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Original article

The size and shape of shells used by hermit crabs: A multivariate analysis of *Clibanarius erythropus*

Tancredi Caruso [a,*], Renato Chemello [b]

[a] *Department of Environmental Sciences "G. Sarfatti", University of Siena, via A.P. Mattioli 4, 53100 Siena, Italy*
[b] *Department of Ecology, University of Palermo, via Archirafi 18, 90123 Palermo, Italy*

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ABSTRACT

Shell attributes such as weight and shape affect the reproduction, growth, predator avoidance and behaviour of several hermit crab species. Although the importance of these attributes has been extensively investigated, it is still difficult to assess the relative role of size and shape. Multivariate techniques allow concise and efficient quantitative analysis of these multidimensional properties, and this paper aims to understand their role in determining patterns of hermit crab shell use. To this end, a multivariate approach based on a combination of size-unconstrained (shape) PCA and RDA ordination was used to model the biometrics of southern Mediterranean *Clibanarius erythropus* populations and their shells. Patterns of shell utilization and morphological gradients demonstrate that size is more important than shape, probably due to the limited availability of empty shells in the environment. The shape (e.g. the degree of shell elongation) and weight of inhabited shells vary considerably in both female and male crabs. However, these variations are clearly accounted for by crab biometrics in males only. On the basis of statistical evidence and findings from past studies, it is hypothesized that larger males of adequate size and strength have access to the larger, heavier and relatively more available shells of the globose *Osilinus turbinatus*, which cannot be used by average-sized males or by females investing energy in egg production. This greater availability allows larger males to select more suitable shapes.

1. Introduction

The role of host structures as a major resource and a limiting factor for hermit crabs has been extensively investigated (Fotheringham, 1976; Bertness, 1981; Blackstone, 1985; Elwood et al., 1995), and general reviews on the biology and ecology of these decapods are available (Hazlett, 1981; Lancaster, 1988; Elwood and Neil, 1992; Williams and McDermott, 2004). Adoption of a soft, coiled abdomen has allowed crabs to colonize protective structures, but has also created a need to search for such structures (Conover, 1978; Hazlett, 1981). Although a small percentage of hermit crabs use bivalve and scaphopod shells, hollowed cylinders of wood (Lemaitre, 1995; McLaughlin and Lemaitre, 1997; Forest, 1987) or sessile calcareous tubes of polychaetes or vermetid gastropods (i.e. *Calcinus* spp., Gherardi, 1996), most species live in empty gastropod shells.

Shell attributes such as weight and size are known to affect the reproduction, growth, predator avoidance and behaviour of several hermit crab species (i.e. Fotheringham, 1976; Bertness, 1981; Elwood et al., 1995). Accordingly, the strong correlation usually found between crab size and the dimensions of inhabited shells or shelters is usually ascribed to the accurate selection of suitable shelters by crabs (Reese, 1963; Conover, 1978). Field data show that although body size largely accounts for the morphological covariance between crab and shell biometrics, it does not fully explain the whole observable covariance (i.e. Kuris and Brody, 1976; Caruso et al., 2005). According to studies on other invertebrates (i.e. Cadima and Jolliffe, 1996; Madec et al., 2003; Fiorentino et al., 2008), weight or shape components (e.g. Kuris and Brody, 1976) must also be taken into account. Random shifts in the composition of the inhabited shells due to local limits in the availability of empty shells may also account for the morphological variance observed in shells used by crabs. It is well documented that the availability of portable shelters is a constraint on the fit between crab and shelter, and shell availability is also known to limit hermit crab populations in certain areas (Kellogg, 1976; Scully, 1979; Barnes, 1999). Based on these considerations, the effective study of shell utilization patterns should involve statistical analysis of shell species occupancy and of biometrics such as crab and shell weight, shell length, shell aperture width and volume, crab cephalothorax length and width, etc. (Kuris

* Corresponding author. Tel.: +39 0577232877; fax: +39 0577232806.
E-mail address: tancredicaruso@unisi.it (T. Caruso).

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and Brody, 1976; Conover, 1978; Barnes, 1999). The frequency distribution of inhabited shell species and simple indices based on the ratio between metrics such as shell length and width can provide generic proxies for shell shape, but only multivariate techniques allow a synthetic and efficient quantitative analysis of such a multi-dimensional property (Kuris and Brody, 1976; Cadima and Jolliffe, 1996; Legendre and Legendre, 1998; Quinn and Keough, 2002; Madec et al., 2003; Chiba and Davison, 2007; Fiorentino et al., 2008). Moreover, multivariate approaches are justified because it is assumed that crabs select shells on the basis of their overall morphological properties, including both shell size and shape (Reese, 1963; Kuris and Brody, 1976). Advanced PCA-based approaches (Cadima and Jolliffe, 1996; Madec et al., 2003; Paquette and Lapointe, 2007; Fiorentino et al., 2008) can possibly improve earlier PCA-based analyses of shell–crab relationships (e.g. Kuris and Brody, 1976; Benvenuto and Gherardi, 2001; Caruso et al., 2005). In particular, these approaches distinguish between size and shape components, whereas classic PCA tends to reflect the effect of size and/or size-biased shape variations (e.g. Cadima and Jolliffe, 1996).

