

ALLOMETRIC GROWTH, HANDEDNESS, AND MORPHOLOGICAL
VARIATION IN *POTAMONAUTES WARRENI* (CALMAN, 1918)
(DECAPODA, BRACHYURA, POTAMONAUTIDAE) WITH A
REDESCRIPTION OF THE SPECIES

BY

S. R. DANIELS

Zoology Department, University of Stellenbosch, Private Bag X1, Matieland, 7602, South Africa

ABSTRACT

Some morphological relationships are investigated amongst three populations of *Potamonautes warreni* (Calman, 1918) and the species is redescribed. Differences between sexes as well as the growth of the carapace, chelipeds, and handedness are quantified. Sex ratios did not differ significantly from 1 : 1 among sites, and no differences in the carapace variables were evident between sexes. Both sexes were heterochelous, with the right chela usually being larger in males than in females. Sexual dimorphism is evident for the width of the abdominal somites. The functional significance of an enlarged right chela, and that of patterns of allometric growth are discussed. In addition, the structure of pleopod 1, mandibular palp, chelipeds, and the third maxilliped are described and illustrated. The distribution of *P. warreni* is re-examined and the species appears to be restricted to the Orange River System and its major tributaries such as the Vaal River in South Africa and Namibia.

RÉSUMÉ

Quelques relations morphologiques ont été étudiées chez trois populations de *Potamonautes warreni* (Calman, 1918) et l'espèce est redécrite. Des différences entre les sexes ainsi que la croissance de la carapace et des chélipèdes, la proportion de droitiers et gauchers, ont été quantifiés. Les sex ratios n'ont pas différé significativement de 1 : 1 sur les différents sites et aucune différence dans les variables de la carapace n'est évidente entre les sexes. Les deux sexes sont hétérochèles, avec la pince droite habituellement beaucoup plus grande chez les mâles que chez les femelles. Le dimorphisme sexuel est évident sur la largeur des somites abdominaux. La signification fonctionnelle d'une pince droite agrandie et celle des modèles de croissance allométrique sont discutées. De plus, la structure du pléopode 1, du palpe mandibulaire, des chélipèdes et les troisièmes maxillipèdes sont décrits et illustrés. La distribution de *P. warreni* est réexaminée et l'espèce apparaît comme limitée au système de la rivière Orange et de ses principaux tributaires comme la rivière Vaal en Afrique du Sud et Namibie.

INTRODUCTION

Freshwater crabs of the family Potamonautidae are common in freshwater systems throughout South Africa (Barnard, 1935, 1950; Bott, 1955). All the freshwater crabs described from this region belong to the genus *Potamonautes*, which is the most speciose of the genera in this family (Cumberlidge, 1999). Calman's (1918) original description of *P. warreni* was based on a female collected from Potchefstroom in Transvaal (now, North West Province), South Africa. The original description consisted of only a brief note on the carapace morphology, without any reference to the taxonomically-important gonopods, mandibular palp, maxillipeds, or chelipeds. As a result, the morphological features that distinguish *P. warreni* from other potamonautid river crabs remained unknown, warranting a more comprehensive description. More recently Daniels et al. (in prep.) noted that the dentition pattern commonly used to distinguish *P. warreni* from other freshwater crabs is highly variable among certain populations. These authors noted that the dentition pattern in this species may range from the presence of a single tooth to 5-10 well-defined teeth on the epibranchial corner of the carapace. Intraspecific patterns of morphological variation in this species have, however, not been investigated, and the degree of morphological variation among populations of *P. warreni* is consequently unknown. Few detailed morphometric studies of freshwater crabs exist. As in other heterochelous crabs, one claw is often enlarged, and generally thought to play a role in food acquisition and crushing. Yet, the functional significance of an enlarged cheliped in freshwater crabs has not been explored. In addition, the changes in overall body morphology have been poorly documented in this group. In the present study, morphological variation among populations of *P. warreni* is quantified and the diagnostic morphological features of this species are described and illustrated.

MATERIALS AND METHODS

A total of 249 *Potamonautes warreni* specimens of (118 males and 131 females) were collected from three geographical areas of the Orange River system. Group 1 is from the lower section near Upington, group 2 from Bothaville (Vaal River system), and group 3 from Bloemfontein (Vaal River system). The carapace and limbs were measured to the nearest 0.1 mm using digital calipers attached to a portable computer. The following measurements were taken: carapace length along the medial line (CL); carapace width at the widest part (CWW); distance between postfrontal crest and anterior margins of the carapace (PFCD); distance between medial margin of the orbits (ED); distance between the exorbital teeth (CWA); carapace height (depth) (CH); width of the fifth (AW5) and sixth (AW6)

abdominal somites: right and left cheliped propodus length (CLPL; CRPL) and width (CLPW; CRPW); length of propodus of pereopod 2 (P2PL); width of propodus of pereopod 2 (P2PW); length of merus of pereopod 2 (P2ML); width of merus of pereopod 2 (P2MW); length of propodus of pereopod 5 (P5PL); width of propodus of pereopod 5 (P5PW); length of merus of pereopod 5 (P5ML) and width of merus of pereopod 5 (P5MW).

The overall sex ratio (S_0) was determined according to the formula modified from Christiansen et al. (1990):

$$S_0 = (M_0 - F_0)/(M_0 + F_0)$$

where M_0 is the number of males in the sample and F_0 the number of females in the sample. The sex ratio of the crabs was analysed using a two-tailed χ^2 test to determine if there was a significant deviation from an expected 1 : 1 sex ratio. The effective population size (N_e) was determined according to the equation given in Li & Graur (1991):

$$N_e = 4N_m N_f / (N_m + N_f)$$

where N_m and N_f are the respective proportions of males and females in a population of N individuals. Student's t -test was used to test for significant differences between variables for males and females. Size distribution was plotted for both sexes using 5 mm carapace length intervals. Bivariate scatter plots were drawn for selected variables using the software package STATISTICA (Stat Soft Inc.).

