Allometry and sexual dimorphism in the chela shape in the squat lobster *Munida rugosa*

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ABSTRACT: Sexual selection generally promotes the development of ornaments or weapons that improve an individual's chance of mating. The squat lobster *Munida rugosa* exhibits a range of variation in chela (claw) morphology, with some individuals having a particular arched chela morphology, apparently specialized as a weapon. Geometric morphometric techniques were used to compare chela morphology across a wide size range and between sexes. The most fully developed arched morphology only occurred in large males, although not all large males possessed an arched claw, while smaller males retained straight, slender claws. Some large females exhibited a reduced version of the arched morphology. The pattern of occurrence of the arched morphology suggests that it is, or has been, subject to sexual selection through male–male competition for mates.

KEY WORDS: *Munida rugosa* · Secondary sexual dimorphism · Chela shape · Sexual selection · Weapon · Geometric morphometric

INTRODUCTION

Evolution of morphology in animals can be directed by natural selection (Darwin 1859) and sexual selection (Darwin 1871). In a given species, pressures directed by natural selection favour morphologies that facilitate individual survival, growth and reproduction, leading to an increase in fitness in a given environment (the 'struggle for life', Darwin 1859). Pressures associated with sexual selection directly promote traits that facilitate success in mating either through intrasexual competition or mate choice (Kodric-Brown & Brown 1984). For example, across a wide range of taxa, weapons in males appear to have evolved through intrasexual selection (Emlen 2008). There are costs in developing such traits and only an increase in overall fitness can explain the evolution of a costly morphology (Bonduriansky & Day 2003, Emlen 2008). In general, the magnitude of a sexually selected trait such as a weapon is related to the quality of the individual, in terms of competitive ability (i.e. honest signalling,

Emlen 2008). Growth of such structures is often positively allometric, with weapons or ornaments becoming disproportionately developed in larger or older individuals (Petrie 1988, 1992, Simmons & Tomkins 1996, Knell & Fortey 2005, Emlen 2008), but allometry is neither necessary nor sufficient evidence for a sexually selected trait (Bonduriansky 2007). Evolution of allometry in such traits requires individual condition to be related to body size and the selected trait to be under directional selective pressure (Bonduriansky 2007). Emlen (2008) also noted that the morphology of all exaggerated male weapons vary greatly among individuals within populations. Consequently, based on empirical evidence (Petrie 1988, 1992, Simmons & Tomkins 1996, Knell & Fortey 2005, Emlen 2008), a trait acting as a weapon has a good chance of being a sexually dimorphic structure that is positively allometric and variable in shape or size in mature males.

In decapod crustaceans, the first pereiopod generally bears a chela (claw) formed by a modification of the dactylus and propodus and is known as a cheliped.

This appendage is typically used in feeding, defence against predators and agonistic behaviour, and has therefore been considered a multifunctional organ (Brown et al. 1979, Lee 1995). When this appendage is used as a weapon, it is to be expected that dominant individuals will have larger or stronger chelipeds and this has indeed been found in the few studies in which this has been investigated (Barki et al. 1997, Sneddon et al. 1997, 2000). Furthermore, allometric growth and sexual dimorphism in cheliped size is common in decapods, with males having larger chelipeds than females (Hartnoll 1974).

The squat lobster *Munida rugosa* has a peculiar chela morphology that can fulfil various functions, such as fighting and feeding (Claverie & Smith 2007). There is sexual dimorphism in cheliped length (Claverie & Smith 2009) but, in addition, some males develop a modified form (arched morphology, Fig. 1A) that is stronger and appears to be adapted to inflict puncture wounds on other males during intense agonistic interactions (Claverie & Smith 2007). Moreover, field obser-

vations indicate that large males chase other males away from their vicinity and they are often surrounded by females (T. Claverie pers. obs.). A closely related species, *M. sarsi*, has a similar claw morphology; claws are used in agonistic encounters involving cheliped grabbing (Berrill 1970) and male *M. sarsi* use chelipeds to restrain females during mating (Pothanikat 2005). Assuming that the arched chelae are better weapons than straight chelae (Claverie & Smith 2007) and that agonistic interactions between males are primarily for access to females (intrasexual selection), we predict that arching is a sexually dimorphic feature with a high degree of variation in mature males. However, it is not clear to what extent the amplitude of arching is correlated to cheliped size, nor the relative contributions of these attributes to agonistic success.

