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Geometric morphometric analysis discriminates native and non-native species of Caprellidae in western North America

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Characteristics of the second gnathopod are traditionally used to distinguish between species of caprellid amphipods. However, these distinctions are often subjective and can be variable within a species. Geometric morphometrics were used to quantitatively assess shape variation of the second gnathopod propodus of three species of caprellids in North America, including the non-native Caprella mutica. *Gnathopod shapes of* C. mutica *specimens from different latitudes revealed distinct morphologies; the factors responsible for the shape variations are unknown. Allometric change of propodus shape was observed in* C. mutica. *Larger individuals showed a wide array of possible propodus morphologies. Despite this variability, there were clear differences between large specimens of* C. mutica *and two species native to North America:* C. alaskana *and* C. kennerlyi. *The use of geometric morphometrics and the thin-plate spline method can serve to both complement descriptions using traditional keys and aid in identification of non-native species in novel geographical regions.*

Keywords: allometry, amphipod, *Caprella mutica*, latitudinal variation, morphology, shape

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INTRODUCTION

Crustacea are typically identified taxonomically using morphological distinctions in the exoskeleton. Within the amphipod genus *Caprella*, these characters include the presence, size, shape and position of pereonite projections, relative size of the antennae, and the size and shape of the second gnathopod (e.g. Laubitz, 1970; Smith & Carlton, 1975; Arimoto, 1976; Hayward & Ryland, 2000). However, these distinctions are often described subjectively (e.g. a little shorter, very small, quite large, sparse and many) and can be variable within a species, especially since morphology can change due to ontogenetic development or environmental influences (Vermeij, 1978; Caine, 1989). Confusion and incorrect identifications can occur when morphological descriptions are based on a few individuals, sizes, or geographical locations. As a result, newly introduced species can be difficult to distinguish from native congeners (Wasson *et al.*, 2000).

Caprella mutica Schurin, 1935 (Figure 1), has the potential to create considerable taxonomic confusion, as it has been widely introduced throughout the world (Ashton, 2006). Its native range includes coastlines of Japan and Eastern Russia, whilst the known introduced range now spans across all temperate coastlines in the northern hemisphere (Ashton *et al.*, 2007) and New Zealand in the southern hemisphere (Inglis *et al.*, 2006). In the native range, *C. mutica* inhabits algal beds, particularly in association with algiculture. Where introduced, individuals are most commonly found associated with fouling communities on man-made structures, including submerged areas of buoys, fish farms and marina or pontoon structures (Ashton, 2006). The identification of *C. mutica* has already been problematic on a number of occasions in northern Europe. For example, in The Netherlands, Platvoet *et al.* (1995) described specimens of *C. mutica* as *C. macho* sp. nov. (Wolff, 2005). In Scotland, *Caprella* specimens collected in 1999 were initially unrecognized and later described as *C. mutica* upon closer scrutiny (O'Reilly, 2006).

In western North America, *C. mutica* co-occurs with several other congeners and may be mistaken for native species, especially if significant geographical variation exists in morphological characteristics. For example, in a guide to the seashore life of the northern Pacific coast of America, Kozloff (1993, Figure 91, p. 114) showed an illustration that was described as the native *C. californica* Stimpson, 1856. The illustrated specimen is clearly setose on pereonites 1 and 2 and gnathopod II, and has dorsal spines on pereonites 3–5; it seems likely that this was *C. mutica*, which was described from the area in 1977 (USGS, 2005). This interpretation is consistent with a recently updated guide to the intertidal organisms of California (Carlton, 2007), where *C. mutica* was described as having several to many sharp spines on pereonites 3, 4 and 5. This contrasts with the description of two of the native caprellids: (a) *C. alaskana* Mayer, 1903 (Figure 1), with one or two small blunt spines on pereonites 5–7, although spines may extend as far as the cephalon (Laubitz, 1970); and (b) *C. kennerlyi* Stimpson, 1864 (=*Metacaprella kennerlyi*) (Figure 1) that is distinguished by the presence