The relative growth of crustaceans is generally in accordance with the simple allometry rule, $Y = aX^b$. Traditionally, allometric growth equations describe a power curve that can be linearized by logarithmic transformation to $\log Y = \log a + b \log X$. Despite arguments against log transformation of variables (Zar, 1968), this transformation has remained widely in use (Finney & Abele, 1981). The least square method of regression is also commonly used. However, this method has received criticism (Ricker, 1973, 1975), because it assumes that the independent variable is measured without error. The constant of allometry was determined for a selection of parameters by logarithmic transformation of the data and subsequent log-log regression equations. A Student's t -test was used to determine the allometric status of structures against the isometric standard slope. Analysis of covariance (ANCOVA) was performed on the log-transformed variables and used to test for significant differences between sexes. Scatterplots of the log transformed variables were drawn for females and males.

A Wild stereomicroscope was used to examine the right third maxilliped, mandible, and mandibular palp, and pleopods (gonopods) 1 and 2. In addition, the carapace outline as well as the dactylus and propodus of the left and right chelipeds of the *P. warreni* holotype, while the gonopods of a male specimen were examined.

Abbreviations: BMNH = British Museum (Natural History); SAM = South African Museum, Cape Town, South Africa.

TAXONOMY

Potamonautes warreni (Calman, 1918)

Material examined. — One female (holotype) Potchefstroom, Transvaal, coll. 1918 by E. Warren (BMNH, 1918.3.30.1); one male, Potchefstroom, Transvaal, coll. December 1917 by Cawston (BMNH, 1918.5.14.1); one male, one female Vioolsdrift; lower Orange river, South Africa (SAM A 41143), coll. 20 May 1992 by B. Stewart and L. Hoenson; four males and four females Gifkloof, Orange river, South Africa, coll. 21 March 1994 by R. Palmer and M. Scheepers (SAM A 41150); one female Fish River, near Seehiem, Namibia, coll. February 1969, coll(s). unknown (SAM A 41152); eight males, four females, Modder river, Glen, South Africa, coll. date unknown, coll. by R. Bigalke (SAM A 6358); three males, Zak River, Willinston, South Africa, coll. in 1939 by K. Barnard, (SAM A 8345); two females, one male Barberspan, South Africa, coll. 6 April 1928 by Hutchinson (SAM A 6899); one male, Kroonstad, unknown date, coll. by Brunette (SAM A 10885); one male Rehoboth, Namibia, date and coll. unknown (SAM A 10886); two males and two females, Glen, date unknown, coll. by R. Bigalke (SAM A 6366); three females, one male, Leber River near Gibeon, Namibia, January 1916, coll. by R. W. Tucker (SAM A 3953); one female, Warrendon, Vaal River system, coll. 1939 by Hess, Boonstra, and Thorne (SAM A 8393); one female, Barkely West, date unknown, coll. by T. Clayson (SAM A 10887).

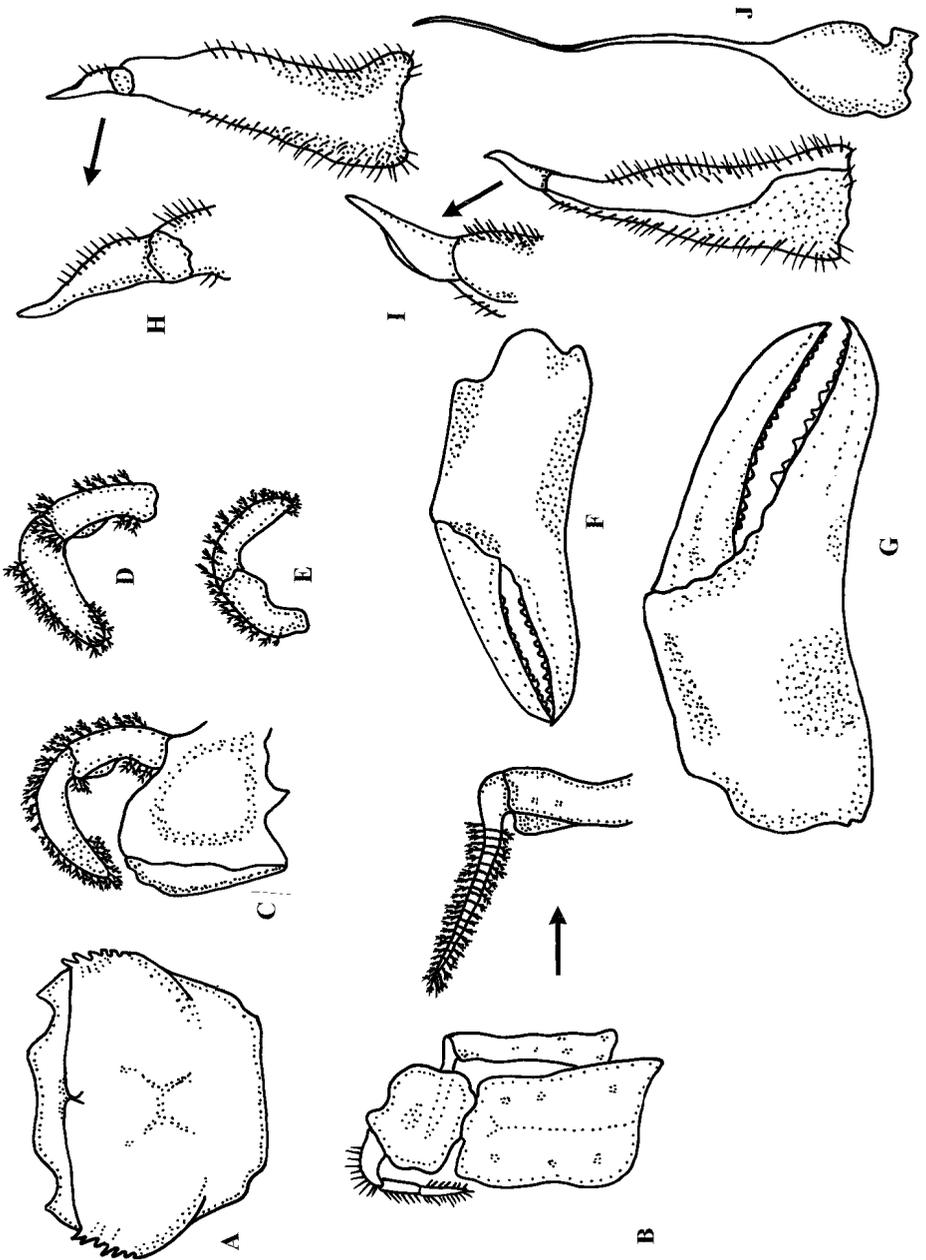
Type locality. — The holotype was originally described from near Potchefstroom, South Africa, from a tributary that flows into the Vaal River system, a major tributary of the Orange River system.