Left–right asymmetry in chela shape (heterochely) is frequently observed in decapods (Crane 1975, Lee 1995, Mariappan et al. 2000) and is generally associated with adaptations for capture and handling of prey (Govind & Pearce 1989, Lee 1995) but, as in the case
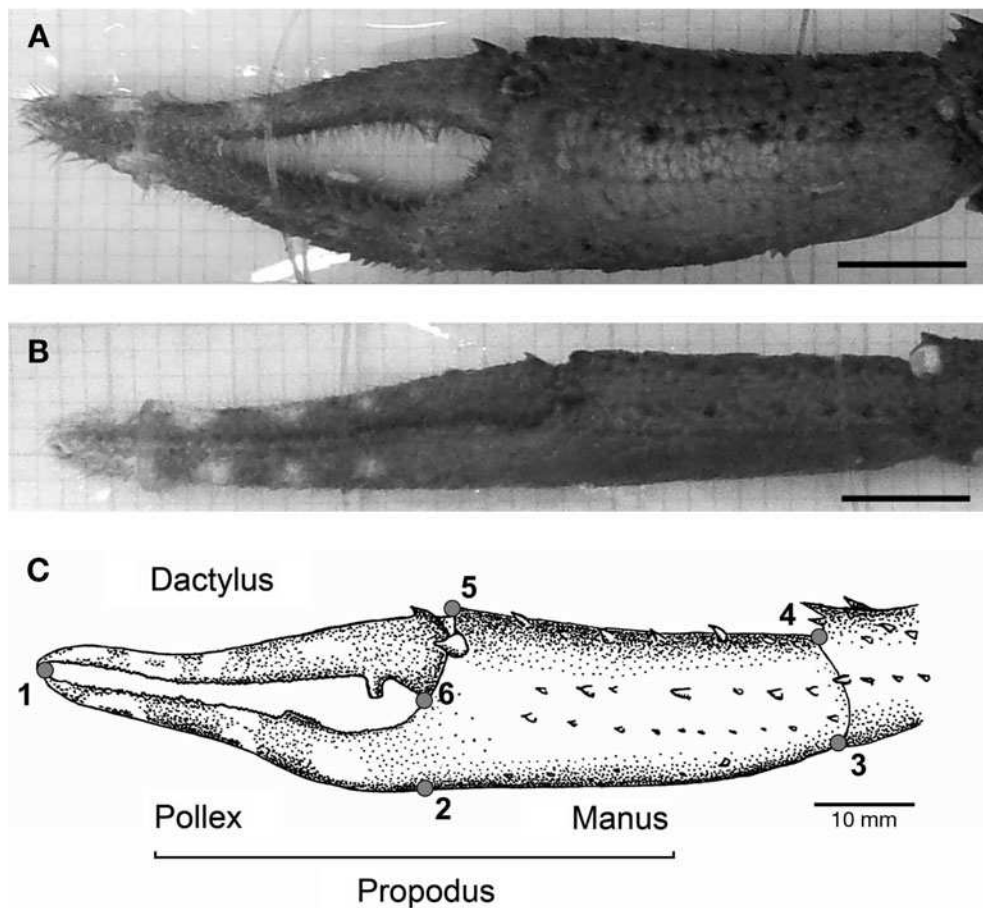

Fig. 1. *Munida rugosa*. Different chela morphologies encountered in *Munida rugosa*, (A) arched and (B) straight, and (C) associated landmarks (1 to 6) whose coordinates were recorded from each chela for analysis of shape. Drawing modified from Claverie & Smith (2007)

of fiddler crabs, can also be adapted for agonistic behaviour and female attraction (Crane 1975, Levinton et al. 1995). Heterochely is generally triggered at an early stage in development, either because of the loss of one cheliped or differential usage between left and right chelae (Govind & Pearce 1989, Young et al. 1994, Goldstein & Tlusty 2003). Moreover, in heterochelous species, homochelous specimens are rare (if they exist naturally at all) and occur generally only when animals are raised in artificial situations, such as in isolation (Govind & Pearce 1989, Goldstein & Tlusty 2003). Consequently, heterochely can be an important morphological feature in crustaceans arising from an underlying ontogenic mechanisms linked with the functional significance of particular chelae designs.

Claverie & Smith (2007) argued that the arched morphology of *Munida rugosa* was better adapted to inflict injuries while retaining functionality for feeding (probably with the same effectiveness). Also, *M. rugosa* was observed to use both chelipeds during agonistic interactions (T. Claverie pers. obs.), as described for *M. sarsi* (Berrill 1970). Consequently, it is unlikely that selective pressures that normally act on decapod cheliped asymmetry (i.e. feeding ecology in durophagous crabs or agonistic interaction in fiddler crabs) would promote asymmetry in *M. rugosa*, since feeding and fighting could be performed with the arched design (Claverie & Smith 2007). We therefore predict that there should be no consistent chela shape asymmetry in this species.

To investigate whether patterns in chela arching in *Munida rugosa* follow our predictions and are consistent with sexually selected traits, chela shape, symmetry and allometry were analysed in relation to body size, sex and cheliped size.