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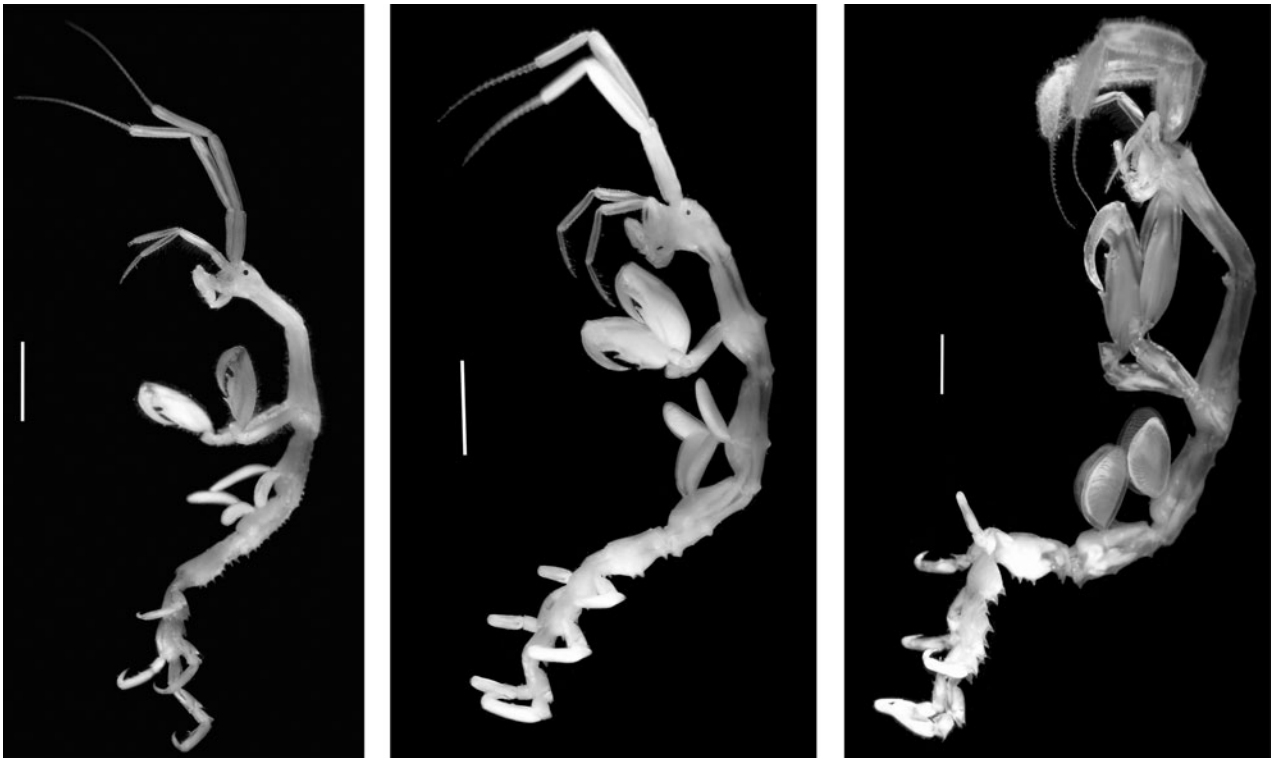

Fig. 1. Adult male individuals of *Caprella mutica* (left), *Caprella alaskana* (middle) and *Caprella kennerlyi* (right). Scale bars 2 mm.

of a pair of head spines (Laubitz, 1970). The head spination is the only characteristic described to reliably define between these two native species (Laubitz, 1970). However, it is noteworthy that species of caprellid amphipods are often discriminated on the basis of the second gnathopods, which are morphologically similar for *C. mutica*, *C. alaskana* and *C. kennerlyi* (Table 1). Moreover, the extent of morphological variation has not been quantitatively assessed for these species. The terms tubercle, spine and projection have been used in the description of caprellids. It is the authors' impression that a spine is typically longer and more pointed than a tubercle, which would be shorter and blunter. The term projection would describe both the aforementioned and setae. However, these terms are subject to personal interpretation and for the purposes of this paper the term spine has been used to describe all spine- and tubercle-like features.

Table 1. Descriptions of the second gnathopods of the three caprellid species found on the northern Pacific coast of America.

Species	Description
Caprella alaskana	'Palm with proximal grasping spine and accessory spine, medial to distal poison spine, distal triangular projection' (Laubitz, 1970) 'Proximal spine is located quite proximally, accessory thorn is missing. The small distal spine is completely distal. Inner margin of the claw is angular. One male diverges from this description due to a different shaped palm and greater spination' (translated from Mayer, 1903)
Caprella kennerlyi	'Palm with proximal grasping spine, small distal poison spine, and large triangular distal projection' (Laubitz, 1970) 'Proximal spine is rather close to the middle of the palm, the relatively small median spine is extremely distal. The accessory thorn is missing in very large males. The inner margin of the claw is angular' (translated from Mayer, 1903)
Caprella mutica	'Bearing a palmar spine, poison tooth situated near by a triangular tooth at distal angle of palm' (Arimoto, 1976) 'The middle projection is most prominent on the grasping margin of the propodus' (Willis *et al.*, 2004)

