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Differences in the structure and functioning of two communities: Frondose and turf-forming macroalgal dominated habitats

Gustavo M. Martins [a, b, *], Cláudia Hipólito [a, b], Filipe Parreira [b], Afonso C.L. Prestes [a, b], Maria A. Dionísio [c], José M. N. Azevedo [a, b], Ana I. Neto [a, b]

[a] CE3C — Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group, Portugal
[b] Universidade dos Açores — Departamento de Biologia, 9501-801, Ponta Delgada, Açores, Portugal
[c] ICNF — Instituto da Conservação da Natureza e das Florestas, 1050-191, Lisboa, Portugal

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In many coastal regions, vegetated habitats (e.g. kelps forests, seagrass beds) play a key role in the structure and functioning of shallow subtidal reef ecosystems, by modifying local environmental conditions and by providing food and habitat for a wide range of organisms. In some regions of the world, however, such idiosyncratic ecosystems are largely absent and are often replaced by less notable ecosystem formers. In the present study, we empirically compared the structure and functioning of two distinct shallow-water habitats present in the Azores: one dominated by smaller frondose brown macroalgae (Dictyotaceae and *Halopteris*) and one dominated by low-lying turfs. Two replicated areas of each habitat were sampled at two different times of the year, to assess spatial and temporal consistency of results. Habitats dominated by small fronds were significantly (ca. 3 times) more productive (when standardized per algal mass) compared to the turf-dominated habitats, and supported a distinct assemblage (both in terms of composition and abundance) of associated macrofauna. Unlike other well-known and studied vegetated habitats (i.e. kelp forests), however, no effects of habitat were found on the structure of benthonic fish assemblages. Results were spatially and temporally consistent suggesting that, in warmer temperate oceans, habitats dominated by species of smaller frondose brown algae can also play an important role in the structure and functioning of subtidal communities and may, to a certain extent, be considered analogous to other well-known vegetated habitats around the world (i.e. kelp forests, seagrass beds).

1. Introduction

Ecological systems are heterogeneous and structured by complex and dynamic processes (Anand et al., 2010; Burkhard et al., 2010) that operate at a range of spatial and temporal scales. Understanding such complexity is essential if we are to identify the impact of anthropogenic activities, which can lead to changes in community structure and functioning (Steele, 1996; McLeod and Leslie, 2009).

In coastal areas of the world, marine vegetation plays an important structuring role, delivering key functions and services to coastal systems and to the human well-being (Boström et al., 2011; Schmidt et al., 2011; Tuya et al., 2014). For example, marine vegetated ecosystems provide important habitats, including nursery grounds, for many species of economic interest, nitrogen and carbon storage services, and wave energy attenuation and dissipation (Orth et al., 2006; Waycott et al., 2009; Filbee-Dexter and Scheibling, 2014; Hurd et al., 2014).

The extent of functioning and services provided by marine vegetated ecosystems depend on the foundation species and their architecture. In many cold temperate oceans, for instance, large forests of brown seaweeds (e.g. kelps) are the structural element of the ecosystems (Schiel, 1988; Steneck et al., 2002; Goodsell et al., 2004; Smale et al., 2013; Hurd et al., 2014). Kelp forests influence local environmental conditions by (i) reducing light intensity reaching the bottom and increasing its heterogeneity (Wernberg et al., 2005; Hurd et al., 2014), (ii) reducing water velocity, creating a relatively quiescent environment in which seaweed and invertebrate propagules can settle and recruit (Hurd et al., 2014),

* Corresponding author. Universidade dos Açores — Departamento de Biologia, 9501-801, Ponta Delgada, Açores, Portugal.
E-mail address: gustavo.om.martins@uac.pt (G. M. Martins).

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(iii) providing habitat and food for a wide range of invertebrates and fish (Steneck et al., 2002; Thomsen et al., 2010; Boström et al., 2011; Smale et al., 2013; Hurd et al., 2014). Therefore kelp forests are considered one of the most productive coastal habitats and provide high-value ecosystems services. Other ecologically and functionally important well-known coastal vegetated habitats include seagrass beds (i.e. Jackson et al., 2001), mangrove forests (i.e. Nybbaken, 2001) and salt marshes (i.e. Ranwell, 1972).

The Azores are located at the transition between the temperate and subtropical regions and are surrounded by oligotrophic waters (Morton et al., 1998; Palma et al., 2012; Silva et al., 2013). Large brown canopy algae (e.g. kelps) are generally absent or reduced in extent, whereas other iconic vegetated habitats (i.e. seagrass beds) are not found. Nevertheless, the Azorean shallow subtidal (up to 40 m depth) supports extensive beds of frondose vegetation mostly dominated by *Dictyota* spp., *Halopteris filicina*, *Sphaerococcus coronopifolius* and, most commonly, *Zonaria tournefortii* (Tittley and Neto, 2000; Neto, 2000a,b; Neto, 2001). Although these macroalgae have not traditionally been coined as canopies, they too can attain considerable sizes (>30 cm) and effectively cast shade on the understory assemblage. Moreover, like many of the larger brown algae, Dictyotaceae species also produce secondary metabolites and are thus able to deter the activities of many grazers (Paul and Hay, 1986; Hay, 1992; Goecke et al., 2010; Hurd et al., 2014). Despite the above, we still know comparatively very little about the ecological and functional role of these less iconic habitats dominated by smaller brown algae.

