



Post larval, short-term, colonization patterns: The effect of substratum complexity across subtidal, adjacent, habitats

Sara García-Sanz^{a,*}, Fernando Tuya^a, Pablo G. Navarro^b, Carlos Angulo-Preckler^c, Ricardo J. Haroun^a

^a BIOGES, Department of Biology, Marine Sciences Faculty, Campus Tafira, Universidad de Las Palmas de Gran Canaria, Canary Islands, 35017 Tafira, Las Palmas, Spain

^b ICCM, Instituto Canario de Ciencias Marinas, 35200 Telde, Gran Canaria, Canary Islands, Spain

^c Department of Animal Biology (Invertebrates), Biology Faculty, Universitat de Barcelona, 08028 Barcelona, Catalunya, Spain

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ABSTRACT

Benthic habitats are colonized by organisms from the water column and adjacent habitats. There are, however, variations in the 'acceptability' of any habitat to potential colonists. We assessed whether the structural complexity of artificial substrata affected patterns of short-term colonization of post larval faunal assemblages across subtidal habitats within a coastal landscape. Specifically, we tested whether short-term colonization patterns on 3 types of artificial substrata encompassing a range of complexities, including a leaf-like unit, a cushion-shaped leaf-like unit and a cushion-shaped unit, were consistent across 4 adjacent habitats: macroalgal-dominated bottoms, urchin-grazed barrens, seagrass meadows and sandy patches, at Gran Canaria (eastern Atlantic). A total of 16,174 organisms were collected after 4 weeks and 4 taxonomic groups (Crustacea, Chordata, Echinodermata and Mollusca) dominated the assemblage. Despite considerable among-taxa variability being observed in response to habitat effects, the total abundance of colonizers, as well as the abundance of Arthropoda, Chordata and Echinodermata, was affected by the habitat where collectors were deployed, but did not differ among types of collectors. Similarly, the assemblage structure of colonizers was mainly affected by the habitat, but not by the type of collector; habitat contributed to explain most variation in the assemblage structure of the four dominant taxonomic groups (from ca. 5.44–19.23%), and obscured, in all cases, variation explained by the type of collector. As a result, the variation in short-term colonization patterns of faunal assemblages into artificial collectors was mostly affected by variation associated with habitats rather than by differences in the structural complexity of collectors. The largest abundances of colonizers, particularly Echinodermata, were found on sandy patches relative to other habitats, suggesting that the 'availability', rather than any particular attribute related to the 'acceptability' of artificial collectors, e.g. its structural complexity, was the main driver of patterns of faunal short-term colonization.

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1. Introduction

Benthic subtidal habitats are continually colonized by organisms from the water column, mainly as juveniles through larval dispersal, and organisms migrating from adjacent habitats, mainly as sub-adults and adults through crawling, active swimming, rafting on the surface of the water, or being transported passively by wave action (Underwood and Keough, 2001; Chapman, 2002). There are, however, variations in space and time in the suitability or 'acceptability' of a habitat to potential colonizers (Singer, 2000). The selection of any habitat by the potential pool of colonizers depend on, amongst other factors, the physical characteristics, as

the architecture of the habitat (Srinivasan, 2003) and sensory signs (Gardner et al., 2005) that include sensory cues related to the presence of benthic organisms (conspecifics living in the surroundings of any habitat (Lecchini, 2005; Wright et al., 2005)). An understanding of the effects of these factors is needed to explain the spatial and temporal patterns in adult abundances.

The structural complexity of any benthic habitat is a key attribute to explain patterns in the arrival of new colonizers (Bourget et al., 1994; Beck, 2000; Kelaher, 2003; Jenkins et al., 2009). For example, it has long been recognized that benthic habitats with a high structural complexity provide new, small-sized, colonizers with a shelter against predators (e.g. Robertson and Blaber, 1992; Nagelkerken et al., 2000; Hereu et al., 2005). Our understanding, however, is biased towards observational, rather than experimental studies. This precludes a general assessment of the importance of habitat complexity as a factor affecting patterns of colonization of

* Corresponding author.

E-mail address: sarags81@yahoo.es (S. García-Sanz).

subtidal biota, particularly across a range of coastal habitats (Underwood and Keough, 2001).

Artificial Substrata (hereafter ASs) provide a unique opportunity to test specific models of colonization patterns into new habitats by faunal assemblages (e.g. Olabarria et al., 2002; Underwood and Chapman, 2006; Cole et al., 2007; Rule and Smith, 2007). These artificial habitats may attract most elements of the mobile fauna in their near vicinity. Our perception of the relative importance of different ecological mechanisms on patterns of colonization into ASs is, however, rather limited (Rule and Smith, 2007; Chapman et al., 2008). Indeed, most studies using ASs have exclusively analyzed patterns of colonization into ASs across a set of spatial and temporal scales, as a way to indirectly infer the relative importance of different ecological mechanisms. Patterns of colonization of faunal assemblages in any AS are likely to be influenced by the structural complexity of collectors; for example, there are larger numbers of species and individuals on highly-complex artificial substrata than on smooth, low complexity, substrata (Christie et al., 2007). However, differences in complexity between types of ASs can be confounded by differences in the amount of available habitat provided by ASs, because often the more complex an AS is, the larger the amount of provided habitat is. In fact, the potential separate effects of complexity and area on species richness and abundance have rarely been addressed (Johnson et al., 2003) and, therefore, statistical routines that specifically correct this issue should be implemented, for example, through the use of covariates (Kostylev et al., 2005).