MATERIALS AND METHODS

Collection of specimens. *Munida rugosa* were collected in the Clyde Sea area, Scotland, by beam-trawling (2 m beam trawl, 50 mm mesh) on a gravel–mud sea bed at water depths ranging from 35 to 40 m during spring 2005. Individuals with both chelipeds intact (no injury or mark of any previous moulting problem) were returned alive to the laboratory for examination. The carapace length (CL, from the base of the rostral spine to the posterior margin of the carapace at the mid-line) of each individual was measured with vernier callipers to 0.1 mm accuracy. A total of 265 animals were measured (130 male and 84 female), ranging in CL from 13 to 38 mm.

A digital photograph of the lateral surface of each cheliped was taken. Chelipeds were held extended and horizontal for the photograph using a custom-made jig. A small translucent elastic band was used to hold the chela closed. Photographs were taken with a digital camera (Fujifilm Finepix F810 in a WP-FX701 waterproof housing) in macro mode and mounted on the jig 25 cm vertically above the cheliped to standardize the picture and minimize distortion. The prodopus and dactylus are only slightly curved laterally, so analysis of chela shape in 2 dimensions was considered adequate. Cheliped length of each animal was measured from the photographs using the image analysis software SigmaScan Pro 5.0.0.

Variation in chela morphology. Geometric morphometric methods (Zelditch et al. 2004) were used to investigate variation in chela shape. Images of the right cheliped were reflected (in Adobe Photoshop Elements 2.0) to appear like the left cheliped to minimize digitising error (Rosenberg 2002) and to simplify symmetry analysis (Klingenberg & McIntyre 1998, Klingenberg et al. 2002). 'Landmark' coordinates were recorded (pixel coordinates were subsequently scaled to distances in mm) from the image with TpsDig2 (Rohlf 2005a). The 6 landmarks used were the same as those used previously (Claverie & Smith 2007; Fig. 1C). They were: (1) the tip of the pollex; (2) the junction between the pollex and the manus on the inferior margin of the propodus; (3,4) the lower and upper attachment points of the carpus with the propodus; and (5,6) the upper and lower points marking the junction of the dactylus with the propodus.

A principal components analysis (PCA) was performed on the landmark coordinates, after procrustes superimposition using the TpsRelw program (Rohlf 2005b), to examine major trends of chela shape variation.

Relationship between chela shape and body size. Relationships between chela shape and CL, and between chela shape and cheliped length, were tested with multivariate regression. Separate analyses were performed for the left and right chelae for males and females. Significance was tested using the Wilks' lambda determinant ratio (Zelditch et al. 2004).

Variability of chela morphology in relation to CL was quantified for males and females. The first principal component (PC1) was plotted against CL. A running mean of PC1 was calculated on a 3 mm CL window across the full range of CL. Squared residual variation (standardised to CL) of the PC1 value from the running mean was then calculated and the cumulative squared standardised residuals were plotted against CL. Residuals were divided by associated CL to represent a standardized measure of the shape variation (scaled to the size of animal) in order to correct for the amplitude of shape difference due to animal size. A deviation from a constant increase of cumulative standardised squared residual (greater or lesser rate of increase) would indicate variation in variability of chela shape

for a given CL. PC1 was used to describe chela shape because it explained most of the variability (Claverie & Smith 2007).

Chela shape difference between sexes and appendage side was tested using a 2-way permuted multivariate analysis of covariance (PERMANCOVA, 1000 permutations) on shape variables (partial procrustes distances) with sex and side as factors and cheliped length as the covariate. In order to exclude any bias from the analysis, only specimens of each sex within the same size range were included (cheliped length 54 to 114 mm). The program Manovaboard 6.4 (Sheets 2006) was used for this analysis. This program uses a permutation test to determine significance (based on the sum of squared partial procrustes distances — shape variables — between and within groups) rather than a conventional MANCOVA procedure (i.e. using an *F*-test of a variance ratio).

Assessment of cheliped asymmetry. In addition to the PERMANCOVA described above, the correlations between chela shape difference (left versus right chelae) and cheliped length difference (left versus right cheliped), as well as the correlation between chela shape difference and CL, were tested with Spearman's rank correlation in order to assess whether chela shape asymmetry was related to body size or cheliped length asymmetry (i.e. regeneration of one of the chelipeds, Claverie & Smith 2009). Shape differences were quantified using procrustes distance between left and right chelae (calculations were performed using the software Coordgen from the IMP series, Zelditch et al. 2004).

