

Stock structure analysis of the Arabian red shrimp (*Aristeus alcocki* Ramadan, 1938) in the Indian coast with truss network morphometrics

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Abstract: The Arabian red shrimp (*Aristeus alcocki* Ramadan, 1938) is a deep-sea penaeoid shrimp that forms a major commercial fishery in the Indian coast. However, the spawning population of this species along the Indian coast is poorly known. To study this, stock structure of *A. alcocki* using truss morphometry was employed. A total of 1842 matured specimens were collected from five geographical locations (Tuticorin (SET), Chennai (SEC), Nagapattanam (SEN), Sakthikulangara (SWS), and Kalamuku (SWK)) along the Indian coast. Thirty-nine truss distances were extracted from each specimen and analyzed by multivariate methods (i.e., principal component analysis (PCA), discriminant functions (DF), and hierarchical cluster analysis). The results of the PCA indicated that the first two components cumulatively explained >70% (female: 72.1%; male: 71.5%) of the total morphometric variation. Stepwise DF analysis indicated that abdominal variables significantly discriminated the populations at different locations. The results clustered the five samples into a minimum of two groups: samples from SWK clustered in group I, whereas rest of the samples clustered in group II. Morphometric variation between the groups was significant for each sex. Significant differences between the groups may be attributed to geographical and environmental conditions, suggesting separate management strategies for resource sustainability.

Key words: *Aristeus alcocki*, truss morphometry, PCA, deep sea shrimp, DF.

Résumé : Le gambon d'Arabie (*Aristeus alcocki* Ramadan, 1938) est une crevette péneïde à la base d'une importante pêche commerciale le long du littoral indien. La population reproductrice de cette espèce le long du littoral indien demeure toutefois méconnue. Pour examiner cette question, la structure des stocks d'*A. alcocki* a été étudiée en utilisant la morphométrie de treillis. Un total de 1842 spécimens adultes a été prélevé de cinq lieux géographiques distincts (Tuticorin (SET), Chennai (SEC), Nagapattanam (SEN), Sakthikulangara (SWS) et Kalamuku (SWK)) le long du littoral indien. Trente-neuf distances de tronçon de treillis ont été mesurées pour chaque spécimen et analysées par des méthodes multivariées en utilisant l'analyse en composantes principales (ACP), les fonctions discriminantes (FD) et la classification hiérarchique. Les résultats de l'ACP indiquent que les deux premières composantes expliquent cumulativement >70 % (femelles : 72,1 %; mâles : 71,5 %) de la variation morphométrique totale. L'analyse discriminante pas-à-pas indique que les variables abdominales distinguent significativement les populations dans des lieux différents. Les résultats permettent de regrouper les cinq échantillons en un minimum de deux groupes : les échantillons de SWK forment le groupe I, alors que le reste des échantillons forment le groupe II. Les différences morphométriques entre les groupes sont significatives pour chaque sexe. Des différences significatives entre les groupes pourraient être attribuables aux conditions géographiques et ambiantes, ce qui indiquerait que des stratégies de gestion différentes pourraient être nécessaires pour assurer la pérennité de la ressource. [Traduit par la Rédaction]

Mots-clés : *Aristeus alcocki*, morphométrie de treillis, ACP, crevettes d'eau profonde, FD.

Introduction

In fisheries management, the term “stock” refers to a subset of a particular fish or shellfish species inhabiting a particular geographical area with the same growth and mortality parameters (Gulland 1983). Stock structure is the contribution of stock units that represent the entire population and not the population structure in terms of their length or size. The major objective of stock assessment programs is to manage fishery resources by providing advice on the optimal exploitation of the resource (Sparre and Venema 1998). Thorough knowledge of the stock structure of the target species in commercial fisheries is the first step in formulat-

ing resource management strategies (Shaklee and Bentzen 1998). If the stock structure is not considered while formulating plans for fisheries management, then it can lead to the collapse of the population due to the changes in biological attributes and loss in productivity rates (Begg et al. 1999; Cadrin 2005). Stock structure analysis is, therefore, a prerequisite for developing fishery management plans to understand the existing levels of recruitment that may replenish the population (Cadrin et al. 2005).

The study of morphometrics using truss network is a quantitative method to represent the complete shape of the fish (Strauss and Bookstein 1982). This representation is formed by interlinking the measurements between morphometric landmarks that

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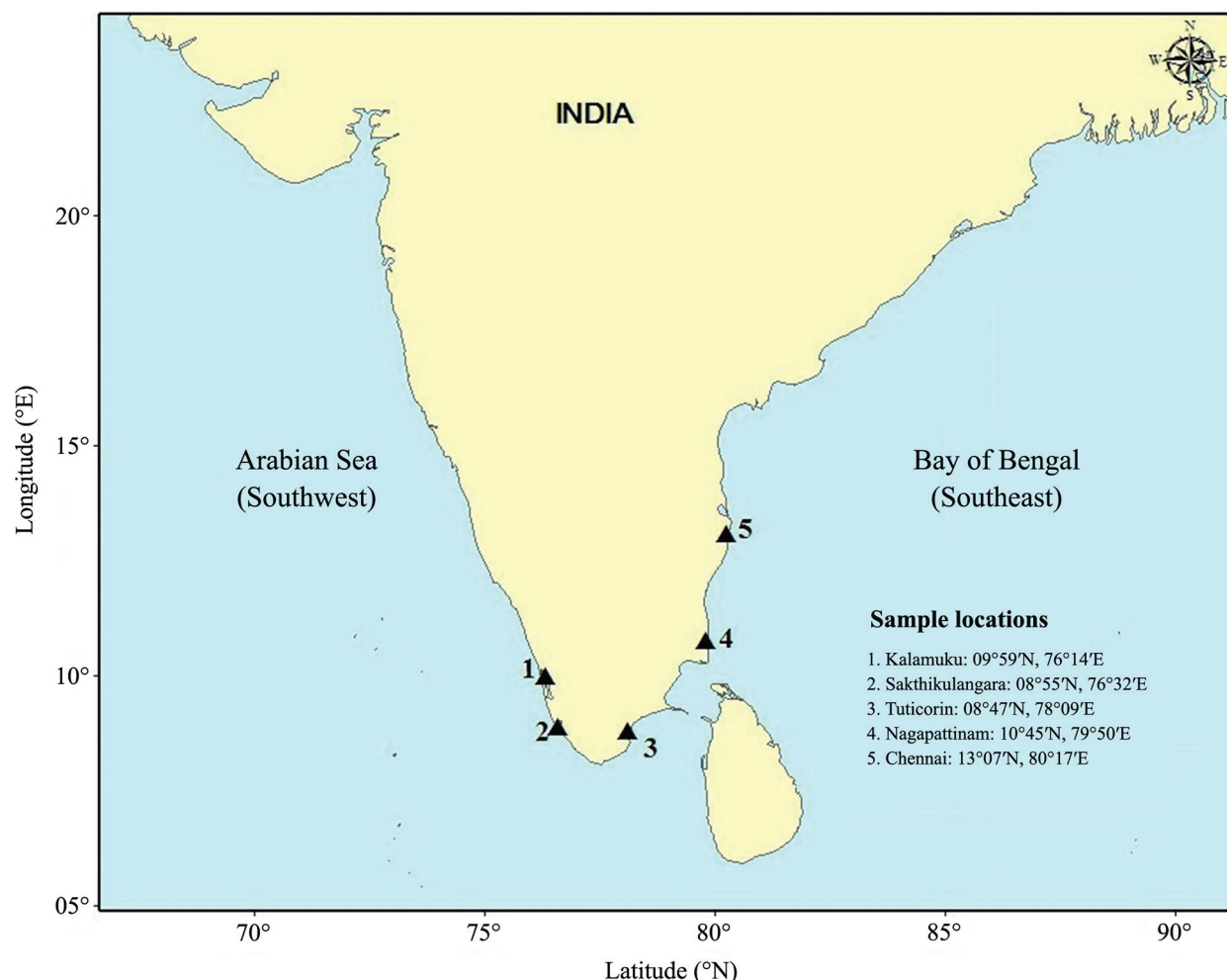
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Fig. 1. Sampling locations used for the collection of Arabian red shrimp (*Aristeus alcocki*) specimens. Color version online.



give rise to a systematic pattern of connected cells covering the entire body structure (Turan 1999); this quantitative method has been successfully used for population and taxonomic studies (Lin et al. 2005; Mevlut et al. 2006). Stock identification by truss network analysis is a practically useful and effective strategy for the description of the body shape compared with the traditional morphometric method (Cadrin 2005). It is effectively used to discriminate the stocks and differentiate between the population's shapes (Strauss and Bookstein 1982).

A large number of studies using the box-truss network method reported better results in categorizing individuals accurately and classifying them to their intraspecific groups (Turan 1999). In particular, the truss is a landmark-based technique that poses no restriction on the direction and localization of change in shape and is highly effective in capturing data on the shape of the organism (Cavalcanti et al. 1999). Phenotypic characters have been successfully used for stock differentiation in many shrimps (e.g., African river prawn, *Macrobrachium vollehovienii* (Herklots, 1857): Konan et al. 2010; oriental river prawn, *Macrobrachium nipponense* (De Haan, 1849): Chen et al. 2015) and fish species (e.g., northern mackerel scad, *Decapterus russelli* (Rüppell, 1830): Sen et al. 2011; Bombay Duck, *Harpodon nehereus* (Hamilton, 1822): Pazhayamadam et al. 2015; Indian oil sardine, *Sardinella longiceps* Valenciennes in Cuvier and Valenciennes, 1847: Remya et al. 2015; Japanese threadfin-bream, *Nemipterus japonicus* (Bloch, 1791): Sreekanth et al. 2015), whereas homogeneity was reported in the population of southern pink shrimp (*Farfantepenaeus notialis* (Pérez Farfante, 1967)) from the Caribbean Sea (Paramo and Saint-Paul 2010). Homogenous fish

populations are often composed of discrete stocks that may have unique demographic properties and responses to exploitation, which should be managed separately to ensure sustainable fishery benefits and efficient conservation (Kinsey et al. 1994; Begg and Brown 2000; Stransky et al. 2008; Neves et al. 2011).

The Arabian red shrimp (*Aristeus alcocki* Ramadan, 1938) (Decapoda, Aristeidae) is distributed along the southern Indian coast at a depth range of 200–1000 m (Silas 1969; Suseelan 1989; Madhusoodana Kurup et al. 2008; CMFRI 2015). It forms a commercial fishery that is confined along the southeast and southwest coasts of India; it is not recorded along the northern coast of India (Mohamed and Suseelan 1973). The catch landed between 2008 and 2015 indicate that *A. alcocki* is the prime species in order of biomass among the deep-sea penaeoid catch, accounting for about 36% of the catch for the whole Indian coast, and the trend in catch rates indicates a decline in these deep-sea shrimps (CMFRI 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015). In this study, we aim to investigate the effectiveness of the truss variables in differentiating the populations of *A. alcocki* along the Indian coast using truss morphometry to provide management advice regarding the sustainability of the fishery.

