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Patterns of morphological and genetic variability in UK populations of the shore crab, *Carcinus maenas* Linnaeus, 1758 (Crustacea: Decapoda: Brachyura)

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Abstract

Previous research has identified extensive inter-population variability in the morphology of the shore crab (*Carcinus maenas* L.). To determine the source of this variation (genetic or environmental), morphological and genetic data were analysed from crabs collected from eight sites around the coast of the UK. Ten morphometric traits were measured from over 800 crabs and the degree of morphological similarity among sites was calculated using multivariate techniques. Allozyme electrophoresis was used to investigate patterns of genetic similarity. Extensive morphological variability was detected: eight out of the ten morphometric traits analysed were useful when discriminating between crabs from each site. Discriminant function analysis revealed that over 35% of individuals could be classified to their site of origin on the basis of their morphology. In contrast, the allozyme analysis revealed low levels of genetic variability, both within the meta-population and among the crab population at each site. Pairwise comparisons revealed a moderate correlation between the degree of morphological and genetic similarity of crabs at each site, which suggests that the observed phenotypic variability has a genetic component. However, only around 20% of the phenotypic variability detected was associated with the patterns of genetic similarity. This means that patterns of morphological variability in this species are largely determined by the local environmental conditions: local factors could have a within-generation selective influence on mean trait values or *C. maenas* may exhibit phenotypic plasticity.
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1. Introduction

Until recently, the analysis of inter-population variability in the morphology of the shore crab, *Carcinus maenas*, has focused on the longstanding debate regarding the classification of this species in European waters (Yamada and Hauck, 2001). A number of studies have provided evidence that variations in male pleopod structure and carapace length-to-width ratio, combined with differences in the distribution of setae on the front distal region of the cheliped carpus, which supports the separation of shore crab specimens from Atlantic and Mediterranean regions into two distinct species: *C. maenas* (Linnaeus, 1958) and *Carcinus aestuari* (Nardo, 1847) (Demeusy and Veillet, 1953; Zariquiey Alvarez, 1968;

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Yamada and Hauck, 2001). In contrast, other research has demonstrated that there is a degree of overlap between the morphological features of crabs from each region, which means that an individual cannot be unequivocally assigned to the Atlantic or Mediterranean group on the basis of shape (e.g. Clark et al., 2001). The controversy regarding the taxonomy of this species is ongoing and shore crab specimens are still classified by locality as opposed to any biological means.

The classification of Atlantic and Mediterranean shore crabs on the basis of their genetic population structure is similarly controversial. Patterns of allozyme variation revealed a lack of complete separation among regional populations (Bulnheim and Bahns, 1996), whereas gene-sequencing studies have detected significant divergence. For example, Geller et al. (1997) assigned *C. maenas* and *C. aestuari* the status of sibling species on the basis of their genetic population structure and Roman and Palumbi (2004) identified a clear break at the species level. The ambiguity concerning the classification of this species is likely to have arisen as a result of its immense capacity for dispersal: shore crabs can be transported over vast distances by tides and currents during their planktonic larval stage, which can last for up to 90 days (Crothers, 1967; Rainbow et al., 1999). Organisms that exhibit this type of dispersal pattern typically lack clear patterns of population divergence due to low levels of genetic differentiation and limited inter-population variability (Hilbish, 1996).

It is therefore surprising that a number of recent studies have detected extensive phenotypic variability in shore crabs within relatively restricted geographical areas. For example, specimens collected from locations around the coast of the UK have been found to differ in terms of their morphology (Bentley et al., 2002; Brian, 2005; Lye et al., 2005) and camouflage pigmentation (Todd et al., 2005). Given that population divergence is prevented by gene flow, these patterns of phenotypic variability are likely to reflect differences between the local environmental conditions, resulting in within-generation selection pressures and/or phenotypic plasticity.

The aim of this study is to assess patterns of morphological and genetic variability in UK shore crab populations in order to investigate the source of this inter-population variability. The decoupling of these parameters will help to establish the extent to which environmental factors influence the expression of phenotypic variability in *C. maenas*, as well as in improving our understanding of the ecology and biogeography of this species. These fundamental issues are of current interest given that the shore crab is a highly successful global invader, having colonised Australia, Tasmania, South Africa, Japan and both coasts of North America (in Roman and Palumbi (2004)). It poses a significant risk to the inter-tidal ecosystem in these areas, causing changes in the abundance, size structure and defence response of native species (Yamada, 2001). The expression of inter-population variability in this species is also of interest from the perspective of biomonitoring: the shore crab has recently been championed as a sentinel for assessing the effects of chemical contamination (e.g. Galloway et al., 2004). However, in order to detect the effects of anthropogenic factors, it is important to consider the potential for natural variation in the biomarker response to establish the limits of normality (Brian, 2005; Sumpter and Johnson, 2005).

2. Materials and methods

Adult green shore crabs (classified as those with a carapace width of >30 mm) were collected by hand from the inter-tidal zone at eight sites around the coast of the UK (Fig. 1). Sites on the west coast consisted of the Dee, Mersey and Clyde estuaries, as well as two Scottish sea lochs, located near Appin and Arisaig. East coast sites comprised the Tyne and Tees estuaries and the Firth of Forth. All specimens were collected within a six-week period during the summer of 2001. Individuals that exhibited symptoms of infection by *Sacculina carcinii* were discarded. The remaining crabs were transported live, back to the laboratory, in cool-boxes for the morphometric and genetic analyses.

The morphological dimensions are illustrated in Brian (2005). These measurements were made using digital callipers (±0.01 mm). The length and width of the carapace and the depth of the cephalothorax were measured at the widest, longest and deepest points, respectively. Chelae depth was measured at the deepest points and the degree of heterochely was calculated as the depth of the right cheliped minus that of the left. The morphology of each claw was also determined by dividing the depth of the cheliped by its width. Individuals that had lost chelae, or that were suspected to have regenerated one or more cheliped (on the basis of their body size ratio), were omitted from the analysis of claw morphology. Periopod and propodus lengths were recorded by averaging these measurements for the fourth and fifth pairs of limbs, respectively. Again, data from individuals with missing or regenerating limbs were excluded. The area of the abdomen was

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