Distribution. — This species is restricted to the middle reaches of the Orange and Vaal River systems and their major tributaries in South Africa and southern part of Namibia.

Diagnosis. — The anterolateral margin of the carapace usually with a series of eight well-defined teeth; certain specimens possesses a series of 5 to 10 well-defined teeth, while a single epibranchial toothed form has also recently been discovered.

Description. — Carapace margins characterized by eight well-defined teeth, branchial region convex, maximum height and width at anterior third (ratio CH/CL = 0.49; CWW/CL = 1.36) (fig. 1A). Postfrontal crest complete, well-developed, granulated and with a groove at midpoint. Anterolateral margins between exorbital

Fig. 1. *Potamonautes warreni* (Calman, 1918). A-G, female holotype. A, carapace outline; B, right third maxilliped, posterior view; C, right mandible and mandibular palp, posterior view; D, right mandibular palp, posterior view; E, right mandibular palp, anterior view; F, left cheliped, dactylus and propodus; G, right cheliped, dactylus and propodus. H-J, male specimen from Gifkloof. H, left gonopod 1, anterior view; I, left gonopod 1, posterior view; J, right gonopod 2, anterior view. Scale bar 1 mm except for A, F, and G, where it is 10 mm.



and epibranchial tooth finely beaded. Urogastric and cardiac grooves moderately deep and well defined. Sternites 1 and 2 fused, no suture discernible, suture (first sternal groove) between sternites 2 and 3 complete. Second sternal groove between sternites 3 and 4 complete laterally, becoming shallow towards the middle and sloping sharply towards the abdominal area.

Mandibular palp composed of two segments; terminal segment undivided and with a dense tuft of setae on the posterior flange, margins very setose (fig. 1B). The third maxillipeds fill the entire buccal frame, except for a small, oval respiratory opening; flagellum present on exopod, ischium possessing a faint but distinct vertical groove (fig. 1C). Chelipeds unequal, dactylus of right and left chelipeds arched. Dactylus of right cheliped more mildly arched, and 1.08 times length of dactylus of left cheliped. Both dactyli armed with several small to medium sized cutting teeth. Right propodus swollen, 1.12 times longer and 1.29 times wider than propodus of left cheliped, with a series of well-defined teeth. Carpus of both chelipeds with two prominent teeth (fig. 1D). Antero-inferior margins of merus with prominent spine, postero-inferior margins without a spine. Pereopods broad ($P2ML/P2MW = 2.46$; $P5ML/P5MW = 2.51$) with P3 being the longest and P5 the shortest. Dactyli ending in sharp pointed margin with spine-like bristles. Terminal segment of first gonopod short, curving away from the midpoint, wider at the base when viewed posteriorly and ending in a pointed tip. Sub-terminal segment of gonopod 1 tapering distally, with a relatively smooth inner margin, posterior surface with longitudinal groove (fig. 1E). Gonopod 2 terminal segment filamentous and hollow, widest at its base and tapering off sharply inwards, to form an upright process that supports the terminal segment (fig. 1F).

Variation. — The dentition pattern on the anterolateral margin of the carapace may vary from a single tooth in certain specimens to a series of 5-10 well-defined teeth in others. Both sexes exhibit heterochely. Pubertal moult occurring approximately in size classes with CL = 25-33 mm.

Colouration. — Carapace and limbs chocolate brown when alive, fading to light brown when preserved in 70% ethanol.

Remarks. — Apart from *Potamonautes warreni*, six of the potamonautid river crab species described in South Africa so far have epibranchial teeth on the anterolateral margins of the carapace. In *P. dentatus* (Stewart, Coke & Cook, 1995) the anterolateral margin posterior to the epibranchial tooth contain 4 to 5 small but distinct, pointed teeth and the postfrontal crest contains an epibranchial sinus posterior to the exorbital tooth. The terminal segment of gonopod 1 also differs between *P. dentatus* and *P. warreni*. These two species are also geographically quite distinct, as *P. dentatus* is a KwaZulu-Natal endemic. The remaining toothed river crabs have a single epibranchial tooth. These include *P. bayonianus bayonianus* (Brito Capello, 1864), *P. b. dubius* (Brito Capello, 1873), *P. obesus calcaratus*

Bott, 1955, *P. parvispina* Stewart, 1997 and *P. unispinus* Stewart & Cook, 1998. The variation in dentition patterns observed in *P. warreni* may make it difficult to discern this species from *P. unispinus*. Where populations of the single-toothed *P. warreni* variety and *P. unispinus* occur in close proximity, they may be considered cryptic species (Daniels et al., in prep.). However, *P. unispinus* always possesses a single, well-defined epibranchial tooth at the epibranchial corner of the carapace and is genetically distinct from *P. warreni*. *P. parvispina* is a species with a small, but distinctive epibranchial tooth at the corner of the anterolateral margins of the carapace and is endemic to high mountain streams of the Western Cape. In *P. bayonianus bayonianus*, *P. b. dubius*, and *P. obesus calcaratus*, the postfrontal crest slopes backward to meet the epibranchial tooth, forming a distinct epibranchial sinus anterior to this tooth, and their distribution does not overlap with that of *P. warreni*.