Materials and methods

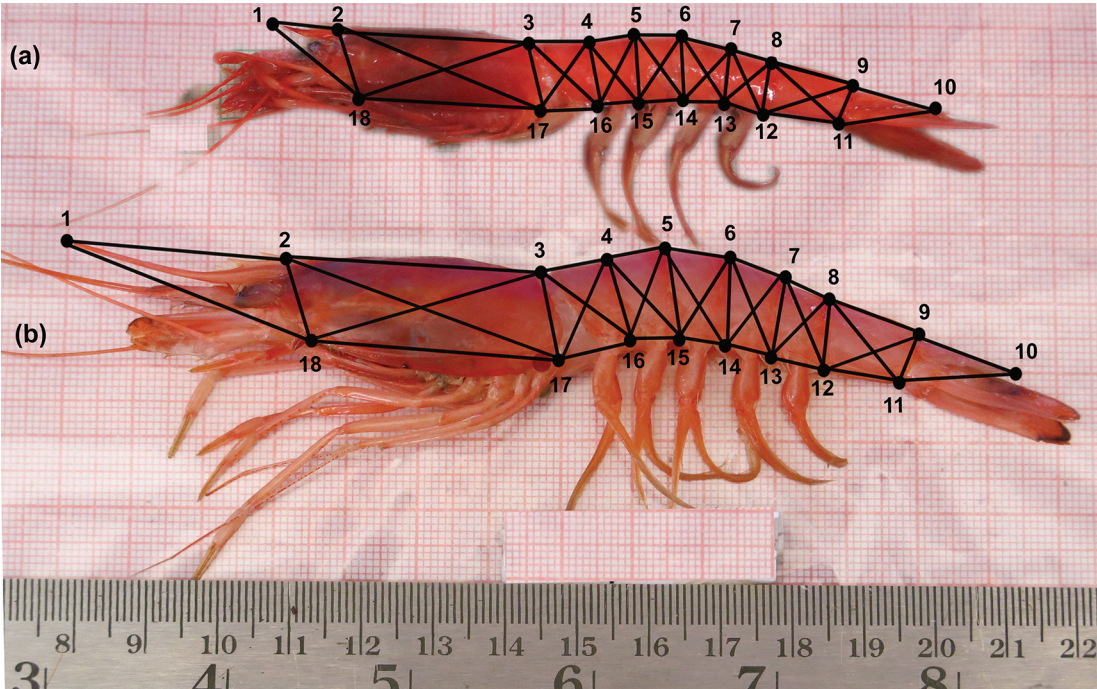
Sampling

Samples of *A. alcocki* were collected from five different fishing harbors, i.e., Tuticorin (SET), Chennai (SEC), and Nagapattinam (SEN) on the southeast Indian coast and Sakthikulangara (SWS)

Table 1. Details of sampling locations, geographical coordinates, time of sampling, and length ranges of the Arabian red shrimp (*Aristeus alcocki*).

| Coast | Location | Collection date | Latitude and longitude | Sex | Length ranges (cm) | Sample size (n) |
|-----------|-----------------------|-----------------|-------------------------------|--------|--------------------|-----------------|
| Southwest | Kalamuku (SWK) | December 2014 | 09°59′01.60″N, 76°14′32.50″E | Female | 12.0–19.0 | 226 |
| | | | | Male | 8.5–10.5 | 205 |
| | Sakthikulangara (SWS) | December 2014 | 08°55′58.38″N, 76°32′30.97″E | Female | 11.3–20.2 | 215 |
| | | | | Male | 8.5–10.8 | 192 |
| | Tuticorin (SET) | January 2015 | 08°47′41.85″N, 78°09′33.80″E | Female | 12.6–17.0 | 204 |
| Southeast | Nagapattinam (SEN) | January 2015 | 10°45′36.54″N, 79°50′57.27″E | Male | 8.4–10.1 | 114 |
| | | | | Female | 12.3–20.1 | 194 |
| | Chennai (SEC) | January 2015 | 13° 07′27.05″N, 80°17′48.90″E | Male | 8.2–10.5 | 158 |
| | | | | Female | 12.0–20.6 | 198 |
| | | | | Male | 8.0–10.0 | 136 |
| Total | | | | | | 1842 |

Fig. 2. (a) Male and (b) female Arabian red shrimp (*Aristeus alcocki*) placed on the graph paper showing 18 landmarks and 39 truss distances. Color version online.



and Kalamuku (SWK) on the southwest Indian coast (Fig. 1). The sampling sites were chosen such that they are distantly apart in latitude to reduce the chances of mixing specimens from the same population. In total, 1842 specimens were collected from the selected sampling sites, i.e., from commercial fishing harbors where the catch is landed by multiday trawlers along the southern coast during December 2014 and January 2015. The samples were collected during peak breeding season (November to January) to ensure that they represent their parent population. The matured specimens (carapace length — female >3.5 cm; male: >2.0 cm) were sorted from the samples collected from each fishing location and used for truss morphometric analysis. The species exhibit a high degree of sexual dimorphism where males were identified by the presence of petasma and females were sorted based on the presence of thelycum. Specimens showing physical damage, namely, broken rostrum or any other body parts, may distort the shape characteristics and hence they were not included in the samples for the study (Table 1).

Digitization of specimens and fixing anatomical landmarks

Shrimp samples were first cleaned with running water, after which the water was allowed to drain, the shrimps were wiped

with tissue paper, and finally placed on a graph paper (Figs. 2a, 2b). Each specimen was placed on a flat platform with a graph paper over a thermofoam, appendages (pereopods and pleopods) and telson were erected by positioning the rostrum portion towards the left side and the telson towards the right side, assuming symmetry between left and right sides of the shrimps, and was labeled with a specific ID code. This helped us in identifying specimens if more landmarks were required to be fixed or if the morphometric measurements were to be repeated. Digital images of the specimens were captured using a camera (Canon G-15) that was fixed on a tripod directly above the specimen and the lens was adjusted so that the margins of viewfinder aligned with the margins of the graph paper in the X–Y directions and each image included a scale to standardize the individual sizes and further scaling was applied in tpsDig using the millimetre grid of the graph paper (Figs. 2a, 2b). These images were used further in fixing the anatomical landmarks and measuring linear distances between them, i.e., truss variables. In previous studies, it has been found that differences in sex are likely to contribute to shape differences that affect the total variance in morphometric distances (Sajina et al. 2011; Pazhayamadam et al. 2015; Reiss and Grothues 2015). In the

Table 2. Descriptive statistics of morphometric variables from the Arabian red shrimp (*Aristeus alcocki*) at the five locations.