Geometric morphometric techniques are being increasingly used to quantify organisms' shapes. Traditional morphometrics include size and shape variables and also include qualitative variables. Descriptions are often accompanied by an illustration drawn from a single specimen. Like traditional morphometrics, geometric morphometric methods allow statistical inference, but importantly, they preserve information about the geometry of the object. The use of landmarks yields variables of significance and the technique is independent of measurements which must be chosen prior to the analysis (Zelditch *et al.*, 2004). They often enable the quantification of features that are difficult to measure with traditional measurements, and are therefore usually described qualitatively. For example, semi-landmarks provide the opportunity to describe curvature. Consequently, geometric morphometrics generates large amounts of useful shape information which previously were unattainable. Finally, they allow morphological differences to be visualized using interactive computer graphics. Therefore, a hypothetical mean 'shape reference' of a species derived from several specimens could be used during identification as opposed to traditional drawings, which originate from only one specimen. Variation among the specimens can also be described visually using deformation grids. This ability to visualize morphological differences is invaluable to help identify and validate simple morphological measurements that can be used in future studies and identification keys (Rohlf & Marcus, 1993). With their hard exoskeletons, crustaceans should be excellent candidates for such analyses (Rufino *et al.*, 2006). The method used in this study has been applied to quantify claw-shape differences in members of the genus *Uca* (Rosenberg, 2002) and to discriminate fishery stocks of the American lobster *Homarus americanus* Milne-Edwards 1837 (Cadrin, 1995).

The current study demonstrates the use of geometric morphometrics to contribute increased clarity in species descriptions, serving to both substantiate and quantify taxonomic differences and to help identify introduced species. The objectives were to use shape differences in the gnathopod II propodus: (1) to measure latitudinal variation in *C. mutica*; (2) to assess allometric growth of *C. mutica*; and (3) to determine and quantify morphological differences between *C. mutica* and two North American caprellids with similar gnathopod shapes: *C. alaskana* and *C. kennerlyi*. In order to investigate the influence of size on the ability to differentiate the species, small and large individuals were treated independently for the final objective.

MATERIALS AND METHODS

Sample collection and specimen classification

Male caprellid specimens were collected from the Pacific coast of North America during summer periods between 2001 and 2003. Several keys to the Caprellidae were used to identify the species (Mayer, 1903; Laubitz, 1970; Arimoto, 1976). Distinguishing characteristics were used as follows: *Caprella mutica* have setation on pereonites 1 and 2 and gnathopod II, and multiple dorsal and lateral spines on pereonites 3–7, including more than 3 pairs of dorsal spines on pereonite 5; *Caprella alaskana* do not have body setation, have fewer dorsal spines (3 pairs on pereonite 5) and no lateral spines; *Caprella kennerlyi* can be distinguished by paired head spines. Several *C. mutica* from non-native populations in Scotland were also included in the analyses. The individuals from Scotland did not form an outlying group in the analyses and were therefore not treated independently. Two hundred and twelve individual caprellids were isolated, including 29 *C. alaskana*, 25 *C. kennerlyi* and 153 *C. mutica*. Male individuals greater than 15 mm total length were considered adults. Caprellids were used in different combinations according to the objectives (see below).

DATA ACQUISITION

Only the outer surface of the right gnathopod II propodus was used in this study. Images were acquired using a binocular microscope equipped with an Olympus 750 camera connected to a computer. All images were saved as TIF files using *Scion Image* software (Scion, Frederick, MD). Coordinates of landmarks and semi-landmarks (Figure 2) were digitized and recorded using *tpsDig2* (Rohlf, 2006). Landmarks 1 through to 7 captured shape information on all three spines: the comparatively large distal triangle (landmark 2; Figure 2), the medial (landmark 4; Figure 2) and proximal spines (landmark 7; Figure 2). Landmarks 8 and 9 marked the points where the propodus and carpus meet. Landmark 16 represents the end of the upper margin of the propodus where the dactyl is connected.