RESULTS

Variation in chela morphology

The first 3 principal components of the PCA together accounted for 94.7% of the shape variation (76.48% for PC1, 13.78% for PC2 and 4.44% for PC3). Examination of the thin plate spline (TPS) representations of extreme forms on each axis indicates that the first axis mainly represents an inverse relationship between pollex (distal extension of the propodus) length and both manus (proximal part of the propodus) length and propodus height (Fig. 2a). Data points for females are mainly clustered on the negative part of the first axis, associated

with narrower chelae, and only males reach high values on the first axis, associated with high propodus, long manus and short pollex. The second axis represents the degree of bending of the chela in the vertical plane, with an inflection point at the base of the pollex (Fig. 2a). The third axis represents variation in chela height (Fig. 2b).

Relationship between chela shape and body size

There was a significant relationship between chela shape and CL for both left (Wilks' λ = 0.35, p < 0.001) and right chelae (Wilks' λ = 0.39, p < 0.001) in males;
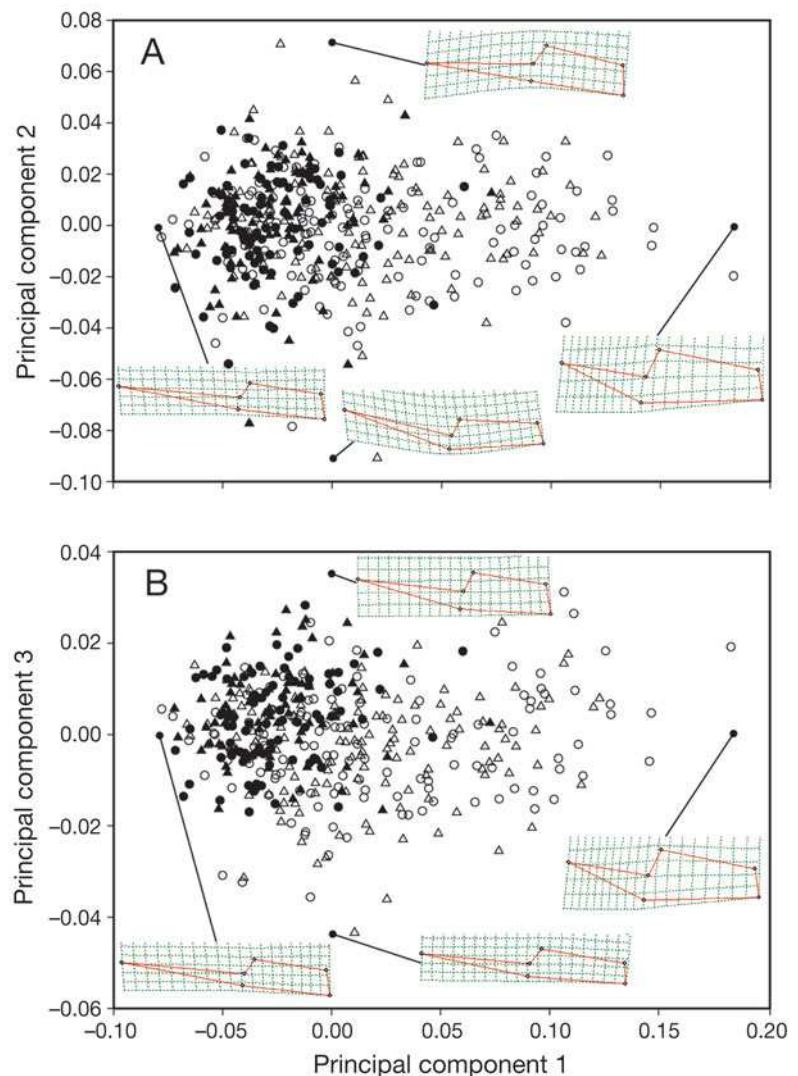

Fig. 2. *Munida rugosa*. Results of a principal components analysis, with thin plate spline representations of extreme landmark configurations on each axis. Relationships between (A) principal components 2 and 1, and (B) principal components 3 and 1. Filled symbols: females; open symbols: males; circle: left chela; triangle: right chela

the linear model explained 35.39% of the variation of chelae shape for both sides. For females, similar relationships were found for the left (Wilks' λ = 0.58, p < 0.001) and right chelae (Wilks' λ = 0.57, p < 0.001), but the linear model explained only 14.71 and 13.45% of the variation in chela shape, respectively.

There was also a significant linear relationship between chela shape and cheliped length for both left (Wilks' λ = 0.27, p < 0.001) and right chelae (Wilks' λ = 0.30, p < 0.001) in males, with the linear model explaining 40.24 and 40.41% of the shape variation, respectively (Fig. 3a). For females, the corresponding regressions were also significant (left: Wilks' λ = 0.60, p < 0.001; right: Wilks' λ = 0.59, p < 0.001; Fig. 3b), but again the linear model explained only 12.02 and 10.93% of the chela shape variation for left and right sides, respectively. In males, chela shape became higher with a relatively shorter pollex and a longer manus (i.e. more arched) with increasing cheliped length and CL, on average (Figs. 3a & 4a). However, in females, chela shape changed little with increasing cheliped length and CL (Figs. 3b & 4b).