| Variable | Statistic | SEC | | SEN | | SET | | SWK | | SWS | |
|-----------------|--------------------|------------------|------------------|------------------|------------------|-----------------|------------------|-----------------|-----------------|-----------------|------------------|
| | | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male |
| Carapace length | Mean \pm SE (mm) | 40.0 \pm 0.26 | 25.15 \pm 0.16 | 41.1 \pm 0.40 | 25.19 \pm 0.19 | 35.8 \pm 0.29 | 22.14 \pm 0.39 | 38.4 \pm 0.47 | 23.7 \pm 0.14 | 37.3 \pm 0.51 | 25.09 \pm 0.16 |
| | Range (mm) | 29.96–49.14 | 21.1–29.01 | 26.92–51.04 | 19.47–30.39 | 25.6–51.3 | 14.8–27.1 | 20.6–50.5 | 19.6–29.7 | 20.0–50.4 | 18.10–29.86 |
| | SD (mm) | 3.78 | 1.58 | 5.2 | 2.38 | 4.18 | 2.4 | 6.9 | 1.9 | 7.4 | 2.34 |
| | CV (%) | 9.45 | 6.29 | 13.3 | 9.48 | 11.6 | 10.9 | 18.0 | 8.2 | 19.9 | 9.32 |
| 1–2 | Mean \pm SE (mm) | 38.25 \pm 0.33 | 10.78 \pm 0.15 | 39.0 \pm 0.38 | 11.00 \pm 0.18 | 34.0 \pm 0.27 | 12.09 \pm 0.30 | 37.0 \pm 0.38 | 11.6 \pm 0.16 | 35.6 \pm 0.37 | 11.26 \pm 0.17 |
| | Range (mm) | 23.96–53.12 | 8.53–15.47 | 26.2–53.6 | 7.43–22.29 | 25.2–44.2 | 8.5–16.4 | 17.4–50 | 7.7–19.7 | 21.8–49 | 7.44–18.63 |
| | SD (mm) | 4.72 | 1.58 | 5.2 | 2.37 | 3.8 | 1.9 | 5.6 | 2.2 | 5.4 | 2.48 |
| | CV (%) | 11.5 | 6.29 | 13.4 | 21.62 | 11.4 | 15.7 | 15.2 | 19.2 | 15.2 | 21.07 |
| 1–18 | Mean \pm SE (mm) | 45.95 \pm 0.37 | 15.65 \pm 0.15 | 47.2 \pm 0.43 | 15.98 \pm 0.17 | 40.8 \pm 0.32 | 16.3 \pm 0.28 | 44.8 \pm 0.45 | 16.4 \pm 0.15 | 43.4 \pm 0.44 | 16.67 \pm 0.16 |
| | Range (mm) | 29.42–61.14 | 12.7–20.08 | 32.8–60.7 | 12.18–25.00 | 28.6–53.6 | 13.0–19.9 | 21.5–59.2 | 11.4–24.8 | 25.3–59.1 | 12.15–23.23 |
| | SD (mm) | 5.30 | 1.43 | 5.9 | 2.17 | 4.6 | 1.7 | 6.7 | 2.1 | 6.4 | 2.29 |
| | CV (%) | 11.54 | 9.16 | 12.6 | 13.59 | 11.3 | 10.8 | 15.0 | 12.9 | 14.8 | 13.74 |
| 2–17 | Mean \pm SE (mm) | 45.01 \pm 0.29 | 28.65 \pm 0.16 | 46.2 \pm 0.43 | 28.54 \pm 0.20 | 40.3 \pm 0.32 | 25.7 \pm 0.43 | 43.3 \pm 0.50 | 27.3 \pm 0.15 | 41.8 \pm 0.54 | 28.39 \pm 0.18 |
| | Range (mm) | 31.41–55.72 | 23.7–32.89 | 30.5–56.3 | 22.53–34.51 | 30.0–55.2 | 20.06–31.9 | 24.1–56.2 | 22.5–34.6 | 23.2–56.0 | 21.02–33.74 |
| | SD (mm) | 4.19 | 1.61 | 5.8 | 2.57 | 4.5 | 2.7 | 7.3 | 2.1 | 7.9 | 2.60 |
| | CV (%) | 9.31 | 5.65 | 12.7 | 9.03 | 11.3 | 10.5 | 17.0 | 7.9 | 19.12 | 9.15 |
| 2–18 | Mean \pm SE (mm) | 14.67 \pm 0.12 | 9.71 \pm 0.16 | 15.3 \pm 0.14 | 9.60 \pm 0.07 | 13.5 \pm 0.12 | 8.9 \pm 0.12 | 14.2 \pm 0.16 | 9.0 \pm 0.06 | 13.7 \pm 0.17 | 9.19 \pm 0.06 |
| | Range (mm) | 9.84–18.65 | 7.50–11.05 | 10.0–19.5 | 6.89–11.84 | 9.7–18.9 | 6.7–10.3 | 6.6–19.7 | 6.5–11.6 | 7.4–19.2 | 6.77–11.47 |
| | SD (mm) | 1.73 | 0.70 | 1.9 | 0.95 | 1.7 | 0.77 | 2.4 | 0.89 | 2.5 | 0.96 |
| | CV (%) | 11.82 | 7.23 | 12.8 | 9.99 | 12.7 | 8.7 | 17.4 | 9.8 | 18.4 | 10.49 |
| 3–4 | Mean \pm SE (mm) | 10.98 \pm 0.09 | 8.49 \pm 0.10 | 11.8 \pm 0.11 | 8.39 \pm 0.08 | 10.5 \pm 0.08 | 7.7 \pm 0.19 | 10.0 \pm 0.12 | 8.0 \pm 0.07 | 10.5 \pm 0.13 | 8.47 \pm 0.07 |
| | Range (mm) | 7.80–14.32 | 5.74–10.45 | 6.4–14.9 | 5.38–11.84 | 6.9–14.1 | 5.1–10.2 | 5.9–14.3 | 4.8–10.1 | 5.5–14.8 | 4.99–10.67 |
| | SD (mm) | 1.31 | 0.99 | 1.56 | 1.06 | 1.16 | 1.19 | 1.8 | 1.00 | 1.9 | 1.05 |
| | CV (%) | 11.94 | 11.67 | 13.2 | 12.67 | 11.10 | 15.4 | 18.6 | 12.5 | 18.3 | 12.44 |
| 3–16 | Mean \pm SE (mm) | 18.35 \pm 0.11 | 12.91 \pm 0.09 | 18.6 \pm 0.15 | 12.70 \pm 0.09 | 17.2 \pm 0.11 | 11.9 \pm 0.21 | 17.3 \pm 0.16 | 12.3 \pm 0.07 | 17.2 \pm 0.18 | 13.11 \pm 0.08 |
| | Range (mm) | 12.69–22.29 | 10.7–15.26 | 12.5–23.0 | 9.27–16.23 | 12.7–22 | 9.6–14.1 | 10.0–21.9 | 9.5–15.1 | 9.6–22.6 | 9.71–15.63 |
| | SD (mm) | 1.65 | 0.89 | 2.14 | 1.21 | 1.6 | 1.3 | 2.4 | 1.0 | 2.7 | 1.21 |
| | CV (%) | 9.00 | 6.93 | 11.4 | 9.52 | 9.5 | 10.8 | 14.2 | 8.5 | 15.9 | 9.25 |
| 3–17 | Mean \pm SE (mm) | 12.97 \pm 0.09 | 9.25 \pm 0.09 | 13.5 \pm 0.10 | 8.95 \pm 0.06 | 12.4 \pm 0.09 | 8.7 \pm 0.12 | 12.6 \pm 0.12 | 8.6 \pm 0.05 | 12.1 \pm 0.13 | 8.99 \pm 0.06 |
| | Range (mm) | 8.82–16.96 | 7.12–11.60 | 9.9–16.8 | 7.05–11.52 | 9.2–15.8 | 7.0–10.0 | 7.8–17.8 | 6.6–10.8 | 6.87–17.6 | 6.83–11.18 |
| | SD (mm) | 1.34 | 0.866 | 1.4 | 0.83 | 1.3 | 0.75 | 1.9 | 0.79 | 1.9 | 0.94 |
| | CV (%) | 10.32 | 9.35 | 10.4 | 9.28 | 10.4 | 8.64 | 15.0 | 9.16 | 15.9 | 10.53 |
| 3–18 | Mean \pm SE (mm) | 38.43 \pm 0.24 | 24.96 \pm 0.15 | 39.3 \pm 0.36 | 24.79 \pm 0.18 | 34.3 \pm 0.26 | 21.9 \pm 0.35 | 36.6 \pm 0.44 | 23.1 \pm 0.13 | 35.0 \pm 0.48 | 24.24 \pm 0.16 |
| | Range (mm) | 27.61–47.00 | 21.2–27.91 | 25.3–48.4 | 19.00–30.78 | 25.3–45.9 | 17.9–26.6 | 19.0–48.0 | 19.1–27.6 | 19.0–47.2 | 17.59–29.80 |
| | SD (mm) | 3.48 | 1.47 | 4.9 | 2.34 | 3.8 | 2.1 | 6.5 | 1.9 | 7.0 | 2.38 |
| | CV (%) | 9.07 | 5.89 | 12.6 | 9.45 | 11.16 | 9.8 | 17.8 | 8.2 | 19.9 | 9.83 |
| 4–5 | Mean \pm SE (mm) | 8.69 \pm 0.05 | 6.73 \pm 0.77 | 8.89 \pm 0.067 | 6.53 \pm 0.05 | 8.15 \pm 0.05 | 6.19 \pm 0.09 | 8.6 \pm 0.08 | 6.3 \pm 0.04 | 8.6 \pm 0.09 | 6.92 \pm 0.05 |
| | Range (mm) | 5.57–11.17 | 5.20–8.55 | 6.47–11.49 | 5.13–8.57 | 6.17–10.7 | 5.05–7.7 | 4.8–11.5 | 4.8–8.4 | 5.2–11.7 | 5.25–8.70 |
| | SD (mm) | 0.82 | 0.77 | 0.92 | 0.71 | 0.80 | 0.60 | 1.3 | 0.66 | 1.3 | 0.71 |
| | CV (%) | 9.46 | 11.47 | 10.45 | 10.87 | 9.8 | 9.7 | 15.15 | 10.3 | 15.2 | 10.38 |
| 4–15 | Mean \pm SE (mm) | 16.22 \pm 0.10 | 11.63 \pm 0.85 | 16.2 \pm 0.12 | 11.33 \pm 0.07 | 15.2 \pm 0.09 | 10.5 \pm 0.16 | 15.6 \pm 0.14 | 10.9 \pm 0.05 | 15.4 \pm 0.15 | 11.64 \pm 0.07 |
| | Range (mm) | 11.09–19.97 | 9.53–13.95 | 11.07–19.5 | 8.88–13.82 | 11.9–19.5 | 8.45–12.4 | 8.5–19.6 | 8.9–13.1 | 8.9–20.3 | 8.72–14.05 |
| | SD (mm) | 1.50 | 0.81 | 1.76 | 1.00 | 1.3 | 0.99 | 2.1 | 0.80 | 2.2 | 1.05 |
| | CV (%) | 9.28 | 7.04 | 10.8 | 8.86 | 9.0 | 9.4 | 13.8 | 7.3 | 14.8 | 9.09 |
| 4–16 | Mean \pm SE (mm) | 13.03 \pm 0.08 | 9.15 \pm 0.73 | 13.14 \pm 0.09 | 8.83 \pm 0.05 | 11.9 \pm 0.07 | 8.3 \pm 0.09 | 12.4 \pm 0.11 | 8.55 \pm 0.04 | 12.0 \pm 0.11 | 8.93 \pm 0.05 |
| | Range (mm) | 8.79–16.10 | 7.74–11.48 | 9.3–15.7 | 6.97–10.33 | 9.3–15.7 | 7.05–9.2 | 7.11–15.5 | 6.7–10.2 | 7.12–16.0 | 6.92–10.93 |
| | SD (mm) | 1.20 | 0.70 | 1.31 | 0.71 | 1.13 | 0.61 | 1.65 | 0.6 | 1.7 | 0.75 |
| | CV (%) | 9.26 | 7.68 | 9.9 | 8.11 | 9.4 | 7.32 | 13.2 | 7.4 | 14.3 | 8.40 |

Table 2 (continued).

