of the endopod of the second pleopod. It is leaf-like, with a broad base and distally narrow, and fringed with tightly arranged short setae on its lateral side. The appendix interna is thin, with an acutely

pointed apex covered entirely by the appendix masculina when seen dorsally; fringed with long setae along outer margins.

The female ovary consists of two symmetrical lobes, located dorso-laterally, and divided into cephalic, thoracic, and abdominal sections (Fig. 3A, B). The cephalic section contains two lobules lying on either side of the cardiac stomach, whereas the thoracic section has 5–6 lobules and it is located in the pancreatic region, with the gonopores located at the coxa of the third pereopod. The abdominal section of the ovary extends dorsally as a pair of tubular lobules over the entire length of the midgut.

The paired testes are located in the posterior thoracic region (Fig. 3C). The vas deferens extends from the testis to the gonopores and is differentiated into three sections. The proximal section is narrow, coiled, folded inwardly; the middle section is thick and its terminal section is dilated to form a conical-shaped ampulla located at the coxa of the fifth pereopods, where the gonopore is found.

Female stages

Stage I (immature). The ovary is thin, translucent, colorless, tubular, and located postero-dorsally from the carapace to the fifth abdominal segment in two parallel, empty branches. The oocytes are not visible with the naked eye and are undeveloped, small, and in a previtellogenic condition (Fig. 4A); oocytes 3.88–13.98 μm , concentrated in the cephalic region, with few specimens carrying oocytes of up to 28 μm wide.

Stage II (early mature). The ovary size is increased, extending antero-posteriorly; light pinkish. The previtellogenic oocytes are round, measuring 13.0–55.6 μm wide; larger number of oocytes than in Stage I, 25% undeveloped and 75% developed. Cytoplasm of oocyte reduced in size; enlarged nuclei (Fig. 4B).

Stage III (late mature). The two lobes of the ovary expand towards the cephalothoracic, hepatopancreatic, and abdominal regions above the gut; pinkish; clearly visible through exoskeleton and observable under the microscope (10 \times). previtellogenic cells are irregular in shape and with a reduced size of the nuclei at the cell center. The oocytes, located in the abdominal portion, are tightly arranged and flattened (Fig. 4C). The ovary consists of four types of cells: resting (5%), developing (20%), expanding (60%), and mature (15%) cells. Most of the expanding oocytes are triangular in shape; size 50.0–136.5 μm .

Stage IV (mature). Ovary dark pink or violet, distinctly visible through exoskeleton from cephalothorax to sixth abdominal segment. The ovary expands, with anterior and middle lobes occupying 50% of cephalothorax. On average 75% of the ovary lies in the anterior portion of the body, Ovary with 60% mature oocytes, along with oocytes in resting condition (3%), developing oocytes (7%), expanding oocytes (40%), and mature oocytes (50%); size 120.0–334.5 μm (Fig. 4D).

Stage V (spent). After maturation, eggs were extruded and ovary was found to be flaccid and pale white (Table 1)

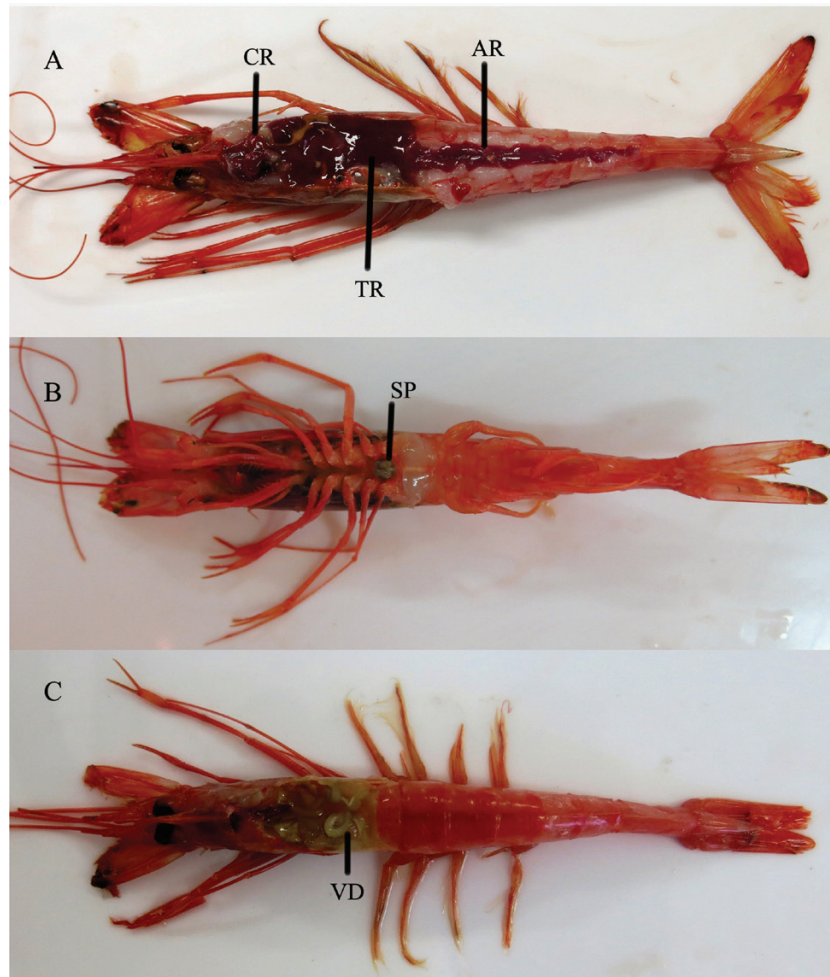


Figure 3. Dorsal view of the ovary of mature females of *Aristeus alcocki* (A); CR, cephalic region; TR, thoracic region; AR, abdominal region; spermatophore (sp) on female thelycum (B); male testes (C); VD, vas deferens. This figure is available in colour at *Journal of Crustacean Biology* online.