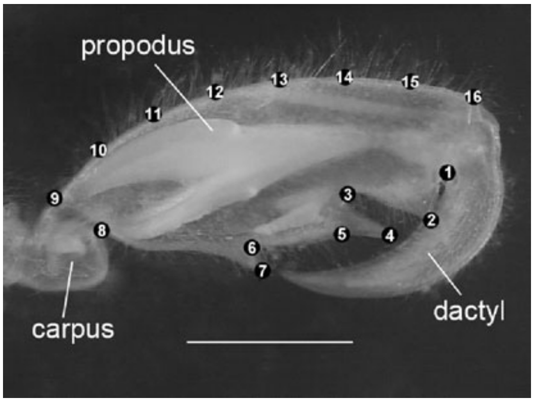

Fig. 2. Digital image of second gnathopod of *Caprella mutica* with landmarks 1 through to 9 and 16 and semi-landmarks 10 through to 15. Scale bar 1 mm.

Landmarks 10 through to 15 were semi-landmarks, used due to a lack of homologous points along the upper margin of the propodus. Semi-landmarks can be used in such cases, as *tpsRelw* (Rohlf, 2005b) includes a command allowing semi-landmarks to slide along a tangent to the traced curve in order to remove tangential variation but retain information on contour (Bookstein, 1997). Semi-landmarks will hereafter be referred to as landmarks.

Shape variables were constructed from the landmarks through the following steps in *tpsRelw*. Landmark configurations were superimposed using the generalized least squares Procrustes superimposition (GLS). Scaling, translation and rotation was employed to minimize the Procrustes distance, the sum of squared distances between corresponding landmarks. In short, the object was centred at the origin by subtracting the coordinates of its centroid from the coordinates of each landmark. Then each object was scaled to unit centroid size by dividing each coordinate of each landmark by its centroid size. One configuration was used as a reference and all others were rotated to minimize partial Procrustes distance. The average shape was then calculated and became the new reference to which all objects were rotated again. This step was repeated until rotation ceased to occur.

The thin-plate spline procedure was used to describe the observed morphologies. This method generates deformation grids by dividing shape change into uniform and non-uniform shape components (Bookstein, 1991; Rohlf & Marcus, 1993). Uniform shape change occurs when parallel lines remain parallel in a deformation grid and alterations occur equally across the entire grid. Non-uniform aspects lead to varying shape changes throughout the grid. Deformation grids depict shape change over the entire object by interpolating between landmarks. The metaphor upon which the thin-plate spline method is based and which intuitively explains a deformation grid is an extremely thin metal plate which can be rotated or bent to conform to shape variation. The plate is bent so as to minimize the energy expended to achieve the shape change and therefore also minimizes highly localized shape variation. Not only is a thin-plate spline an effective visualization tool but its coefficients (partial warps scores) can be used in descriptive and inferential statistical tests as well (Rohlf, 1999). This method provides variables with the correct number of degrees of freedom ($2k-4$ where k is the number of landmarks) and employs the Procrustes distance as a metric. The partial warps scores represent the non-uniform shape variation between the specimens and the consensus.

In *tpsRelw* a principal components analysis (PCA) of the partial warps matrix, including the uniform components as a pair of partial warps, was carried out to describe major trends in morphological variation. Principal components of the partial warps scores are referred to as relative warps. The total variability described by each principal component axis was noted and included in PCA figures. Statistical analyses were performed, including the testing of assumptions (normality and homogeneity of variance), using both uniform and non-uniform components in Statistica 6.0. (StatSoft, Inc., 2001). A fully detailed description of the mathematics underlying these geometric morphometric methods is beyond the scope of this paper. For further information see the works by Bookstein (1991), Rohlf & Marcus (1993) and Slice (2005).

ANALYSIS

Latitudinal variation

To investigate intraspecific shape variation in *C. mutica* at different latitudes, three regions on the west coast of North America were chosen: San Francisco Bay (California (CA), 37.7°N; N = 18), Puget Sound (Washington (WA), 47.4°N; N = 24) and Dutch Harbor (Alaska (AK), 53.9°N; N = 18). Adult male specimens from these regions were used to gather landmark data used in a relative warps analysis (Rohlf & Marcus, 1993). *tpsRelw* yielded a PCA to observe regional clustering and deformation grids based on the average individual from each location to describe morphology. Shape variation was assessed using multivariate analysis of variance (MANOVA) on both uniform and non-uniform components.

