Journal of Experimental Marine Biology and Ecology 473 (2015) 195–201

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Barnacle settlement on rocky shores: Substratum preference and epibiosis on mussels

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ARTICLE INFO

Article history:
Received 15 December 2014
Received in revised form 10 September 2015
Accepted 11 September 2015
Available online 20 September 2015

Keywords:
Barnacle settlement
Settlement
Rocky shore
Substratum choice

ABSTRACT

Understanding the dynamics of epibiosis is fundamental to understanding the role of biological interactions in the functioning of marine ecosystems. At many coastal sites, barnacles are abundant as epibionts on the shells of mussels. As they approach the shore, cypris larvae explore the environment, actively seeking suitable settlement sites and rejecting unsuitable substrata. Suitability involves micro-features of the surface, including its texture and contours, chemical signals and the presence of conspecifics. To investigate whether epibiosis on mussel shells indicates a preference for this substratum on the part of the barnacle *Chthamalus dentatus*, artificial plates were deployed at two rocky shore sites on the south coast of South Africa. These plates offered settling cyprids four habitat choices: a live mussel, the shell of a recently dead mussel, a fine resolution resin replica of a mussel shell to mimic architectural micro-surface, without the chemical characteristics of natural shells and a rock mimic, a surface covered in a film of hard plastic that resembled natural rock surface as closely as possible. Settling surfaces were photographed monthly, and new barnacles were counted and allocated to size classes, so that survival could be estimated over a period of several months. Barnacles showed a clear preference for the rock mimic surfaces, which on average supported double the number of settlers found on mussel replicas. These in turn were significantly higher than the numbers on live and dead mussel shell surfaces, implying that there are features of both dead and live mussel shells that deter barnacle settlement. In contrast, final abundances of adults showed no significant effect of settling surface. The results suggest that during settlement, cyprids avoid chemical cues from mussel shells that persist even after the death of the mussel. This suggests that the high numbers of barnacles often found on the surface of live mussels could be due to saturation of substratum.

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1. Introduction

Marine benthic organisms frequently show initial settlement patterns that are highly variable in space and time. Following settlement on a hard substratum, post-larval stages experience high rates of mortality through interactions with each other, as well as other species, while facing the effects of abiotic stressors (Pineda et al., 2009). As a result, post-settlement mortality (mortality immediately after settlement), is an important determinant of species success, defining the distinction between settlement and recruitment (Connell, 1985; Minchinton and Scheibling, 1993; Porri et al., 2006). Recruitment can be regarded as the rate at which juveniles join the adult population (i.e. become sexually mature), or as the number of juveniles that survive for a defined period of time after settlement (Bayne, 1964; Connell, 1985; Pineda, 2000). For benthic invertebrates, this period is usually a few days or weeks, after which mortality rates decline markedly (Connell, 1985; Nakaoka, 1993; Pineda et al., 2009). In the case of sessile organisms, the selection of the settlement site is particularly critical as it has an enormous influence on post-settlement mortality and overall fitness.

Barnacles are sessile and exhibit spatial patterns of settlement that reflect the effects of several, at times opposing, factors. These include a preference for cracks and pits (Crisp and Barnes, 1954), gregarious larval behaviour (Knight-Jones, 1953; Crisp and Meadows, 1962, 1963) and the need to maintain sufficient inter-individual distance to allow for growth within the maximum spacing that will allow internal fertilisation (Crisp, 1990). Barnacles are well known to show preferences for settlement sites (Crisp, 1961) and once cyprids reach the near shore environment, they actively seek out and evaluate the micro-environment, rejecting unsuitable positions (e.g. Rittschof et al., 1984). What constitutes a suitable position involves the micro features of the surface, its texture and contours and the presence of conspecifics. Surface topography can be classified according to scale, as texture (the irregularities of the surface that are smaller than the larvae) and contour (irregularities larger than the larvae) (Le Tourneux and Bourget, 1988). One measure of texture is roughness and most studies have shown that