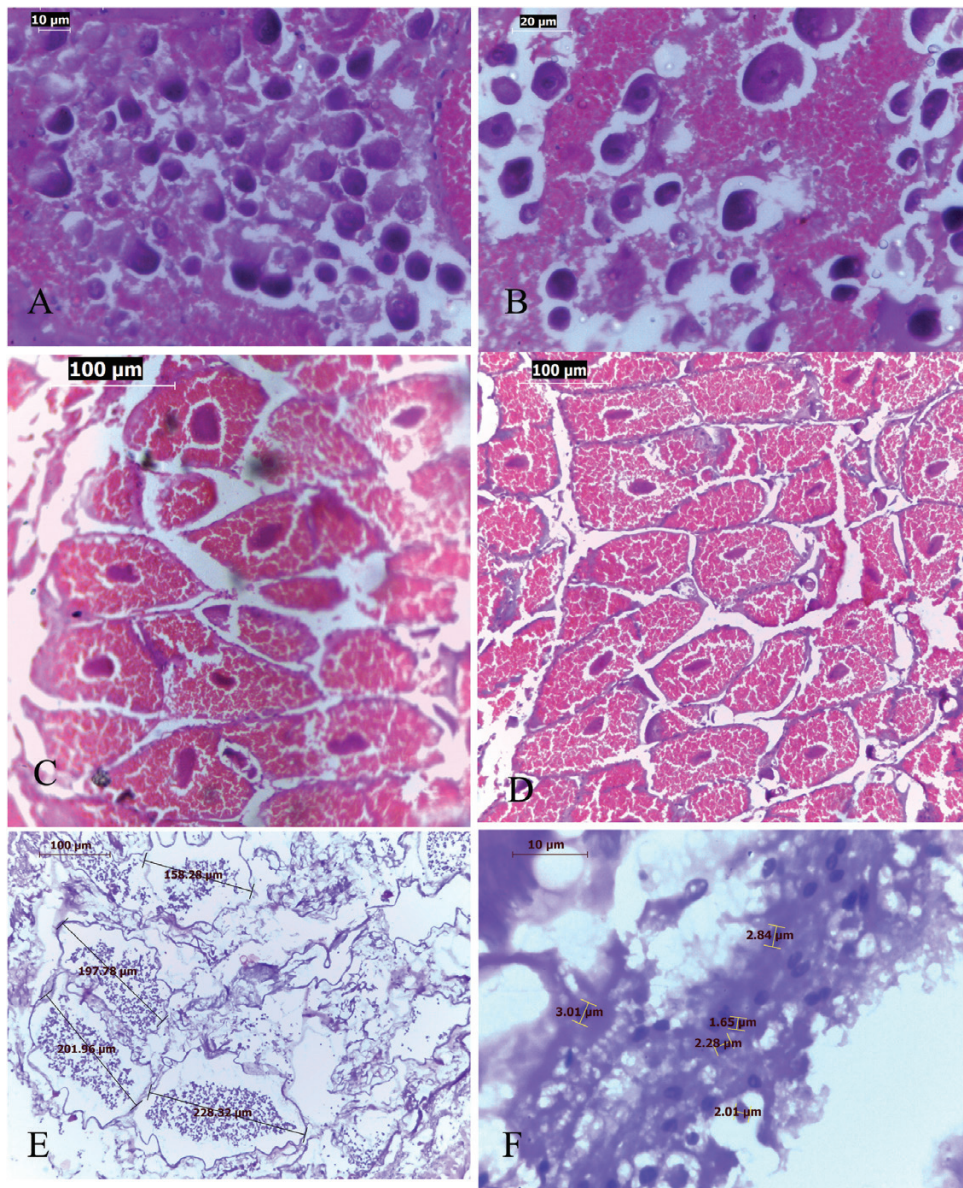


Figure 4. Microscopic view of maturation stages in females of *Aristeus alcocki*: stage I (A); stage II, previtellogenic oocytes (B); stage III, vitellogenic oocytes with expanded (C); stage IV, fully developed oocytes with flattened nucleoli (oc, oocyte, nc, nucleoli) (D); microscopic view of the male (E) follicular chamber (fc) with matured sperm; and sperm cells (sp) (F). This figure is available in colour at *Journal of Crustacean Biology* online.

Male stages

Stage I (immature). Testes quite thin, translucent, and coiled, showing undeveloped or developing spermatophores.

Stage II (mature). Testes fully developed, thick and pale white due to the presence of fully developed spermatophores, forming a tubular structure with inwardly folding anteriorly. Spermatophores are tightly packed in compact chambers; size 122–228 µm; size of single mature spermatophore 2.0–3.9 µm (Fig. 4E, F).

Insemination

Oda total of 2,090 females examined, 68.6% were found to have been inseminated (Fig. 5A). These females ranged in size from CL 22.0–53.0 mm (mean \pm SD 38.78 \pm 4.28 mm). Non-inseminated females showed a wide size range (CL 13–43 mm), but were dominated by small-size classes (mean CL 29.00 \pm 4.78 mm). Medians and size frequency distributions differed significantly between these

two groups (two-sample Kolmogorov-Smirnov test: $z = 15.783$, $P < 0.001$; Mann-Whitney test: $U = 61775.6$, $P < 0.001$). The ratio of inseminated females showed a proportionate increase with CL size. The maximum number of inseminated females were observed in the medium-size classes (CL 30–40 mm), whereas all females were inseminated in large-size classes (> 52 mm).

The level of inseminated females was high throughout the study period. The highest level (> 60%) was recorded consistently from January to May, with a peak in November 2013 (97.0%; $N = 66$) and May (100.0%; $N = 40$), while low levels were registered from September to December 2014 (< 5.0%) and December 2013 (20%) (Fig. 5B).

Maturity stages in relation to carapace length

Stage I appeared in CL ranges from 13–37 mm; its presence decreased with increasing size until it disappeared in females CL > 37 mm. Females in Stage II appeared at CL 21–47 mm, with

Table 1. Ovarian developmental stage in the deep water red shrimp, *A. alcocki*.

| Stages | Macroscopic definition | Microscopic definition | Oocyte size ranges (µm) | Condition of the Oocytes |
|--------------|---|---|-------------------------|---|
| Immature | Tubular translucent, colorless, and thin. | Undeveloped oocytes | 4.01 – 13.88 | Resting oocytes & started develop |
| Early mature | Light pinkish and semi translucent. | Undeveloped with Previtellogenic oocytes | 13 – 55.6 | Resting oocytes ~ 25 % Developing oocytes ~ 75% |
| Late mature | Pinkish in color, swollen appearance. | Previtellogenic oocytes | 50 – 136.5 | Resting oocytes ~ 5 % Developing oocytes ~ 20% Expanding oocytes ~ 60% |
| Mature | Dark pinkish or violet, and fully occupied carapace | Vitellogenic oocytes | 120 – 334.5 | Mature oocytes ~ 15% Resting oocytes ~ 3 % Developing oocytes ~ 7% Expanding oocytes ~ 40% |
| Spent | Lilac, very flacid | | | Mature oocytes ~ 50% Mature oocytes ~ 20% |

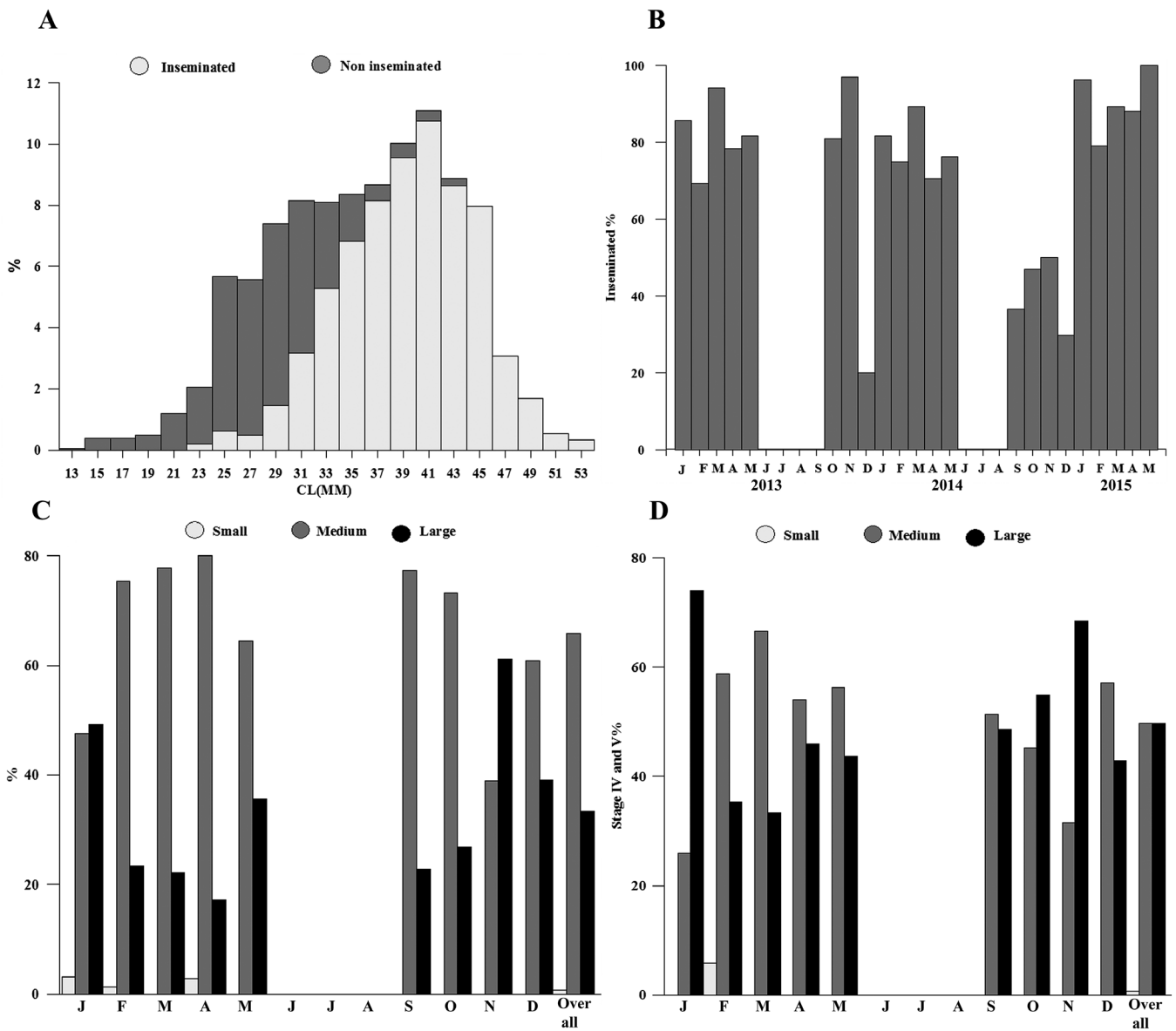


Figure 5. Insemination and non-insemination frequency of females of *Aristeus alcocki* in relation to carapace length (CL) (A); monthly insemination of females during 2013–2015 (B); monthly distribution of females in relation to size classes; inseminated (C); mature (D).

its maximum at CL 31 mm. Stage III occurred in females measuring CL 29–49 mm with a peak observed at CL 37 mm. Females with maturity stages IV and V ranged from CL 33–53 mm. The appearance of Stage V increased gradually with increasing size up to CL 53 mm (Fig. 6A).