Allometry

A PCA of the partial warps scores of 142 *C. mutica* individuals was carried out, using *tpsRelw*, to examine trends in morphological change throughout growth. Specimens were categorized into 4 size-classes according to total body length: (1) greater than 20 mm; (2) 15–20 mm; (3) 10–15 mm; and (4) less than 10 mm. This included individuals from the Pacific coast of North America and the west coast of Scotland. In addition, a multivariate regression analysis of shape against total length (mm) was carried out using principal component scores 1 through to 3 to determine which shape change best described allometry. *tpsRegr* (Rohlf, 2005a) provided a visualization window allowing to monitor how shape changes with size. Shape variation was assessed using MANOVA on both uniform and non-uniform components.

Species

The GLS method and thin-plate spline procedures (*tpsRelw*) were used to discern significant variations in propodus shape between *C. alaskana, C. kennerlyi* and *C. mutica*. Specimens from the small and large sizes were treated separately. Small individuals were those less than 10 mm length: 15, 13 and 17 individuals of *C. alaskana*, *C. kennerlyi* and *C. mutica*, respectively, from Alaska. Large individuals were greater than 15 mm length: 14 *C. alaskana* from Ketchikan (N = 12), Kodiak (N = 2); 12 *C. kennerlyi* from Prince William Sound (AK, N = 5), Kodiak (AK, N = 2) and Kachemak Bay (AK, N = 5); 47 *C. mutica* from Dutch Harbor (N = 7), Humboldt (CA, N = 1), Ketchikan (N = 6), Puget Sound (N = 9), San Francisco Bay (N = 7), Sitka (AK, N = 9) and the west coast of Scotland (N = 8). Shape variation was assessed using MANOVA on both uniform and non-uniform components.

RESULTS

Latitudinal variation

Principal components analysis shows clustering of adult male *Caprella mutica* according to source region (Figure 3). There was some overlap in propodus morphology, but the differences between populations were significant (MANOVA, Wilks' lambda = 0.046, $F_{28,60} = 3.94$, $P < 0.001$). The gradation of shape change did not follow a linear latitudinal trend. Thin-plate splines illustrate that the main area of shape variation was located around the median spine (Figure 3). The size of the spine changed from being most massive in individuals from Dutch Harbor to a much reduced size in individuals from Puget Sound. Another area of variation was the relative build of the propodus, with those from Dutch Harbor typically broad and short, those from Puget Sound long and thin. Individuals from San Francisco Bay were intermediate in propodus shape.

ALLOMETRY

Propodus shape and variability changed with the size-class of the individual (Figure 4). Larger individuals (>15 mm) showed more shape variation than smaller ones, with variation in both the propodus curvature and relative size of the median spine between large individuals with extreme morphologies (D and E; Figure 4). Shape variation between the size-classes was significant (MANOVA, Wilks' lambda = 0.08, $F_{28,142} = 5.1$, $P < 0.001$). Eighty per cent of the shape variation was described in principal components 1 through to 3, all of which correlated significantly with individual size (PC1 Rsq = 0.165, $P < 0.001$; PC2 Rsq = 0.379, $P < 0.001$; PC3 Rsq = 0.087, $P < 0.001$). The strongest relationship was with principal component 2 (Figure 5), which describes a continuous elongation and

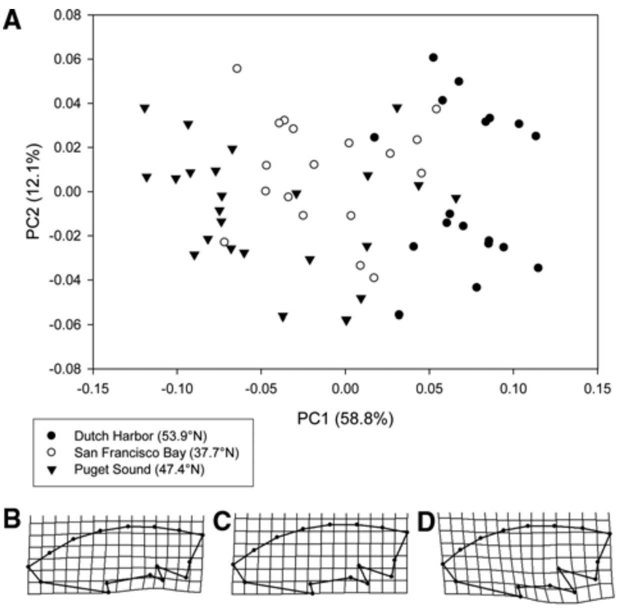

Fig. 3. Scores on the first two principal components of Procrustes shape coordinates for *Caprella mutica* males, >15 mm, from 3 geographical locations. (A) Thin-plate spline deformation grids show the deviation from the total mean individual to mean individuals from (B) Dutch Harbor, (C) San Francisco and (D) Puget Sound.

thinning of the propodus and extension of the median spine as body size increases (Figure 4).