RESULTS

Population structure

Group 1 was represented by 32 males and 45 females, which meant a sex ratio of 1 : 1.45 ($S_0 = -0.16$) and an effective population size, $N_e = 77$; group 2 was represented by 15 males and 13 females which meant a sex was ratio of 1 : 0.86 ($S_0 = 0.07$) and $N_e = 28$; group 3 was represented by 71 males and 73 females which meant a sex ratio of 1 : 1.02 ($S_0 = 0.02$) and $N_e = 144$. Overall, 118 males and 131 females were collected and the sex ratio thus was 1 : 1.11 ($S_0 = -0.05$) which did not deviate significantly ($\chi^2 = 0.04$; $df = 2$; $P > 0.05$) from a 1 : 1 ratio. The estimated effective population size ($N_e = 248$) was similar to the actual population size ($N = 249$) due to the high similarity in the overall sex ratio. No significant difference was seen ($P > 0.05$) in the frequency of the carapace length (CL) per size group between sexes (fig. 2). In addition, no significant differences ($P > 0.05$) in the mean size between males and females existed for the following variables: CL, CWW, PFCD, ED, CH, P2PL, P2PW, P2ML, P2MW, P5PL, P5PW, P5ML, P5MW, CLDL, CLPL, and CLPW. However, when the mean width of the fifth and six abdominal segments were compared between sexes, significant differences ($P < 0.001$) were obtain for both AW5 ($t = -12.61$) and AW6 ($t = -13.43$). Females had significant larger abdominal segments (mean AW5 = 23.37 mm; mean AW6 = 24.29 mm) than males (mean AW5 = 9.74 mm; mean AW6 = 11.93 mm). When the mean width of the right dactylus length (CRDL), and the right propodus length (CRPL), and right propodus width (CRPW) were compared between sexes, statistically significant ($P < 0.05$) results were obtained CRDL ($t = 2.42$); CRPL ($t = 2.29$) and CRPW ($t = 2.34$). Males

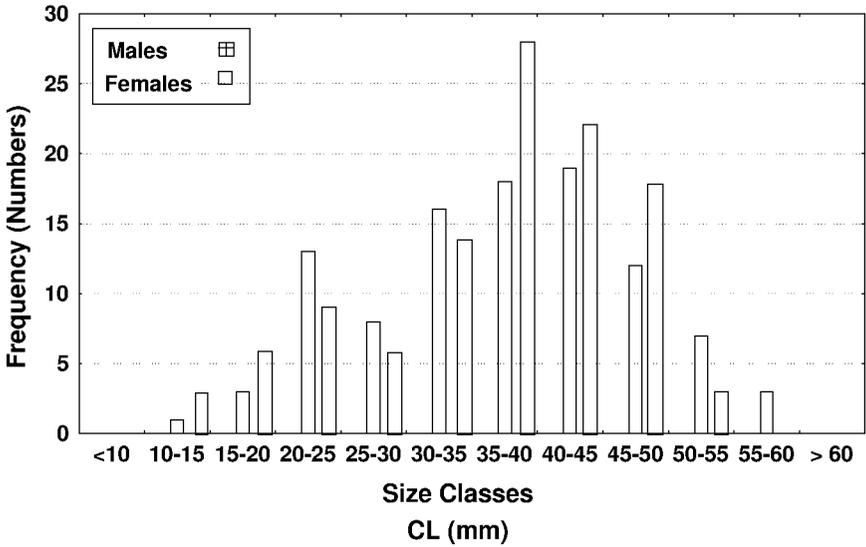


Fig. 2. *Potamonautes warreni* (Calman, 1918). Histogram of carapace length frequencies for females and males.

had larger right chelipeds (mean CRDL = 22.03 mm; mean CRPL = 36.07 mm, and CRPW = 14.34 mm) than females (mean CRDL = 19.68; CRPL = 32.42 mm and mean CRPW = 12.77 mm). A histogram of frequencies of observation for males and females per size class using CL (carapace length) showed no significant differences between size class frequencies for males and females ($P > 0.05$) and between sexes ($P > 0.05$).