| Variable | Statistic | SEC | | SEN | | SET | | SWK | | SWS | |
|----------|--------------------|------------------|------------------|-----------------|------------------|-----------------|------------------|-----------------|-----------------|-----------------|------------------|
| | | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male |
| 4–17 | Mean \pm SE (mm) | 16.52 \pm 0.11 | 12.25 \pm 0.12 | 17.4 \pm 0.12 | 12.12 \pm 0.09 | 15.7 \pm 0.10 | 11.5 \pm 0.17 | 16.0 \pm 0.16 | 11.5 \pm 0.07 | 16 \pm 0.15 | 12.07 \pm 0.08 |
| | Range (mm) | 11.55–21.03 | 8.87–15.22 | 13.1–21.0 | 9.44–15.58 | 12.0–21.8 | 9.6–14.3 | 10.2–21.4 | 8.9–14.3 | 10.0–21.5 | 8.67–15.07 |
| | SD (mm) | 1.60 | 1.19 | 1.7 | 1.15 | 1.5 | 1.10 | 2.3 | 1.0 | 2.2 | 1.20 |
| | CV (%) | 9.70 | 9.76 | 10.1 | 9.55 | 9.5 | 9.58 | 14.7 | 9.4 | 14.3 | 9.95 |
| 5–6 | Mean \pm SE (mm) | 8.65 \pm 0.06 | 6.50 \pm 0.89 | 8.8 \pm 0.06 | 6.72 \pm 0.06 | 8.27 \pm 0.05 | 6.3 \pm 0.09 | 8.6 \pm 0.08 | 6.5 \pm 0.05 | 8.6 \pm 0.07 | 6.86 \pm 0.05 |
| | Range (mm) | 5.95–11.20 | 4.72–8.69 | 5.9–11.2 | 5.06–9.19 | 6.04–10.7 | 5.0–7.8 | 4.6–11.5 | 4.9–8.6 | 5.8–11.7 | 4.99–9.34 |
| | SD (mm) | 0.89 | 0.85 | 0.92 | 0.84 | 0.81 | 0.59 | 1.2 | 0.74 | 1.14 | 0.74 |
| | CV (%) | 10.37 | 13.13 | 10.4 | 12.62 | 9.8 | 9.46 | 14.7 | 11.4 | 13.2 | 10.81 |
| 5–14 | Mean \pm SE (mm) | 16.31 \pm 0.10 | 11.68 \pm 0.09 | 16.2 \pm 0.12 | 11.66 \pm 0.08 | 15.4 \pm 0.09 | 10.75 \pm 0.14 | 15.4 \pm 0.13 | 11.0 \pm 0.06 | 15.4 \pm 0.14 | 11.65 \pm 0.06 |
| | Range (mm) | 11.79–20.12 | 9.27–13.63 | 11.8–18.9 | 9.29–14.32 | 11.7–20.1 | 9.13–12.5 | 8.6–19.1 | 8.7–13.2 | 9.3–19.7 | 9.14–13.78 |
| | SD (mm) | 1.40 | 0.90 | 1.64 | 1.02 | 1.3 | 0.86 | 2.05 | 0.86 | 2.12 | 0.95 |
| | CV (%) | 8.62 | 7.76 | 10.1 | 8.76 | 8.85 | 8.03 | 13.2 | 7.7 | 13.7 | 8.16 |
| 5–15 | Mean \pm SE (mm) | 13.22 \pm 0.08 | 9.44 \pm 0.078 | 13.2 \pm 0.09 | 9.14 \pm 0.05 | 12.5 \pm 0.08 | 8.78 \pm 0.10 | 12.5 \pm 0.10 | 8.7 \pm 0.04 | 12.3 \pm 0.11 | 9.24 \pm 0.05 |
| | Range (mm) | 9.09–16.02 | 7.54–11.72 | 9.9–15.6 | 7.49–10.97 | 9.6–16.1 | 7.3–9.7 | 7.6–15.5 | 7.27–10.1 | 7.3–16.0 | 7.06–11.15 |
| | SD (mm) | 1.21 | 0.74 | 1.2 | 0.72 | 1.14 | 0.6 | 1.5 | 0.61 | 1.6 | 0.74 |
| | CV (%) | 9.19 | 7.91 | 9.6 | 7.88 | 9.14 | 7.5 | 12.4 | 7.03 | 13.6 | 8.09 |
| 5–16 | Mean \pm SE (mm) | 14.22 \pm 0.08 | 10.43 \pm 0.07 | 14.8 \pm 0.09 | 10.24 \pm 0.06 | 13.3 \pm 0.08 | 9.82 \pm 0.10 | 13.5 \pm 0.11 | 9.7 \pm 0.05 | 13.4 \pm 0.12 | 10.58 \pm 0.06 |
| | Range (mm) | 9.79–17.68 | 7.54–11.72 | 11.3–17.7 | 8.10–12.21 | 10.0–17.6 | 8.15–11.05 | 9.08–16.7 | 7.9–11.5 | 7.9–16.4 | 7.87–12.57 |
| | SD (mm) | 1.24 | 0.763 | 1.3 | 0.79 | 1.25 | 0.66 | 1.6 | 0.74 | 1.7 | 0.87 |
| | CV (%) | 8.72 | 7.31 | 8.8 | 7.73 | 9.3 | 6.7 | 12.2 | 7.6 | 13.2 | 8.25 |
| 6–7 | Mean \pm SE (mm) | 9.44 \pm 0.06 | 6.84 \pm 0.096 | 8.7 \pm 0.08 | 6.98 \pm 0.07 | 8.13 \pm 0.05 | 6.4 \pm 0.13 | 8.4 \pm 0.09 | 6.7 \pm 0.06 | 8.8 \pm 0.09 | 6.91 \pm 0.06 |
| | Range (mm) | 7.01–12.12 | 4.66–8.65 | 4.7–11.2 | 4.37–9.50 | 5.59–11.3 | 4.4–8.1 | 5.0–11.5 | 4.6–8.8 | 5.6–12 | 4.60–9.49 |
| | SD (mm) | 0.96 | 0.919 | 1.16 | 0.92 | 0.80 | 0.85 | 1.42 | 0.85 | 1.3 | 0.87 |
| | CV (%) | 10.26 | 13.48 | 13.2 | 13.26 | 9.94 | 13.2 | 16.7 | 12.5 | 15.3 | 12.71 |
| 6–13 | Mean \pm SE (mm) | 16.15 \pm 0.09 | 11.46 \pm 0.09 | 15.7 \pm 0.12 | 11.57 \pm 0.09 | 14.8 \pm 0.08 | 10.6 \pm 0.16 | 14.7 \pm 0.13 | 10.9 \pm 0.06 | 14.9 \pm 0.14 | 11.50 \pm 0.06 |
| | Range (mm) | 11.52–19.15 | 8.56–13.52 | 11.2–19.3 | 8.58–14.92 | 11.2–19.2 | 8.6–12.6 | 8.9–18.8 | 8.8–13.7 | 9.3–19.2 | 9.08–13.90 |
| | SD (mm) | 1.33 | 0.90 | 1.6 | 1.16 | 1.27 | 1.0 | 1.9 | 0.87 | 2.04 | 0.98 |
| | CV (%) | 8.23 | 7.91 | 10.47 | 10.05 | 8.6 | 9.6 | 13.3 | 7.9 | 13.6 | 8.56 |
| 6–14 | Mean \pm SE (mm) | 13.02 \pm 0.08 | 9.20 \pm 0.07 | 13.1 \pm 0.09 | 9.04 \pm 0.05 | 12.2 \pm 0.07 | 8.7 \pm 0.10 | 12.11 \pm 0.1 | 8.5 \pm 0.04 | 12.1 \pm 0.11 | 9.11 \pm 0.05 |
| | Range (mm) | 9.20–15.56 | 7.25–11.10 | 9.5–15.4 | 7.30–11.47 | 9.4–15.5 | 7.5–9.8 | 7.7–15.4 | 7.04–10.6 | 7.4–15.5 | 7.28–10.73 |
| | SD (mm) | 1.13 | 0.66 | 1.29 | 0.71 | 1.06 | 0.6 | 1.5 | 0.63 | 1.6 | 0.73 |
| | CV (%) | 8.72 | 7.27 | 9.8 | 7.88 | 8.69 | 7.7 | 12.5 | 7.44 | 13.8 | 8.02 |
| 6–15 | Mean \pm SE (mm) | 14.06 \pm 0.08 | 10.40 \pm 0.08 | 14.5 \pm 0.09 | 10.16 \pm 0.06 | 13.2 \pm 0.08 | 9.9 \pm 0.11 | 13.3 \pm 0.11 | 9.7 \pm 0.05 | 13.3 \pm 0.12 | 10.53 \pm 0.06 |
| | Range (mm) | 10.02–16.77 | 7.83–13.28 | 10.9–17.1 | 8.25–12.04 | 10.6–17.4 | 8.3–11.5 | 8.9–17.3 | 8.2–11.3 | 7.8–16.9 | 8.07–12.52 |
| | SD (mm) | 1.21 | 0.85 | 1.2 | 0.76 | 1.17 | 0.72 | 1.6 | 0.75 | 1.7 | 0.91 |
| | CV (%) | 8.72 | 8.16 | 8.6 | 7.55 | 8.8 | 7.2 | 12.4 | 7.80 | 13.11 | 8.71 |
| 7–8 | Mean \pm SE (mm) | 6.76 \pm 0.04 | 5.52 \pm 0.06 | 7.2 \pm 0.06 | 5.46 \pm 0.05 | 6.3 \pm 0.05 | 4.8 \pm 0.07 | 6.6 \pm 0.06 | 5.13 \pm 0.04 | 6.9 \pm 0.07 | 5.28 \pm 0.04 |
| | Range (mm) | 4.59–8.66 | 3.96–7.11 | 4.7–9.5 | 3.93–7.25 | 4.6–9.1 | 4.03–5.8 | 4.3–9.6 | 3.7–7.1 | 4.07–9.4 | 3.88–7.71 |
| | SD (mm) | 0.69 | 0.57 | 0.9 | 0.66 | 0.72 | 0.48 | 1.02 | 0.60 | 1.1 | 0.67 |
| | CV (%) | 10.23 | 10.39 | 12.5 | 12.19 | 11.3 | 9.9 | 15.3 | 11.8 | 15.9 | 12.73 |
| 7–12 | Mean \pm SE (mm) | 13.52 \pm 0.08 | 9.98 \pm 0.07 | 13.8 \pm 0.11 | 9.95 \pm 0.07 | 12.9 \pm 0.08 | 9.18 \pm 0.12 | 12.7 \pm 0.11 | 9.3 \pm 0.05 | 12.9 \pm 0.12 | 9.95 \pm 0.05 |
| | Range (mm) | 9.63–16.53 | 8.20–12.24 | 10.0–17.1 | 7.70–12.02 | 9.3–16.6 | 7.8–10.7 | 8.11–16.8 | 7.64–11.6 | 7.6–16.6 | 7.81–11.86 |
| | SD (mm) | 1.20 | 0.68 | 1.54 | 0.90 | 1.27 | 0.74 | 1.6 | 0.75 | 1.8 | 0.83 |
| | CV (%) | 9.45 | 6.86 | 11.15 | 9.07 | 9.8 | 8.16 | 13.0 | 8.08 | 14.1 | 8.37 |
| 7–13 | Mean \pm SE (mm) | 10.91 \pm 0.07 | 7.97 \pm 0.05 | 11.1 \pm 0.08 | 7.67 \pm 0.05 | 10.4 \pm 0.06 | 7.38 \pm 0.08 | 10.2 \pm 0.09 | 7.15 \pm 0.04 | 10.2 \pm 0.10 | 7.66 \pm 0.04 |
| | Range (mm) | 7.12–13.70 | 6.54–9.24 | 7.8–13.7 | 6.25–9.43 | 7.6–13.1 | 6.3–8.5 | 6.5–13.8 | 5.8–8.7 | 6.3–13.2 | 5.99–9.09 |
| | SD (mm) | 1.30 | 0.52 | 1.15 | 0.63 | 0.98 | 0.54 | 1.3 | 0.56 | 1.4 | 0.65 |
| | CV (%) | 9.45 | 6.57 | 10.3 | 8.21 | 9.4 | 7.4 | 13.1 | 7.8 | 14.3 | 8.57 |

Table 2 (continued).