Immature males (Stage I) ranged in size from CL 17–24 mm, whereas mature individuals measured between CL 19–26 mm. Mature males occurred throughout the study period in large numbers (Fig. 6B).

Monthly maturity variation

Females in Stage I and II occurred during September to November, with peaks during December 2013 (76 %; $N = 42$);

these stages disappeared during March to May. Mature females (Stages III, IV, and V) were recorded from mid-January to May (> 50%); higher percentages were obtained in October (72%; $N = 36$) and November 2013 (95%; $N = 64$). Stage III females reached a maximum (57%; $N = 34$) in March 2015, Stage IV in March 2013 (72%; $N = 42$), and spent ovaries (Stage V) showed an increasing trend (5–62%) during November to May, with highest values in May 2015 (62 %; $N = 38$) (Fig. 6C). Mature males were present during the entire year, with the exception of January 2013 and February 2014. Immature males were observed in lower frequencies throughout the study period, with a peak (55%; $N = 35$) recorded in January 2013 (Fig. 6D).

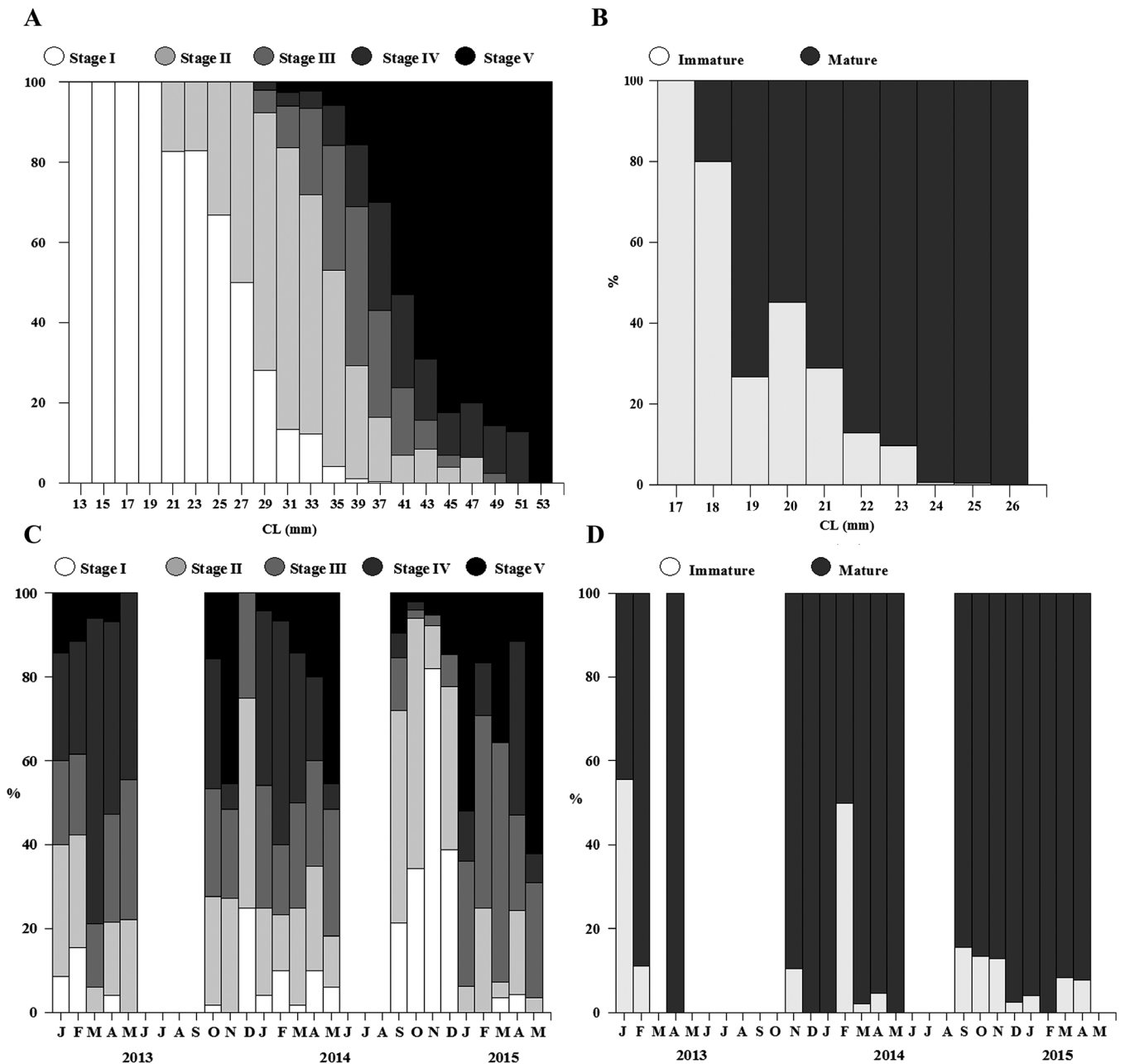


Figure 6. (A) Relationship of developmental stages in ovarian stages and carapace length (CL) in *Aristeus alcocki*; relationship of developmental stages of testes and carapace length (B); monthly maturity variation of females (C) and males (D).

Relationship of insemination and maturity stages in females

The lowest (0.7%) and highest insemination levels (> 60%) were found in the smallest and medium-size classes, respectively, whereas larger-size females had an insemination level of < 40% on a monthly basis. The two latter stages were inseminated throughout the year. In the medium-size classes, however, insemination level increased consistently from November to May, with peaks during September and October; in large-size classes, 80% of the specimens were inseminated throughout the year (Fig. 5C).

Throughout the study period, small-size classes were not observed in a mature stage. However, 45% of medium-size classes was mature except in January (25%; $N = 20$) and November (31%; $N = 23$). In large-size classes (Fig. 5D), a high proportion of females (> 50%) was mature in all the months except February (35%; $N = 30$) and March (33%; $N = 35$).

Size at maturity

The CL of the smallest mature female was 35 mm and the largest mature specimen measured 53 mm. Mean size at maturity (CL_{50ms}) of females (stage III and IV) was CL 35.07 mm (120–170 mm TL) predominating in the inseminated medium-size classes specimens (CL_{50is}) showed maturity at CL 31.45 mm (120–152 mm TL). The size at maturity of males (CL_{50ms}) was CL 19.6 mm (75–96 mm TL), with higher numbers in the range of 80–90 mm TL (Fig. 7).

Fecundity and gonadosomatic index (GSI)

The average gonad weight (GW) of 110 mature females was 1.91 g, with a range of 1.02–3.33 g. Fecundity increased with female size (CL) (Fig. 8). The average absolute fecundity was 131,750 oocytes (50,240–288,965) and average relative fecundity was 7,808 oocytes g^{-1} (2,132–12,765). The relationships of AF, RF, CL, BW, and GW were analyzed by the regression method (Table 2). Significant relationships were observed in AF/CL, BW, GW, and GW/BW, CL; non-significant for RF/CL, BW, and GW.

The mean GSI of *A. alcocki* varied significantly with the developmental stages, ranging from 1.47 ± 0.27 (Stage I) to 9.04 ± 0.19 (Stage IV), and increased with female size (CL) except in stage V (Table 3).

DISCUSSION

Our study is the first contribution to the knowledge of reproductive biology of *A. alcocki* in India. It complements studies on the taxonomy (Suseelan *et al.*, 1989b), distribution (Madhusoodana *et al.*, 2008; Radhika, 2011), economics (Shanis *et al.*, 2014), and molecular characterization on the species in southwestern coast (Chakraborty *et al.*, 2015).

The morphology of the reproductive system of *A. alcocki* is similar to that of other groups of Dendrobranchiata (Pérez Farfante, 1969; 1975; 1988; Heldt, 1938; Tuma, 1967; King, 1948; Subrahmanyam, 1965; De Freitas, 1985; Orsi Relini & Tunesi, 1987; Primavera, 1979), and specifically resembles that of *Aristeus antennatus* (Risso, 1816) (Demestre & Fortulio, 1992). The female reproductive system in penaeoid shrimps consists of a pair of ovaries extending from the esophageal region to the sixth abdominal somite, with a pair of oviducts attached to the ovaries (Dall *et al.*, 1990). The oviducts open to the surface through gonopores located at the coxae of the third pair of pereopods (Dall *et al.*, 1990; Krol *et al.*, 1992). The male reproductive system consists of endopods at the first pleopod modified as a complex organ, the petasma, whereas the endopod of the second pleopod forms the appendix masculina, which is involved in the transfer of spermatophores to females during copulation (Heldt, 1938; Dall *et al.*, 1990).

