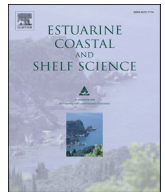




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Benthic community responses to macroalgae invasions in seagrass beds: Diversity, isotopic niche and food web structure at community level

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ABSTRACT

Trophic paths between species are a useful tool for analysing the impact of species invasions of a biotic community. Species invasions produce changes at trophic level and diversity shifts by replacing native species with species of similar ecological niche. This study focused on the effects of macroalgal invasions on seagrass ecosystems. We conducted two – year bimonthly sampling of a pristine *Posidonia oceanica* seagrass meadow and dead matte colonized by three *Caulerpa* species bimonthly. The largest changes in faunal composition were found in meadows colonized by *Caulerpa prolifera*, where major differences in infaunal taxonomic distinctness were apparent. On the other hand, the infaunal community was quite similar between the two invasive *Caulerpa* species (*Caulerpa taxifolia* and *Caulerpa racemosa*). The isotopic niche based on the main trophic guilds established using stable isotope signatures at community level resulted in a highly compacted and 15N-enriched *C. prolifera* food web structure, indicating high overlap of food source utilization among faunal components, which is typical of degraded systems. Conversely, the *P. oceanica* ecosystem presented the most complex food web, while the influence of the 2 invasive species were similar. An attempt to reconstruct the food web at each vegetated habitat revealed high trophic linkages among the different trophic levels with a continuous transition among them by the various trophic guilds suggesting an adaptation response of the different organisms to the new habitat forming species.

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1. Introduction

Food webs are being increasingly used to address important questions in conservation, the impact of species invasions being one of the areas where they have proved successful in hypotheses building, both in terrestrial (Aizen et al., 2008; Bartomeus et al., 2008; Heleno et al., 2009) and marine (Levin et al., 2006; Byrnes et al., 2007) environments. In general, trophic paths between species are a useful tool for conservation managers by indicating whether and how species affect each other. Invasions produce changes in trophic level and diversity shifts by replacing native species with species of similar ecological niche. Given the strong connectance between trophic groups (Williams et al., 2002), any addition or modification in the trophic web is supposed to have

strong effects on the whole community (Williams et al., 2002; Byrnes et al., 2007), which may result in major changes to ecosystem structure and function (Duffy, 2003).

Despite a thorough understanding of the consequences of changing species abundances within a particular trophic level, the ecological consequences of simultaneous biodiversity changes as a result of these modifications at multiple trophic levels remain poorly understood (Byrnes et al., 2007). Biodiversity loss within a trophic level is likely to impact on species at other levels, whether directly through changes in competitive and consumer–resource interactions, or indirectly via changes in ecosystem processes. On the other hand, heterogeneity within a trophic level, is likely to trigger compensatory responses as a result of biodiversity changes occurring elsewhere in the food web, which will have effects on ecosystem processes (Raffaelli et al., 2002).

The Mediterranean basin is highly affected by marine bio-invasions (Galil, 2007), which are modifying natural and native

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communities. Specifically, *Posidonia oceanica* seagrass beds, which are the dominant ecosystem in coastal areas of the Western Mediterranean Sea, are highly invaded by macroalgae (Montefalcone et al., 2010). *Caulerpa* species in particular, have monopolized the benthos in some areas of the Mediterranean sea, and through increased competition have caused significant changes to community composition, usually evident as reduced cover and richness of native marine plants (Boudouresque and Verlaque, 2002; Wallentinus and Nyberg, 2007). The effects of *Caulerpa taxifolia* in natural benthic Mediterranean communities are well documented (Boudouresque et al., 1995; Longepierre et al., 2005), but other *Caulerpa* species are becoming more abundant, causing also heavy impacts on the habitats they colonize. The alga *Caulerpa racemosa* has now widely colonized the Mediterranean (Klein and Verlaque, 2008), causing biotic changes either at species or community level (Deudero et al., 2011; Lorenti et al., 2011; Vazquez-Luis et al., 2012). It has widely spread onto seagrass beds altering beta diversity (Piazzi and Balata, 2008), reducing the diversity and abundance of native macroalgae, especially turf and encrusting species (Piazzi et al., 2001). Similar to the native *Caulerpa prolifera*, it has been found to cause deterioration in sediment quality of the *Posidonia* meadows it colonises, increasing organic matter and sulphide levels, as well as microbial activity in the sediments, and contributing to seagrass decline (Holmer et al., 2009). These changes are likely to have an impact on the trophic structure of infaunal communities associated with *Posidonia* meadows (Casu et al., 2009; Deudero et al., 2011) and may have far-reaching negative consequences for ecosystem stability.

We conducted a study to examine changes in the community and trophic structure of *Posidonia oceanica* meadows colonized by three different *Caulerpa* species in the Balearic Islands (NW Mediterranean Sea) using stable isotopes over a two-year period.