A plot of the first axis of the PCA of chela shape (which accounted for most of the shape variation) against CL for males and females illustrates considerable variability in chela shape across the whole range of sizes (Fig. 4a,b). In males, there was a pronounced increase in chela shape variation at CL >30 mm (Fig. 5a). Females, however, did not show such a distinct increase in chela shape variability with increasing CL (Fig. 5b).

Results from the PERMANCOVA showed that chela shape was significantly affected by cheliped size (p < 0.001) and differed between sexes (p < 0.001), but there was no interaction between cheliped size and sex (p = 0.322), nor was there a difference between sides (p = 0.437). There was still no effect of side (p = 0.230) if all the specimens were included in the analysis (including the differing size ranges of males and females).

Assessment of cheliped symmetry

Difference in shape between left and right chelae (i.e. procrustes distance between the 2 chelae) was highly correlated with difference in cheliped length for males (r_S = 0.55, p < 0.001) and females (r_S = 0.32, p = 0.003; Fig. 6a). However, the difference in chela shape between left and right was not correlated with CL for males (r_S = 0.15, p = 0.086) or females (r_S = 0.13, p = 0.226; Fig. 6b).

DISCUSSION

Variation in chela morphology in *Munida rugosa* has been recorded in previous studies (Ingrand 1937, Zainal 1990, Hartnoll et al. 1992, Combes 2002, Claverie & Smith 2007), but was not investigated further than a qualitative description in relation to body size. Claverie & Smith (2007) noted variation from a straight morphology, with a narrow propodus and straight pollex and dactylus, to an arched morphology, with a higher propodus and bent pollex and dactylus leaving a gap in between. In the present study, a large variety of intermediate shapes was observed from narrow (straight) to broad (arched) propodi, with the greatest propodus heights observed only in males (represented by PC1). There was a positive relationship between the
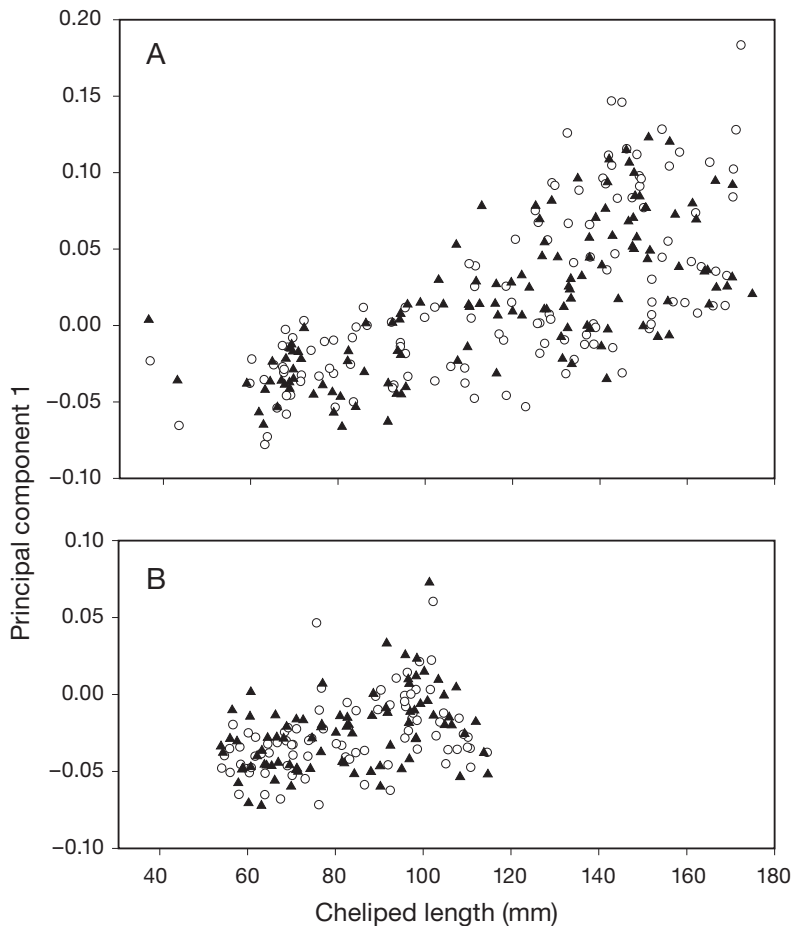

