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Behaviour of mobile macrofauna is a key factor in beach ecology as response to rapid environmental changes

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ABSTRACT

Sandy beach animals show behavioural adaptations that are expressed as contingencies during the life history of individuals to face periodic and episodic environmental changes. Such adaptations include activity rhythms, orientation, zonation, burrowing, escape responses and feeding strategies, the first two being common adaptations to all mobile animals. The complex conditions of a particular beach environment may be integrated in a learning process enhancing the adaptation and survival of individuals and eventually of populations. Evidence exists of genetic determination of some behavioural features that are adaptive in the long term (throughout generations) by increasing individual survival and reproductive potential. The environmental features integrated with the life history of beach animals shape the individual behaviour through ontogenetic processes, as well as population behaviour through evolutionary processes. Thus, behavioural differences among individuals may reflect environmental variation at the local and small/medium temporal scales of beach processes, whereas within-population behavioural coherence and differences among populations may reflect variation at the geographic scale. The different foci stressed by different authors and the variety of evidence dependent upon local geographical and ecological conditions have often resulted in compartmentalised explanations, making generalizations and the repeatability of behavioural studies of beach ecology challenging. There was a need to developing a more synthetic paradigm for beach animal behaviour. This paper gives a brief overview of the theoretical background and keystone studies, which have contributed to our understanding of animal behaviour in sandy beach ecology, and proposes testable hypotheses to be integrated in the beach ecology paradigm.

1. Introduction

Behavioural adaptations are key features in sandy beach ecology and are expressed as prompt and flexible responses to environmental changes (Brown, 1996; McLachlan and Brown, 2006). Behaviours are contingencies by definition, i.e. *hic et nunc* reactions, occurring in a particular place and at a particular time, modifiable by internal and external factors and individual experience (Campan and Felicita, 2002). Behaviour has a key role in evolutionary processes, as it contributes to maintain the populations in a suitable environment throughout, thus permitting the selection of adaptations to particular environmental features; behaviour may also favour the colonisation of new environments and introduce novelty that may help animals in facing unpredictable, potentially stressful events.

On sandy beaches, the mobile macrofauna are arrayed in zones extending from the sea to the dunes (McLachlan and Brown, 2006). These zones span environmental changes, such as sediment grain size, moisture, temperature, salinity, organic content and pH gradients, as well as the physical actions of waves, winds and run-off (Colombini et al., 2002). Mobile beach animals respond to environmental changes or stressful physical and chemical factors by moving away from unsuitable beach zones to reach more favourable ones, thus optimizing their living conditions. It has been stressed that physical constraints determine the community distribution on sandy beaches (McLachlan and Brown, 2006; Defeo et al., 2009). The physical and chemical gradients across the shore may guide the animals' movements on the beach-dune system, according to their ecological needs, eventually generating an overall community zonation that, in turn, may modify some characteristics of the beach ecosystems, not only in terms of community distribution and abundance (Defeo et al., 1997), but also because the action of burrowing into the sand may mix the sediments and render them more incoherent and mobile (Dorgan et al., 2006).

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Navigation mechanisms are expressed by beach animals that are able to return to specific points on the beach (goal orientation) or the most suitable beach zone (zonal orientation) from a distant point, not directly connected to the goal (Pardi and Ercolini, 1986). In this case, navigation across a beach may be guided by opposite features occurring seawards or landwards, which determine the sea–land axis, or may refer to geographical coordinates, such as celestial and astronomic cues or the geomagnetic field. Pardi and Ercolini (1986) defined these cues as local (linked to the beach features) and universal (not specific to the beach environment), respectively. Navigation may be a complex process, including different mechanisms, such as tactic movements (oriented responses to light, dark shapes, beach-slope, winds or waves, etc.) and biological clocks that drive the expression of orientation depending on the needs (e.g., feeding, mating, releasing of eggs/larvae) and threats (e.g., dehydration or submersion by waves and tides) (Fig. 1). Several studies have thrown light on the temporal features of zonation and navigation that are clearly linked to the natural rhythms of environmental changes (tidal, diel, semilunar, lunar and seasonal) and in some cases are supported by a system of internal (biological) clocks (Naylor, 1988, 2005, 2010; Palmer, 1995; Ugolini, 2003). A variety of evidence has demonstrated that beach animals use different cues and mechanisms to navigate on beaches, dependent on the population and/or environmental features (Felicita, 1997, 2006, for beach amphipods).