In parts of temperate coasts of the world, habitats occurring at small scales ($<10^2$ m) are arranged in mosaics within large landscapes ($>10^3$ m). These habitats can vary substantially in the composition and abundances of their associated biotas (e.g. Taylor and Cole, 1994; Tuya et al., 2008), which may reflect changes in the intensity of ecological mechanisms among habitats, such as the arrival of new individuals. For example, colonization by polychaetes into ASs was notably influenced by the type of biogenic habitat (the 'matrix of habitats') that surrounded ASs in the intertidal (Cole et al., 2007).

This study aimed to assess whether the structural complexity of artificial substrata affected patterns of short-term colonization of post larval faunal assemblages across a range of subtidal habitats arranged in mosaics within a coastal landscape. Specifically, we tested whether short-term colonization patterns in 3 types of ASs, encompassing a range of substratum complexities, were consistent across four subtidal habitats: algal-dominated rocky bottoms, rocky urchin-grazed barrens, seagrass meadows and sandy patches that are arranged in mosaics within landscapes in the eastern Atlantic.

2. Materials and methods

2.1. Study area

This study was carried out at two localities off the east coast of Gran Canaria (Canary Islands, Spain): Risco Verde ($27^{\circ}51'25.94''$ N,

$15^{\circ}23'10.26''$ W) and Playa del Cabrón ($27^{\circ}52'14.43''$ N, $15^{\circ}23'00.31''$ W) (Fig. 1). Both localities encompass a mosaic of subtidal, neighboring, habitats, including seagrass meadows constituted by the marine phanerogam *Cymodocea nodosa* and sandy patches on soft substrata, as well as urchin-grazed barrens and macroalgal-dominated beds (mainly dominated by the frondose fucoid genera *Cystoseira* and *Sargassum*, as well as *Dyctiota* spp., *Padina pavonica* and *Lobophora variegata*) on adjacent rocky substrata. All habitats are found interspersed at ca. 5–10 m depth.

2.2. Type of collectors

Three types of ASs were designed, based on previous studies (e.g. Phillips and Booth, 1994; Butler and Herrnkind, 2001; Phillips et al., 2006), to encompass a range of substratum complexities (Fig. 2). A Leaf-Like Unit (LLU, Fig. 2a) consisted of a plastic mesh frame (50 cm², 2 cm of diameter of mesh size) to which artificial leaves (green plastic raffia, 35 cm long and 10 mm wide) were attached every ca. 4 cm. Raffia is positively buoyant underwater and so floats upright. The Cushion-shaped Leaf-Like unit (CLLU, Fig. 2b) was the same collector as the LLU, but folded as a cushion. A total of 75 cm² of concealment gardening mesh (≤ 1 mm diameter) was included inside, creating small holes and shelters. Finally, the Cushion-shaped Unit (CU, Fig. 2c) was morphologically identical to the CLLU, but without the artificial leaves. The amount of habitat provided by each type of collector differed; the LLUs and CLLUs had a similar mean displaced volume (ca. 1.4 l), but larger than the mean volume of CUs (ca. 0.8 l).

2.3. Experimental set up

Four replicates of each type of collector were deployed on each habitat at each locality. Adjacent ASs within each type of habitat were, in all cases, 3–5 m apart; ASs from any two adjacent habitats were 100 s of m apart. ASs were fixed through cable ties on hard substrata and by iron rods (ca. 50 cm long) on soft substrata. In all cases, ASs were in contact with the seabed. A total of 48 ASs were deployed at both localities on the start of August 2008 and were subsequently retrieved on the start of September 2008; this period of time (4 weeks) encompassed an entire lunar cycle. Each AS was removed by divers by carefully enclosing each unit within a cloth bag. The bags were carried to the laboratory, where each collector was cleaned with freshwater, and all organisms retained by a 0.5 mm mesh sieve subsequently identified to the lowest possible taxonomic level, mostly to taxonomic identifiable units corresponding to families.

2.4. Data analysis

Differences in the total abundance of colonizers, including the total abundance of the 4 dominant phyla: Arthropoda, Chordata, Echinodermata and Mollusca, which accounted for the 96.85% of individuals, and the abundance of the 16 dominant taxonomic



Fig. 1. Location of the study area in the eastern Atlantic Ocean; (A) Playa del Cabrón and (B) Risco Verde.

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