Our aim was threefold: 1- to analyse abundance and diversity changes in infaunal species at community level as a result of colonization by each of the three species; 2- to test for functional changes in the trophic structure of the invaded communities based on stable isotope signatures; and 3- to examine the structure of each food web through the establishment of trophic levels from stable isotope data.

Since we expected the infauna to be the community component that would be potentially be most affected by changes in habitat characteristics promoted by the algae, we examined community changes (aim 1) based on this group. On the other hand, since we expected trophic changes to be propagated throughout the food web, we investigated variations in food web structure and functionality of the various trophic guilds (aims 2 and 3) considering the whole community inhabiting these habitats.

2. Material and methods

2.1. Study sites

Sampling sites were located in Mallorca (Balearic Islands, NW Mediterranean) and had similar bathymetries (5–8 m depth) and hydrodynamic regimes (i.e. enclosed bays). Four habitats were sampled: un-invaded *Posidonia oceanica* meadows, and *P. oceanica* meadows colonised by the invasive *Caulerpa racemosa*, and *Caulerpa taxifolia*, and the native *Caulerpa prolifera* (hereafter referred to by naming only the respective *Caulerpa* species). Sampling sites could not be equitably separated in distance since they were conditioned by the presence of the various target species, as simultaneous combination of the four habitats does not occur in the Balearic Islands. However, all sampling locations were relatively close and separated kilometres, considering the small size of the Island of Mallorca, and no particular features such as rivers or

concrete anthropogenic modifications were identified, so spatial variation between them can be considered minimal. Uninvaded *P. oceanica* meadows and those colonised by *Caulerpa taxifolia* were sampled at Cala d'Or Bay, (N 39° 22.164'/E 3° 13.887'); *Caulerpa prolifera* – colonised *P. oceanica* meadows were sampled at Cala Llonga (N 39° 22.039'/E 3° 13.400), and *P. oceanica* meadows invaded by *C. racemosa* were sampled at Portals Vells (N 39° 28.321'/E 2° 31.320'). In general, the invasive species occupied patches of cleared *P. oceanica*, over dead “matte”, interspersed among living ones. All samples were collected at sites where the cover of *Caulerpa* spp. on the *P. oceanica* matte was 100%.

2.2. Sampling and sample processing

Sampling was carried out bimonthly from February, 2003 to February, 2005. Each time, three sampling points separated by about tens of meters from each other were identified at each of the habitats. At each of these sites, 3 random replicates located within 10 m were taken by inserting 20 × 20 cm quadrats, 5 cm into the sediment. The quadrats were sampled during morning hours (10–12 h GTM) by SCUBA diving. Samples were placed within a 0.5 mm mesh bag and later sorted in the laboratory. Algae and other macroinvertebrates such as echinoderms were sampled manually and also placed inside 0.5 mm mesh bags and transported to the laboratory. Ichthyofauna was intensively sampled during 4 days and their nights during summer 2004 using angling and fish-traps left overnight. Planktonic organisms were sampled with a WP2 plankton net with 220 µm mesh designed to collect mesozooplankton.

Seawater and sediments were sampled for analysis of the particulate and sediment organic matter (POM and SOM), respectively at each sampling event. Sea water samples (10 l) were collected at approximately 0.5 m over the sea-bottom and filtered through pre-combusted (450 °C, 4 h) Whatman GF/F filters (1.2 µm pore size). Sediment organic matter (SOM) was sampled by inserting three cores (3.5 cm diameter), 5 cm into the sediment at each meadow and on each sampling date.

Once in the laboratory, all macrofauna was macroscopically sorted using binocular microscopes and identified to the lowest taxonomic level possible. Organisms were frozen at –20 °C until tissue preparation for isotopic analyses.

Sediment samples were oven-dried at 60 °C until constant weight to calculate total organic matter content. Then, samples were ashed in a muffle furnace at 525 °C for 3 h until constant weight in order to remove the total organic matter. Weight loss after ashing was calculated as the proportion of organic matter in the sample (Skilleter et al., 2006).

2.3. Isotopic analyses

Sediment organic matter for $\delta^{13}\text{C}$ isotopic analysis were acidified by adding 2 N HCl dropwise (the cessation of bubbling was used as criterion to determine the amount of acid to add) and left for 3 h (Carabel et al., 2006), while for $\delta^{15}\text{N}$ analysis non-acidified replicates were used. Tissue samples for stable isotope analyses were extracted from muscle tissue of megafauna or whole body for small invertebrates (mainly pooled crustaceans and polychaetes). The dissected tissue was rinsed with distilled water to remove residual salt and carbonates. *Posidonia oceanica* and macroalgae were rinsed in distilled water, and visible epiphytes were removed before drying the seagrass and the macroalgae (60 °C, 48 h). In the case of crustaceans and molluscs, the exoskeletal parts, valves or shells, were removed, and only the soft body tissues were considered for isotope analysis in order to avoid acidification (Ng et al., 2007).

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