Heterochely

Crabs that were missing either cheliped were excluded from the analyses. Of the 208 crabs examined, 17% (35 of 208) had the left propodus and dactylus enlarged (left handed) and 84% (175 of 208) had the right propodus and dactylus enlarged (right-handed). No homochelous individuals were found. Amongst the 100 females sampled, 21% were left-handed and 79% were right handed, while amongst the 105 males examined, 12% were left-handed and 88% were right-handed. No significant difference in handedness between sexes was observed ($\chi^2 = 3.80; P > 0.05$). Handedness between the sexes was compared relative to CL to assess if any changes occur as animals grow. For females with a CL < 30 mm, 68% (17 of 25) were right handed, while 80% (20 of 25) males in the same size class were right handed. In the range 30 to 40 mm CL, 77% (34 of 44) females were right handed, while 95% (38 of 40) of males were right handed. Of the crabs with a CL > 40 mm, 86% of females (24 of 28) and 83% (33 of 40) of males were right handed. Scatterplots of the width of the left and right propodus against their lengths

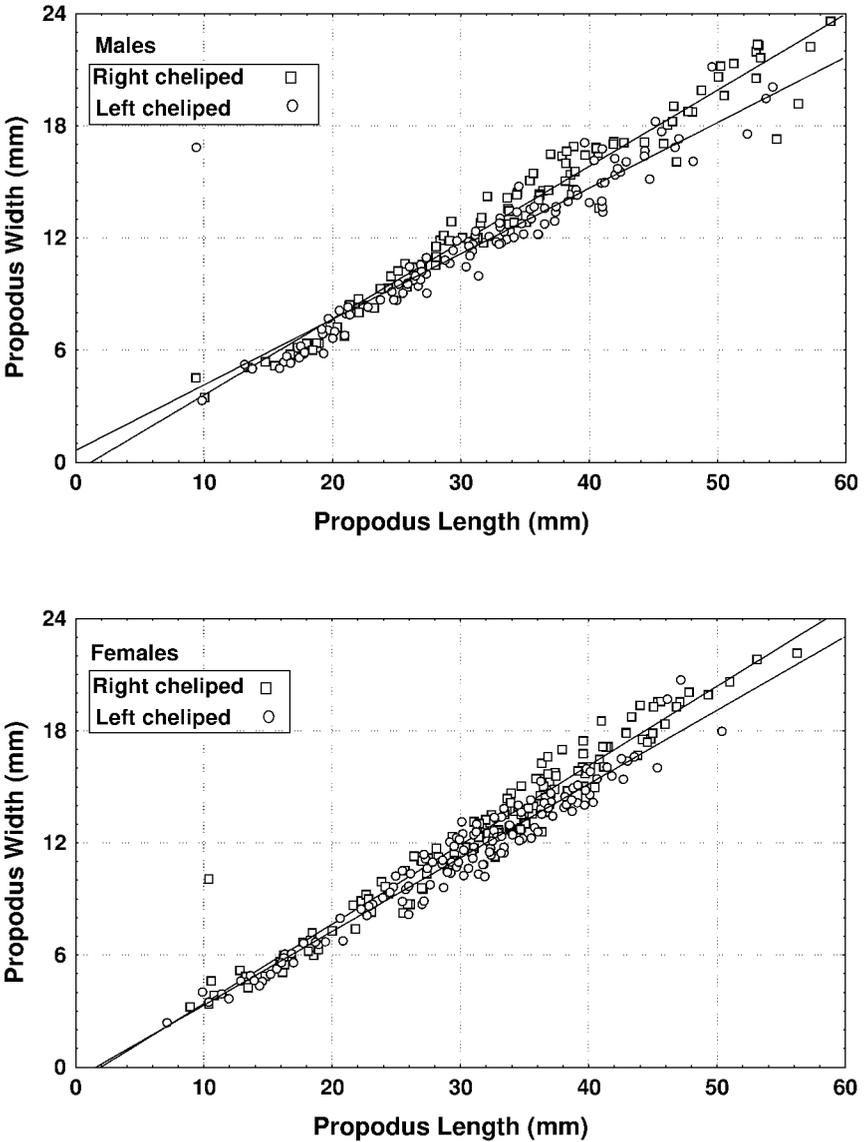


Fig. 3. *Potamonautes warreni* (Calman, 1918). Plot of propodus width against propodus length of the left and right cheliped for male and female specimens.

for both sexes show that the right chelae in males and females grow proportionally larger than the left chelae (fig. 3). When the slope of the regression was compared between the right and left propodus length relative to CL within sexes, significant differences between the right and left propodus was evident for both females ($F = 3.99; P < 0.05$), and males ($F = 4.69; P < 0.05$). In addition, when the regression for the slope of right propodus was compared between sexes statistically significant

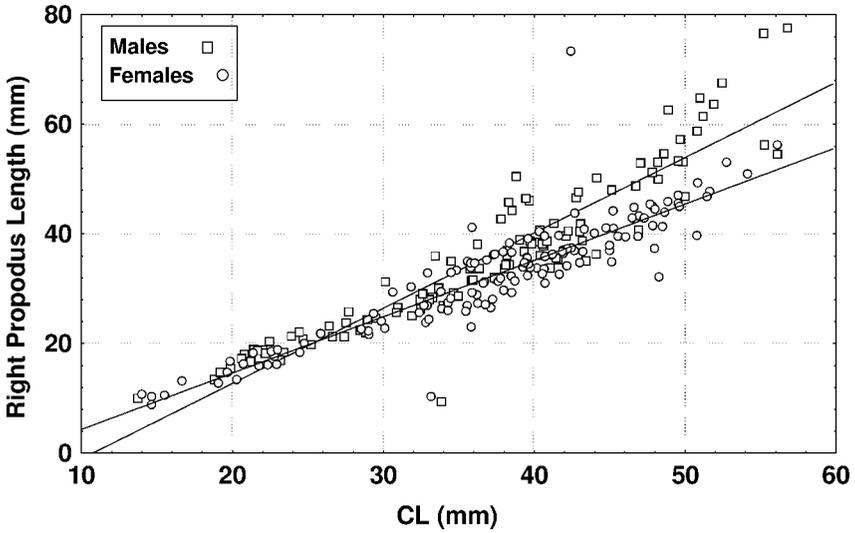


Fig. 4. *Potamonautes warreni* (Calman, 1918). Plot of the right propodus length against carapace length (CL) for males and females.

($F = 37.05$; $P < 0.001$) results were obtained, with males growing larger in the right propodus length relative to CL (fig. 4).

