Multi-scale phenotype-substrate matching: Evidence from shore crabs (*Carcinus maenas* L.)

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ABSTRACT

Phenotype-environment correlations can be caused by various overlapping ecological processes (e.g. differential mortality, phenotypic plasticity and adaptation) operating over a range of spatial and temporal scales. However, multi-scale studies of the relationship between specific traits and environmental variables are rare, even though such a holistic view may have greater predictive value than the more typical single-scale observations. Here, we investigate the relationship between cryptic colouration and environmental characteristics at a range of spatial scales for the shore crab (*Carcinus maenas* L.), a common intertidal species. Using existing data sets at macro-scale (10,000s m^2) and meso-scale (100s m^2) and previously unpublished data at a micro-scale (<1 m^2) we demonstrate that phenotype-substrate associations in this species are sampling-scale invariant. The association is strongest at the micro-scale, possibly because the advantages of cryptic colouration for visual predator avoidance are dependent on close concordance between prey phenotype and the surrounding substrate. By contrast, correlations at greater spatial scales may reflect longer term processes such as phenotypic plasticity or the accumulated effects of predator mediated differential mortality.

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1. Introduction

Correlations between phenotypic traits and environmental characteristics have been fundamental to the development of evolutionary theory; indeed, adaptation has been defined as conformity between the organism and its environment (Pianka, 1994). However, as recently pointed out by McLachlan and Ladle (2011), adaptation (as inferred from environment-trait correlations) is only apparent within a specific range of space–time frames due to multiple interacting and overlapping ecological processes (Fig. 1). At very small spatial scales and over small times frames animals may seek micro-habitats that 'match' their phenotype (Donnelly and Dill, 1984; Edelaar et al., 2008) and, over slightly larger scales, predators might selectively remove individuals that are poorly matched (Cox and Cox, 1974). Over even longer time periods and larger spatial scales phenotypic plasticity can also result in a match between trait and environment (Pigliucci, 2005; Todd, 2008). When the time period covers several generations then environment-trait correlations may be produced by natural selection on available genetic variability or through evolution by phenotypic assimilation (McLachlan and Ladle, 2011). Finally, biogeographic processes (e.g. adaptive radiation of taxa with traits that enable them to colonize new habitats and geographic areas) can, over geological time frames, produce a degree of environment-trait matching at the crudest level of spatial analysis (Harmon et al., 2009).

The ecological/evolutionary processes outlined above overlap in time and space and it is therefore likely that, for any given spatio-temporal frame of sampling, phenotype-environment correlations will be caused by one or more hierarchically organized ecological processes. By extension, for many traits we would expect a degree of scale invariance where associations with environmental characteristics are detectable at a range of sampling scales, but which are probably driven by different underlying processes. Thus, it is perhaps surprising that there are very few studies that have assessed phenotype-environment correlations at different spatial scales in an attempt to identify and tease apart the relative importance of these processes. Such multi-scale studies have other potential advantages: variation in scale may reveal different patterns for a single ecological phenomenon (Wheatley and Johnson, 2009) or identify trends that any of the individual spatial scales could not have shown. Thus, a phenomenon simultaneously observed at multiple scales provides a more holistic perspective and has greater predictive value in exploring

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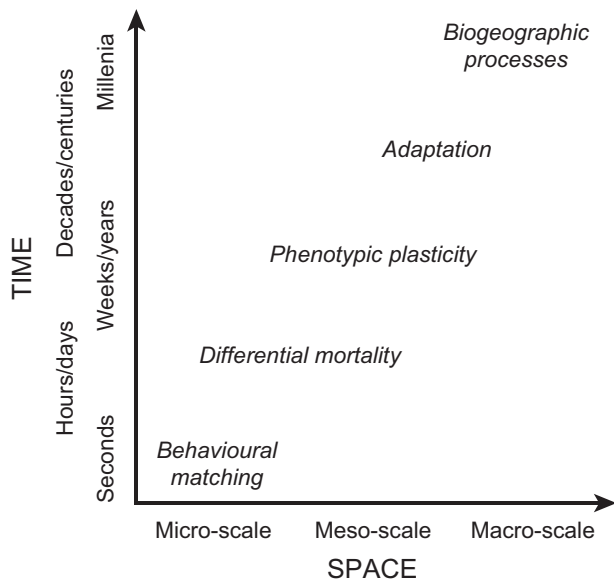*E-mail address:* dbspat@nus.edu.sg (P.A. Todd).

Fig. 1. A hierarchical schemata to explain phenotype-environment correlations. Phenotype matching emerges at different spatial-temporal scales due to multiple interacting and overlapping ecological processes (after McLachlan and Ladle, 2011).

the underlying ecological processes than single-scaled observations (Milne, 1992).

