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Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae

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ABSTRACT

Patterns of distribution and abundance of epifauna often differ markedly among macroalgal species. The hypotheses tested were that (1) assemblages of mobile epifauna associated with *Laminaria ochroleuca* and *Sargassum muticum* differed because they have different structure, and (2) assemblages of mobile epifauna associated with *S. muticum* differed between heights on the shore because tidal height affects physical and biological conditions. We also investigated the effect of epiphytic biomass on the composition of epifaunal assemblages. Hypotheses were tested with measuring and manipulative experiments using natural and artificial algae, and by measuring uni- and multivariate assemblage descriptors. The results indicated that epifaunal assemblages associated with natural *L. ochroleuca* and *S. muticum* differed, but only differences in epifaunal densities were likely to be related to the structure of algae since all other variables did not clearly differ between the two algae. Although structure might play an important role, other factors need to be taken into account and further experimental tests are necessary. Epifaunal assemblages associated with *S. muticum* did vary depending on the height on the shore, but inconsistently over time in the case of natural algae. In addition, epifaunal densities of natural algae were positively related to biomass of epiphytes in both species. Time of sampling, epiphytic load and height on the shore were the most important factors in structuring epifaunal assemblages rather than complexity of the host algae.

1. Introduction

In rocky intertidal habitats, one of the most limiting resources for benthic organisms is space (Dayton, 1971). Some marine organisms, however, can act as foundation species (*sensu* Dayton, 1972), thereby increasing substrate heterogeneity and the area available for settlement. Biological substrates indeed have a major influence on the organization of shallow water communities by diversifying the spatial resources that can be used, by increasing the area available for colonisation by sessile species, and by providing refuges against predators and unfavourable environmental conditions (Monteiro et al., 2002). Previous studies have pointed out the important role that habitat-forming species can play in facilitating associated organisms (Stachowicz, 2001; Bruno et al., 2003). For example, marine macroalgae serve as both primary space holders in communities, competing for resources such as space, as well as a secondary substratum, acting as biological habitat structure (*sensu* Jones and Andrew, 1992; Chemello and Milazzo, 2002; Wikström and Kautsky, 2004) and providing suitable habitat for abundant and diverse organisms. There is evidence that different macrophytes support different assemblages of mobile epifauna (Taylor and Cole, 1994; Schreider et al., 2003; Vazquez-Luis et al., 2008), and this may be due to several biological factors such as life cycles, algal structure (*sensu* McCoy and Bell, 1991; Gee and Warwick, 1994), habitat complexity (Schreider et al., 2003), chemical defences (Wernberg et al., 2004) or physical factors (e.g. wave exposure or tidal height) (Chemello and Milazzo, 2002; Schreider et al., 2003).

Shape and structural complexity of macroalgae are important factors in determining patterns of abundance and size structure of associated epifaunal organisms. The most structurally complex algae harbour more abundant and diverse assemblages of invertebrates because among other effects, they provide a larger availability of surface for colonisation by fauna and epiphytic algae (Gee and Warwick, 1994; Chemello and Milazzo, 2002). In this context, quality and quantity of epiphytic load may play an important role by increasing the structural complexity of the habitat, determining habitat preferences for some invertebrates (Schneider and Mann, 1991; Martin-Smith, 1993; Schreider et al., 2003), and providing additional new resources (i.e. food, habitat) for invertebrates (Viejo, 1999; Jones and Thornber, 2010). Thus presence of epiphytes can influence strongly the structure of epifaunal assemblages (Attrill et al.,

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2000). In addition, any factor related to different elevations on the shore may be also important in shaping patterns of abundance of epifaunal organisms. For example, height above sea level is important for many organisms on rocky shores, because it may affect physical conditions (e.g. desiccation levels, changes in water currents), availability of food, rate of predation or availability of recruits (Underwood, 1984; Martin-Smith, 1993; Schreider et al., 2003).

Spatial variability of epifaunal assemblages among and within habitats may be shaped by temporal variation at different scales ranging from weeks to months. Epifauna frequently undergoes strong temporal fluctuations, due to a range of physical and biological factors (e.g. Taylor, 1998; Jones and Thornber, 2010). Changes in several factors such as temperature, abundance of epiphytic algae, productivity, predation pressure, competition or recruitment are likely to influence the patterns of epifaunal abundance at different spatial and temporal scales (Taylor, 1998; Jones and Thornber, 2010).

Several papers have dealt with the role of marine macroalgae in structuring epifaunal assemblages, some of them comparing how different species of macroalgae influence the abundance, richness, and diversity of assemblages associated (e.g. Taylor and Cole, 1994; Chemello and Milazzo, 2002). Special attention has been only recently given to comparisons among native and invasive habitat-forming macroalgal species (Wernberg et al., 2004; Wikström and Kautsky, 2004; Schmidt and Scheibling, 2006; Harries et al., 2007; Vazquez-Luis et al., 2008; Gestoso et al., in press).