Gonad stages

Macroscopic and microscopic observations of ovarian stages of *A. alcocki* indicate distinct morphological changes in size, shape, and color of the female gonad. During developmental stages, color changes of the ovary are well documented in decapods crustaceans (i.e., Heldt, 1938; King, 1948; Eldred, 1958; Champion, 1987; Burukovsky, 1978; Demestre & Fortulio, 1992; Balasubramanian & Suseelan, 1998), and also observed in all penaeoids (Dall *et al.*, 1990). The mature ovaries of *A. alcocki* are dark pink but pink or purple ovaries were reported for *A. antennatus* (Demestre & Fortulio, 1992) and bluish gray or pale black in *Aristaeomorpha foliacea* (Risso, 1827). These color differences in the gonads of aristeid shrimps could be influenced by temperature and quality and quantity of food, all of which may vary along the latitudinal range of distribution.

A proportionate increase in oocyte size with the developmental stage was reported in penaeoid shrimps by Demestre & Fortulio (1992) and Kao *et al.* (1999). The diameter of oocytes of *A. alcocki* increased in size 3.8–334 μm , which differs in other penaeoid shrimps from Indian coasts: *Metapenaeus monoceros* (Fabricius, 1798) (6.4–232 μm) (Nandakumar, 2001; Abraham & Manisseri, 2012) and *Solenocera choprai* Nataraj, 1945 (3.0–320 μm) (Dineshbabu & Maniserry, 2008).

The mean GSI value increased gradually from Stage I to IV with female size, whereas the maximum GSI values were obtained in larger specimens (CL > 50 mm). Similarly, the decrease of GSI in larger specimens was reported in the penaeid *Melicertus plebejus* (Hess, 1865) (CL > 60 mm) (Courtney *et al.*, 1995), indicating a reduction of oocyte production with age. It has been previously suggested that gonadal development is controlled by ecological factors (e.g., salinity, organic matter, and temperature), which are assumed to play a crucial role in penaeoid reproduction (Tyler *et al.*, 1994; Courtney *et al.*, 1995; Company & Sardà, 1997; Tuset *et al.*, 2009). In the present study, however, the GSI values overlapped in all of the three classes (small, medium, and large) as well as stages (I–V). Medium and large-size classes had a maximum GSI, indicating a proportionate increase in GSI with maturation. Similar observations were made in *Melicertus kerathurus* (Forskål, 1775) (Conides *et al.*, 2008; Lumare *et al.*, 2011; Kevrekidis & Thessalou-Legaki, 2013), indicating that GSI is dependent on size.

Insemination

The presence of spermatophores in females was observed in a wide size range, with a maximum at CL 41 mm; there was a gradual increase from January to April, with a peak during January to May. This pattern might be due to the high availability of food and warmer conditions during these periods, which are important key factors for the development of nauplii (Devi *et al.*, 2010). From October to November 2013 we observed a high level (> 80%) of insemination, with 100% inseminated females in May 2015 (Fig. 5B). The high proportion of inseminated females year-round suggests a continuous reproductive cycle. Similar results were reported in penaeoids such as *Melicertus laticulatus* (Kishinouye, 1896), *M. longistylus* (Kubo, 1943) (Courtney & Dredge, 1988), and *M. kerathurus* (Kevrekidis & Thessalou-Legaki, 2013).

Non-inseminated females were recorded at a wider CL range (13–43 mm), with its maximum (> 50%) in immature females from September to December 2014 (Fig. 5A). Females bearing spermatophores with immature gonads were also reported for other aristeids, suggesting that copulation and gonadal development could take place non-synchronously during different periods of the year (Papaconstantinou & Kaporis, 2003; Politou, *et al.*, 2004; Kaporis & Thessalou-Legaki, 2009).

Lower percentages of insemination were recorded in specimens of the small-size classes, with a monthly mean insemination of 0.7%. This finding could be associated with the relatively high number of molts typical for small-size females,

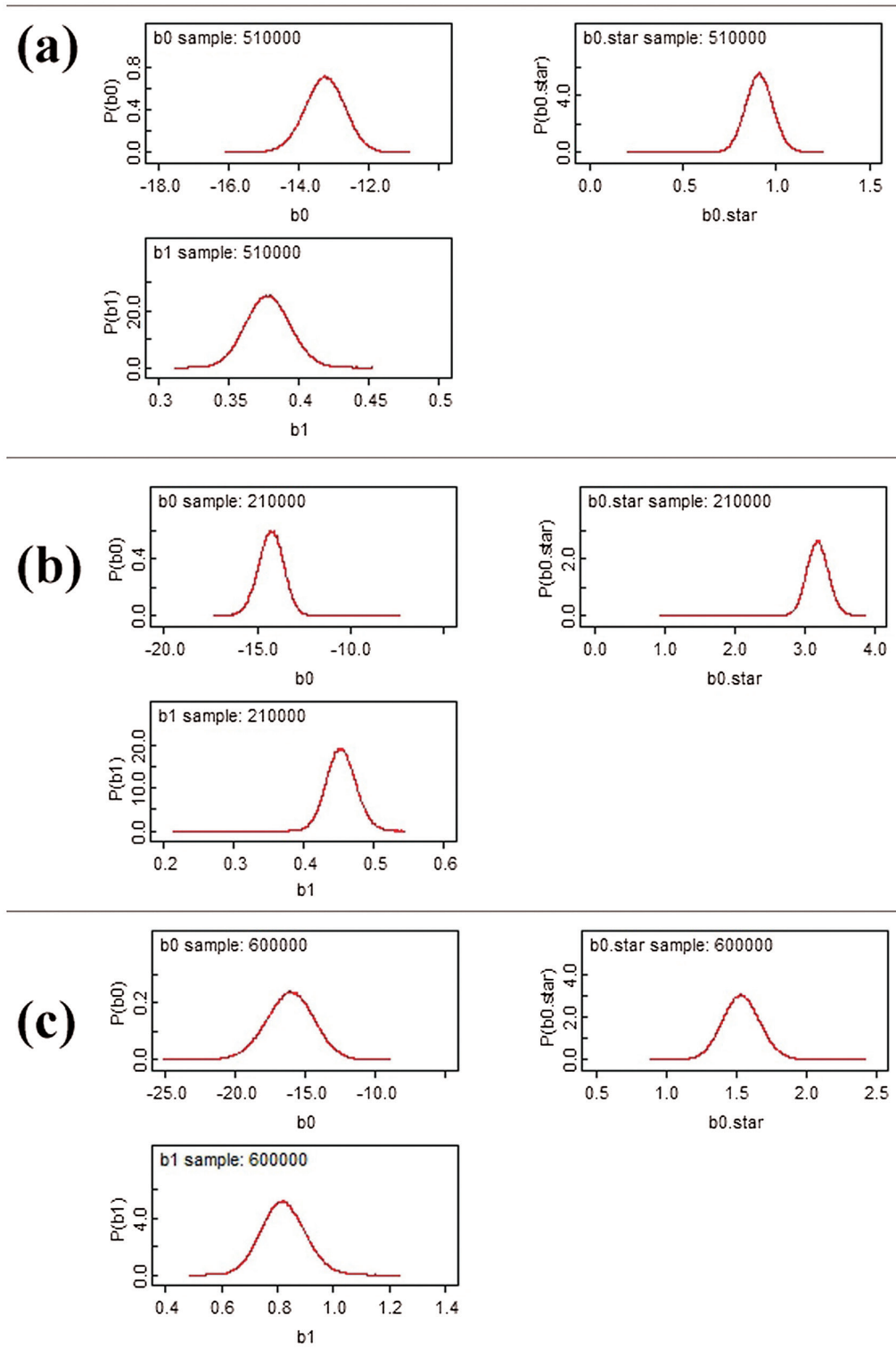


Figure 7. Estimation of size at maturity of *Aristeus alcocki* by non-linear iteration method: mature female (a); inseminated female (b); mature males (c).

which increases the likelihood of losing the attached spermatophore (Sardà *et al.*, 2004). Medium and large-size classes were inseminated (> 40%) during all the months. High percentages of insemination in medium-size females were noticed throughout the year, suggesting that females CL > 30 mm are

predominantly more involved in mating than smaller females. It also indicates that spermatophore insemination is positively related to size. These findings are in agreement with similar observations made in penaeids such as *Fenneropenaeus merguensis* (de Man, 1888) (Crococ & Kerr, 1983), *Penaeus semisulcatus*

