



Effects of macroalgae on the recruitment, growth, and body condition of an invasive reef forming polychaete in a south-western Atlantic coastal lagoon



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ABSTRACT

Species interactions could mediate species invasive processes. In Mar Chiquita coastal lagoon (37° 40'S, 57° 23'W, Argentine), the invasive reef building polychaete *Ficopomatus enigmaticus* (Fauvel 1923) enhances the biomass of the red alga *Polysiphonia subtilissima* Montagne 1840 on reef surfaces, and excludes green macroalgae (mainly *Cladophora* sp. Kützing, 1843) from sediment between reefs. In turn, macroalgae could have several community structuring effects (e.g., as food or by competing for space). Therefore, macroalgae may affect *F. enigmaticus*. To evaluate this hypothesis we studied (1) the interaction between macroalgae and *F. enigmaticus* during the colonization of new substrates and (2) the effects of macroalgae on the recruitment, growth, and body condition of *F. enigmaticus*. Field sampling and experiments suggested a lack of competition on new substrates. However, there was a positive effect of macroalgae on *F. enigmaticus* during the warm season, since its recruitment, tube length, and body condition were higher in areas with macroalgae on reef surfaces. Considering that previous studies showed that reefs positively affect macroalgae, our results suggest that there is a positive feedback on *F. enigmaticus* created by macroalgae on established reefs and during the reefs' growing season. This interaction may contribute to the maintenance and growth of established reefs.

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1. Introduction

Biological invasions are an important research topic because of the impact they can have on the conservation of natural ecosystems (e.g., Troost, 2010; Vitousek et al., 1996) through changes of ecosystem states (Sakai et al., 2001). When the invader is an ecosystem engineer, changes in the habitat structure are an important pathway of community modification (Crooks, 2002, 2009). Ecosystem engineers modify the physical environment through their own structures and modulate the availability of biotic and abiotic resources for other species (e.g., shelter from predators or physical stress, Jones et al., 1994), and can indirectly affect their own performance (i.e., ecosystem engineering feedback, Jones et al., 2010).

Concurrently, species interactions may mediate invasive processes. For example, consumption could promote a patchy distribution, or the exclusion, of species primarily affected by an invasive species (see Bazterrica et al., 2012, 2013). In particular, invading ecosystem engineers may be affected by ecosystem engineering feedback (see Jones and Gutiérrez, 2007). For example, feedback could enhance the ecosystem

engineer nutritional state or decrease their growth, abundance and distribution at a landscape scale (see Bouma et al., 2009). These interactions may be important factors affecting invasive processes.

The invasive reef forming polychaete, *Ficopomatus enigmaticus* (Fauvel 1923), is distributed worldwide in estuarine environments (e.g., North America: Cohen and Carlton, 1995; UK: Thorp, 1994; Italy: Bianchi and Morri, 1996; Spain: Fornós et al., 1997; Africa: Davies et al., 1989; Asia and Oceania: Read and Gordon, 1991). In estuaries of the Southwestern Atlantic, *F. enigmaticus* was reported in the mid-19th century (Borthagaray et al., 2006; Brankevich et al., 1988; Obenat and Pezzani, 1994). In the Mar Chiquita coastal lagoon (37° 40'S, 57° 23'W, Argentina; A UNESCO Man and the Biosphere Reserve), reefs are large, reaching up to 0.5 m in height and 7 m in diameter (Schwindt et al., 2001). There, reefs occupy up to 86% of the coastal lagoon (Schwindt et al., 2001) with densities of about 89 reefs·ha⁻¹ (Schwindt et al., 2004b), but there are several areas without reefs (see Bazterrica et al., 2012).

In the Mar Chiquita coastal lagoon, biomass of the red macroalga *Polysiphonia subtilissima* Montagne 1840 is highest on reef surfaces, but reefs exclude macroalgae (mainly the green macroalga *Cladophora* sp.) from surrounding sediments (Bazterrica et al., 2012). The effects of *F. enigmaticus* on macroalgae could have consequences for other trophic levels, since macroalgae have several mechanisms to structure communities: as autogenic ecosystem engineers (Stewart and Carpenter, 2003; Wallentinus and Nyberg, 2007), by bottom-up control

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as food (Alfaro et al., 2006; Bruno and O'Connor, 2005), by assimilation/dissimilation processes (Jones and Gutiérrez, 2007) and also by other interactions such as competition (Lubchenco, 1982; McCook et al., 2001).