Fig. 3. *Munida rugosa*. The first axis of the principal component analysis of chela landmark configurations as a function of cheliped length for (A) males and (B) females. (○): left cheliped; (▲): right cheliped
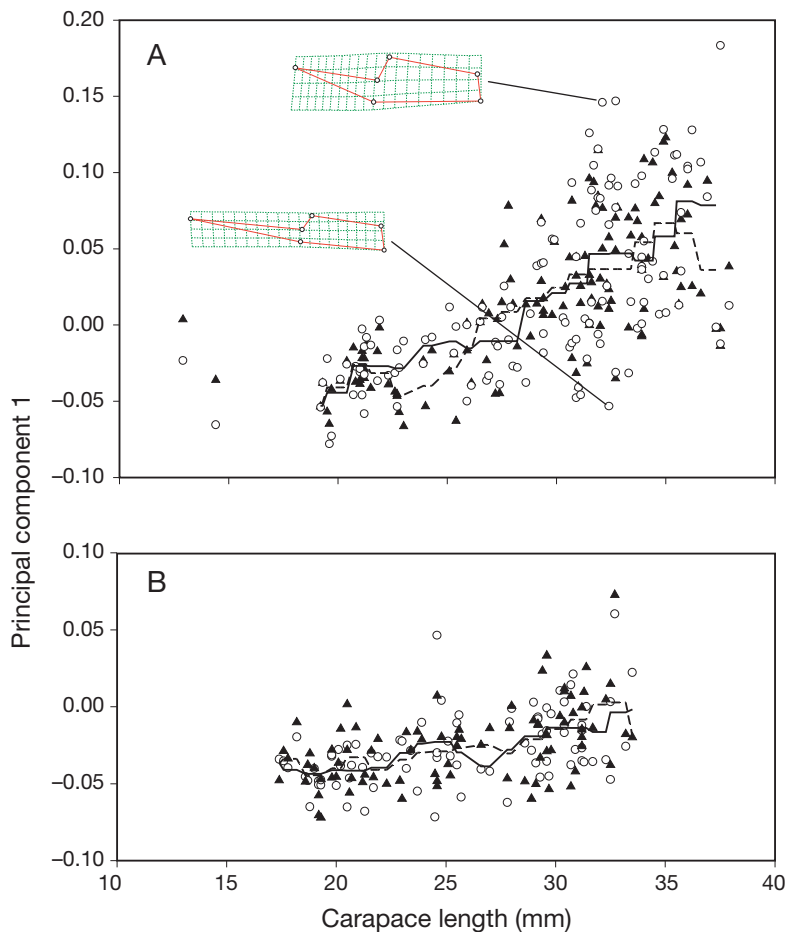
Fig. 4. *Munida rugosa*. The first axis of the principal component analysis as a function of carapace length with associated running means (window of 3 mm) for (A) males (with thin plate spline representations of extreme landmark configurations) and (B) females. (○, solid line): left cheliped; (▲, dashed line): right cheliped

Smith 2009). It therefore appears that one secondary sexual feature (arched chelae) becomes prevalent 3 to 4 moults later than another (allometric cheliped growth, commonly encountered in decapods). This could be due to a slow development of arched morphology over several moults, perhaps because change in chela mass takes longer than an increase in cheliped length.