A good candidate for such a multi-scale study is the association between carapace patterns and substrate in shore crabs (*Carcinus maenas* L.), a common intertidal species found in a wide variety of coastal environments (Amaral et al., 2009; Crothers, 1966). The carapace of the mature crab is usually a drab greenish-grey or brown, however, many juveniles and some adults (especially the younger ones) possess patterns of white, and sometimes red, pigmentation (Bedini, 2002; Hogarth, 1975, 1978; Todd et al., 2005, 2006). These patterns vary among individuals, but it is not known whether the patterns are polymorphisms, polyphenisms, or a combination of both genetic and environmental factors (Todd et al., 2006). Various studies have shown a relationship between *C. maenas* morphs and the physical structure of their environment (Bedini, 2002; Hogarth, 1975, 1978; Todd et al., 2005, 2006) and it has been suggested that carapace patterns provide defence against visual predators. The detection of phenotype-environment associations is unsurprising, given that the effectiveness of cryptic (specifically background-matching) phenotypes is dependent on the degree of concordance with their immediate environment (Endler, 1978, 1984; Stevens and Merilaita, 2009). Phenotype-substrate matching in *C. maenas* has previously been demonstrated at both meso-scale (Todd et al., 2006) and macro-scale (Hogarth, 1978), but no studies to date have examined this relationship at the micro-scale.

Here, we provide a multi-scale analysis of cryptic colouration in shore crabs by collating and synthesizing the macro-scale data published by Hogarth (1978) and meso-scale data collected by Todd et al. (2006), and augmenting them with micro-scale data original to this study. Our primary objective is to test the hypothesis that associations between phenotype and substrate in *C. maenas* are scale-independent due to overlapping ecological processes that may include (but are not necessarily limited to) behavioural choice of microhabitat, differential mortality by predators, adaptive phenotypic plasticity and natural selection. Each sampling scale was approximately two orders of magnitude different to the next, i.e. from 10,000s m^2 to 100s m^2 to <1 m^2; large enough to be considered hierarchical shifts in spatial scale (Walker and Walker, 1991).

2. Methods

2.1. Study species

The shore crab *C. maenas* (L.) is a common inhabitant of the British coast, as well as being widespread in some countries of mainland Europe (e.g. Norway and Iceland), Western Africa, and parts of northwestern America (Stewart and Ryland, 1998). It inhabits a large variety of habitat types from the sub-littoral zone to the intertidal area, including rocky shores, salt marshes and estuaries. At an age of three to four years old *C. maenas* reaches terminal anecdysis after going through approximately 18 moults (Crothers, 1966). Most of the young are permanently in the littoral zone, hiding during low tide and emerging to forage at high tide. Adults are more willing to emerge onto the shore when the tide is low but generally move with the tide between the sub-littoral and littoral zones (Edwards, 1958).

2.2. Macro-scale data

Macro-scale data were extracted from Table 2 in Hogarth (1978), representing 35 study shores around the UK that were classified, at the level of the entire *Fucus serratus* zone, as having low (≤10%), medium (11–89%), or high (≥90%) fucoid seaweed cover. For each of these shore types, Hogarth provided the percentage of high and low contrast patterned *C. maenas* (data pooled for the present study) and the percentage of un-patterned crabs. Hogarth (1978) also listed the sample sizes from each shore so it was possible to convert his percentage data into numbers of crabs for additional analysis.

2.3. Meso-scale data

Meso-scale data were retrieved from Todd et al. (2006) who collected *C. maenas* from three shores situated to the east of Edinburgh along the southern shore of the Firth of Forth, Scotland. Within each of these shores, crabs were collected from 15 large (10 × 40 m) quadrats and classified into eight morphs: seven patterned (pooled into 'patterned' for the present study) and one plain. The substrate in every quadrat was determined using line intercept transect methodology (English et al., 1997), i.e. the quantity of each of eight substrate types that was encountered under a nylon tape was measured. The 6000 m^2 area sampled from each shore can be thus be described by the ratio of (polychromatic) mussel-bed cover to (more monochromatic) algae&rocks ('rocks' for the present study being pooled data for 'rock and barnacle', 'bare rock' and 'rocks'). The mussel-bed:algae&rocks ratios for the three shores are as follows: Ferny Ness (41:42), Long Craigs (13:69) and Milsey Bay (0:78).

2.4. Micro-scale data

During the summers of 2003, 2004 and 2005, *C. maenas* from six Scottish shores were sampled, i.e. those near North Berwick, Longniddry, Dunbar, Seahouses, Brighouse, and Beadnell. All sites hosted a variety of habitats. Crabs were collected from within 0.5 m^2 quadrats, positioned so that only one substrate was represented. The patches of substrate that the quadrats were placed on were generally quite small (1–10 m^2), therefore the opportunity for the crabs to move among different habitats during their natural activities remained. Thorough searches were conducted which included disturbing the substratum; all crabs were recorded as plain or patterned before being placed in aquaria for release at the end of the sampling occasion. Altogether, a total of 70 'macro-algae quadrats', 60 'rocks quadrats', and 30 'mussel quadrats' were deployed, distributed approximately evenly both temporally (2003–2005) and spatially (among the six shores).