SPECIES

Propodus shape is clearly distinct in large individuals of the 3 caprellid species (Figure 6) (MANOVA, Wilks' lambda = 0.00, $F_{28,73} = 24.05$, $P < 0.001$). No overlap of the species was observed. The outer surface of the propodus of *Caprella alaskana* was more rounded than the other species, the median spine being small. *Caprella kennerlyi* was less rounded, but maintains the small median spine. Propodus shape was most variable in individuals of *C. mutica*. The mean *C. mutica* gnathopod was much less curved and had a massive median spine relative to the other species.

Small individuals of the three species often overlapped in the PCA, although shape variation was statistically significant (MANOVA, Wilks' lambda = 0.00, $F_{28,45} = 15.97$, $P < 0.001$). Characteristics for differentiating between species could not be deciphered from the deformation grids (Figure 7).

DISCUSSION

Morphology of the second propodus of *Caprella mutica* was much more variable than expected, showing significant geographical variation among populations in western North America. However, there was no direct relationship between latitude and shape variation which would enable morphology to be predicted according to latitude. The results suggest that external or biological influences, which do not co-vary with latitude, are driving the observed morphologies. Environmental factors such as temperature, salinity and chlorophyll-*a* concentrations are known to have an impact on body size and various life history traits in crustaceans (Frank, 1975; Dugan *et al.*, 1994; Contreras & Jaramillo, 2003). Turbulence has also been described to affect the 'robustness' or ratio between segment depth and length at the widest portion, of several caprellid species (Bynum, 1980; Caine, 1989). Individuals were found to become more robust with increasing wave exposure. Caine (1989) described a process by which changes in the musculature of an appendage should be reflected by changes in the dimensions of that appendage. In addition, changes in the appendage may affect the musculature (and thus dimensions) of the pereonite which supports the appendage. In the decapod *Munida rugosa*, an arched chelate morphology was able to generate greater force than a straight chela (e.g. Smith, 2004; Claverie

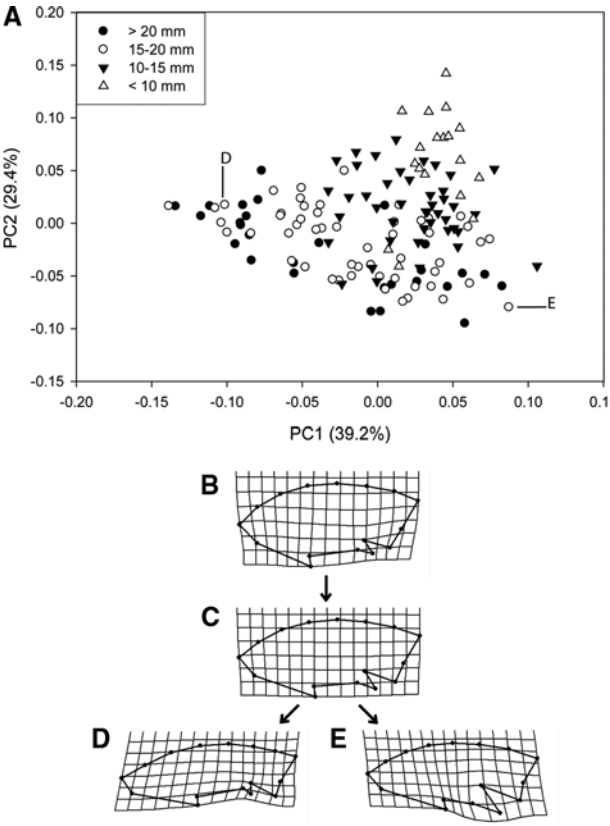

Fig. 4. Scores on the first two principal components of Procrustes shape coordinates for *Caprella mutica* individuals of 4 size-classes. (A) Thin-plate spline deformation grids show the deviation from the total mean individual to (B) mean small (<10 mm) (C) mean medium (10–15 mm) (D) and (E) two extreme shapes of large (>15 mm) individuals as indicated in (a).