Claw morphology in *Munida rugosa* exhibits patterns previously observed for sexually selected traits (i.e. greater weapons in larger males, Petrie 1992, Simmons & Tomkins 1996, Knell & Fortey 2005, Emlen 2008), assuming that arched chelae are more effective weapons (Claverie & Smith 2007). Alternative chela morphologies (i.e. straight) may represent alternative reproductive phenotypes within sexes associated with alternative tactics (phenotypic outcome) within a common strategy (decision rules, Dominey 1984). Such a strategy is commonly called a conditional strategy and is thought to be the most common evolutionary stable strategy in nature (Gross 1996). Using this strategy, males may adopt different tactics depending on their status in the population and fitness among tactics is not necessarily equal (Gross 1996). There is evidence for conditional strategies in some crustaceans. In *Macrobrachium rosenbergii* and *Rhynchocinetes typus*, for example, dominant or alpha males are more aggressive, have well-developed chelipeds and are superior in competition for access to food, shelter or mates. Subordinate males, on the other hand, retain relatively small chelipeds and use sneaking tactics to obtain these resources (Barki et al. 1992, Correa et al. 2003). When dominant males disappear, subordinate males replace them and become morphologically the new alpha males (Karplus 2005). In *M. rugosa*, one morphology (apparently the arched one since it is exaggerated only in large males) may be costly to develop, but could have greater benefits in terms of intrasexual competition or intersexual attraction and could be associated with dominant males (Claverie & Smith 2007). The second morphology (in this case the straight one, since it appears more like a juvenile form) may be less costly to develop, but could confer limited disadvantages in intrasexual competition or intersexual attraction (e.g. not being able to hold firmly or injure conspecific) and would consequently be associated with subordinate males. Costs
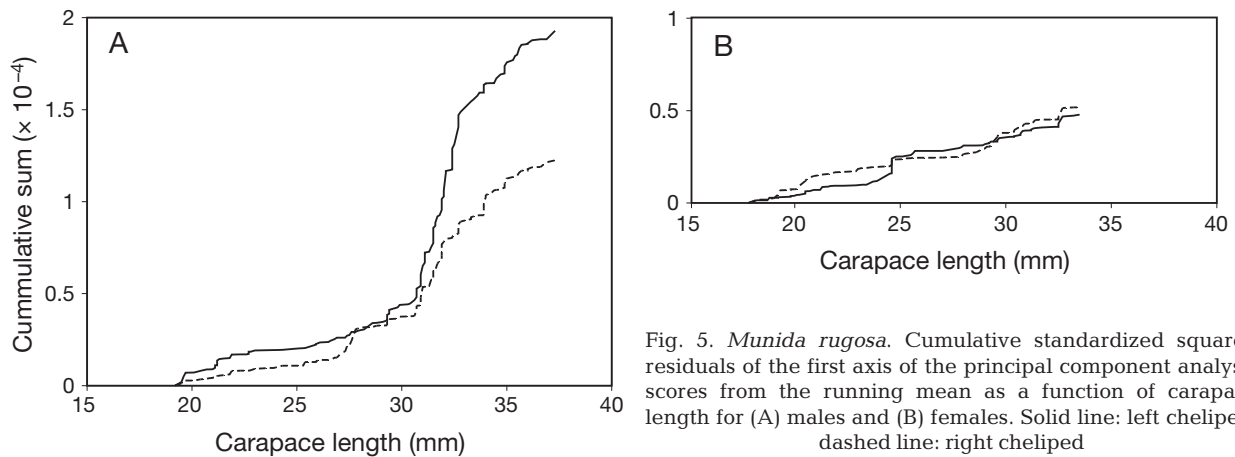
amplitude of arching and CL and cheliped length, but with considerable variability. The amplitude of arching depended on cheliped size (the greatest arching was encountered in the longest chelipeds), but the reciprocal was not true, as the longest chelipeds were not always arched.

Chela shape varied from the straight towards the arched morphology in both sexes, but the fact that the degree of arching was greater in males (for equivalent female cheliped size and also because males developed longer chelipeds than females), suggests that there is stronger selection for this character in males. In both sexes, the arched morphology appeared only in individuals larger than the morphological size of maturity (Claverie & Smith 2009). In males, however, variation in chela shape (due to development of the arched morphology) increased markedly above a CL of 30 mm, whereas the size of morphological maturity indicated by cheliped length is 22 mm CL (Claverie &

Fig. 5. *Munida rugosa.* Cumulative standardized squared residuals of the first axis of the principal component analysis scores from the running mean as a function of carapace length for (A) males and (B) females. Solid line: left cheliped; dashed line: right cheliped

associated with the arched morphology could relate to the production of larger muscular and exoskeletal mass and greater energetic cost to maintain a bigger claw. The arched morphology could also impose a longer moulting time to extract the cheliped from exuvia, which may increase exposure to predators. Intermediate morphologies may represent a development towards the arched form. Under this hypothesis, both morphologies (representing different tactics) would likely be associated with behavioural adaptations appropriate to the difference in competitiveness (Dominey 1984).

Another possible explanation for the occurrence of straight chelae in large males is that autotomised chelipeds may take several moults to reacquire the arched morphology during regeneration, as suggested by Ingrand (1937) and Hartnoll et al. (1992). Intermediate morphologies would occur during regeneration. Studies in other decapods have shown that a particular cheliped morphology may take several moults to regenerate (Wilson 1903, Juanes & Smith 1995, Read & Govind 1997). In that case, the loss of an arched cheliped would have a high cost, since regeneration would be long (this species moult onces or twice a year depending on size) and fitness would consequently be adversely affected due to a reduction in competitive status.

