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ORIGINAL PAPER

Interaction between the invasive macroalga *Lophocladia lallemandii* and the bryozoan *Reteporella grimaldii* at seagrass meadows: density and physiological responses

**S. Deudero · A. Blanco · A. Box · G. Mateu-Vicens ·
M. Cabanellas-Reboredo · A. Sureda**

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Abstract Invasive epiphyte *Lophocladia lallemandii* macroalga induces changes in the erect bryozoan *Reteporella grimaldii* at shallow *Posidonia oceanica* meadows at a Mediterranean pristine location. Bryozoan densities at noninvaded seagrass plots (88.32 ± 3.11 colonies m^{-2}) are higher than those at invaded plots (13.39 ± 1.09 colonies m^{-2}) with a fourfold decrease in number of colonies. Activation of enzymatic pathways (catalase, superoxide dismutase, glutathione peroxidase) and increase in lipid peroxidation malondialdehyde (MDA) [0.80 ± 0.06 nmol/mg prot at *Posidonia oceanica* plots to 1.08 ± 0.04 nmol/mg prot at *L. lallemandii* ($P < 0.05$)] is observed on sessile bryozoans as response to anoxia caused by *L. lallemandii*. δ^{13}C of bryozoan isotopic composition differed among treatments, covering a broad range (−19.30‰ invaded to −2.84‰ at noninvaded plots), suggesting modification of food sources. Induced shifts of a filter-feeding erect bryozoan by dense algal turfs at invaded seagrasses are demonstrated, highlighting the need to further address interaction across natural communities and alien species invaded systems before further cascade effects are driven.

Keywords Bryozoans · Seagrass · *Lophocladia lallemandii* · Invasive species · ROS · Stable isotopes

Abbreviations

ROS	Oxygen species production
CAT	Catalase
SOD	Superoxide dismutase
GPx	Glutathione peroxidase
MDA	Malondialdehyde

Introduction

Biological invasions, considered as the introductions of nonnative species, represent a threat to biodiversity and ecosystem functioning (Bax et al. 2003; Galil 2007). Studies on the effects of invasive species on native biota report either a facilitation interaction among invaders (Parker et al. 2006) or a "biotic resistance" (sensu Elton 1958; Britton-Simmons 2006). Biotic interactions between native and introduced species are often inferred from correlational

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S. Deudero (✉) · A. Blanco · A. Box ·
M. Cabanellas-Reboredo
Laboratorio de Biología Marina, Universitat de les Illes Balears, Ctra. de Valldemossa s/n km. 7.5, 07022 Palma de Mallorca, Illes Balears, Spain
e-mail: salud.deudero@uib.es

G. Mateu-Vicens
Departament de Ciències de la Terra, Universitat de les Illes Balears, Ctra. de Valldemossa s/n km. 7.5, 07022 Palma de Mallorca, Illes Balears, Spain

A. Sureda
Laboratori de Ciències de l'Activitat Física, Universitat de les Illes Balears, Ctra. de Valldemossa s/n km. 7.5, 07022 Palma de Mallorca, Illes Balears, Spain

evidence (Scheibling and Anthony 2001) and experimental testing (Scheibling and Gagnon 2006). Competitive exclusion by invasive species has been reported as a cause of the progressive regression of seagrasses (Williams 2007). Seagrasses are very sensitive to environmental degradation and physical disturbances (Hemminga and Duarte 2000).

The endemic *Posidonia oceanica* (L.) Delile is the most widespread seagrass species in the Mediterranean Sea. Nowadays, more than 60 species of macrophytes have been introduced in the Mediterranean Sea (Boudouresque and Verlaque 2002), inducing community shifts (Piazzi and Balata 2008a). The red algae *Lophocladia lallemandii* (Montagne) *F. Schmitz* is widespread throughout the tropics and subtropics and is considered an alien species in the Mediterranean, being probably introduced via Suez Channel (Boudouresque and Verlaque 2002). *L. lallemandii* grows on a wide range of substrates (bare bedrocks, rocky macroalgae bottoms, *Posidonia oceanica* seagrass meadows, and over coralligenous communities; Ballesteros 2006). *L. lallemandii* displays a particular pattern of invasion in *P. oceanica* meadows (Ballesteros et al. 2007). The alga initially settles on rhizomes and occasionally settles over old leaves, growing as an epiphyte, and finally completely overgrows the benthic communities. *L. lallemandii* invasion induces a decrease in size and weight of the seagrass shoots, leaf chlorosis, leaf necrosis, and shoot death of *P. oceanica* plants (Ballesteros et al. 2007). The development of turfs, which occurs widely in western Mediterranean seagrass beds, seems to modify strongly the structure of macroalgal assemblages of rhizomes, mostly via the decrease in species and functional diversity (Piazzi et al. 2002). The modification of the microhabitat characteristics of the seagrass beds induced by the presence of *L. lallemandii* translated into a decrease in size and weight of the canopy and also affects the faunal communities associated to the seagrasses (Patzner 1998).

