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Cheliped morphological variation of the intertidal crab *Eriphia verrucosa* across shores of differing exposure to wave action

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ABSTRACT

Understanding the effects of predator–prey interactions at a community level requires robust information on the mechanisms determining these interactions at the individual level. Here we use the intertidal crab *Eriphia verrucosa* (Forskål) as a model species to examine patterns of association between functional morphology (cheliped size and form) and patterns of prey consumption on shores of differing exposure to wave action. The size and form of the cheliped of crabs are known to be related to feeding performance and thus influence the outcomes for prey assemblages. Multivariate analyses showed that the claw size and shape of *E. verrucosa* varied between shores of differing exposure to wave action. Individuals from exposed locations had larger claws than those from sheltered locations. This shift in size was accompanied by differences in the composition of stomach contents between locations. Crabs from exposed shores had ~55% more hard shell prey (mussels and limpets) in their diet than those from sheltered shores. Crabs were more abundant on sheltered shores, but those from exposed locations were larger in carapace width. The relative abundance of prey varied between shores of differing exposure. Patterns of claw functional morphology provided a mechanistic explanation for the differences in prey consumption along the wave exposure gradient, although it remains to be tested whether there is a phenotypic plasticity response of crab claw to patterns of prey consumption. The interaction between prey abundance and morphology of the cheliped will likely shape the diet of this crab species, and this may have implications for the relative impact of this predator between shores of differing exposure.

1. Introduction

Predation is known to be an important biological factor with direct (e.g. prey mortality) and indirect effects (e.g. effects on organisms associated with the prey species) on population dynamics and community structure of marine ecosystems (e.g. Hughes, 1980; Menge et al., 1986). The rocky intertidal is recognised as a particularly tractable system to examine predator–prey interactions since predation effects are thought to be stronger here than in freshwater and terrestrial habitats (Sih et al., 1985). Predation is also known to interact with other biological (e.g. competition, Menge and Sutherland, 1976) and physical factors (e.g. wave exposure, Menge, 1978a), influencing its effects on prey populations (Menge, 1991, 2000; Menge and Sutherland, 1987). Hence, predator foraging and therefore predation pressure, are modulated by biological constraints and environmental factors, which subsequently determine realized foraging patterns (Lawton and Zimmerfaust, 1992; Thompson et al., 2004).

Crabs are highly mobile and are known to have an important role in structuring assemblages on rocky shores worldwide (e.g. Burrows et al., 1999; Ebling et al., 1964; Rilov and Schiel, 2006; Robles, 1987; Silva et al., 2008). It is therefore important to better understand the mechanisms of crab predation at the individual level in order to better understand their effects on prey populations. Traditionally, studies on predator–prey interactions have focused either on lethal effects on prey such as mortality (e.g. Rilov and Schiel, 2006; Silva et al., 2004, 2008; Thompson et al., 2000), or on non-lethal effects such as morphology (e.g. Dalziel and Boulding, 2005; Trussell, 1996; Vermeij, 1978), physiology (e.g. Moller and Beress, 1975), life history or behaviour (e.g. Phillips, 1976; Sih, 1987). As for specific predator–prey studies involving hard-shelled prey, durophagous crabs have been observed to crush and/or peel molluscan shells (Shoup, 1968; Takeda and Suga, 1979; Vermeij, 1977). Many crabs such as *Calappa* spp. crabs, are capable of accessing prey by peeling the shell aperture and thus avoid amore time and energy-consuming behaviour such as shell crushing (e.g. Shoup, 1968). This specialization of crab feeding behaviour reflects also on morphology,

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with changes in claw dentition developing to meet the demands of peeling the prey shell (Yamada and Boulding, 1998). Despite such a specialization in feeding behaviour of crabs towards their molluscan prey, there are also reports of generalization in crab feeding, such as a widespread preference to feed on small-sized molluscan prey, which are presumably easier to crush and so offer higher net energy gain (Juanes, 1992).

Studies on the predator–prey arms race between crabs and their gastropod prey are abundant (e.g. Bertness and Cunningham, 1981; Boulding, 1984; Brookes and Rochette, 2007; Cotton et al., 2004; Lowell, 1986), and crabs have been reported to have larger claws in locations where the most consumed prey are shelled molluscs (e.g. Yamada and Boulding, 1998). These studies have, however, mainly focused on consequences in terms of defences developed by prey, and predator responses to the interaction with prey often are overlooked. Hence, there is limited information on the cheliped morphological responses to the crab foraging behaviour, taking into consideration variations in the physical environment and in prey availability (interpreted here as abundance).