Ficopomatus . enigmaticus and macroalgae might compete for new substrates for recruitment since both recruit on the same substrate (i.e., bivalves and snail valves (Bazterrica et al., 2012; Schwindt and Iribarne, 2000)). Additionally, macroalgae could enhance (or reduce) the recruitment and development of *F. enigmaticus* in substrates occupied by macroalgae (valves and reef surfaces; Bazterrica et al., 2012; Obenat and Pezzani, 1994; Schwindt and Iribarne, 2000). For example, macroalgae may positively affect *F. enigmaticus* recruitment by enhancing the refuge, modifying physical conditions (e.g., Daleo et al., 2006; Stewart and Carpenter, 2003), or enhancing food concentration (see Rabaut et al., 2007; Wahl, 1989). On the other hand, macroalgae could negatively affect *F. enigmaticus*, for example, by interfering with their filtering performance (see Dittman and Robles, 1991).

The morphology of the tubes of *F. enigmaticus* is variable according to environmental or biological conditions (e.g., wall thickness of tubes depends on the distance between individuals, Nishi and Nishihira, 1997; tube growth rates are low during gametogenesis, Bianchi and Morri, 1996). The biomass of the worms also can increase under appropriate temperature and nutrient conditions (Schwindt et al., 2004a). Therefore, several parameters of *F. enigmaticus* morphology may change according to macroalgae presence, including the shape of the tubes (length) and the body condition of the worms inside the tubes (weight · height⁻¹).

Reef spread is thought to be mainly controlled by environmental variables (e.g., salinity, nutrients, and current speed; Bianchi and Morri, 2001; Schwindt et al., 2004b) and the availability of nuclei (i.e., hard substrate for settlement of the polychaete that may generate a new reef; see Schwindt et al., 2004a). Less evidence exists about biotic controlling factors (e.g., predation, competition; see Bianchi and Morri, 2001; Schwindt et al., 2004b). A possible biotic factor is the effect of macroalgae on the density and growth of the reefs of *F. enigmaticus* by affecting their colonization of new substrates or the addition of new individuals to reef surfaces. But also macroalgae could affect the tube length or worm biomass, having cascading effects on processes such as fertility and gamete production (see Charles et al., 2003; Dittman and Robles, 1991). Therefore, our objective is to investigate the effect of macroalgae on *F. enigmaticus* in the colonization of new bare substrate, in their recruitment on areas previously occupied with macroalgae, and in their growth and body condition.

2. Methods

2.1. Study site

We worked in the Mar Chiquita coastal lagoon, a body of brackish water (46 km²) permanently connected to the sea (Isla, 1997). It has a wide salinity range (2 to 35; Schwindt et al., 2004a, 2004b) with low amplitude tides (≤ 1 m) that decrease towards the main body of the lagoon (Isla, 1997). *Ficopomatus F. enigmaticus* reefs are found everywhere from C.E.L.P.A. bridge to Channel 7 (Fig. 1), with the highest abundance in the center (Schwindt et al., 2004b). To accomplish our objective, we performed surveys and field experiments in the low intertidal (a site located approximately 6 km inland from the lagoon inlet; San Gabriel; Fig. 1).

