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Arctic field experiment shows differences in epifaunal assemblages between natural and artificial substrates of different heterogeneity and origin

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ABSTRACT

Many studies have the aim of increasing our knowledge on settlement and colonization of epifauna. Despite broad interest these important processes have proved to be very complex and there are still issues which need more attention. Experiments presented here, performed in the Arctic, aim to explore colonization of epifauna on hard substrates in relation to: (1) site, (2) depth, and (3) substrate characteristics (i.e. heterogeneity and biotic/abiotic origin). Three different substrate types (pebbles, empty *Buccinum undatum* shells and artificial shells made of granite) were prepared and deployed on the seabed in four Arctic sites (two at Spitsbergen 78°N, two in Northern Norway 69°N) for one year. After recovery, epifaunal assemblage structure, species richness, abundance, and Shannon-Wiener diversity of each substrate was estimated, subjected to a three-factor fixed experimental design and analysed using permutational multivariate analysis of variance (PERMANOVA). As hypothesized, site (i.e. colonizer species pool, local environmental conditions) explained most of the variation, and proved to be most influential factor in determining epifaunal assemblage structure. However, where the spatial scale of investigation was lower, as at Spitsbergen where study sites were in close vicinity (2 nm apart), factors that varied with depth (e.g. macrofaunal cover) predominated. The study indicated that epifaunal assemblages are influenced to a different degree at various sites. Depending on the region (Spitsbergen or Northern Norway), the substrate surface area or substrate type were the least important factors, but still made some contribution. Results suggest also that among substrate features surface heterogeneity is of high importance, higher than its biotic/abiotic character. In most of the cases rough surfaces of artificial shells supported the highest species richness, abundance and diversity.

1. Introduction

Settlement and colonization of benthic habitats by marine invertebrates is determined by the composition of the colonizer source species pool and a complex set of factors, which include physical, chemical and biological components (Osman, 1977; Harms and Anger, 1983; Wahl, 1989; Rodriguez et al., 1993; Fernandez-Leborans, 2010; Pineda et al., 2010). Among the most commonly studied features are the properties of the substratum (Kuklinski et al., 2006) as larvae frequently exhibit specific preferences for surface settling (Fernandez-Leborans, 2010 and references therein) and are sometimes found only on one type of substrate (e.g. Jirkov, 2001). Investigations emphasising the role of different factors influencing epifaunal settlement include studies focusing on substrate: size (Jackson, 1977), orientation (Glasby, 2000), contour, texture (heterogeneity) (Crisp and Barnes, 1954; Crisp, 1974), chemical composition (Little et al., 1986; Bavestrello et al., 2000; Rodriguez et al., 1993), thermal capacity, colour and electrical charge (Holmes et al., 1997). The role of biofilms (Maki et al., 1992; Faimali et al., 2004), already attached species, including conspecifics (Crisp, 1961; Keough, 1998), light conditions (Crisp and Barnes, 1954), and available food resources (Kuklinski et al., 2005) have also been studied.

Gastropod shells protecting hermit crabs are used as a substrate by a variety of epibionts (Williams and McDermott, 2004; Balazy and Kuklinski, 2013). The vast majority of hermit crab populations are shell limited which means that they are restricted to specific shell sizes, and to shells of different gastropod species (Kellogg, 1976; Balazy et al., 2015). This creates large spectrum of substrate sizes and shapes which serve as a perfect model system to study the influence of substrate properties on epifaunal settlement patterns. Previous work (Balazy et al., 2016), where hermit crabs served as model organisms representing a hard mobile substrate, showed that crab host species, local species pools and local environmental settings significantly affected epifaunal assemblages. Additionally, the substrate identity (i.e. gastropod shell inhabited by the hermit crab) was also of

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significance. Whether this is an effect of shell shape complexity, or its biogenic character is still not clear (but see Balazy and Kuklinski, 2013). Movement of shells inhabited by hermit crabs, as well as crab "messy feeding" behaviour, is believed to influence their epifaunal assemblages – it can increase epifaunal species richness and abundance when compared with similar substrates that do not share these properties, such as rocks of an equivalent size (Balazy and Kuklinski, 2013).

In this study we designed a field experiment to test the impact of substrate complexity and its biogenic characteristics on the structure of epifaunal settlement. The experiment has a fully stationary character; with substrates for colonization fixed to the seabed rather than mobile as is the case with crab shells. This was intended to exclude those variables (e.g. shell movement, plus no food supply) which could influence the structure of epifauna on the shell. This study aims to explore colonization of epifauna in relation to site, depth and substrate characteristics (heterogeneity and biotic/abiotic origin) using underwater field experiments deployed over a large geographic scale ranging from metres to thousands of kilometres. The strategy is intended to test whether potential influence of shell shape complexity, or biotic character, is restricted to the local environment or occurs over a large scale. The degree to which large scale processes, including hydrology or different local species pools influence observed patterns is also of interest. Based on our previous work (Balazy et al., 2016) we hypothesize that factors describing local conditions, for example colonizer species pool, environmental attributes and depth, are likely to exert a major influence over the substrate characteristics. Among substrate features (i.e. heterogeneity, biotic/abiotic origin) we anticipate surface heterogeneity to be the strongest.