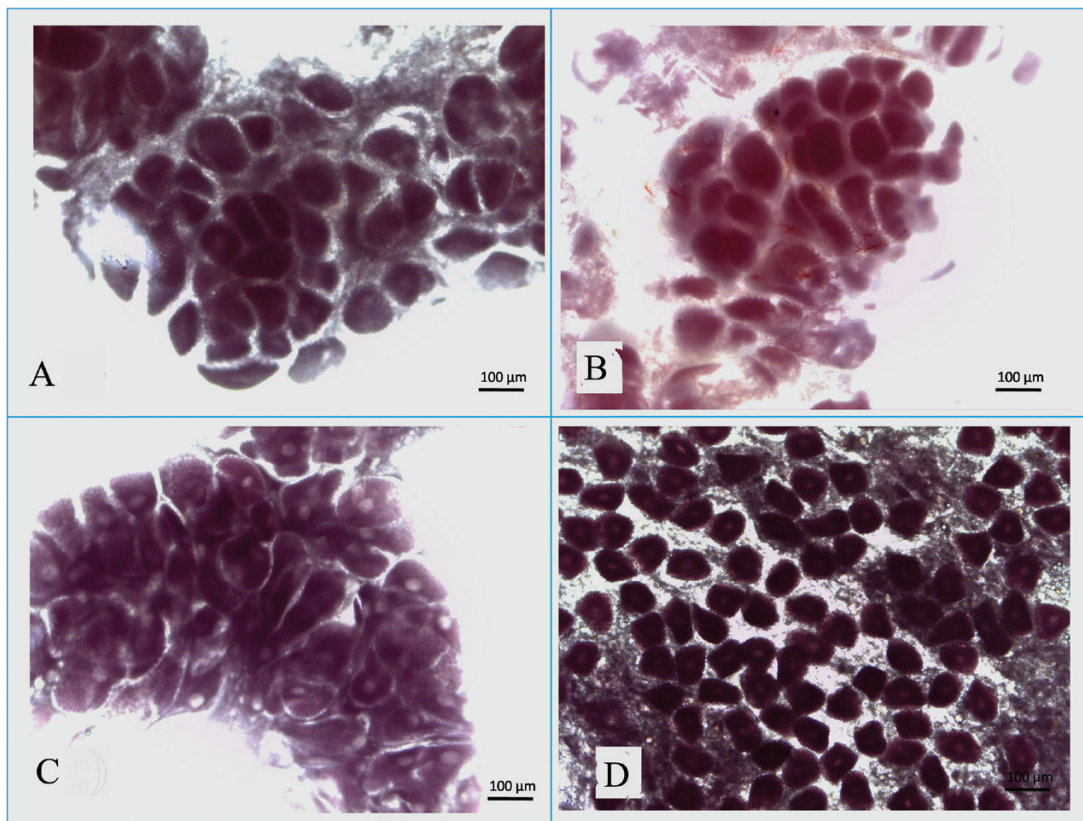


Figure 8. Oocytes of *Aristeus alcocki* treated with sodium hypochlorite solution: cephalic (A); thoracic (B); abdominal (C); oocyte in fresh condition (D). This figure is available in colour at *Journal of Crustacean Biology* online.

Table 2. Regression analysis for absolute fecundity (AF) and relative fecundity (RF).

| variable | b value | SE | a | F | r |
|----------|---------|--------|--------|--------|---------|
| AF/CL | 2.65 | 0.40 | 1.78 | 43.66 | 0.572* |
| AF/BW | 0.592 | 0.308 | 9.895 | 3.70 | 0.299** |
| AF/GW | 0.379 | 0.058 | -3.796 | 42.683 | 0.567* |
| RF/CL | 0.061 | 0.045 | 2.92 | 1.78 | NS |
| RF/BW | 0.006 | 0.041 | 2.884 | 0.025 | NS |
| RF/GW | 0.089 | 0.053 | -0.561 | 2.833 | NS |
| GW/CL | 0.614 | 0.0289 | 3.465 | 4.50 | 0.218** |
| GW/BW | 0.851 | 0.313 | 2.56 | 7.40 | 0.276* |

Carapace length (CL), Body weight (BW), Gonad Weight (GW), b = regression coefficient (slope), SE = standard error of b, n = number of individual females used, F = variance ratio, r = correlation coefficient, ** $P < 0.05$, * $P < 0.01$, NS- non-significant.

De Haan, 1844 (Crococ, 1987a), *Penaeus esculentus* Haswell, 1879 (Crococ, 1987b), *M. longistylus*, *M. latisulcatus* (Courtney & Dredge, 1988), and *M. kerathurus* (Kevrekidis & Thessalou-Legaki, 2013).

The ripe ovary stage is a useful and accurate index to determine the reproductive cycle, season, and spawning ground of a species (Minagawa *et al.*, 2000). The monthly frequency of ovarian maturation and spermatophore insemination has shown that *A. alcocki* exhibits year-around spawning, with a peak from January to April (Fig. 5B & 6C). Similar spawning activities were reported in *S. choprai*, with a peak in January to February and a second peak in November and for *Metapenaeus monoceros* and *Metapenaeus dobsoni* (Miers, 1878) from the Bay of Bengal, India are shown similar spawning activity (Nandakumar, 2001).

Size at maturity

The size at maturity of female *A. alcocki* was at CL 35.07 mm (CL_{50ms}) and CL 31.45 mm (CL_{50fs}), revealed that the ovarian development follows insemination, which coincides with all the species of Penaeidae. These species first undergo maturation followed by mating (Penn, 1980; Dall *et al.*, 1990). The CL_{50} of *A. alcocki* varied considerably in relation to other aristeids (Table 4). This might due to the environmental parameters (season, latitude, depth temperature) or size, and the growth rate of the species in different locations.

Most males of *A. alcocki* with CL under CL 18 mm (90%) had undeveloped petasma, and the size at maturity was CL 19.6 mm, smaller than size of female maturity. Similar results were observed in *A. antennatus* and *A. foliaceus* in different regions, indicating that males of aristeid shrimps reach maturity at a considerably smaller size than females, which favors mating (Sardà & Demestre, 1987).

Fecundity

The average absolute fecundity in *A. alcocki* (size CL 42.8 mm) was estimated as 131,750 oocytes female⁻¹, which was higher than its relative fecundity (7,808 oocytes g⁻¹). These values are comparable with fecundity data published for other aristeid shrimps from different locations. Kapiris & Thessalou-Legaki (2006) observed the absolute and relative fecundity in *A. foliaceus* (CL 44.6 mm) as 151,956 oocytes and 5,477 g⁻¹, respectively, from Mediterranean regions, whereas in *A. antennatus* (CL 40.6 mm) was 200,472 oocytes and 9,386 g⁻¹, respectively. Orsi Relini & Semeria (1983) reported the absolute fecundity of *A. foliaceus* (CL 40–55 mm) in the range of 100,000–250,000 oocytes in the Ligurian Sea and 140,000–900,000 oocytes in each ovulation for *A. antennatus* (Catalan Sea; CL 35–65 mm) which is greater than that reported for *A. alcocki*. This difference in fecundity could be due to location or climatic conditions.

Table 3. Gonadosomatic index of various developmental stages.

| Stages | GSI ranges | CL (mm) Avg | CL (mm) ranges | Spermatopore presence | GSI Mean \pm Standard Error |
|--------------|-------------|-------------|----------------|-----------------------|-------------------------------|
| Immature | 0.65 – 2.06 | 23 | 20 – 25 | Partially | 1.47 \pm 0.27 |
| Early mature | 1.86 – 3.26 | 28.6 | 26 – 32 | Yes | 2.29 \pm 0.15 |
| Late mature | 2.91 – 10.2 | 35.5 | 33 – 37 | Yes | 5.95 \pm 0.35 |
| Mature | 6.3 – 14.20 | 41.9 | 38 – 45 | Yes | 9.04 \pm 0.19 |
| Spent | 4.11 – 7.13 | 47.8 | 45 – 54 | Yes | 5.81 \pm 0.13 |

Table 4. Size at maturity of aristeid shrimps in different regions; M(CL), mature size range of carapace length; CL_{50ms}, size at maturity based on mature gonads; CL_{50is}, size at maturity based on insemination; AAT, *Aristeus antennatus*; AATL, *Aristeus antillensis*; AF, *Aristaeomorpha foliacea*; AA, *Aristeus alcocki*.