Similar allometric slopes were found in the size-related change in chelae shape for males and females (i.e. non-significance of the interaction term between cheliped size and sex). Consequently, there may be a common genetic basis for chela arching in both sexes, with degree of arching being largely determined by the length of the cheliped (and maybe social status in the hypothesis of

a conditional strategy). Females have shorter chelipeds than males, on average (Claverie & Smith 2009) and may, as a result, be less likely to develop the arched form exhibited by large males. However, the differences in shape between males and females were
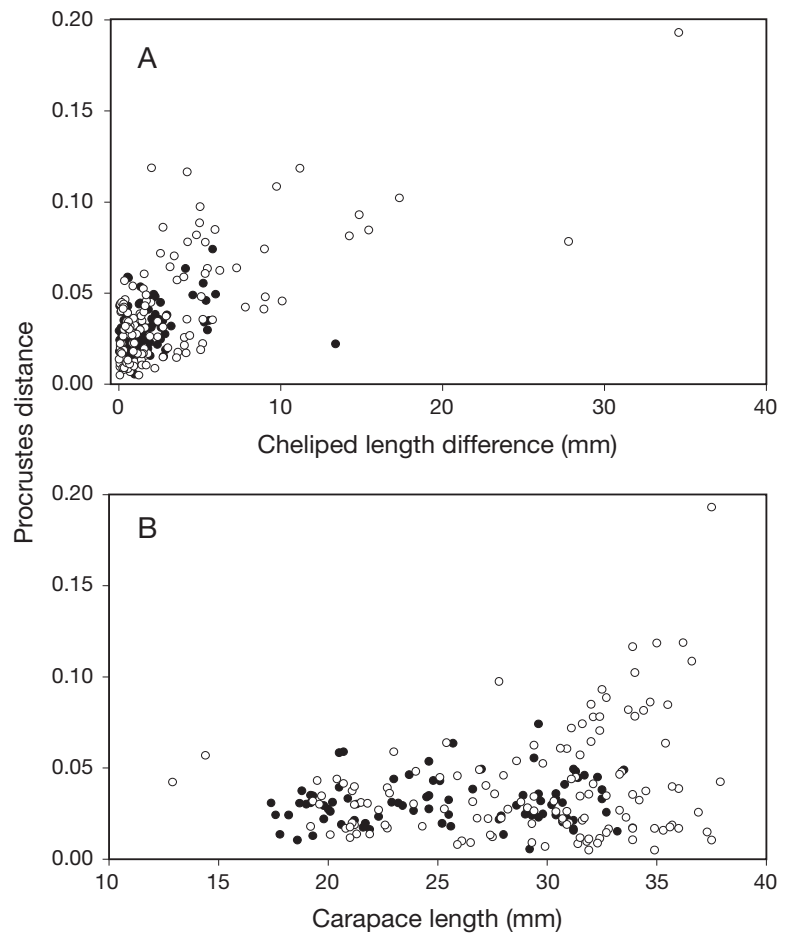

Fig. 6. *Munida rugosa.* Procrustes distance between left and right chelae as a function of (A) absolute cheliped length difference between left and right chelae and (B) carapace length. (○): males; (●) females

not solely due to cheliped length, since females had less arched chelae than males of equivalent size. Nevertheless, there may be intrasexual competition among females, giving rise to a certain level of selection for this trait (Kodric-Brown & Brown 1984). If so, the limited degree of arching in females implies lower selection pressure for arched chelae and correspondingly lower intensity of competition mediated through agonistic interactions using the chelipeds than in males.

No significant asymmetry was measured in chela shape of *Munida rugosa* and most specimens were approximately symmetrical in cheliped length (Claverie & Smith 2009). In the present study, some specimens were heterochelous but no specific handedness was observed, and shape asymmetry was correlated with the asymmetry in cheliped length (with the longer claw being the most arched). Some asymmetry in arching was previously reported for this species (Zainal 1990, Hartnoll et al. 1992, Combes 2002), but findings were not consistent. *M. rugosa* possess long and slender chelipeds and autotomise these appendages more readily when handled (particularly ovigerious females, T. Claverie pers. obs.) than crabs or lobsters with more robust chelipeds. Hartnoll et al. (1992) suggested that arching could take several moults to develop. The high prevalence of symmetric specimens in the population sampled, combined with the correlation between shape and length difference, strongly suggests that the observed asymmetries in cheliped length and chela shape could be the result of regeneration after autotomy.

In summary, *Munida rugosa* exhibit a sexual dimorphism where males are larger than females, possess longer chelipeds and can have a greater degree of chela arching. However, considerable variation in the degree of arching was observed for large males and only some of the largest individuals fully developed arched chelae. Considering the various examples of exaggerated traits occurring in the animal kingdom related to sexual selection (Zahavi 1975, Siva-Jothy 1987, Emlen & Nijhout 2000, Hongo 2003, Emlen 2008) and similar patterns observed in other decapods associated with male–male interactions (Crane 1975, Barki et al. 1992), it seems possible that sexual selection has favoured the evolution of longer chelipeds with a greater degree of chela arching (weapons) in mature male *M. rugosa*. However, the effect of arching on the outcome of intrasexual conflict remains to be quantified. It is to be expected that males with arched chelae would be more successful in agonistic interactions or in obtaining and handling mates than similar-sized males with straight chelae. These predictions are readily testable with behavioural experiments.

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