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http://dx.doi.org/10.1016/j.jembe.2015.09.006
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surface roughness generally promotes barnacle settlement (see review in Berntsson et al., 2000a). There are also chemical cues to settlement, for example from conspecifics (Knight-Jones, 1953; Crisp and Meadows, 1962, 1963; Chabot and Bourget, 1988; Raimondi, 1988), and final larval choice at settlement will involve a combination of chemical and physical cues (Wethey, 1984). Selection of microhabitat, at scales of heterogeneity larger than 10 cm, in combination with the presence of conspecifics, at scales smaller than 1.5 cm, seems to drive settlement of *Semibalanus balanoides* (Chabot and Bourget, 1988).

A more cryptic factor influencing barnacle settlement may be the bacterial film that develops on surfaces that have been immersed in the sea and many marine larvae settle readily on such surfaces (Zobell and Allen, 1935; Tighe-Ford et al., 1970), though Maki et al. (1988) and Nasrolahi et al. (2012) found that bacterial films generally inhibited the attachment of barnacle larvae. Larval age is important, with older larvae attaching more readily to clean surfaces that lack a biofilm than younger individuals, perhaps an example of the desperate larva hypothesis (Knight-Jones, 1951, 1953).

By increasing surface complexity, the shells of bivalves in the intertidal increase the available surface for larval settlement. Despite the fact that shells offer substantial space, mytilids often appear to support fewer fouling organisms than adjacent non-biological substrata (Wahl et al., 1998; Bers and Wahl, 2004). One possible explanation is that many marine species have evolved behavioural, chemical, physical or mechanical defence mechanisms to prevent or minimise epibiotic settlement (Wahl, 1989). Given the possibility of harmful effects of epibiosis, one might expect surfaces of endemic species to evolve preventative measures to inhibit the settlement of local epibionts, while cosmopolitan species should show a generalised antifouling strategy (Bers et al., 2006). The texture of the periostracum influences the antifouling capacity of the shells of the mussel *Mytilus edulis* (Wahl et al., 1998; Bers and Wahl, 2004) and *Mytilus galloprovincialis* (Scardino et al., 2003) and there are indications of adaptation to local and abundant epibionts (Bers et al., 2006). The periostracum can inhibit damage to mussel shells by boring endolithic organisms (Kaehler, 1999) and general fitness is improved by an intact periostracum texture, which reduces the incidence of epibiosis on *M. galloprovincialis* (Scardino and de Nys, 2004).

It is clear that settlement is affected by factors that operate across a wide range of scales, from kilometres to sub-millimetres (Pineda, 2000), and settlement of barnacles may be limited by multiple elements, from planktonic larval supply (Buschbaum, 2000), linked to oceanic and tidal features (Raimondi, 1990; Pineda, 1994; Hills and Thomason, 1996), to micro-heterogeneity of the available surface (Le Tourneux and Bourget, 1988). The choice of settlement sites by sessile organisms on rocky shores is especially important, as it determines their final position, directly influencing the structure of the intertidal assemblage (reviewed by Chan and Høeg, 2015). In the case of epibiosis, this also affects biological interactions within the community, including those between epibiont and host (Laihonen and Furman, 1986; Garner and Litvaitis, 2013). In order to clarify whether the selection of mussels as a settlement substratum by barnacles is due to active choice, and how such choices affect survival, we addressed the question of whether the physical and chemical properties of mussel shells influence barnacle settlement and their survival to adulthood. We hypothesised that the surface texture of mussel shells and chemical properties of their periostracum would deter barnacle settlement and reduce barnacle survival.

2. Methods

Artificial plates were deployed at two rocky shores separated by approximately 10 km on the south coast of South Africa: Beacon Isle (34°3′ 35″ S; 23°22′ 49″ E) and Keurboomstrand (34°0′ 18″ S; 23° 27′ 30″ E). Both sites are situated within Plettenberg Bay and mussels at both sites experience high levels of epibiosis by barnacles (per. obs.).