| Species | Females (mm) | | | Males (mm) | | References |
|---------|--------------|--------------------|--------------------|------------|--------------------|---|
| | M(CL) | CL _{50ms} | CL _{50is} | M(CL) | CL _{50ms} | |
| AAT | | 26 | | 20 | | Demestre, 1995 (Ionian Sea) |
| | 22–59 | 21.9 | | 19–37 | 18.1 | García-Rodríguez & Esteban, 1999 (Ibiza Channel) |
| | 15–65 | 26.6–29.2 | | 15–38 | 21.3–22.3 | Carbonell et al., 1999 (Balearic Islands) |
| | 22–62 | 31.3 | 35.4 | | | Carlucci et al., 2006 (northwestern Ionian Sea) |
| | 26–64 | 29.4 | 26.3 | | 20 | Kapiris & Thessalou-Legaki, 2009 (Greek Ionian Sea) |
| AATL | 32–66 | 40.2 | | 24–39 | 25.4 | Pezzuto & Dias, 2009 (Brazil) |
| AF | | 43.0 | 39.3 | | 26 | D'Onghia, et al., 1998 (northwestern Ionian Sea) |
| | 28–66 | 40.5 | 35.1 | | 30 | Belcari et al., 2003 (northern Tyrrhenian Sea) |
| | 34–52 | 44.1 | 35.9 | | | Carlucci et al., 2006 (northwestern Ionian Sea) |
| | 32–66 | 38.8 | 36.8 | | 26 | Kapiris & Thessalou-Legaki, 2009 (Greek Ionian Sea) |
| | 41–66 | | | 25–45 | | Perdichizzi et al., 2012 (southern Tyrrhenian Sea) |
| AA | 35–53 | 35.0 | 31.4 | 19–24 | 19.6 | Present study |

Our results revealed that fecundity in *A. alcocki* was positively associated with BW, GW, and CL. Similar results have been observed in *A. foliacea*, *A. antennatus* (Kapiris & Thessalou-Legaki, 2006), *Penaeus duorarum* Burkenroad, 1939 (Martosubroto, 1974), and *M. kerathurus* (Kevrekidis & Thessalou-Legaki, 2013). According to the regression coefficient value, absolute fecundity can be predicted using the CL, BW, and GW. The number of oocytes was found to be directly proportional to the increase in CL, BW, and GW.

Our results revealed that ovarian maturation and spermatopore insemination in *A. alcocki* exhibits a year-round spawning activity, with a peak extends from January to April. Information on the reproductive traits of a species is important for managing the fishery and in particular for the protection of breeding grounds and maintenance of spawning stocks. Deep-sea catches, particularly *A. alcocki*, are high during January to April, which coincides with its peak spawning season. This could explain the significant decline in landings during 2014 to 2016 (unpublished data). The current ban period (June to August) for the deep-sea trawl fishery should be shifted to January to April in order to conserve the spawning stocks of this species.

ACKNOWLEDGEMENTS

We thank the Department of Science and Technology, Ministry of Science and Technology, India, for a grant towards the Fast Track Scheme for Young Scientists (SR/FT/LS-73/2012, SERB). We also thank the Dr A. Gopalakrishnan (Director, Central Marine Fisheries Research Institute, Kerala) for the encouragement and for the facilities provided. Thanks are also due to Dr. T.Y. Chan (National Taiwan Ocean University) for confirming the identification of *A. alcocki*. We also thank the anonymous reviewers for improving the manuscript with their comments.

REFERENCES

- Abraham, J. & Manisseri Mary, K. 2012. Histological and morphological changes associated with ovarian development of speckled shrimp *Metapenaeus monoceros* (Fabricius, 1798) conservation and management. *Indian Journal of Fisheries*, **59**: 119–124.
- Alcock, A. 1901. *A descriptive catalogue of Indian deep-sea Crustacea, Decapoda, Macrura and Anomala in the Indian Museum*. Indian Museum, Calcutta, India.
- Bagenal, T.B. & Braum, E. 1978. Eggs and early life history. In: *Methods for assessment of fish production in fresh waters* (Bagenal, T., ed.), IBP Handbook No 3, Blackwell Scientific, Oxford.
- Balasubramanian, C.P. & Suseelan, C. 1998. Natural diet of the deep water crab *Chaybdis smithii* Macleay (Brachyura: Portunidae) of the seas around India. *Indian Journal of Fisheries*, **45**: 407–411.
- Belcari, P., Viva, C., Mori, M. & De Ranieri, S. 2003. Fishery and biology of *Aristaeomorpha foliacea* (Risso, 1827) (Crustacea: Decapoda) in the northern Tyrrhenian Sea (Western Mediterranean). *Journal of Northwest Atlantic Fishery Science*, **31**: 195–204.
- Bell, T.A. & Lightner, D.V. 1988. *A Handbook of normal penaeid shrimp histology*. Special Publication No. 1. World Aquaculture Society, Baton Rouge, LA, USA.
- Burkenroad, M.D. 1939. Further observations on Penaeidae of the northern Gulf of Mexico. *Bulletin of the Bingham Oceanographic Collection*, **6**: 1–62.
- Burukovsky, R.N. 1978. On the biology of the shrimp *Aristeus varidens*. *Biologiya Morya* (Vladivostok), **3**: 70–77.
- Carbonell, A., Carbonell, M., Demestre, M., Grau, A. & Monserrat, S. 1999. The red shrimp *Aristeus antennatus* (Risso, 1816) fishery and biology in the Balearic Islands, western Mediterranean. *Fisheries Research*, **44**: 1–13.
- Carlucci, R., D'Onghia, G., Sion, L., Maiorano, P. & Tursi, A. 2006. Selectivity parameters and size at first maturity in deep-water shrimps, *Aristaeomorpha foliacea* (Risso, 1827) and *Aristeus antennatus* (Risso, 1816), from the northwestern Ionian Sea (Mediterranean Sea). *Hydrobiologia*, **557**: 145–154.
- Chace, F.A. Jr. 1985. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907–1910, Part 3: Families Thalassocarididae and Pandalidae. *Smithsonian Contributions to Zoology*, **411**: 1–143.
- Chakraborty Rekha, D., Purushothaman, P., Kuberan, G., Sebastian, J. & Maheswarudu, G. 2015. Morphological analysis and molecular