Phenotypic plasticity is the ability of a particular genotype to produce different phenotypes in response to environmental variation (DeWitt and Scheiner, 2004). Studies on crab flexibility have, however, mainly been investigated in terms of behaviour (e.g. Briffa et al., 1998; Hazlett, 1995), and there is little information on phenotypic flexibility according to differing environmental conditions (but see for example Freire et al., 1996; Hughes, 2000; Yamada and Boulding, 1996) and associated functional responses. The cheliped of crabs are important for reproduction (Hughes, 2000; Lee, 1995) and are crucial for feeding, being used to crush or detach molluscan prey (Hughes and Elner, 1979; Iwasaki, 1993; Silva et al., 2008; Yamada and Boulding, 1998). Cheliped morphology is known to vary according to both diet (Brown et al., 1979; Elner, 1978; Freire et al., 1996; Hughes, 2000; Smith and Palmer, 1994) and mating interactions (Lee and Seed, 1992). To our knowledge, there is no evidence that chelipeds are a key feature in the reproduction for *Eriphia verrucosa*. Little has been done, however, to describe relationships between external physical factors and variation in the cheliped size and shape (but see Takeda and Murai, 2003), and the mechanisms underlying phenotypic responses to the environment are not well understood (DeWitt and Scheiner, 2004). Specifically, differences in predator morphological traits in relation to wave action have not previously been examined. Such information is important because patterns of claw morphology can have direct consequences for prey populations and potentially also have evolutionary consequences for their morphology (see Vermeij, 1982; Vermeij et al., 1981).

In the intertidal, prey composition and abundance vary along environmental gradients (Lewis, 1964; Raffaelli and Hawkins, 1996; Stephenson and Stephenson, 1949); thus it becomes important to examine differences in predator foraging characteristics at this scale. Here we focus on the role of exposure to wave action, an important environmental gradient in intertidal habitats, on the foraging pattern of the xanthid crab *E. verrucosa*. This species was used as a model organism because it is ubiquitous on exposed and sheltered shores in southern Europe (for a Portuguese reference see Flores and Paula, 2001). We examined natural variations in stomach content composition of *E. verrucosa* and hypothesized that crabs from sheltered locations would differ in cheliped form and size from those at exposed locations, and that this would be related to differences in prey abundance and consumption. At the same time, we aimed to describe the abundance, stomach content composition and population structure of *E. verrucosa* on shores of differing exposure. The sex of predators was included in the analysis since this can influence predator distribution, behaviour and diet (e.g. Bishop and Wear, 2005; Brousseau et al., 2001; Buck et al., 2003; Mascaró and Seed, 2001; Spooner et al., 2007). Patterns of prey abundance were also examined between shores of differing exposure and related to stomach content composition of *E. verrucosa*.

The following specific null hypothesis were examined in relation to shores of differing exposure: (1) there are no differences in prey abundance; (2) there are no differences in the abundance and population structure of *E. verrucosa*; (3) there are no differences in stomach content composition; (4) there are no differences in claw size or shape between sexes; (5) claw shape and/or size do not explain possible differences in stomach content composition; (6) there is no relationship between crab size (carapace width and claw size) and the percentage of hard-shelled prey found in their stomachs.

2. Methods

2.1. Study sites and collection methods

Two moderately exposed (Peralta — 39°17′26.56″N, 9°20′36.20″W and Porto Dinheiro — 39°13′54.99″N, 9°20′13.61″W) and two relatively sheltered rocky shores (Paimogo — 39°17′11.65″N, 9°20′25.88″W and Vale Pombas — 39°17′27.42″N, 9°20′27.27″W), hereafter named exposed and sheltered shores, were examined on the central coast of Portugal. Levels of shore exposure were confirmed using measures of mean flow conditions via the dissolution of gypsum ($CaSO_4$) disks following Jonsson et al. (2006). Sets of twelve disks were attached to the rock surface ~3 m above CD for a single high-tide on two occasions at each location. Disks on exposed shores dissolved significantly ($p<0.05$) faster (7 g/h) than on more sheltered shores (3 g/h), giving a clear separation of exposure between locations. There were no significant differences ($p>0.1$) between shores within exposures.

2.2. Prey abundance

To quantify prey abundance, ten randomly deployed 50 cm × 50 cm quadrats were sampled at two sites on the midshore at all four shores. The abundance of all species was recorded.

2.3. Abundance, population structure and stomach contents of E. verrucosa

In order to assess crab population structure and collect specimens for stomach content analysis and cheliped morphology, three nocturnal collections were made on each shore during August–September 2007. A transect, approximately 100 m × 50 m, was walked by two observers for approximately 1 h. The crabs were hand-collected by hand as individuals were found to be active on the rock surface and little disturbed by human presence, and these were subsequently frozen upon return to the laboratory. Since the presence of parasites or the moulting of crabs can hinder their feeding behaviour (Williams, 1982), we only considered the intermoult stage of parasite free crabs.

The stomachs of 30 individuals per sex collected on each shore were analysed. We aimed to assess the importance of intertidal prey in the diet composition of crabs, particularly of prey with hard body parts including limpets, barnacles and mussels. The points method was used to examine occurrence of prey species in the diet of these predators since it is suitable for prey that are ingested in large recognisable pieces or in their entirety (Williams, 1981). The presence of hard body prey parts was then used to quantify the composition of prey within predator stomachs (Hill, 1976; Jones, 1968; Wear and Haddon, 1987; Williams, 1981): for limpets the number of radulae and pieces of shell (apex) were counted; for topshells the number of opercula or shell parts (apex); for chitons the number of radulae and anterior and posterior plates; for mussels the number of valves or umbos; and for barnacles the number of pairs of opercular plates.

2.4. Morphometric analyses of cheliped size and shape

Linear measures of claw morphology were taken from approximately thirty *E. verrucosa* of each sex at each shore (Fig. 1a). Only