| Variable | Statistic | SEC | | SEN | | SET | | SWK | | SWS | |
|----------|--------------------|------------------|------------------|------------------|------------------|-----------------|------------------|-----------------|-----------------|-----------------|------------------|
| | | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male |
| 7–14 | Mean \pm SE (mm) | 13.09 \pm 0.07 | 9.89 \pm 0.07 | 13.5 \pm 0.09 | 9.42 \pm 0.06 | 12.4 \pm 0.07 | 9.2 \pm 0.11 | 12.3 \pm 0.10 | 9.0 \pm 0.05 | 12.5 \pm 0.11 | 9.72 \pm 0.05 |
| | Range (mm) | 9.55–15.56 | 7.42–11.23 | 10.06–15.9 | 7.55–11.32 | 9.48–15.0 | 7.6–10.8 | 8.17–15.4 | 7.27–10.8 | 8.4–15.5 | 7.50–11.42 |
| | SD (mm) | 1.14 | 0.70 | 1.25 | 0.75 | 1.08 | 0.73 | 1.5 | 0.75 | 1.6 | 0.82 |
| | CV (%) | 8.43 | 7.07 | 9.2 | 8.02 | 8.7 | 7.9 | 12.5 | 8.3 | 13.2 | 8.47 |
| 8–9 | Mean \pm SE (mm) | 13.16 \pm 0.07 | 11.21 \pm 0.07 | 13.9 \pm 0.09 | 10.66 \pm 0.07 | 12.7 \pm 0.07 | 9.7 \pm 0.11 | 13.16 \pm 0.1 | 10.1 \pm 0.06 | 13.5 \pm 0.11 | 10.83 \pm 0.05 |
| | Range (mm) | 10.03–15.83 | 8.79–12.95 | 10.7–16.9 | 8.28–13.18 | 10.0–16.1 | 8.09–10.8 | 9.29–16.1 | 7.9–12.8 | 8.7–17.1 | 8.73–13.12 |
| | SD (mm) | 1.08 | 0.70 | 1.24 | 0.93 | 1.06 | 0.713 | 1.5 | 0.89 | 1.67 | 0.84 |
| | CV (%) | 8.22 | 6.25 | 8.9 | 8.79 | 8.3 | 7.3 | 11.7 | 8.7 | 12.4 | 7.75 |
| 8–11 | Mean \pm SE (mm) | 15.40 \pm 0.08 | 12.40 \pm 0.06 | 16.1 \pm 0.11 | 11.95 \pm 0.07 | 14.7 \pm 0.08 | 10.9 \pm 0.13 | 15.1 \pm 0.12 | 11.5 \pm 0.05 | 15.2 \pm 0.13 | 12.27 \pm 0.06 |
| | Range (mm) | 11.41–18.78 | 10.74–13.9 | 12.1–19.4 | 9.56–14.95 | 11.6–18.5 | 9.2–12.7 | 10.6–18.6 | 9.7–13.7 | 9.9–19.4 | 9.6–14.74 |
| | SD (mm) | 1.20 | 0.60 | 1.55 | 0.98 | 1.22 | 0.85 | 1.8 | 0.81 | 1.9 | 0.95 |
| | CV (%) | 7.85 | 4.91 | 9.6 | 8.20 | 8.33 | 7.8 | 12.0 | 7.08 | 12.7 | 7.75 |
| 8–12 | Mean \pm SE (mm) | 9.54 \pm 0.06 | 6.98 \pm 0.05 | 9.72 \pm 0.07 | 6.71 \pm 0.04 | 9.19 \pm 0.06 | 6.5 \pm 0.08 | 8.86 \pm 0.07 | 6.25 \pm 0.03 | 8.9 \pm 0.08 | 6.81 \pm 0.04 |
| | Range (mm) | 6.76–11.86 | 5.62–7.98 | 6.9–11.8 | 5.13–7.96 | 6.3–11.5 | 5.3–7.4 | 5.57–11.3 | 5.1–7.5 | 5.6–11.8 | 5.20–8.05 |
| | SD (mm) | 0.87 | 0.49 | 1.03 | 0.53 | 0.86 | 0.5 | 1.11 | 0.51 | 1.2 | 0.58 |
| | CV (%) | 9.12 | 7.09 | 10.6 | 7.98 | 9.3 | 7.7 | 12.5 | 8.18 | 14.17 | 8.51 |
| 8–13 | Mean \pm SE (mm) | 11.3 \pm 0.06 | 8.72 \pm 0.06 | 11.9 \pm 0.08 | 8.42 \pm 0.05 | 10.7 \pm 0.06 | 8.18 \pm 0.09 | 10.8 \pm 0.08 | 7.9 \pm 0.05 | 11.0 \pm 0.10 | 8.43 \pm 0.05 |
| | Range (mm) | 7.97–13.58 | 6.55–9.92 | 9.09–14.4 | 6.35–10.35 | 8.3–13.5 | 6.6–9.2 | 7.2–13.2 | 6.5–10.7 | 7.0–14.1 | 6.60–10.70 |
| | SD (mm) | 0.96 | 0.62 | 1.12 | 0.69 | 0.9 | 0.6 | 1.3 | 0.73 | 1.4 | 0.77 |
| | CV (%) | 8.52 | 7.10 | 9.4 | 8.22 | 8.66 | 7.4 | 11.9 | 9.2 | 13.3 | 9.16 |
| 9–10 | Mean \pm SE (mm) | 15.76 \pm 0.10 | 12.02 \pm 0.09 | 16.7 \pm 0.13 | 11.18 \pm 0.08 | 15.0 \pm 0.10 | 10.6 \pm 0.13 | 15.4 \pm 0.16 | 10.8 \pm 0.08 | 15.6 \pm 0.16 | 11.16 \pm 0.07 |
| | Range (mm) | 10.75–20.69 | 9.79–15.33 | 11.5–20.8 | 8.82–14.31 | 10.3–18.9 | 9.16–12.5 | 8.6–20.7 | 8.5–19.7 | 9.3–20.3 | 8.27–14.09 |
| | SD (mm) | 1.52 | 0.89 | 1.87 | 1.03 | 1.4 | 0.84 | 2.4 | 1.2 | 2.4 | 1.12 |
| | CV (%) | 9.67 | 7.42 | 11.2 | 9.26 | 9.9 | 7.9 | 15.7 | 11.15 | 15.5 | 10.11 |
| 9–11 | Mean \pm SE (mm) | 7.15 \pm 0.05 | 5.51 \pm 0.04 | 7.21 \pm 0.05 | 5.27 \pm 0.04 | 6.7 \pm 0.04 | 4.9 \pm 0.08 | 6.6 \pm 0.06 | 4.6 \pm 0.03 | 6.6 \pm 0.06 | 5.05 \pm 0.03 |
| | Range (mm) | 4.89–9.29 | 4.42–6.44 | 5.5–9.2 | 3.82–7.35 | 4.2–8.9 | 3.8–5.8 | 3.8–9.0 | 3.7–6.0 | 4.04–8.8 | 3.65–6.21 |
| | SD (mm) | 0.70 | 0.41 | 0.756 | 0.50 | 0.66 | 0.50 | 0.9 | 0.42 | 1.0 | 0.49 |
| | CV (%) | 9.87 | 7.55 | 10.4 | 9.67 | 9.87 | 10.10 | 13.6 | 9.0 | 15.17 | 9.76 |
| 9–12 | Mean \pm SE (mm) | 14.10 \pm 0.07 | 11.76 \pm 0.08 | 14.8 \pm 0.08 | 11.31 \pm 0.06 | 13.4 \pm 0.07 | 10.76 \pm 0.12 | 13.9 \pm 0.11 | 10.7 \pm 0.06 | 14.4 \pm 0.11 | 11.29 \pm 0.06 |
| | Range (mm) | 10.49–16.53 | 9.03–13.51 | 11.6–17.8 | 9.25–14.18 | 10.4–17.2 | 8.9–12.5 | 9.25–17.6 | 8.4–13.2 | 9.7–17.8 | 8.16–13.79 |
| | SD (mm) | 1.08 | 0.78 | 1.2 | 0.87 | 1.02 | 0.8 | 1.6 | 0.95 | 1.6 | 0.97 |
| | CV (%) | 7.68 | 6.67 | 8.08 | 7.75 | 7.6 | 7.4 | 12.0 | 8.8 | 11.5 | 8.60 |
| 10–11 | Mean \pm SE (mm) | 16.9 \pm 0.12 | 13.33 \pm 0.11 | 17.9 \pm 0.14 | 12.34 \pm 0.10 | 15.8 \pm 0.11 | 11.7 \pm 0.15 | 16.8 \pm 0.18 | 11.8 \pm 0.10 | 17.0 \pm 0.17 | 11.87 \pm 0.08 |
| | Range (mm) | 12.33–21.16 | 10.4–17.25 | 12.4–22.8 | 9.18–16.31 | 11.4–20.3 | 9.3–13.9 | 9.12–22.7 | 8.8–20.3 | 10.4–22.4 | 9.13–15.47 |
| | SD (mm) | 1.68 | 1.09 | 1.9 | 1.28 | 1.58 | 0.93 | 2.7 | 1.3 | 2.6 | 1.20 |
| | CV (%) | 9.93 | 8.20 | 10.7 | 10.39 | 9.9 | 8.0 | 16.3 | 11.7 | 15.3 | 10.17 |
| 11–12 | Mean \pm SE (mm) | 11.35 \pm 0.07 | 9.59 \pm 0.07 | 12.1 \pm 0.080 | 9.39 \pm 0.06 | 10.7 \pm 0.06 | 8.8 \pm 0.11 | 11.5 \pm 0.10 | 9.3 \pm 0.05 | 11.8 \pm 0.09 | 9.65 \pm 0.06 |
| | Range (mm) | 8.21–14.61 | 7.97–11.29 | 8.7–14.8 | 7.32–11.16 | 8.7–13.5 | 7.2–10.6 | 7.8–19.7 | 7.13–11.5 | 8.13–15.0 | 7.06–12.56 |
| | SD (mm) | 0.98 | 0.71 | 1.10 | 0.77 | 0.96 | 0.72 | 1.57 | 0.79 | 1.3 | 0.95 |
| | CV (%) | 8.68 | 7.47 | 9.10 | 8.24 | 8.97 | 8.24 | 13.6 | 8.5 | 11.8 | 9.86 |
| 12–13 | Mean \pm SE (mm) | 7.71 \pm 0.05 | 5.88 \pm 0.07 | 8.17 \pm 0.07 | 6.21 \pm 0.05 | 7.22 \pm 0.05 | 5.7 \pm 0.10 | 7.53 \pm 0.07 | 5.9 \pm 0.04 | 7.6 \pm 0.07 | 6.30 \pm 0.05 |
| | Range (mm) | 5.40–10.30 | 4.42–7.43 | 5.7–10.3 | 4.37–8.57 | 5.45–9.5 | 4.3–7.3 | 5.14–10.2 | 4.5–8.2 | 4.3–10.14 | 4.55–8.61 |
| | SD (mm) | 0.77 | 0.68 | 1.00 | 0.64 | 0.81 | 0.6 | 1.0 | 0.67 | 1.1 | 0.77 |
| | CV (%) | 10.06 | 11.62 | 12.3 | 10.30 | 11.3 | 11.3 | 14.2 | 11.2 | 14.7 | 12.28 |
| 13–14 | Mean \pm SE (mm) | 7.86 \pm 0.05 | 6.11 \pm 0.07 | 7.9 \pm 0.07 | 6.02 \pm 0.06 | 7.2 \pm 0.06 | 5.4 \pm 0.11 | 7.1 \pm 0.08 | 5.89 \pm 0.05 | 7.54 \pm 0.08 | 6.30 \pm 0.05 |
| | Range (mm) | 6.04–9.75 | 4.62–8.44 | 5.2–9.8 | 4.26–8.24 | 4.27–9.87 | 4.2–7.0 | 4.07–9.7 | 4.12–7.9 | 4.7–9.9 | 4.42–8.34 |
| | SD (mm) | 0.79 | 0.71 | 0.96 | 0.76 | 0.87 | 0.71 | 1.20 | 0.71 | 1.1 | 0.71 |
| | CV (%) | 9.75 | 11.67 | 12.03 | 12.65 | 12.18 | 13.0 | 16.7 | 12.0 | 15.6 | 11.41 |

Table 2 (continued).

