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Response of rocky invertebrate diversity, structure and function to the vertical layering of vegetation

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ABSTRACT

Macroalgae comprise a prominent part of the rocky benthos where many invertebrates develop, and are believed to be undergoing severe declines worldwide. In order to investigate how the vegetation structure (crustose, basal and canopy layers) contributes to the diversity, structure and function of benthic invertebrates, a total of 31 subtidal transects were sampled along the northeast Atlantic coast of Spain. Significant positive relationships were found between the canopy layer and faunal abundance, taxonomic diversity and functional group diversity. Canopy forming algae were also related to epiphytic invertebrates, medium size forms, colonial strategy and suspensivores. By contrast, basal algae showed negative relationships with all variables tested except for detritivores. Multivariate multiple regression analyses (DISTLM) point to crustose as well as canopy layers as the best link between seaweeds and invertebrate assemblage structure. A close relationship was found between taxonomic and functional diversities. In general, low levels of taxonomic redundancy were detected for functional groups correlated with vegetation structure. A conceptual model based on the results is proposed, describing distinct stages of invertebrate assemblages in relation to the vertical structure of vegetation.

1. Introduction

Human activities affect the composition of biological assemblages at all ecological levels, from increasing rates of species invasions and species extinctions to large-scale alterations in community structure and function, leading to complex and unpredictable consequences for ecosystem processes (Hooper et al., 2005). One of the most severe alterations described recently in marine communities is the decline of canopy forming algae (Bennedetti-Cecchi et al., 2001; Steneck et al., 2002; Graham, 2004; Airoldi and Beck, 2007; Díez et al., 2012; Borja et al., 2013). Given that macroalgae are dominant colonisers of rocky marine substrata, where a large variety of invertebrates live, the relationship between the vegetation and coexisting faunal assemblages is of major interest in quantifying the implications of human threats to the marine environment.

Seaweeds represent an essential biological resource for rocky invertebrates for a number of reasons. Macrophytes provide biogenic habitats, adding further space to be colonised; they provide refuge, constitute a source of food and have the potential to modify physical factors such as light, water flow and sedimentation (Bégin et al., 2004; Eckman et al., 1989). Investigations on the links between seaweeds and invertebrate assemblages have principally focused on taxonomic composition. Significant relationships have been detected for fauna associated with the canopy layer (Saiz-Salinas and Urdangarin-Isasi, 1994; Bégin et al., 2004; Tuya et al., 2010; Crowe et al., 2013), whereas weak relationships have been found for invertebrates inhabiting the basal layer of the vegetation (Attril et al., 2000; Thrush et al., 2011). These investigations have focused on particular layers of vegetation. An overall assessment gathering information on more than one layer at the same time is likely to provide a more comprehensive view of the community assembly.

In order to assess environmental impact, what response variables are investigated is of particular relevance. Benthic invertebrates offer a wide range of possibilities, and environmental assessment has developed different approaches that provide complementary and essential information for interpreting biological issues (Addison, 1996). Besides established taxonomic analyses, functional categorisation of marine species has proven to be a valuable tool for detecting environmental change, linking shifts in structure to ecological function (Micheli and Halpern, 2005; Bremner et al., 2006). The ecological relevance of functional traits in ecosystem processes has led to an increasing number of studies focused on this subject in the marine environment. The evidence

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that loss of species diversity accelerates the simplification of ecological communities (McCann, 2000) has focused scientific research on the relationship between species diversity and functional diversity (Emmerson et al., 2004; Micheli and Halpern, 2005; Solan et al., 2006; Canning-Clode et al., 2009; Wahl et al., 2011). Changes in the structure of marine communities can also alter the ecological functions that species assemblages perform (Hughes et al., 2003). However, the effect of seaweed structure alterations on invertebrates functional traits has been less widely investigated, although there is evidence that it could result in significant changes in ecosystem processes (Crowe et al., 2013).

In terrestrial habitats, a limited number of groups of organisms may control critical processes necessary for an ecosystem to function (Bengstsson, 1998). A challenging task for marine ecologists is to identify how a variety of elements such as species composition, traits and biogenic habitats in a biological system influence its functioning (Duffy, 2013). Considering changes in the vegetation structure worldwide, the first important step for research would be to distinguish general patterns in the flora–fauna association. This would be valuable in drawing attention to the existence of key relationships in benthic assemblages that may, if altered, entail unexpected consequences for ecosystem functioning.

Assemblages in the Cantabrian Sea are predicted to be among the most affected by future sea-temperature warming (Müller et al., 2009). Investigations of subtidal vegetation have already documented local declines (Díez et al., 2012; Borja et al., 2013) and morphological and biochemical stress symptoms (Quitano et al., 2013) for habitat-forming macrophytes from this area. The present study aims: (1) to examine the relative role of seaweeds in the genotypic (i.e. taxonomic) and phenotypic (i.e. functional) structure of zoobenthos, and (2) to identify which features of invertebrate assemblages are most closely linked to different layers of vegetation.