2. Material and methods

2.1. Experimental set-up

For the purpose of the experiment three types of substrates (pebbles, empty *Buccinum undatum* shells and artificial shells) were prepared. Pebbles and empty *B. undatum* shells were collected from the sea bottom at each of the experiment localities. All flora and fauna covering the shells was cleaned off. Artificial shells, resembling the shape and texture of natural *B. undatum* shells, were made of granite (Fig. 1). Pebbles (average surface area of 92 cm^2) were larger than artificial shells (on average 83 cm^2). Empty *B. undatum* shells were the smallest (with an average area of 54 cm^2). Ten items of each substrate type were bolted to a single metal frame forming three rows (Fig. 2). In August 2009 frames with substrates were placed by SCUBA divers at the sea bottom, secured with rocks to make them less susceptible to water movement, and left for one year at either of two depths (shallow – 6 m, and deep – 12 m) at each of the four sites (two sites at Spitsbergen Island in Isfjord - S1, S2; and two in Northern Norway – T1 Kvalsund, T3 Grotfjord; Fig. 3). The Spitsbergen sites (two nautical miles apart) consisted of hard bedrock shelves with sediment patches and similar environmental characteristics. Shallower depths were typically covered with dense kelp forests while deeper rocky barrens were colonized by diverse and abundant epibenthos. The Northern Norway sites consisted of a mixed bottom with pebbles, cobbles and boulders overlying coarse sand and gravel. Both regions (Spitsbergen and Northern Norway) are under the influence of warm North Atlantic Current, and thus although there is a high Arctic setting the Isfjord hydrology is more typical of sub-Arctic conditions. Descriptions of environmental settings of experimental sites are described in more detail in Balazy and Kuklinski (2013) and Zmudczyńska-Skarbek et al. (2015, see SEABIRD site).

Fig. 2. One of the metal frames with the three substrate types prior to deployment on the sea bed.

2.2. Protocol

In August 2010 after one year of deployment, frames with experimental substrates were recovered from the sea floor and epifauna on the substrata was analysed. The external surface area of each experimental substrate was calculated according to the method of Bergey and Getty (2006). Each shell was wrapped carefully in a thin layer of aluminium foil and any overlapping or excess foil was trimmed off. The foil was weighed (B) and the surface area (SA) was calculated from the equation $SA = 0.0495 + 413.59 * B$, $R2 = 0.948$ (this equation was obtained after weighing pieces of foil of known surface area). All organisms larger than 1 mm directly attached to a pebble, *Buccinum* sp. shell and artificial shell were identified to the lowest possible taxonomic level (typically species level). Identification of sedentary polychaete species was made according to Jirkov (2001) from tube morphology

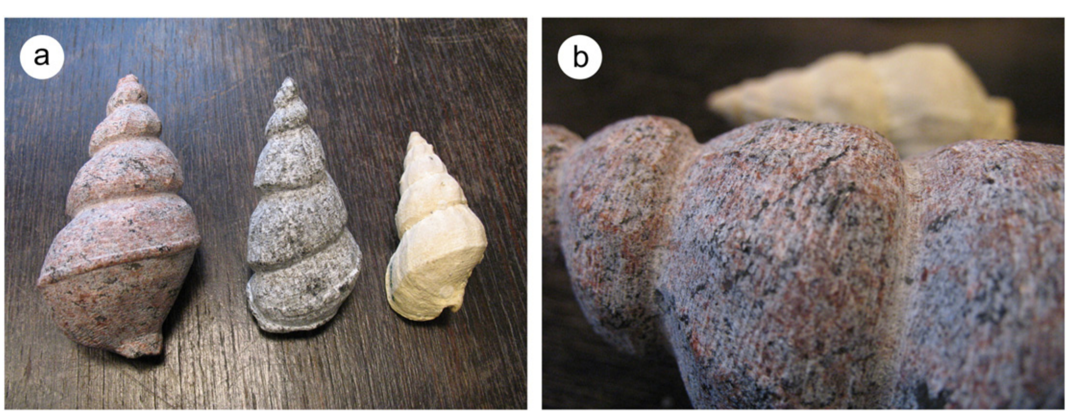

Fig. 1. Artificial shells made of granite (the two largest) and a natural shell of *Buccinum undatum* (a), and magnification of the uneven surface of an artificial shell (b).