2.1. Experimental set up

The following four treatments (termed settling surfaces, hereafter) were fixed to perspex plates for attachment to the shore: live mussels, dead mussels (shell only), resin shells (fine-resolution replicas of shells to mimic the architectural micro-surface but not the chemical characteristics of natural shells) and a rock mimic. Settling surfaces were deployed haphazardly within the mid mussel zone. Live mussels were collected two days prior to field deployment and kept alive in aerated sea water, at ambient temperature (21–25 °C), with the water being changed daily. The dead shell surface was prepared by scraping out the soft tissue, drying the shells and filling the two halves with two-component epoxy adhesive (Abe epidermix 372). The valves were glued back together using clear, two-component epoxy (Alcolin rapid-epoxy) and left for 24 h to set. This was done approximately 24 h before deployment to ensure the periostracum was as intact as possible and its chemical characteristics still present. Resin replicas were made from natural mussel shells from which the soft tissues had been removed. This methodology has been successfully applied to separate the effect of microstructure and shell chemistry (Marrs et al., 1995; Bers et al., 2006; Bers et al., 2010). The shells were then gently washed and dried. Moulds were made of the outer surfaces of the two valves separately, using silicone (Loctite, RTV Silicone 587, Blue 80 ml Tube). These moulds were left to set for 20 to 30 min at room temperature. Resin was mixed at the ratio of 5 ml of catalyst to 300 ml of resin, kept bubble-free by slowly stirring for five minutes. The resin was then carefully poured into the silicone moulds and left overnight to cure at room temperature. Once solid, the resin casts were removed from the moulds and the two halves of the replica mussel were glued together as above.

Live, dead and replica mussels were glued onto clear, perspex plates that had been roughened for better attachment. The rock mimic surfaces were settlement plates that had a film of hard plastic (3M™ Safety-Walk™, Medium duty, Grey) that resembled natural rock surface as closely as possible, attached to them. All settlement plates were 8.0 × 5.5 cm in size and the mussels used for all settling surfaces were *Perna perna* of 3.0–5.0 cm shell length.

Settlement plates were attached to the rocks using battery powered drills and self-tapping screws. Prior to the attachment of the settlement plates, the immediate area around each plate was scraped clean of any barnacles or mussels to avoid attraction by conspecifics. On 8 March 2012, at Beacon Isle, 44 plates ($n = 11$) were arranged within the mid mussel zone, covering a total along-shore stretch of 10 m, while, at Keurboomstrand, 40 plates ($n = 10$) were arranged, across 15 m of shore, on 6 April 2012. All plates were removed in August 2012.

2.2. Data collection

Photographs of each plate were taken every month and new barnacles (*C. dentatus*) on all settling surfaces were counted, using ImageJ 1.45 software. The dates of sampling at Beacon Isle were: 6 April 2012; 7 May 2012; 7 June 2012; 20 July 2012; 4 August 2012, while at Keurboomstrand, they were: 7 May 2012; 7 June 2012; 20 July 2012; 4 August 2012. Barnacles were also allocated to a size class, so that survival over the months could be estimated. Barnacles were divided into size classes on the basis of the basal diameter as follows:

Size class I: visible to the naked eye – 1.00 mm.
Size class II: 1.01 mm – 2.50 mm.
Size class III: 2.60 mm – 3.50 mm.
Size class IV: 3.60 mm – 5.50 mm.

Chthamalus fissus reaches maturity at a basal diameter of 2 mm (Hines, 1978). In the absence of data on size at sexual maturity for our species, we took the conservative approach of considering class IV individuals to be adult.

Prior to analysis, the counts for the rock mimic plates were adjusted by taking the area of the plastic film attached to the plate and scaling it to correspond to the average area of the other mussel shells used.

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