The present study focuses on an intertidal population of *Clibanarius erythropus* (Latreille, 1818). Although this is one of the commonest Mediterranean hermit crabs, reaching high densities in several important habitats such as *Dendropoma* reef formations, knowledge of its biology and ecology is still limited to a few areas of the Mediterranean and eastern Atlantic Ocean (Gherardi, 1991; Busato et al., 1998; Botelho and Costa, 2000; Benvenuto and Gherardi, 2001; Benvenuto et al., 2003). Through innovative multivariate, explorative analysis, the study aimed to explore the role of size and shape in patterns of shell use by the hermit crab. In order to formulate a general, testable hypothesis relating to the poorly known crab-shell relationships, collected multivariate patterns were integrated with findings from other studies on *C. erythropus* (e.g. Benvenuto and Gherardi, 2001; Benvenuto et al., 2003).

2. Materials and methods

2.1. Study area, habitat and sampling

Sampling was performed between June and August 2002 by randomly collecting a total of 312 individuals along a 1 km shoreline in the Barcarello locality (38°12′ N; 13°17′ E; Palermo, NW Sicily), where the gastropod *Dendropoma petraeum* (Monterosato) constructs carbonate reefs (Antonioli et al., 1999). The random collection procedure involved creating a sequence of 400 numbers by "random extraction with repetition" of the numbers 1–10 using a computer routine for random number creation. In the field, the individual representing the first random number from the above series (not the first encountered individual) was collected. For example, if the first random number were three, the third encountered individual would be collected. The procedure was iterated using the second number from the random series. According to Gherardi (1991), animals were found either alone or aggregated in the pools of different depth (from a few to tens of centimetres) typical of *Dendropoma* reefs.

The studied population was promising for the aim of the study because the *Dendropoma* reef formation hosts a highly diversified gastropod assemblage structured by complex hydro-dynamic gradients. These gradients affect shell shape and size distributions, which range respectively from globose to elongate and from large to small (Chemello et al., 1998). This gastropod assemblage thus offers a wide array of shapes and sizes for crabs to choose from.

Inhabited shells were identified to the species level, weighed (dry weight; 0.01 g) and measured (to the nearest 0.1 mm) using a vernier caliper. Shell variables were: shell length, shell width (measured at the largest whorl), shell aperture height and width (defined with respect to the position of the crab) (Fig. 1). Shells were also assigned to arbitrarily defined conservation conditions: good (not broken), broken (breakage that has clearly modified the shell structure), intermediate (old shell with signs of erosion, but mostly intact). Crabs were sexed using gonopore positions, and sized to the nearest of 0.01 mm by ocular micrometry. Crab measures were: cephalothorax length and width, shield length and width, left and right chelae length and width, and crab fresh weight to the nearest 0.01 g (Fig. 2).

2.2. Statistical analysis

The frequency distribution of each inhabited gastropod species (i.e. the fraction of sampled crabs that uses a specific shell) was

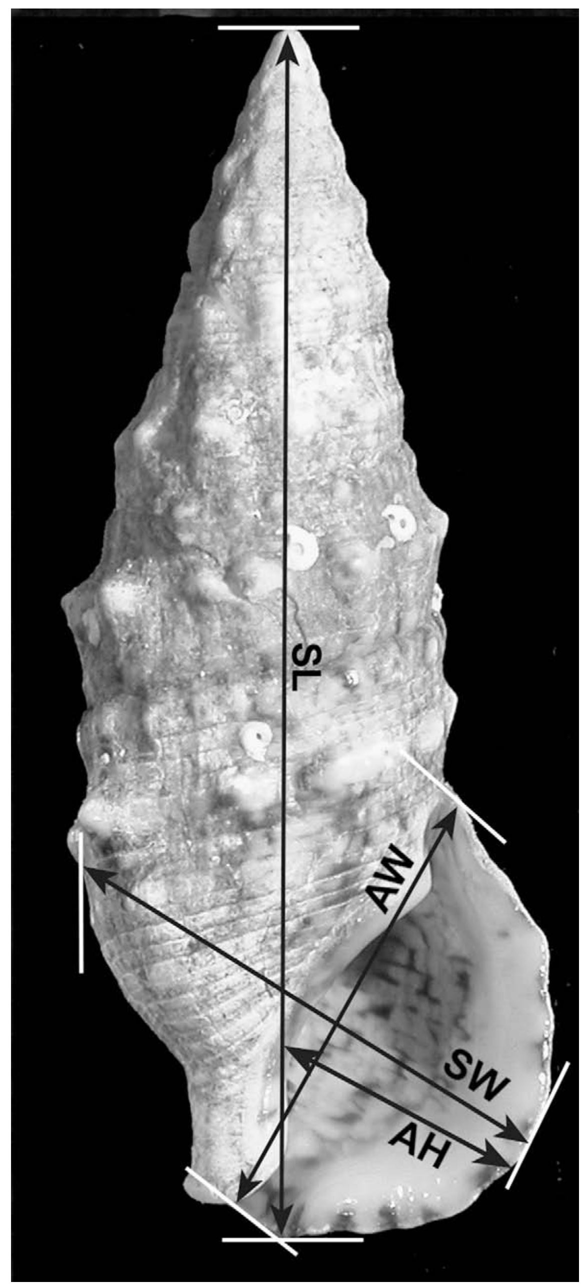

Fig. 1. *Cerithium* sp. shell used by one crab in the studied *Clibanarius erythropus* population. The pictured example shows the shell variables measured for each shell inhabited by a crab: SL, shell length; SW, shell width; AH, shell aperture height; AW, shell aperture width.