Allometry

Table I provides a summary of the allometric statistics for *P. warreni*. The wet weight (WW) of males and females showed positive allometric growth. This demonstrates that the weight of the animal increases as it matures. There was a significant difference in the slope ($F = 7.18$; $P < 0.01$) between log WW and log CL for males and females, due to the small but significant difference in the slope between the two regression lines. The regression of log CWW against log CL showed positive allometry in males, but was negative in females, the slopes between these two variables being significantly different ($F = 17.21$, $P < 0.001$). Both log CWA and log PFCD showed negative allometry for both sexes. Log CWA was significantly different between the two sexes, ($F = 5.78$; $P < 0.05$), for PFCD however no significant differences in the slopes were detected. Log ED against log CL showed negative allometry in males but was positive allometry in females. No significant difference in slope was evident between males and females for this character. Sexual dimorphism in the both the fifth (AW5) and sixth (AW6) abdominal segment width against CL was evident between sexes. The regression for the log AW5 for males showed negative allometry, while in females it showed positive allometry, and a significant difference in slope was evident between sexes ($F = 8.41$; $P < 0.01$). Log of AW6 against CL was slightly positive in males,

TABLE I

Regression analyses of morphometric data for *Potamonautes warreni* (Calman, 1918); M = males; F = females; log indicates logarithms of base 10

X	Y	Sex	Least Square Regression Log Y = log a + b log X	r	t(b - 1) ⁽¹⁾
CL	WW	M	Log WW = -3.441 + 3.187(Log CL)	0.995	3.181
		F	Log WW = -3.515 + 3.226(Log CL)	0.995	3.225*
CL	CWW	M	Log CWW = 0.102 + 1.021(Log CL)	0.995	1.021*
		F	Log CWW = 0.116 + 1.008(Log CL)	0.996	0.674*
CL	CWA	M	Log CWA = 0.242 + 0.832(Log CL)	0.993	0.832*
		F	Log CWA = 0.229 + 0.838(Log CL)	0.993	0.838*
CL	PFCD	M	Log PFCD = -0.809 + 0.995(Log CL)	0.973	0.995*
		F	Log PFCD = -0.721 + 0.935(Log CL)	0.973	0.934*
CL	CH	M	Log CH = -0.578 + 1.199(Log CL)	0.966	1.198*
		F	Log CH = -0.619 + 1.224(Log CL)	0.966	1.224*
CL	ED	M	Log ED = -0.224 + 0.982(Log CL)	0.744	0.982*
		F	Log ED = -0.368 + 1.074(Log CL)	0.744	1.072*
CL	AW5	M	Log AW5 = -0.4545 + 0.975(Log CL)	0.975	0.975*
		F	Log AW5 = -1.460 + 1.798(Log CL)	0.959	1.797*
CL	AW6	M	Log AW6 = -0.644 + 1.039(Log CL)	0.967	1.038*
		F	Log AW6 = -1.832 + 2.018(Log CL)	0.955	2.018*
CL	LCPL	M	Log LCPL = -0.464 + 1.249(Log CL)	0.921	1.249*
		F	Log LCPL = -0.334 + 1.153(Log CL)	0.977	1.153*
CL	RCPL	M	Log RCPL = -0.603 + 1.369(Log CL)	0.929	1.398*
		F	Log RCPL = -0.410 + 1.217(Log CL)	0.932	1.217*
P2PL	P2PW	M	Log P2PW = -0.280 + 0.985(Log P2PL)	0.952	0.984*
		F	Log P2PW = -0.295 + 1.009(Log P2PL)	0.960	1.009*
P2ML	P2MW	M	Log P2MW = -0.272 + 0.907(Log P2ML)	0.940	0.906*
		F	Log P2MW = -0.382 + 1.006(Log P2ML)	0.950	1.006*
P5PL	P5PW	M	Log P5PL = -0.200 + 0.906(Log P5PW)	0.922	0.906*
		F	Log P5PL = -0.156 + 0.867(Log P5PW)	0.954	0.867*
P5ML	P5MW	M	Log P5MW = -0.375 + 0.971(Log P5ML)	0.945	0.971*
		F	Log P5MW = -0.392 + 0.991(Log P5ML)	0.950	0.990*

t-test for b = 1.
P < 0.05 marked with*.

and markedly curvilinear, exhibiting positive allometric growth. The regression between these two sexes was significantly different (F = 901; P < 0.001).

When both the left and right cheliped propodus length (LCPL and RCPL) were compared to CL, positive allometry was evident for both sexes, with males showing slightly higher positive values. When the left propodus length against CL was compared between sexes statistically significant results were detected (F = 8.97; P < 0.01), with males growing slightly faster than females (fig. 5). When the right propodus length against CL was compared between sexes, males grew proportionally larger than females (fig. 6). The slope of this regression between