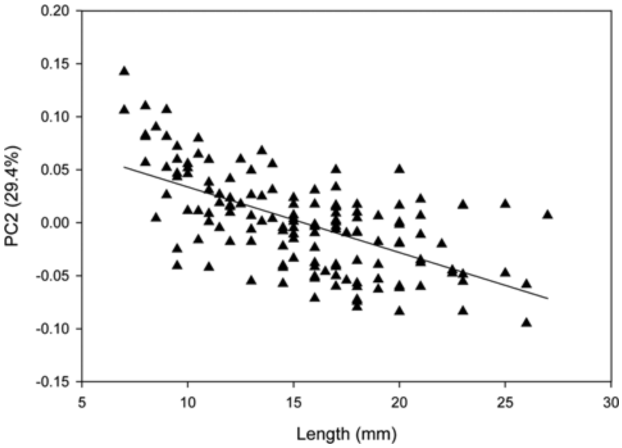

Fig. 5. Regression of principal component 2 of Procrustes shape coordinates against size for 142 *Caprella mutica* individuals (Rsq = 0.379; $P < 0.001$).

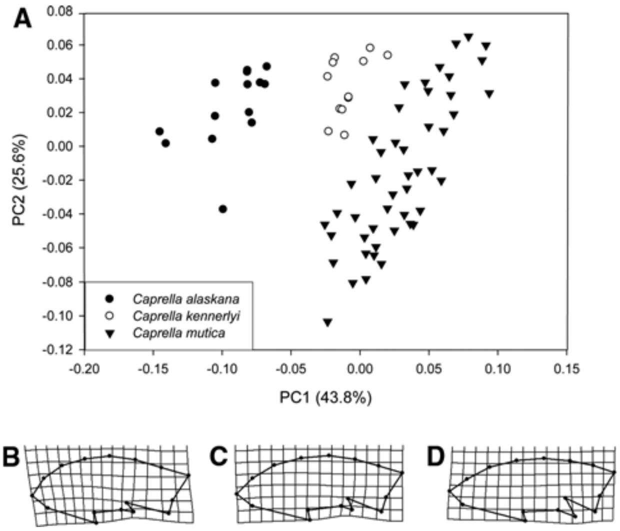

Fig. 6. (A) Scores on the first two principal components of Procrustes shape coordinates for large *Caprella alaskana*, *Caprella kennerlyi* and *Caprella mutica* individuals (>15 mm). Thin-plate spline deformation grids show the deviation from the total mean individual to (B) *C. alaskana* (C) *C. kennerlyi* and (D) *C. mutica* mean individuals.

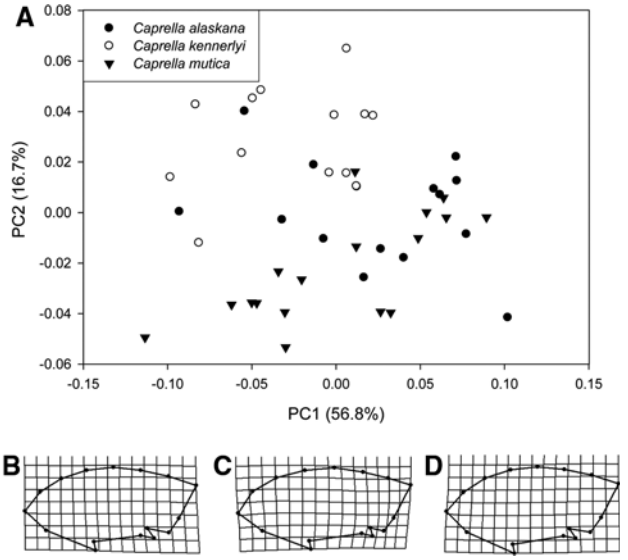

Fig. 7. Scores on the first two principal components of Procrustes shape coordinates for small *Caprella alaskana*, *Caprella kennerlyi* and *Caprella mutica* individuals (<15 mm). (A) Thin-plate spline deformation grids show the deviation from the total mean individual to (B) *C. alaskana* (C) *C. kennerlyi* and (D) *C. mutica* mean individuals.

& Smith, 2007). Claverie & Smith (2007) suggest that the arched morphology has evolved as a result of sexual selection by improving the use of the chela as a weapon in addition to its function during feeding. Thus, sexual selection may also influence shape variation in crustacea. The caprellid gnathopod II is employed in numerous activities (e.g. grasping the substrate, movement, feeding and agonistic interactions), whereby differences in the organism's local environment and behaviour could also explain shape variation. For example filter feeders may be expected to have a more robust gnathopod II for grasping the substrate while filter feeding with the antennae; compared to active predators which develop robust posterior appendages to grasp the substrate while anterior appendages capture prey (Caine, 1989). With decreasing wave exposure, predatory caprellids may be expected to have a more robust gnathopod II, as filter feeders would not develop the increased musculature associated with grasping. Aggressive species are expected to have an enlarged gnathopod II in which the basis is long (Caine, 1974, 1977). The large amount of variability found in gnathopod shape of adult, male *C. mutica* individuals implies aggressive behaviour and an increased level of adaptability to unused trophic niches. This morphological suitability could serve this species in establishing populations outside its native range.