- phylogeny of *Aristeus alcocki* Ramadan, 1938 from south-west coast of India. *Indian Journal of Geo-Marine Sciences*, **44**: 1716–1725.
- Champion, H.F.B. 1987. The functional anatomy of the male reproductive system in *Penaeus indicus*. *South African Journal of Zoology*, **22**: 297–307.
- Company, J.B. & Sardà, F. 1997. Reproductive patterns and population characteristics in five deep-water pandalid shrimps in the western Mediterranean along a depth gradient (150–1100 m). *Marine Ecology Progress Series*, **148**: 49–58.
- Conides, A., Glamuzina, B., Dulčić, J., Kapiris, K., Jug-Dujakovic, J. & Papaconstantinou, C. 2008. Study of the reproduction of the Karamote shrimp *Penaeus (Melicertus) kerathurus* in Amvrakikos Gulf, western Greece. *Acta Adriatica*, **49**: 97–105.
- Courtney, A.J. & Dredge, M.C.L. 1988. Female reproductive biology and spawning periodicity of two species of king prawns, *Penaeus longistylus* Kubo and *Penaeus latissulcatus* Kishinouye, from Queensland's east coast fishery. *Australian Journal of Marine and Freshwater Research*, **39**: 729–41.
- Courtney, A.J., Montgomerie, S.S., Die, D., Andrew, N.L., Cosgrove, M.G. & Blount, C. 1995. Maturation in the female eastern king prawn, *Penaeus plebejus* from coastal waters of eastern Australia, and considerations for quantifying egg production in penaeid prawns. *Marine Biology*, **122**: 547–556.
- Crococ, P.J. 1987a. Reproductive dynamics of the grooved tiger prawn, *Penaeus semisulcatus*, in the north-western Gulf of Carpentaria, Australia. *Marine and Freshwater Research*, **38**: 79–90.
- Crococ, P.J. 1987b. Reproductive dynamics of the tiger prawn *Penaeus esculentus* and a comparison with *P. semisulcatus* in the north-western Gulf of Carpentaria, Australia. *Marine and Freshwater Research*, **38**: 91–102.
- Crococ, P.J. & Kerr, J.D. 1983. Maturation and spawning of the banana prawn *Penaeus merguensis* de Man (Crustacea: Penaeidae) in the Gulf of Carpentaria, Australia. *Journal of Experimental Marine Biology and Ecology*, **69**: 37–59.
- CMFRI (Central Marine Fisheries Research Institute). 2008. *Annual Report 2007–08*. Central Marine Fisheries Research Institute, Kochi, India.
- CMFRI (Central Marine Fisheries Research Institute). 2014. *Annual Report 2013–14*. Central Marine Fisheries Research Institute, Kochi, India.
- CMFRI (Central Marine Fisheries Research Institute). 2015. *Annual Report 2014–15*. Central Marine Fisheries Research Institute, Kochi, India.
- Dall, W., Hill, J., Rothlisberg, P. & Staples, D. 1990. The biology of Penaeidae. *Advances in Marine Biology*, **105**: 1–489.
- Dallagnolo, R., Perez, J.A.A., Pezzuto, P.R. & Wahrlich, R. 2007. Análise da pescaria de camarões-deprofundidade (Decapoda: Aristeidae) no talude das regiões Sudeste e Sul do Brasil. In: *5ª Sessão Ordinária do Subcomitê Científico do Comitê Consultivo Permanente de Gestão de Recursos Demersais de Profundidade (CPG/Demersais)/SEAP/PR*, Itajai, Brazil.
- De Freitas, A.J. 1985. The Penaeoidea of southeast Africa. II – The Families Aristeidae and Solenoceridae. *South African Association for Marine Biological Research*, **1**: 1–69.
- De Grave, S. & Fransen, C.H.J.M. 2011. Carideorum Catalogus: The recent species of the Dendrobranchiate, Stenopodidean, Procarididean and Caridean shrimps (Crustacea: Decapoda). *Zoologische Mededelingen*, **85**: 195–588.
- Demestre, M. 1995. Moulting activity-related spawning success in the Mediterranean deep-water shrimp *Aristeus antennatus* (Decapoda: Dendrobranchiata). *Marine Ecology Progress Series*, **157**: 57–64.
- Demestre, M. & Fortuno, J.M. 1992. Reproduction of the deep-water shrimp *Aristeus antennatus* (Decapoda: Dendrobranchiata). *Marine Ecology Progress Series*, **84**: 41–51.
- Devi Asha, C.R., Jyothibabu, R., Sabu, P., Josia J., Habeebrehman, H., Prabhakaran, M.P., Jayalakshmi, K.J. & Achuthankutty, C.T. 2010. Seasonal variations and trophic ecology of microzooplankton in the southeastern Arabian Sea. *Continental Shelf Research*, **30**: 1070–1084.
- Dineshbabu, A.P. & Manisseri, J.K. 2008. Reproductive biology of ridge back shrimp, *Solenocera choprai* (Decapoda: Penaeoidea, Solenoceridae) off Mangalore coast, South India. *Fisheries Science*, **74**: 796–803.
- D'Onghia, G., Maiorano, P., Matarrese, A. & Tursi, A. 1998. Distribution, biology, and population dynamics of *Aristaeomorpha foliacea* (Risso, 1827) (Decapoda, Natantia, Aristeidae) in the north-western Ionian Sea (Mediterranean Sea). *Crustaceana*, **71**: 518–544.
- Eldred, B. 1958. Observations on the structural development of the genitalia and the impregnation of the pink shrimp, *Penaeus duorarum* Burkenroad. *Florida State Board Conservation Technical Series*, **23**: 1–26.
- Fabricius, J.C. 1798. *Supplementum Entomologiae Systematicae*. Proft & Storch, Hafniae [= Copenhagen].
- Forskål, P., 1775. *Descriptiones Animalium, Aëium, Amphibiorum, Piscium, Insectorum, Vermium; quae in Itinere Orientali Observavit Petrus Forskål. Post Mortem Auctoris editi Carsten Niebuhr. Adjuncta est materia Medica Kahirina*. Mölleri, Hafniae [= Copenhagen].
- García Rodríguez, M. & Esteban, A. 1999. On the biology and fishery of *Aristeus antennatus* (Risso, 1816), (Decapoda, Dendrobranchiata) in the Ibiza Channel (Balearic Islands, Spain). *Scientia Marina*, **63**: 27–37.
- Haan, W. de. 1833–1850. Crustacea. In: *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit* (P.F. von Siebold, ed.). Lugduni-Batavorum [= Leiden].
- Haswell, W.A. 1879. On the Australian species of *Penaeus*, in the Macleay Museum, Sydney. *Proceedings of the Linnean Society of New South Wales*, **4**: 38–44.
- Heldt, J.H. 1938. La reproduction chez les crustacés décapodes de la famille des péneides. *Annales de l'Institut Oceanographique*, **18**: 31–206.
- Hess, W. 1865. Beiträge zur Kenntnis der Decapoden-Krebse Ost-Australiens. *Archiv für Naturgeschichte*, **31**: 127–173.
- Kao, C.H., Chan, Y.T. & Yu, P.Y. 1999. Ovary development of the deep-water shrimp *Aristaeomorpha foliacea* (Risso, 1826) (Crustacea: Decapoda: Aristeidae) from Taiwan. *Zoological Studies*, **38**: 373–378.
- Kapiris, K. & Thessalou-Legaki, M. 2006. Comparative fecundity and oocyte size of *Aristaeomorpha foliacea* and *Aristeus antennatus* in the Greek Ionian Sea (Eastern Mediterranean) (Decapoda: Aristeidae). *Acta Zoologica*, **87**: 239–245.
- Kapiris, K. & Thessalou-Legaki, M. 2009. Comparative reproduction aspects of the deep-water shrimps *Aristaeomorpha foliacea* and *Aristeus antennatus* (Decapoda, Aristeidae) in the Greek Ionian Sea (Eastern Mediterranean). *International Journal of Zoology* [doi:10.1155/2009/979512].
- Kevrekidis, K. & Thessalou-Legaki, M. 2013. Reproductive biology of the prawn *Melicertus kerathurus* (Decapoda: Penaeidae) in Thermaikos Gulf (N. Aegean Sea). *Helgoland Marine Research*, **67**: 17–31.
- King, I.E. 1948. A study of the reproductive organs of the common marine shrimp, *Penaeus styliifera* (Linnaeus). *Biological Bulletin*, **94**: 244–264.
- Kishinouye, K. 1896. Note on a Japanese *Penaeus* and its classification. *Zoological Magazine (Dobutsugaku Zasshi)*, **8**: 372–374 [in Japanese].
- Krol, R., Hawkins, W. & Overstreet, R. 1992. Reproductive components. In: *Microscopic anatomy of the invertebrates* (F.W. Harrison & A.G. Humes, eds.), **10**: 295–343. Wiley-Liss, New York.
- Kubo, I. 1943. Diagnosis of a new species of the genus *Penaeus*. *Suisan Kenkyūsi*, **38**: 200–201.
- Lumare, D., Lumare, L., Vitale, S. & Lumare, F. 2011. Reproduction of the caramote shrimp *Melicertus kerathurus* (Decapoda, Penaeidae) in the South Adriatic Sea (south-eastern coast of Italy). *Crustaceana*, **84**: 4293–4305.
- Lunn D., Spiegelhalter, D., Thomas, A. & Best, N. 2009. The BUGS project: Evolution, critique and future directions. *Statistics in Medicine*, **28**: 3049–3067.
- Madhusoodana Kurup, B., Radhika, R. & Venu, S. 2008. Distribution of deep sea prawns off Kerala. *Journal of Marine Biological Association of India*, **50**: 122–126.
- Man, J.G. de. 1888. Report on the podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson F.R.S., Superintendent of the Museum. *Journal of the Linnean Society (Zoology)*, **22**: 1–305.
- Martosubroto, P. 1974. Fecundity of pink shrimp *Penaeus duorarum* Burkenroad. *Biological Marine Science*, **24**: 606–627.
- Miers, E.J. 1878. Notes on the Penaeidae in the collection of the British Museum, with descriptions of some new species. *Proceedings of the Zoological Society of London*, **1878**: 298–310.
- Minagawa, M., Yasumoto, S., Ariyoshi, T., Umemoto, T. & Ueda, T., 2000. Interannual, seasonal, local and body size variations in reproduction of the prawn *Penaeus (Marsupenaeus) japonicus* (Crustacea: Decapoda: Penaeidae) in the Ariake Sea and Tachibana, Japan. *Marine Biology*, **136**: 223–231.
- Mohamed, K.H. & Suseelan, C. 1973. Deep-sea prawn resources of the south-west coast of India. In: *Proceedings Symposium of Living Resources of the Seas Around India*, pp. 614–633. Special Publication, Central Marine Fisheries Research Institute, Cochin, India.
- Nandakumar, G. 2001. Reproductive biology of the speckled shrimp *Metapenaeus monoceros* (Fabricius). *Indian Journal of Fisheries*, **48**: 1–8.