| Variable | Statistic | SEC | | SEN | | SET | | SWK | | SWS | |
|----------|--------------------|------------------|------------------|-----------------|------------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------|
| | | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male |
| 14–15 | Mean \pm SE (mm) | 6.93 \pm 0.05 | 5.56 \pm 0.06 | 7.27 \pm 0.06 | 5.53 \pm 0.05 | 6.5 \pm 0.05 | 4.8 \pm 0.08 | 6.65 \pm 0.07 | 5.14 \pm 0.04 | 6.75 \pm 0.07 | 5.74 \pm 0.05 |
| | Range (mm) | 4.44–9.34 | 4.14–7.29 | 4.9–9.0 | 3.93–7.32 | 3.8–8.3 | 3.7–5.9 | 3.9–9.5 | 3.6–6.7 | 3.6–8.7 | 3.66–7.63 |
| | SD (mm) | 0.74 | 0.65 | 0.86 | 0.70 | 0.76 | 0.5 | 1.14 | 0.64 | 1.0 | 0.80 |
| | CV (%) | 10.68 | 11.7 | 11.8 | 12.77 | 11.6 | 10.5 | 17.2 | 12.5 | 15.7 | 13.98 |
| 15–16 | Mean \pm SE (mm) | 6.93 \pm 0.05 | 5.34 \pm 0.06 | 7.56 \pm 0.07 | 5.55 \pm 0.06 | 6.86 \pm 0.05 | 4.9 \pm 0.08 | 6.7 \pm 0.07 | 5.29 \pm 0.04 | 7.02 \pm 0.08 | 5.99 \pm 0.05 |
| | Range (mm) | 4.62–8.94 | 3.77–6.70 | 4.9–9.9 | 3.57–7.79 | 4.5–8.9 | 3.7–5.9 | 4.46–9.19 | 3.8–7.02 | 3.6–9.7 | 3.88–8.08 |
| | SD (mm) | 0.80 | 0.66 | 1.02 | 0.76 | 0.80 | 0.5 | 1.08 | 0.65 | 1.2 | 0.74 |
| | CV (%) | 11.32 | 12.49 | 13.5 | 13.76 | 11.6 | 10.9 | 16.16 | 12.3 | 17.15 | 12.48 |
| 16–17 | Mean \pm SE (mm) | 12.36 \pm 0.10 | 8.73 \pm 0.14 | 12.6 \pm 0.13 | 8.99 \pm 0.10 | 11.6 \pm 0.09 | 8.4 \pm 0.2 | 12.0 \pm 0.14 | 8.6 \pm 0.08 | 12.3 \pm 0.13 | 9.30 \pm 0.08 |
| | Range (mm) | 7.79–17.04 | 5.80–11.49 | 7.71–16.6 | 6.20–12.62 | 8.3–15.4 | 6.5–11.4 | 6.64–16.6 | 6.1–11.5 | 6.12–17.3 | 5.96–12.38 |
| | SD (mm) | 1.48 | 1.39 | 1.8 | 1.34 | 1.3 | 1.2 | 2.18 | 1.1 | 2.0 | 1.17 |
| | CV (%) | 11.98 | 15.93 | 14.4 | 14.96 | 11.49 | 15.3 | 18.2 | 13.03 | 16.2 | 12.63 |
| 17–18 | Mean \pm SE (mm) | 39.01 \pm 0.25 | 25.16 \pm 0.17 | 39.7 \pm 0.37 | 24.98 \pm 0.19 | 34.5 \pm 0.28 | 22.3 \pm 0.40 | 37.2 \pm 0.44 | 23.7 \pm 0.14 | 35.3 \pm 0.48 | 24.49 \pm 0.17 |
| | Range (mm) | 26.47–48.16 | 20.8–20.71 | 25.1–48.7 | 18.45–32.17 | 25.9–49.1 | 18.0–28.1 | 20.2–47.7 | 19.2–29.0 | 19.3–47.7 | 17.96–31.03 |
| | SD (mm) | 3.57 | 1.64 | 5.14 | 2.46 | 4.07 | 2.4 | 6.5 | 1.9 | 7.09 | 2.50 |
| | CV (%) | 9.17 | 6.52 | 12.9 | 9.85 | 11.7 | 11.1 | 17.4 | 8.4 | 20.04 | 10.21 |

Note: Locations are Chennai (SEC), Nagapattinam (SEN), Tuticorin (SET), Kalamuku (SWK), Sakthikulangara (SWS).

Table 3. MANCOVA (sex \times location) of carapace size of the Arabian red shrimp (*Aristeus alcocki*) measured at five locations.

| | Wilks' λ | df | F | P |
|-----------------------|------------------|----|-------|--------|
| Sex | 0.310 | 1 | 94.26 | <0.001 |
| Location | 0.385 | 4 | 11.43 | <0.001 |
| Sex \times location | 0.527 | 4 | 7.372 | <0.001 |

present analysis, both males and females were included to accommodate the effect of sex on their morphometry. The extraction of numeric truss distances from the digital images of specimens were carried out using two software platforms: (1) tpsDig2 version 2.1 for marking the landmark coordinates on the digital images (Rohlf 2006) and (2) paleontological statistics (PAST) for extracting the values pertaining to the marked distances (Hammer et al. 2001). The data extracted by these methods ensure stability, accuracy, and repeatability.

Analysis of truss morphometric data

The assumptions of normality and homogeneity of variance were verified with the log-transformed data, using the SAS PROC UNIVARIATE procedure (SAS Institute, Inc. 2014), and the data rows with outliers (7%–10%) were removed from each location before proceeding further with the analysis. MANCOVA was used to establish significant differences between sex and location using the log-transformed data, with carapace length incorporated into the models as a covariate. Therefore, the whole truss measurements (39 distances) were transformed to size-independent shape variables using the allometric method suggested by Reist (1985):

$$M_{\text{trans}} = \log M - \beta[\log \text{CL} - \log(\text{CL mean})]$$

where M_{trans} is the truss measurement after transformation; M is the original truss measurement; CL is the carapace length of the shrimp, which is reported to be more reliable than using total length in the case of crustaceans (FAO 1974); CL mean is the overall mean carapace length; and β is the slope regressions of $\log M$ against $\log \text{CL}$.

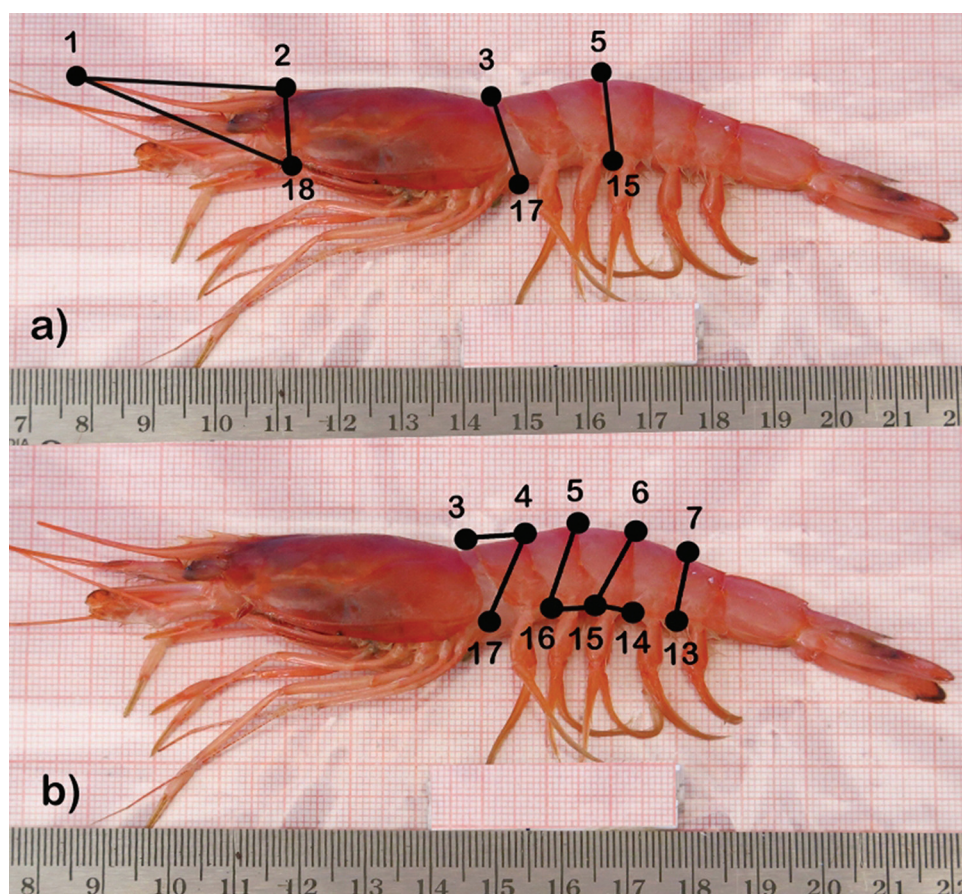
Correlation coefficients were checked between each pair of variables before and after the removal of the size effect. In such analysis, the absolute values of correlation coefficients were expected to decrease after the removal of the size effect (Murta 2000). Mean, standard error (SE), standard deviation (SD), minimum and maximum (range) of all measurements were recorded for each population. The percent coefficient of variation (CV%) was computed as $\text{CV\%} = 100 \times \text{SD}/\text{mean}$ of morphometric variables in each population. Multivariate methods used in this study were principal component analysis (PCA), discriminant functions (DF), and hierarchical cluster analyses.

PCA was used to evaluate morphometric variation among specimens and identify variables contributing substantially to that variation. DF was run to test the effectiveness of variables in predicting different group locations (Tomović and Džukić 2003; Loy et al. 2008). The stepwise inclusion procedure was carried out to reduce the number of variables and identify the combination of variables that best separates the groups (Hair et al. 1996; Jain et al. 2000; Poulet et al. 2005) to obtain a confusion table matrix. Hierarchical cluster analysis based on Mahalanobis distance matrices determined with DF was used to evaluate population relationships, as used by Slabova and Frynta (2007) and Ferrito et al. (2007). All analyses in the present study were carried out in SAS (SAS Institute, Inc. 2014).

Results

Descriptive statistical results showed less CV (<25%) in all the truss variables for both sex at the five different locations (Table 2). The CV ranged from 7.6% to 20% for females and from 4.9% to

Fig. 3. Variables with high loadings observed in the (a) first and (b) second components when morphometric variables were subjected to principal component analysis. Color version online.



21.6% for males. The morphometric variability within populations was low for all the locations.

Correlation coefficients between the morphometric variables were estimated before and after the removal of the size effect (see Supplementary Tables S1 and S2).¹ Before the removal of the size effect, coefficient values were highly significant. After the removal of the size effect, the coefficient values were reduced, which suggested that the effects of size had been effectively removed from the morphometric data. The CL mean specifies that males are much smaller than females, and a significant difference between sex and location was observed (Table 3).

The PCA results indicate that the first two components cumulatively explained >70% (female: 72.1%; male: 71.5%) of the total morphometric variation. A few truss distances loaded heavily on PC1 (1–2, 1–18, 2–18, 3–17, and 5–15), which alone explained >63% of the entire variance. The loadings of two variables, i.e., the 1–2 distance that correspond to the rostral length and the 1–18 distance that connect the rostrum tip to the pterygostomian spine, contributed to a substantial proportion of the total variance. PC2 explained 8.21% of the total variation, and three distance variables (3–4, 15–16, and 4–17) corresponding to the abdominal region of the shrimp loaded heavily on this component. The distances with high loadings on both PC1 and PC2 characterize the rostrum and the second to third abdominal segment portions of the shrimp (Figs. 3a, 3b), which were all found to be positive, thus signifying the positive correlation between the variables within a component, i.e., these attributes grow in proportion with one another. A

scatterplot between PC1 and PC2 resulted in the separation of SWK from other populations (Figs. 4a, 4b).