The semi-exposed low intertidal rocky shores of the Galician coast (north-western Spain) are generally dominated by large macroalgae such as *Laminaria ochroleuca* Bachelot de la Pylaie and *Sacchoriza polyschides* (Lightfoot) Batters (Cremades et al., 2004). Over the past decades, however, kelp beds have been progressively invaded by the invasive brown alga *Sargassum muticum* Yendo (Fensholt), forming dense stands that cover native algal species (Viejo, 1997; Sánchez and Fernández, 2005). *Laminaria ochroleuca* and *S. muticum* form dense forests and house a large number of epiphytes and associated invertebrates, and both species are currently common in the low intertidal habitat of the Galician coast, although *S. muticum* is also found in the mid intertidal area in smaller numbers.

This study focused on assemblages of mobile epifauna associated with *Laminaria ochroleuca* and *Sargassum muticum*. Both species have notable differences in structure; the invasive species being more complex than *L. ochroleuca*, with numerous secondary 3-dimensional branches coming from the primary ones (Arenas et al., 2002). In contrast, structure of *L. ochroleuca* is relatively simple (flat-blades), having long strap-like blades that are suspended above the substratum with a stipe that is firmly attached with a root-like holdfast. The stiff and upright stipes of *S. muticum* and *L. ochroleuca* also provide substrate for a number of macroalgae, being heavily colonised by filamentous algae and macrophytes in the study area. It is important to note that both species differ in various characteristics other than structural complexity, such as colour, surface texture and chemical contents of tissues. We attempted to avoid confounding any effects of these factors with influences in structure. Therefore, artificial mimics of both species were used to separate the effects of structural complexity from other characteristics intrinsic to the algae.

The main goal of this study was to analyse the composition and abundance of mobile epifaunal assemblages associated with two habitat-forming algae, *Laminaria ochroleuca* and *Sargassum muticum*. With measuring and manipulative experiments using natural and artificial algae, we tested the hypotheses that (1) epifaunal assemblages associated with *L. ochroleuca* and *S. muticum* on the low shore differed because they have different structure, and (2) epifaunal assemblages associated with *S. muticum* differed between heights on the shore because a seaweed's position may affect physical and biological conditions of associated epifauna. If this is the case, we would also expect that epifaunal assemblages associated with artificial *S. muticum* placed at two different heights on the shore would be different. In addition, we investigated the role of epiphyte loads on the composition of epifaunal assemblages associated with the two macroalgal species because differences in epiphytes load are likely to occur. Finally, we tested if patterns of abundance and composition of epifaunal assemblages associated with natural algae were consistent over time.

2. Material and methods

2.1. Study area

This study was carried out on the south region of the Galician coast (NW Spain), at mid and low heights on the shore (0.2–0.8 m above the lowest astronomical tide) of an intertidal area, Monte Lourido (42° 7′ 26″N; 8° 49′ 4″W), located on the southern shore at the entrance to Ria de Vigo. This area has rock platforms with numerous pools, and the subtidal and intertidal levels are invaded by *Sargassum muticum* (for more detailed description of the area, see Olabarria et al., 2009).

2.2. Sampling strategy

Natural *Sargassum muticum* and *Laminaria ochroleuca* algae of similar size (average fresh weights (±SE): *S. muticum* $= 149.9 \pm 58.9$ g; *L. ochroleuca* $= 87.78 \pm 22.6$ g, $F_{1,14} = 0.59$, $p = 0.455$) were sampled during low tide on two dates (6 May and 4 June, 2008) ($n = 4$).

Individuals of *Sargassum muticum* were collected at mid and low tidal heights on the shore, whereas individuals of *Laminaria ochroleuca* were collected at low height on the shore. Each alga including the holdfast was gently cut from the substratum with a scraper and immediately transferred into a plastic bag filled with formalin (10%). In the laboratory, mobile epifauna was washed off each alga through 0.5 mm sieves and algae were searched thoroughly for any remaining animals under binocular lens. Animals were fixed in 70% ethanol before being quantified and identified to the lowest taxonomic level feasible. In addition, epiphytes were scraped off the algae and then fixed in 70% ethanol before quantifying biomass. Dry weight of epiphytes was calculated after drying them for 48 h at 60 °C.

The density of each taxon (individuals per alga) was expressed as the number of animals per cm^2 of algal surface (Johnson and Scheibling, 1987). Surface area was estimated by submersing algae in oil of low viscosity (Johnson's Baby®). Assuming equal rates of absorption and retention of oil by algae, the surface area of each alga was proportional to the weight of oil required to cover it. Algae were bottled dry with paper towels, submersed in oil and shaken until oil stopped dripping. Then algae were weighed again, and the weight of oil calculated. Surface area was estimated using relationships between the weight of oil and the true surface area of *Sargassum muticum* and *Laminaria ochroleuca*. To calculate true surface area 10 randomly chosen individuals of each species were collected and scanned (150 dpi, HP Scanjet G4010 scanner) and then their surfaces were measured with ImageJ analysis software. The r^2 values derived from the linear regressions between surface areas and oil weights were 0.94 and 0.96 for artificial *L. ochroleuca* and *S. muticum*, and 0.99 and 0.98 for respective natural species. To evaluate the differences between the two species, the ratios weight/surface areas were calculated and analysed using one-way ANOVA. These ratios significantly differed between natural *S. muticum* and *L. ochroleuca* ($F_{1,14} = 5.39$, $p < 0.05$).