The present review seeks to compare the various perspectives on behavioural adaptation of mobile beach macrofauna, which have emerged in beach ecology since the first classic studies performed in the 1950s (Williamson, 1951a,b; Pardi and Papi, 1952, 1953). It is a critical presentation of previous research, aiming at integrating behavioural adaptation into the existing paradigm of beach ecology and fostering the development of a modified one that includes behavioural development and evolution.

In the study of behavioural adaptation to sandy beaches, different research groups/leaders/schools developed and proposed different hypotheses based on observations under different local conditions, particularly related to various climatic conditions and tidal regimes. The different foci stressed by different authors and the variety of evidence dependent upon local geographical and ecological conditions have often resulted in compartmentalised explanations, making generalizations and the repeatability of behavioural studies of beach ecology challenging. In some cases, the hypotheses, supported by sound arguments and strong experimental evidences, were developed into paradigms that have guided further research on behavioural adaptation to sandy beaches. To overcome the difficulty of conducting experiments on the movements and orientation of animals under natural conditions, where multiple factors may influence behaviour, appropriate statistical methods have been developed to test hypotheses on behavioural responses under (changing) natural conditions (Underwood and Chapman, 1985; Marchetti and Felicita, 2003). The differences observed between the experimental results of different workers may well be a result of the natural variety of adaptations that are the core of the evolutionary processes driven by natural

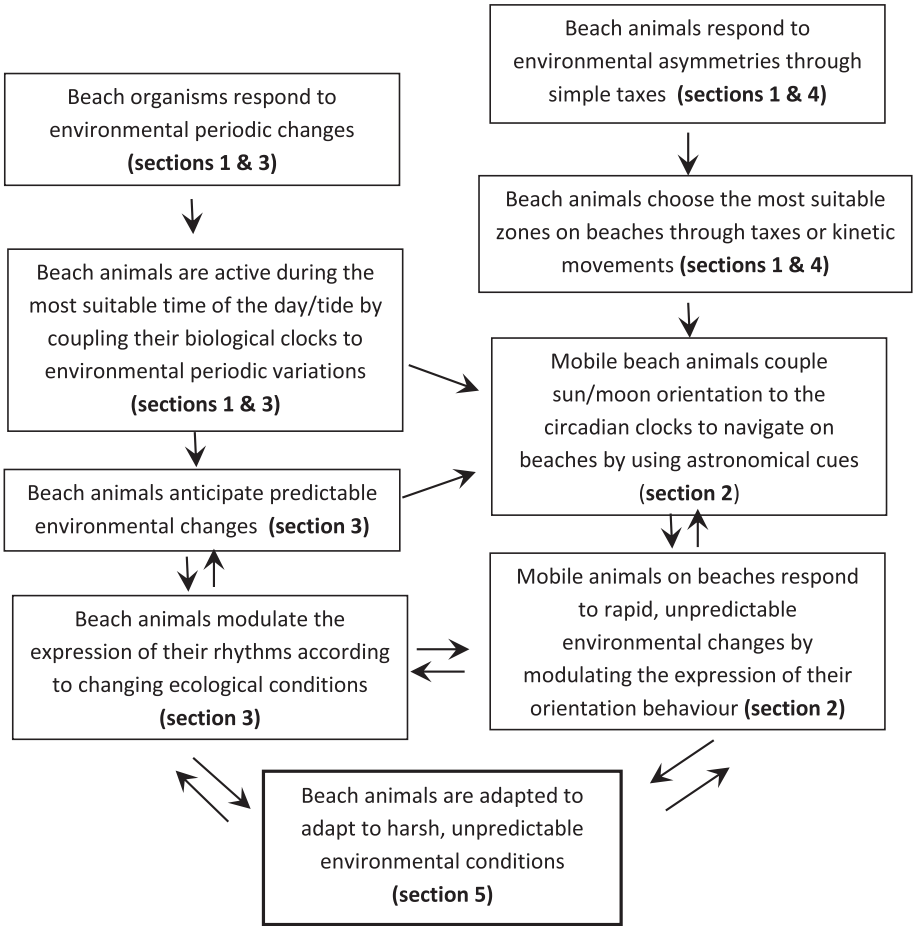

Fig. 1. Hypotheses including behaviour in sandy beach ecology. On the left, the time components of behaviour are listed; on the right the spatial components. The manuscript sections, where the behaviours are referred to are noted in each box.