With respect to the stepwise DF analysis, 6 out of 39 variables were efficiently discriminated in the different populations. The pairwise *F* tests on these primary important characters were obtained and shown in Table 4. The well-defined female populations were from SWK with classified individual percentage >70% (Table 5). A minimum proportion of 1.4% from each population was allocated to every population. The highest misclassification rate of 14.1% was observed between SEN and SWK. In the male population, SWK was classified with >50% individuals, a minimum 5.4% of each population was allocated to other populations, and there was a higher misclassification rate (21.4%) compared with the female population. The overall rate of correct classification was 68.5% in females and 40.0% in males. This analysis revealed that the Mahalanobis distances between the different groups were significant ($P < 0.001$). The well-separated population was SWK and most closely related samples were SEN and SET.

From cross-validation analysis, 64.4% of females and 48.1% of males were correctly classified to their corresponding group (Table 5). The greatest proportion of classification was obtained in SET female populations (83.5%) and SWK male populations (54.1%). The higher proportions of misclassified females from SWK were allocated to SWS and males of SEC were allocated to SET (26.4%).

The first two canonical functions carry the analysis through the 89.9% and 84.7% for female and male, respectively, indicating that the greatest level of variation was due to the first two canonical

¹Supplementary tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2016-0283>.

Fig. 4. Scatterplot of the first two principle components from the principal component analysis for (a) female and (b) male Arabian red shrimp (*Aristeus alcocki*). Color version online.

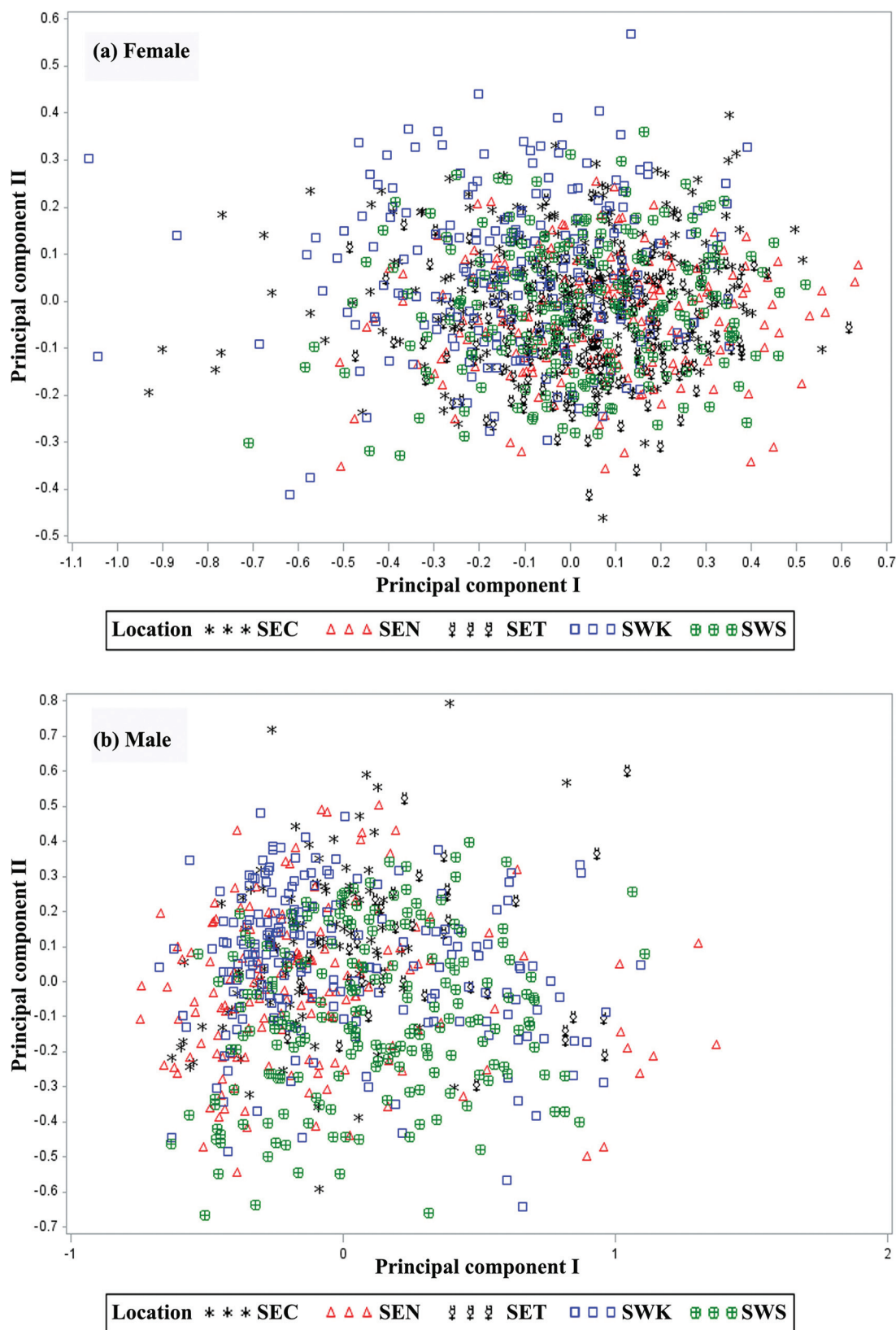


Table 4. Discriminate morphometric characters of the Arabian red shrimp (*Aristeus alcocki*) retained by stepwise discriminant analysis.

| Variable | Female | | | Male | | |
|----------|------------------|-------|-------|------------------|-------|-------|
| | Wilks' λ | F | P | Wilks' λ | F | P |
| T12 | 0.99 | 2.19 | 0.021 | 0.95 | 7.19 | 0.000 |
| T118 | 0.98 | 4.27 | 0.006 | 0.95 | 7.46 | 0.000 |
| T34 | 0.89 | 29.69 | 0.000 | 0.95 | 8.19 | 0.000 |
| T417 | 0.96 | 10.83 | 0.000 | 0.98 | 1.38 | 0.015 |
| T1415 | 0.96 | 8.36 | 0.000 | 0.94 | 9.45 | 0.000 |
| T1516 | 0.93 | 19.31 | 0.000 | 0.87 | 23.28 | 0.000 |

variables. The ordination of females and males on the canonical factors I and II (Figs. 5a, 5b) showed well separation in SWK population from other populations based on the canonical factor II.

The results of the hierarchical cluster analysis showed two distinct groups from the five populations of both sexes (Figs. 6a, 6b). Group I included the SWK population, whereas group II included the SWS, SET, SEN, and SEC populations. This analysis showed that SWK samples constituted phenotypically a separate population, whereas the morphometric resemblance between SWS, SET, SEN, and SEC stocks were found to be high. The analysis of the present study revealed that the variables used in this study were capable of clearly differentiating SWK population from the other groups.

Discussion

This is the first report on the study of *A. alcocki* populations collected from five locations along the southeast and southwest coast of India. The results of the present study demonstrated that *A. alcocki* exhibited morphometric variability revealing two groups: SWK separately clustered in group I, whereas samples collected from other four locations clustered in group II.

MANCOVA showed a clear trend of sexual dimorphism in *A. alcocki*. In males, the rostrum was always noticeably shorter than in females, which helps in mating, swimming behavior (Burukovsky and Romensky 1972), sexual segregation, and feeding activity (Cartes and Sardà 1989; Kapiris and Thessalou-Legaki 2001; Chakraborty et al. 2015). A similar observation was made in the blue and red shrimp (*Aristeus antennatus* (Risso, 1816)) from the Mediterranean Sea (Sardà and Gordo 1986; Sardà and Demestre 1987; Kapiris et al. 2002). Females tend to have greater dimensions in their cephalic and abdominal segments, as well as in the rostral length. The lesser CV (<25%) for all the variables at the five locations was noted, indicating low variation in the intrapopulation from all the locations. It might be due to high inheritability and less influence of environmental parameters (both abiotic and biotic, e.g., availability of food) on the individuals that reduces the expression of significant differences within populations.

The PCA revealed that the phenotypical differences were relatively less between the different populations of SEC, SEN, SET, SWS, except for SWK, suggesting a close relationship that is mainly due to less variation in abdominal segments among these populations. The probable reasons hypothesized for this similarity was larval dispersal and long-distance migration for food, breeding, and current patterns from the Arabian Sea to the Bay of Bengal. SWK population was well separated due to the variability in the shorter abdominal characters (3–4 and 15–16) compared with the other populations. These differences are likely to manifest adaptations to environmental conditions, as such an exhaustive study is required to understand this intricacy. The geographic barrier and uncommon hydrological conditions (e.g., salinity, current flow, and temperature) play an important role in affecting gene flow between populations that is responsible for differentiating individuals (Macholán 2001; Brian et al. 2006; Ferrito et al. 2007; Chamarthi et al. 2008). Bagherian and Rahmani (2009) reported slender body shape in the Danube bleak (*Chalcalburnus*

chalcoides (Güldenstädt, 1772)) due to high water velocity. Also, the current pattern in the Bay of Bengal and the Arabian Sea was found to modify the morphometry of finletted mackerel scad (*Megalaspis cordyla* (Linnaeus, 1758)) (Sajina et al. 2011) and *Macrobrachium nipponense* (Chen et al. 2015).

The consistent level of classification was obtained by DFs owing to the environmentally induced morphological changes between shrimp populations. This demonstrated the efficiency of morphometric variables in distinguishing the populations. In fact, the strong differentiating power of the morphometric variables was found in the comparison between populations (Ferrito et al. 2007; Anastasiadou et al. 2009). The misclassification results of DFs clearly support that similarity between populations within and between coasts can be attributed to a common environment, genetic origin at an earlier period, and associated to genetic introgression of the shrimps particularly those in the transition zones. The present study revealed the close relationship between SET, SEN, SEC, and SWS populations. The highest similarity between SEN and SET specimens was supported by hierarchical cluster analysis (Fig. 6), which grouped the SWK population in group I and grouped the SEC, SEN, SET, and SWS populations in group II by sex, demonstrating the morphometric variability in *A. alcocki* populations. However, these results need to be verified through the molecular genetic studies.

Conclusion

The truss morphometric characters in *A. alcocki* can be efficiently used to discriminate populations as studied in other species found in freshwater and marine environments. The major discriminating variable that differentiated the populations into two groups was the abdominal measurements, suggesting a need to adopt separate management strategies for the resource sustainability and policy regulations. However, future studies based on genetic markers and biochemical methods can be used to validate the findings of this study.