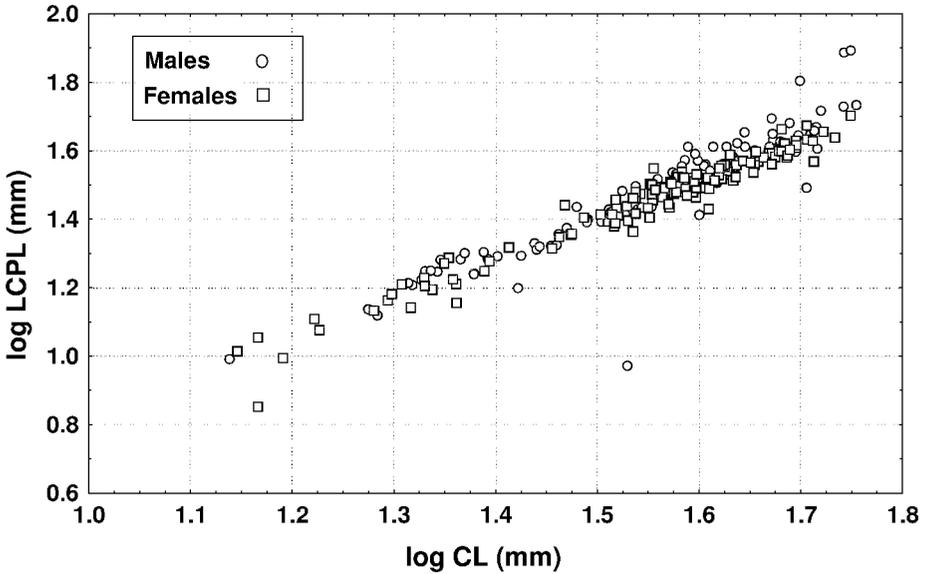


Fig. 5. Plot of log the left chela propodus length (LCPL) against log carapace length (CL) for male and female *Potamonautes warreni* (Calman, 1918) specimens.

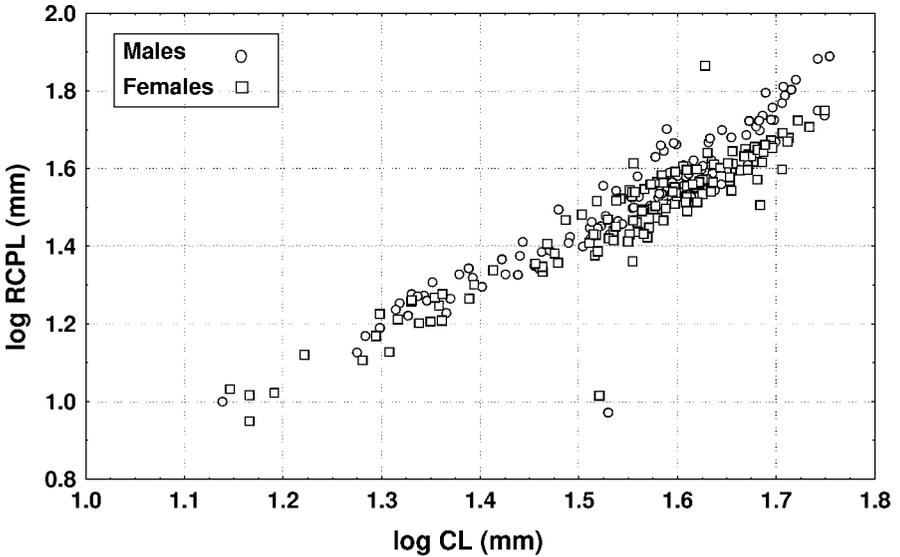


Fig. 6. Plot of log the right chela propodus length (RCPL) against log carapace length (CL) for male and female *Potamonautes warreni* (Calman, 1918) specimens.

the sexes were statistically significant ($F = 26.95$; $P < 0.001$). Log P2PW against P2PL showed negative allometry for males, but was close to isometry in females, while statistically significant results were obtained between sexes ($F = 4.04$;

$P < 0.05$). The regression of P2MW against P2ML showed negative allometry in males, but were close to isometry in females, however no significant differences in the slopes were obtained between sexes. Negative allometry was recorded for both sexes for all the measurements of the fifth pereopod, with no significant differences for P5PL against P5PW and for P5ML against P5MW.

DISCUSSION

The sex ratio within the three population groups was close to 1 : 1. A number of researchers (Raubemheimer, 1986; Cornew, 1990; Mayfield, 1993) reported that female freshwater crabs were the more abundant sex. In this study 52% of the total number of crabs caught was female. Males and females were generally of similar size. Sexual dimorphism was clearly evident between the abdominal segments, and to a lesser degree in the chelipeds of *Potamonautes warreni*.

The growth of the abdominal width in *P. warreni* showed strong positive allometry and was sexually dimorphic. Hartnoll (1982) described such a general pattern of growth in crustaceans. A number of subsequent studies on sexual dimorphism in decapod crustaceans have reported similar results. The growth in the male abdomen approaches isometry, while that in females shows strong positive allometry. The sexual dimorphism of the abdomen is thought to be related to the differences in the function of the male gonopods and female pleopods. In male crabs the gonopods need not increase in size faster than the carapace. Finney & Abele (1981) are of the opinion that this does not have any reproductive advantages. In females, however, the marked increase in abdomen size would increase the area for the fixation of eggs on the setose pleopods and thus act as an incubation chamber for the developing eggs.

Potamonautes warreni is heterochelous, with right handedness in both sexes being the most dominant. Handedness among freshwater crabs in the genus *Potamonautes* (Potamonautidae) is relatively well documented, yet has remained poorly studied (table II). Heterochely showed no sexual dimorphism, as it is equally expressed in both males and females. Similar patterns have also been recorded for freshwater crab of the family Potamidae. For example, Gherardi & Micheli (1989) reported that right handedness in the freshwater crab *Potamon potamios palaestinense* Bott, 1967 is dominant. Hartnoll (1982) stated that in the majority of heterochelous decapod species "there is no preference for handedness of the large chela" and "this must be regarded as the prevalent situation, although isolated examples of handedness are recorded". This dominance in handedness is not restricted to freshwater crabs, but has also been reported amongst marine taxa

TABLE II

A summary of handedness in potamonautid crabs (*Potamonautes* Mac Leay, 1838), expressed as a percentage for the sex examined, where *N* is the total number of individuals examined per species. The missing percentage regards homochelous crabs. R = right-handed, L = left-handed. Unless otherwise stated, data have been taken from descriptive papers