2. Methods

2.1. Study area

The Basque coast stretches for approximately 192 km at the eastern end of the Cantabrian Sea, northern Spain (41°53′ N to 43°40′N and 01°40′W to 09°20′W) (Fig. 1). Wave action is predominantly from the northwest and mean water surface temperature ranges between 12 °C in February and 22 °C in August (Valencia et al., 2004). In the last three decades a gradual warming of surface waters has been reported (Goikoetxea et al., 2009), by as much as 1 °C in summer for the three last decades (1980–2008) (Díez et al., 2012), as has a higher frequency of hot summers.

2.2. Field sampling

Sampling was carried out during the summers of 2008 and 2009. The sampling area covered the entire Basque Coast, from Kobaron to Cape Higer (Fig. 1). The sampling locations were based on baseline information from previous studies in the area (Díez et al., 2003). A total of 31 locations were systematically selected along the coast covering a total distance of approximately 150 km. At each location, a 100 m long transect was placed perpendicularly to the coast. The starting point of each transect was placed at a depth of 3 m below extreme low water spring tides, covering an average depth range of 3–9 m. The assemblages investigated were those inhabiting substrata (continuous bedrock platform or large blocks) with gentle to moderate slopes. Invertebrate abundance was assessed every 5 m along each transect using a non-destructive sampling strategy. This consisted of underwater visual estimates of the cover in 50 × 50 cm quadrats of invertebrate species expressed as a percentage. The abundance-covering scale proposed by Pèrés and Picard (1964) was used: <1%, 1–5%, >5–25%, >25–50%, >50–75% and >75–100%. The mean cover of species was calculated for each quadrat using the median of each range. At each transect, 21 sampling units (i.e. quadrats) were recorded. A total of 636 samples instead of 651 were collected due to the loss of sampling units in few cases.

Taxonomic identification was carried out at species level, but in some cases alternative identifications were provided at family level or lower taxonomic separation categories. Invertebrate species not identified in the field were preserved in formalin or alcohol according to recommended procedures. As a result, a total of 124 taxa were recorded, comprising 24 species of Porifera, 30 Cnidaria, 1 Platyhelminthes, 9 Annelida, 10 Arthropoda, 23 Mollusca, 7 Echinodermata, 13 Bryozoa, 6 Tunicata and 1 Phoronida.

Cover estimations for crustose, basal and canopy layers were recorded in each quadrat. In order to avoid the underestimation of lower layers, particular attention was paid when quantifying the cover of basal and crustose algae under canopies, and of crustose algae under the basal layer. The crustose layer was made up mainly by the calcareous algae *Lithoplyllum incrustans* and *Mesophyllum* spp. Cespitose species and articulated coralline algae formed most of the basal layer. The canopy layer was mostly structured with the perennial canopy of *Gelidium corneum* and *Cystoseira baccata.*

2.3. Functional traits

Different traits can describe distinct aspects of ecological functions and the type of trait included in the statistical analyses might influence the mode assemblages are viewed (Bremner et al., 2006;

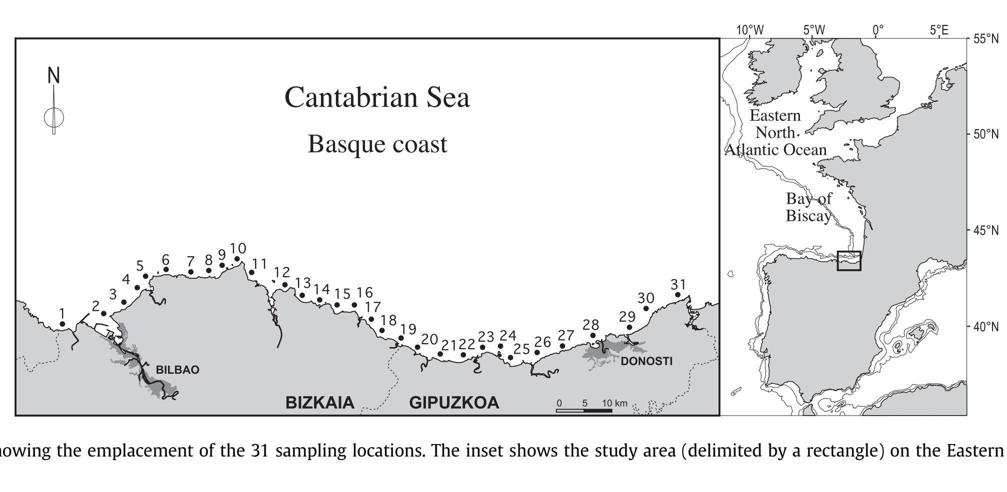

Fig. 1. Study area showing the emplacement of the 31 sampling locations. The inset shows the study area (delimited by a rectangle) on the Eastern North Atlantic coast.