The main goal of this study was to empirically assess and compare the structure and functioning of two distinct shallow-water habitats present in the Azores: one dominated by brown frondose macroalgae (Dictyotaceae and *Halopteris*) and one dominated by low-lying turf-forming algae (e.g. *Corallina* spp., *Gelidium* spp.). In each habitat we estimated and compared (i) macroalgal primary production, (ii) the structure of the associated macrofaunal assemblage, and (iii) the associated fish assemblage. We predicted that like kelp forests in colder temperate regions, habitats dominated by smaller species of brown algae play an important role in the structure and functioning in warmer temperate seas.

2. Materials and methods

2.1. Study sites

Four subtidal communities (each covering more than 100 m^2), two frondose-dominated and two turf-dominated habitats, all on the south coast of São Miguel (Fig. 1), were selected for this study. Sampling locations were similar in depth (depth range 9–12 m), sea water temperature and wave exposure; all places were located near the shore with irregular bedrock and basalt rocky boulders. The four locations were sampled twice (May and October 2014). These two periods of sampling were included in the design to provide temporal replication of the experiment and hence assess the temporal consistency of results.

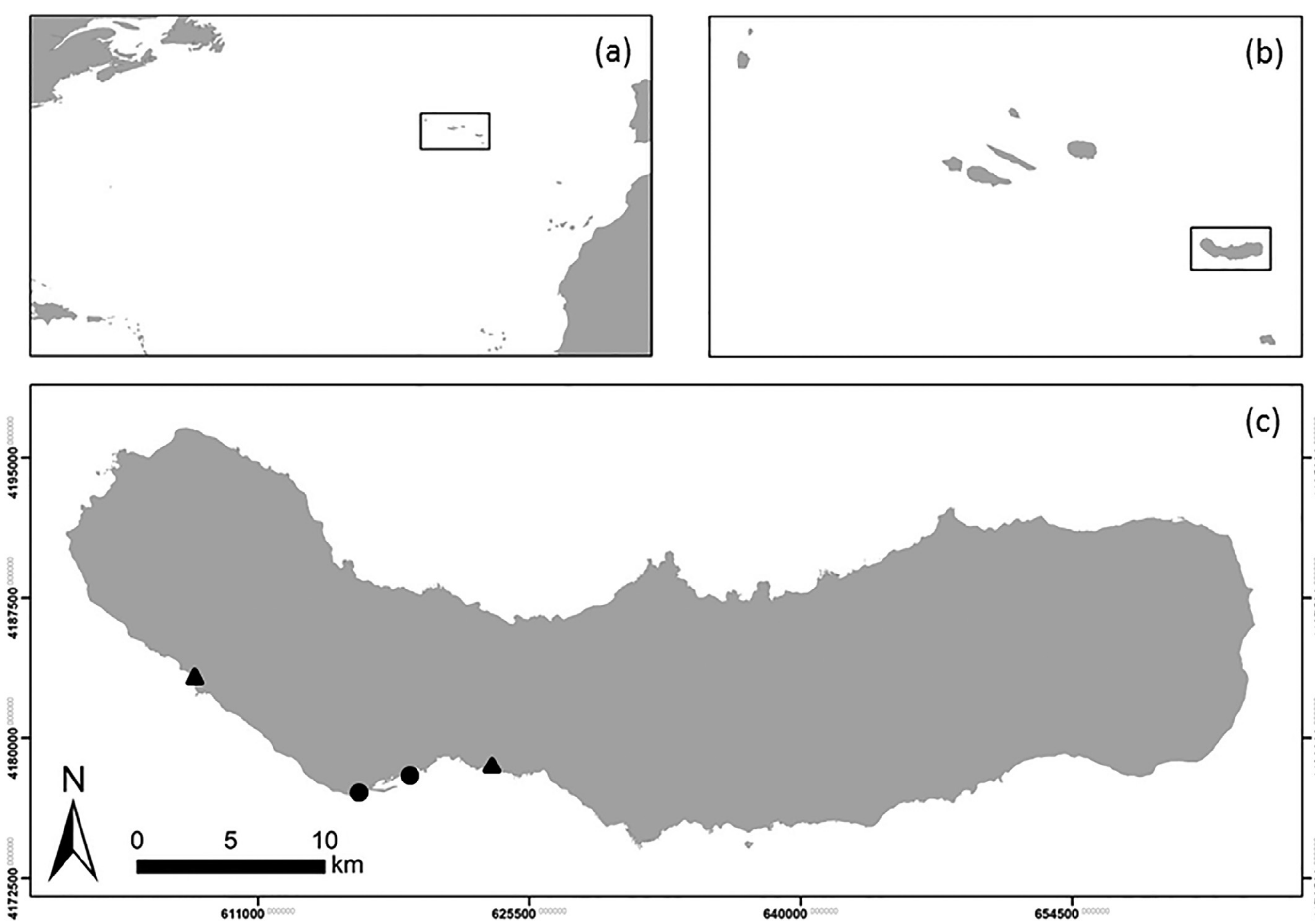

Fig. 1. Map of Azores Archipelago (a), São Miguel Island (b) and sampling locations (c): two frondose-dominated (Feteiras and Lagoa, triangles, sites 1 and 2 respectively) and two turf-dominated habitats (Santa Clara and São Roque, circles, sites 3 and 4 respectively).