Species	Females		Males		<i>N</i>	Reference
	%R	%L	%R	%L		
<i>P. bayonianus bayonianus</i> (Brito-Capello, 1873)	77	23	92	8	61	Unpubl. data
<i>P. brincki</i> Stewart, 1997	58	42	89	11	61	Unpubl. data
<i>P. dentatus</i> Stewart et al., 1995	82	18	75	25	39	
<i>P. depressus depressus</i> (Krauss, 1843)	94	6	94	6	272	Unpubl. data
<i>P. clarus</i> Gouws, 1999	67	7	85	6	75	
<i>P. granularis</i> Daniels, et al., 1998	82	15	73	24	113	
<i>P. lividus</i> Gouws, 1999	74	13	79	8	147	
<i>P. obesus obesus</i> (A. Milne-Edwards, 1868)	87	13	88	12	33	Unpubl. data
<i>P. parvispina</i> Stewart, 1997	61	37	88	12	249	Unpubl. data
<i>P. perlatus</i> (H. Milne Edwards, 1837)	79	21	76	24	374	Siegfried (1972)
<i>P. sidneyi</i> (Rathbun, 1904)	71	29	71	29	1432	Raubenheimer (1986)
<i>P. unispinus</i> Stewart & Cook, 1998	85	15	79	21	274	Unpubl. data
<i>P. warreni</i> (Calman, 1918)	77	23	13	87	201	Present study

in the Calappidae (Ng & Tan, 1985); Portunidae (Hamilton et al., 1976; Abby-Kalio & Warner, 1989; Chu, 1999); Xanthidae (Cheung, 1976); and in the Belliidae (Abby-Kalio & Warner, 1989).

Most of the studies conducted on handedness in marine crabs have concentrated on the crushing of shells by marine crabs. However, feeding studies in freshwater crabs indicate that these crabs are detritivores or feeding generalists (Hill & O'Keeffe, 1992). These authors showed that juvenile crabs (CL = 21-30 mm) of the Cape River crab, *Potamonautes perlatus* (H. Milne Edwards, 1837) ate a significantly higher percentage of aquatic invertebrates than did adults, however, as the crab grows (61-70 and 71-80 mm) vascular plant material becomes more abundant. Raubenheimer (1986) reported a similar trend for *P. sidneyi* (Rathbun,

1905). In freshwater crabs, the enlarged right cheliped may play a less significant role during feeding as no crushing is required for effective feeding (pers. obs.). Cornew (1990) showed an exponential increase in size of the major chelae of *P. perlatus* and suggests that claw dimorphism is related to something other than feeding.

Stein (1976) hypothesized that sexual selection is probably the major driving force in the evolution of large chelae. The larger chela in *P. warreni* may play a role in sexual signalling (pre-mating behavior such as courtship), reproduction (in fighting for females) and in defense (of food, mates or territories). Males with larger chela may have some selective advantage over males with smaller chela, and may thus be more successful at feeding, reproducing and at defending home territories (burrows). Stein (1976) showed that in the crayfish, *Orconectes propinquus* (Girard, 1852), males with larger claws were able to mate with larger females, and that a larger chela determines their superiority during fighting prior to copulation. *Potamonautes warreni* have been observed to burrow extensively (pers. obs.). Individuals with larger claws may thus be more successful at defending their burrows and territories, assuming freshwater crabs are territorial. Barbaresi et al. (1997) have observed that in the freshwater crab *Potamon fluviatile* (Herbst, 1785) animals occupy a different refuge when they return from their nocturnal feeding. These authors did not report any fights for burrows. However, aggressive behaviour is likely to be influenced by densities.

The large claw of females may act as a signal of sexual vitality and reproductive vigour to males. Freshwater crabs are well known to be direct developers with long incubation periods (for up to three months in *P. sidneyi*) and extensive maternal care (Raubenheimer, 1986). Females with larger claws may thus be more successful at mating and have a better chance of defending the developing young against attack from other crabs. More recently, Liu & Li (2000) showed that in the freshwater crab, *Candidiopotamon rathbuni* (De Man, 1914) post-hatching maternal care occurs, for up to two weeks. Ovigerous females of this species have been found to prefer to stay on land, to avoid injury due to flash floods. This behavioural adaptation in females freshwater crabs may have led to the evolution of large chelipeds that can be used to defend the developing young against predators and thus enhance the survival rate of juveniles.

Abellò et al. (1990) reported that isometric growth in the chela of swimming crab would be advantageous, as they would use less energy during swimming. The high positive allometry in both chelae can be related to the fact that freshwater crabs are benthic species, with a reduced swimming capacity.

Clayton (1990) noted that caution should be exercised when interpreting patterns of an allometric growth, as the tests that are used to determine if a set of variables exhibit isometric or allometric growth are designed to detect differences, not

the absence of differences. He warns that the functional significance of allometric growth has received only superficial treatment and that more care needs to be taken when explaining such biological phenomena. Cumberlidge (1999) is of the opinion that the variation in morphometric relationships is correlated with the habitat and lifestyle of freshwater crabs. According to Cumberlidge (1999), most of these changes in the morphology of freshwater crabs is to accommodate changes in the respiratory system. More research on allometric relationships amongst the South African freshwater crab fauna needs to be undertaken in order to corroborate such conclusions.

ACKNOWLEDGMENTS

I wish to thank Dr. Barbara Cook for foresight and encouragement during this study and Gavin Gouws for reading a draft of the manuscript. The National Research Foundation (NRF) and WWF South Africa are thanked for financial assistance. Liz Hoenson of the South African Museum is thanked for her helpful assistance. Miranda Lowe and Paul Clark of the British Museum of Natural History are thanked for allowing me to examine the holotype of *P. warreni*.

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First received 18 April 2000.

Final version accepted 12 September 2000.