Alternative explanations include population genetic differences and reproductive isolation as a result of geographical barriers (Contreras & Jaramillo, 2003; Rufino *et al.*, 2006). The genetic source(s) of the respective *C. mutica* populations examined in this study are presently unknown. This is further complicated by the fact that some morphological traits evolve rapidly (often predictably) in invasive species (Huey *et al.*, 2005).

As a species that is now widespread, invading many regions of the world, the functional significance of the large range of propodus shape in *C. mutica* is of particular interest. Whether the result of phenotypic plasticity or evolutionary change, the observed shape variation may allow this species to successfully exploit a wider range of resources (e.g. habitat types, environmental conditions and food sources) than other congeners and increase success in establishing self-sustaining populations. Although an intriguing possibility, this remains to be tested.

The results indicate a change of allometry in the second propodus of *C. mutica*. The propodus of large individuals becomes more extended, and the median spine can take on a large range of sizes relative to the rest of the propodus, compared to smaller individuals. Inconsistency in median spine size causes more shape variation and less condensed clustering among larger individuals. This indicates that both origin and size of the individual must be considered when using the second gnathopod as a taxonomic feature for identification.

At a large size (>15 mm), geometric morphometric analysis clearly distinguishes between the three species of caprellid. Exploratory analyses, using fewer *C. mutica* individuals originating only from Alaska, indicated that this variation was not biased by the larger sample size or number of source locations included in the analysis (again, individuals from Scotland were not outliers). Figure 6 includes deformation grids depicting the changes responsible for the distinctions between species: position and size of the median spine, build and curvature of propodus. Large males of these morphologically similar species could still be distinguished even though propodus shape in *C. mutica* was highly variable. A study using traditional morphometric techniques also described considerable gnathopod II shape variation in *C. mutica* (Faasse, 2005). The advantage of using geometric morphometrics is that it enables simple quantitative analysis of the characters described by Faasse (2005) from multiple specimens. In addition, sampling images enables the researcher to avoid sacrificing endangered or expensive specimens and any further measurements would no longer require revisiting the individual, which will not be possible if it has been used for genetic analysis (Cadrin, 2000). Using geometric morphometrics, the digital image is saved and can be revisited and any shapes which had not been previously considered important can be included in the analysis.

Smaller individuals of *C. mutica* often have very similar propodus morphology. Therefore when these species co-occur it can be difficult or impossible to identify juveniles to the species level. This must be taken into account when including small individuals in analyses (e.g. of abundance). Further investigation using geometric morphometrics may reveal characteristics which ascertain identification to the species level of the three species. The authors would suggest experimenting with the inclusion of other appendages or pereonites. In studying juveniles, care must be taken to ensure that the identity of the juvenile is known, e.g. by selecting them from a single species community.

In the future, it may be possible to hold digital images and coordinate data in a database to allow insertion of extra landmarks or identify an unknown species. However, geometric mophometrics can be sensitive to inconsistencies in image quality (Rufino *et al.*, 2006). For this reason all images for the current study were taken by a single person using the same equipment and settings. In order to begin a morphological database, care must also be taken to assure the quality of digital images, including size, profile and correct labelling of the images, similar to restrictions implemented on genetic databases. The positioning of landmarks is also critical to the geometric morphometric analysis and a detailed description of the exact position of landmarks would be necessary for any such database. Finally, Saila & Martin (1987) suggest that N (total individuals) should be roughly three times the number of variables (2* number of landmarks – 4). Therefore as the number of landmarks increase, a considerable increase in sample size is required. This is not always possible due to various reasons, e.g. endangered species, and small number of available specimens. In this study, the number of available specimens was limited and this rule of thumb could not always be followed. The authors attempted to find the optimal number of landmarks for shape description.

Overall, this study demonstrates how geometric morphometrics and the thin-plate spline method can contribute to descriptions using traditional keys. In invasion biology, misidentification can lead to errors in the history of patterns and baseline data, especially among closely related natives and non-natives (Müller *et al.*, 2002). In such cases of uncertainty, quantification of morphological characters using geometric morphometrics provides an important tool in taxonomic analysis. This reduces the likelihood of errors that may result from a more qualitative approach to identification.

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