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Table 5. The number of individual Arabian red shrimp (*Aristeus alcocki*) classified and the percentage in each group from the confusion matrix of the discriminant analysis.

| | | | SEC | SEN | SET | SWK | SWS | Total |
|-----------------|-----|------------|-------|-------|-------|-------|-------|--------|
| Female | | | | | | | | |
| Original | SEC | Count | 143 | 16 | 17 | 17 | 5 | 198 |
| | | Percentage | 72.22 | 8.08 | 8.59 | 8.59 | 2.53 | 100.00 |
| | SEN | Count | 24 | 118 | 13 | 18 | 21 | 194 |
| | | Percentage | 12.37 | 60.82 | 6.70 | 9.28 | 10.82 | 100.00 |
| | SET | Count | 15 | 7 | 174 | 3 | 8 | 207 |
| | | Percentage | 7.25 | 3.38 | 84.06 | 1.45 | 3.86 | 100.00 |
| | SWK | Count | 17 | 32 | 20 | 127 | 30 | 226 |
| | | Percentage | 7.52 | 14.16 | 8.85 | 56.19 | 13.27 | 100.00 |
| | SWS | Count | 6 | 24 | 10 | 24 | 151 | 215 |
| | | Percentage | 2.79 | 11.16 | 4.65 | 11.16 | 70.23 | 100.00 |
| Cross-validated | SEC | Count | 134 | 18 | 19 | 20 | 7 | 198 |
| | | Percentage | 67.68 | 9.09 | 9.60 | 10.1 | 3.54 | 100.00 |
| | SEN | Count | 24 | 110 | 15 | 22 | 23 | 194 |
| | | Percentage | 12.37 | 56.7 | 7.73 | 11.34 | 11.86 | 100.00 |
| | SET | Count | 16 | 7 | 173 | 3 | 8 | 207 |
| | | Percentage | 7.73 | 3.38 | 83.57 | 1.45 | 3.86 | 100.00 |
| | SWK | Count | 21 | 36 | 22 | 109 | 38 | 226 |
| | | Percentage | 9.29 | 15.93 | 9.73 | 48.23 | 16.81 | 100.00 |
| | SWS | Count | 6 | 27 | 12 | 26 | 144 | 215 |
| | | Percentage | 2.79 | 12.56 | 5.58 | 12.09 | 66.98 | 100.00 |
| Male | | | | | | | | |
| Original | SEC | Count | 45 | 24 | 29 | 28 | 10 | 136 |
| | | Percentage | 33.08 | 17.64 | 21.32 | 20.58 | 7.35 | 100.00 |
| | SEN | Count | 24 | 51 | 27 | 25 | 31 | 158 |
| | | Percentage | 15.2 | 32.8 | 17.1 | 15.8 | 19.6 | 100.00 |
| | SET | Count | 12 | 12 | 54 | 24 | 12 | 114 |
| | | Percentage | 10.5 | 10.5 | 47.4 | 21.1 | 10.5 | 100.00 |
| | SWS | Count | 41 | 17 | 44 | 54 | 36 | 192 |
| | | Percentage | 21.4 | 8.9 | 22.9 | 28.1 | 18.8 | 100.00 |
| | SWK | Count | 11 | 24 | 36 | 19 | 115 | 205 |
| | | Percentage | 5.4 | 11.7 | 17.6 | 9.3 | 56.1 | 100.00 |
| Cross-validated | SEC | Count | 39 | 11 | 36 | 25 | 25 | 136 |
| | | Percentage | 28.6 | 7.7 | 26.4 | 18.5 | 18.5 | 100.00 |
| | SEN | Count | 25 | 49 | 30 | 24 | 30 | 158 |
| | | Percentage | 15.8 | 30.8 | 19.1 | 15.2 | 19.1 | 100.00 |
| | SET | Count | 18 | 18 | 40 | 27 | 12 | 114 |
| | | Percentage | 15.8 | 15.8 | 34.2 | 23.7 | 10.5 | 100.00 |
| | SWS | Count | 41 | 17 | 44 | 54 | 36 | 192 |
| | | Percentage | 21.4 | 8.9 | 22.9 | 28.1 | 18.8 | 100.00 |
| | SWK | Count | 12 | 25 | 38 | 19 | 113 | 205 |
| | | Percentage | 5.9 | 12.2 | 18.5 | 9.3 | 54.1 | 100.00 |

Note: Locations are Chennai (SEC), Nagapatinam (SEN), Tuticorin (SET), Kalamuku (SWK), and Sakthikulangara (SWS).

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Fig. 5. Scatterplot of the first two discriminant factor from the discriminant functions analysis for (a) female and (b) male Arabian red shrimp (*Aristeus alcocki*). Color version online.

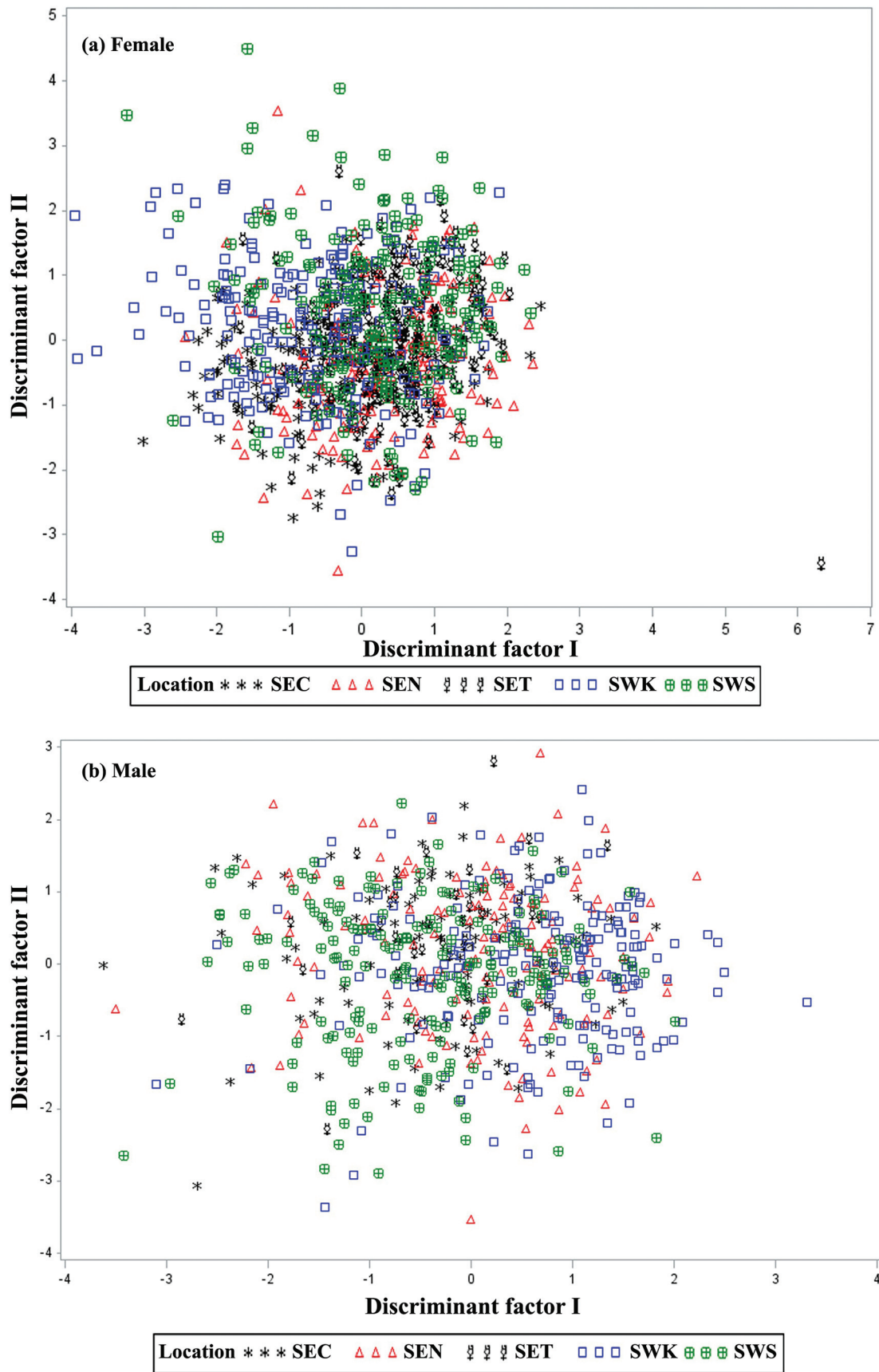
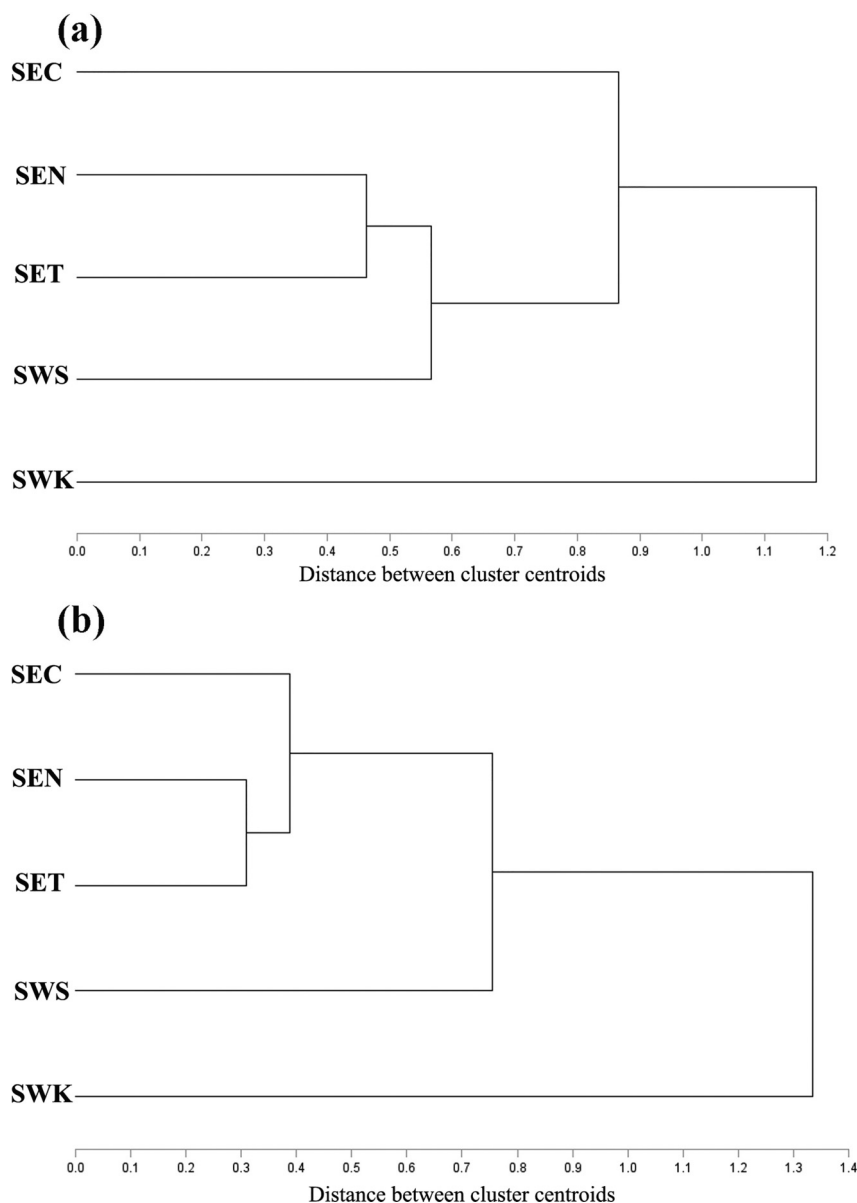


Fig. 6. Dendrogram showing the patterns of morphometric similarity among (a) female and (b) male Arabian red shrimp (*Aristeus alcocki*) from the five locations along the Indian coast.



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