2.2. Relationship between *Ficopomatus F. enigmaticus* and macroalgae recruitment on bare substrates

We described *F. enigmaticus* and macroalgae recruitment on new hard substrate, following the recruitment of both groups of organisms on initially bare valves of the snail *Adelomelon brasiliana* (Lamarck 1811). We used valves of *A. brasiliana* because they are the main “nuclei”

selected by *F. enigmaticus* (Schwindt and Iribarne, 2000). Available valves were collected from C.E.L.P.A. to the inlet of the lagoon (n = 30; Fig. 1). The size range of the valves was 8 to 14 cm between the apex and the siphonal channel (see Fig. 2A). Valves were brushed and placed on sediment tied individually with nylon string (1 m long) to numbered wooden stakes (2 m high). The nylon string was glued to the apex of the valves with a small pellet of putty epoxy. Wooden stakes were buried (1 m depth) in a line (~6 m) parallel to the coast (mean depth during low tide = 0.93 m, SE = 0.10; measured in January 2008 over 11 days). The experiment started in October 2007 and data were collected in December 2007, and January, February, April, June, August and October 2008. The abundances of *F. enigmaticus* (number of recruits · valve⁻¹) and macroalgae (percent cover · valve⁻¹) were registered visually, considering two sides of the valves: the internal and external sides (see Fig. 2A and B). The null hypothesis of no differences in the abundance of *F. enigmaticus* and macroalgae was evaluated with repeated measures ANOVA that included month and valve side (internal and external) as factors (Zar, 1999; n = 10 due to the loss of some experimental units).

During the experiment we observed the recruitment of the barnacle *Balanus improvisus* and the presence of the crab *Cyrtograpsus angulatus*. Both species may affect *F. enigmaticus* and macroalgae. Barnacles may compete for the substrata (e.g., Anderson, 1999) and crabs may consume and/or disturb *F. enigmaticus* (e.g., Schwindt and Iribarne, 2000). To evaluate potential relationships between the abundance of *B. improvisus* (# of individuals · valve⁻¹) and macroalgae percent cover on the external side of the valve; and between the abundance of *C. angulatus* (# of individuals · valve⁻¹) and the number of *F. enigmaticus* recruits inside the valves Spearman correlations (Zar, 1999) were performed.

2.3. Macroalgae effects on recruitment of *Ficopomatus F. enigmaticus*

2.3.1. Description of the recruitment of *Ficopomatus F. enigmaticus* on hard substrates, with and without macroalgae

The recruitment of *F. enigmaticus* in the presence or absence of macroalgae was quantified on the hard substrates available in the sediment on the bottom of the lagoon (“nuclei”) in order to assess a potential relationship between both organisms in the use of the nuclei. For that, we sampled the abundance of *F. enigmaticus* and macroalgae on nuclei of the following categories, collected randomly from the lagoon (January 2008): valves of *Mactra isabelleana* d'Orbigny 1846, valves of *Tagelus plebeius* Lingtfoot 1785, valves of *A. brasiliana* and “others” (i.e., plastics, bottles, etc; see Schwindt and Iribarne, 2000). We determined that a greater number of recruits of *F. enigmaticus* in the presence of macroalgae would suggest a positive interaction. In contrast, a lower number of recruits of *F. enigmaticus* with macroalgae would suggest a negative effect. Finally, if the abundance of recruits of *F. enigmaticus* did not vary, we would conclude no potential effect of macroalgae. The null hypothesis of no differences in the abundance of *F. enigmaticus* and macroalgae in each category of nucleus was tested with a one-way ANOVA (Zar, 1999).

We observed variations in the position of the valves on the sediment, and in the position of macroalgae and *F. enigmaticus* on valves. In order to describe these patterns, we recorded the resting position of the valves and the side of the valves occupied by *F. enigmaticus* and macroalgae. Resting positions were “convex” (i.e., with the internal side, or mantle, of the valve on the sediment; Fig. 2C and D), “concave” (i.e., with the external side of the valve on the sediment; Fig. 2C and D) and “semi-buried” (i.e., semi-buried or upright valves; only considered for bivalve valves); for *A. brasiliana*, the position “convex” corresponded with valves lying with the inside on the sediment, and “concave”, with the valve lying with the outside on the sediment (Fig. 2A). The side of the valve occupied by *F. enigmaticus* and macroalgae was classified as internal or external (see Fig. 2A, C and D). Thus, combining both the resting position and the side of the valve occupied, we considered the following “positions” for *F. enigmaticus* and macroalgae: (1) convex-

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