- Nataraj, S. 1945. On two new species of *Solenocera* (Crustacea Decapoda: Penaeidae) with notes on *Solenocera pectinata* (Spence Bate). *Journal of the Asiatic Society of Bengal*, **11**: 91–98.
- Orsi Relini, L. & Semeria, M. 1983. Oogenesis and reproductive strategies in bathyal penaeid prawns, *Aristeus antennatus* and *Aristaeomorpha foliacea*. *Rapports et Procès-verbaux des Réunions/Conseil permanent international pour l'Exploration de la Mer*, **28**: 1–2.
- Orsi Relini, L. & Tunesi, L. 1987. The structure of the spermatophore in *Aristeus antennatus* (Risso, 1816). *Investigación Pesquera*, **51**: 461–470.
- Papaconstantinou, C. & Kapiris, K. 2003. The biology of the giant red shrimp (*Aristaeomorpha foliacea*) at an unexploited fishing ground in the Greek Ionian Sea. *Fisheries Research*, **62**: 37–51.
- Penn, J.W. 1980. Spawning and fecundity of the western king prawn, *Penaeus latisulcatus* Kishinouye, 1896 in western Australian waters. *Australian Journal of Marine & Freshwater Research*, **31**: 21–35.
- Perdichizzi A., Pirrera, L., Micale, V., Muglia, U. & Rinelli, P. 2012. A histological study of ovarian development in the giant red shrimp *Aristaeomorpha foliacea* (Crustacea: Decapoda: Aristeidae) from the Southern Tyrrhenian Sea (western Mediterranean). *The Scientific World Journal* [doi: 10.1100/2012/289608].
- Pérez Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*. *Fishery Bulletin*, **67**: 461–591.
- Pérez Farfante, I. 1975. Spermatophores and thelyca of the American white shrimps, genus *Penaeus*, subgenus *Litopenaeus*. *Fishery Bulletin*, **73**: 463–486.
- Pérez Farfante, I. 1988. Illustrated key to penaeoid shrimps of commerce in the Americas. *NOAA Technical Report NMFS*, **64**: 1–32.
- Pérez Farfante, I. & Kensley, B. 1997. Penaeoid and sergestoid shrimps and prawns of the world, keys and diagnoses for the species and genera. *Mémoires Muséum national d'Histoire naturelle* (Paris), **75**: 1–233.
- Pezzuto, P.R. & Dias, M.C. 2009. Reproductive cycle and population structure of the deep-water shrimp *Aristeus antillensis* A. Milne Edwards & Bouvier, 1909 (Decapoda: Aristeidae) on southeast Brazilian continental slope. *Latin American Journal of Aquatic Research*, **37**: 443–454.
- Pezzuto, P.R., Perez, J.A.A. & Wahrlich, R. 2006. Deepsea shrimp (Decapoda: Aristeidae): New targets of the deep-water trawling fishery in Brazil. *Brazilian Journal of Oceanography*, **54**: 123–134.
- Politou, C.Y., Kapiris, K., Maiorano, P., Capezzuto, F. & Dokos, J. 2004. Deep-sea Mediterranean biology: the case of *Aristaeomorpha foliacea* (Risso, 1827) (Crustacea: Decapoda: Aristeidae). *Scientia Marina*, **68**: 129–139.
- Primavera, J.H. 1979. Notes on the courtship and mating behaviour in *Penaeus monodon* Fabricius (Decapoda, Natantia). *Crustaceana*, **37**: 287–292.
- Radhika Rajasree, S.R. 2011. Biodiversity of deep sea prawns in the upper continental slope of Arabian Sea, off Kerala (South West India): A comparison between depths and years. *Journal of Fisheries & Aquatic Science*, **11**: 291–302.
- Ragonese, S. & Bianchini, L.M. 1995. Size at sexual maturity in red shrimp females, *Aristaeomorpha foliacea*, from the Sicilian Channel (Mediterranean Sea). *Crustaceana*, **68**: 73–82.
- Ramadan, M.M. 1938. Crustacea: Penaeidae. *Scientific Reports of the John Murray Expedition*, **5**: 35–76.
- Risso, A. 1816. *Histoire naturelle des Crustacés des environs de Nice*. Librairie Grecque-Latine-Allemande, Paris.
- Risso, A., 1827. *Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes*, Vol. 5. F.-G. Levrault, Paris.
- Rhode, F. & Ross, S. 1987. Life history of the Pinewoods Darter *Eltheostoma mariae* (Osteichthyes: Percidae), a fish endemic to the Carolina Sandhills. *Brimleyana*, **13**: 1–20.
- Rohlf, F.J. 2006. *TpsDig2*, Version 2.1. State University of New York, Stony Brook, NY, USA [<http://life.bio.sunysb.edu/morph>].
- Sardà, F., Company, J.B. & Maynou, F. 2003. Deep-sea shrimp *Aristeus antennatus* Risso 1816 in the Catalan Sea, a review and perspectives. *Journal of the Northwest Atlantic Fishery Science*, **31**: 127–136.
- Sardà, F. & Demestre, M. 1987. Estudio biológico de la gamba *Aristeus antennatus* (Risso, 1816) en el Mar Catalán (NE de España). *Investigación Pesquera*, **51**: 213–232.
- Sardà, F., D'Onghia, G., Politou, C.Y., Company, J.B., Maiorano, P. & Kapiris, K. 2004. Deep-sea distribution, biological and ecological aspects of *Aristeus antennatus* (Risso, 1816) in the western and central Mediterranean Sea: preliminary aspects on species distribution, biomass and population structure. *Scientia Marina*, **68**: 117–127.
- Shanis Rajool, C.P., Salim, S.S., Manjebayakath, H., Ganga, U., Manjusha, U. & Pillai, N.G.K. 2014. Deep-sea shrimp fishery operations in Kerala coast: problems and prospects. *International Journal of Fisheries and Aquatic Studies*, **1**: 237–242.
- Silas, E.G. 1969. Exploratory fishing by R. V. Varuna. *Bulletin of Central Marine Fisheries Research Institute (Kochi, India)*, **12**: 1–86.
- Spence Bate, C. 1888. Report on the Crustacea, Macrura collected by the Challenger during the years 1873–76. *Report on the Scientific Results of the Voyage of H.M.S. "Challenger" during the years during the years 1873–76*, **24**: i–xc, 1–942, pls. 1–157.
- Subrahmanyam, C.B. 1965. On the reproductive cycle of *Penaeus indicus* (M. Edwards). *Journal of Marine Biological Association of India*, **7**: 284–290.
- Suseelan, C. 1974. Observations on the deep-sea prawn fishery off the south-west coast of India with special reference to pandalids. *Journal of Marine Biological Association of India*, **16**: 491–511.
- Suseelan, C., Nandakumar, G. & Rajan, K.N. 1989a. Results of bottom trawling by FORV Sagar Sampada with special reference to catch and abundance of edible crustaceans. In: *Proceedings of First Workshop, Scientific Results of FORV Sagar Sampada*, pp. 337–346. Cochin, India.
- Suseelan, C., Muthu, M.S., Rajan, K.N., Nandakumar, G., Kathiravel, M., Neelakanta, N., Pillai, N., Surendranatha, K. & Chellappan, K. 1989b. Results of an exclusive survey for the deep-sea crustaceans off southwest coast of India. In: *Proceeding of First Workshop, Scientific Results of FORV Sagar Sampada*, pp. 347–359. Cochin, India.
- Tudela, S., F. Sardà, F. Maynou & M. Demestre. 2003. Influence of submarine canyons on the distribution of the deepwater shrimp (*Aristeus antennatus*, Risso 1816) in the northwestern Mediterranean. *Crustaceana*, **76**: 217–225.
- Tuma, D.J. 1967. A description of the development of the primary and secondary sexual characters in banana prawn, *Penaeus merguensis* De Man (Crustacea: Decapoda: Penaeinae). *Australian Journal of Marine & Freshwater Research*, **18**: 73–88.
- Tuset, V.M., Pérez Peñalvo J., González, J., Pinho, M.R., Tuset, V.M., Delgado, J. Biscoito, M., Carvalho, D. & Santana, J. 2009. Biology of the deep-water shrimp *Heterocarpus ensifer* (Caridea: Pandalidae) off the Canary, Madeira and the Azores Islands (northeastern Atlantic). *Journal of Crustacean Biology*, **29**: 507–515.
- Tyler, C.R., Nagler, J.J., Pottinger, T.G. & Turner, M.A. 1994. Effects of unilateral ovariectomy on recruitment and growth of follicles in the rainbow trout, *Oncorhynchus mykiss*. *Fish Physiology and Biochemistry*, **13**: 309–316.
- Wood-Mason, J. & Alcock, A. 1891. Natural history notes from H.M. Indian marine survey steamer 'Investigator', Commander R.F. Hoskyn, R.N., commanding Series II, No. 1. On the results of deep-sea dredging during the season 1890-189. *Annals and Magazine of Natural History*, **8**: 268–286.