Among several species *Posidonia oceanica* communities include primary producers such as codiacean and red algae and several faunal taxa epibionts (bryozoans, cnidarians, foraminifers, polychaetes, sponges, etc.) and vagile biota (echinoderms, crustaceans, molluscs, fish; Templado et al. 2004). Seagrass-associated faunal communities encompass many taxonomic groups, including few bryozoans species (Trautman and Borowitzka 1999; Bonhomme et al. 2001; Ben Mustapha et al. 2002). *Reteporella grimaldii* (Jullien in Jullien and Calvet 1903) is a Cheilostomata bryozoan from the Phidoloporidae family morphologically described as a convoluted compact three-dimensional colony spreading up to 40 mm in length and 80 mm horizontally, forming anastomoses defining funnels (Hayward and Ryland 1996). Coevolution of faunal assemblages at seagrasses dates back to the Cretaceous (Ivany et al. 1990) including the cheilostomate bryozoan such as *R. grimaldii* (Voigt 1981), which is coeval with the first documented occurrence of the genus *Posidonia* (*P. cretacea*) (Boudouresque and Jeudy de Grissac 1983). Therefore, epibionts and seagrasses have coevolved since the end of the Mesozoic, which has conduced to highly adapted biocenosis with complex interactions with the substrate and among the different organisms forming such communities. Nowadays, the appearance of erect bryozoans such as *R. grimaldii* on rocky bottom meadows (Reverter-Gil and Fernández-Pulpeiro 1999) and in association with the seagrass rhizomes (Ben Mustapha et al. 2002, Heß 2004) has been documented.

Bryozoan colonies are considered good indicators reflecting changing environmental conditions (Elia et al. 2007). Since the invasive macroalgae *Lophocladia lallemandii* is capable of growth over all types of substrates, including sessile invertebrates, it can potentially induce a shift in regimen fluxes for sessile organisms such as bryozoans. Therefore, evaluation of bryozoan's physiological responses to oxygen depletion and flux modification due to epiphytism can be quantified by determination of antioxidant defenses. It is known that oxidative stress results from the disruption of cellular homeostasis of reactive oxygen species (ROS) production (Halliwell and Gutteridge 1999). Overproduction of ROS causes cell damage through oxidation of membrane lipids, nucleic acids, and proteins (Imlay and Linn 1998; Collen et al. 2003; Li et al. 2006). To counteract these ROS damaging effects, the organisms have developed efficient defense systems in scavenging of cellular ROS (Elias et al. 1999). These protective mechanisms involve a number of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), and glutathione peroxidase (GPx). The antioxidant defense adaptation against ROS is crucial for the survival of organism under stressful conditions. Several reports have shown a tight association between antioxidant capacity and the presence of alien competing species (Sureda et al. 2006, 2007). Nevertheless, studies about the effects of *L. lallemandii* on the antioxidant defenses of invertebrates are lacking.

Another useful tool to determine the energy sources and the functioning of the coastal food webs at altered ecosystems is the analysis of isotopes ratios of carbon and nitrogen ($^{13}\delta$C and $^{15}\delta$N) (Davenport and Bax 2002; Smit et al. 2006; Le Loc'h F Hily and Grall 2007). Comparison of isotopes ratios from the bryozoan of invaded meadows and bryozoans of noninvaded meadows give clues about potential shifts in food sources at filtering sedentary species (Riera 2007). Most isotopic studies of bryozoan community were related with paleoenvironmental and climate change (Brenchley et al. 2006), and only a few address partly contributions of isotopes ratios to bryozoan diets (Dunton 2001; Fredrkinsen 2003). An expectation of the invasion situation is a modification of the trophic pathway and carbon sources for the seagrass beds and associated bryozoans.

Information on erect bryozoan *Reteporella grimaldii* spatial distribution at seagrass beds is very scarce (Heß 2004; Balata et al. 2007). Moreover, knowledge on the bryozoan densities, distribution of colonies, physiological responses, and discrimination of food sources induced by the macroalga *Lophocladia lallemandii* had not been previously addressed. Therefore, the main hypothesis was to test that densities of *R. grimaldii* colonies between invaded and noninvaded *Posidonia oceanica* seagrass meadows plots did not differ as a result of invasion of *L. lallemandii*. A second objective was to test for physiological responses of bryozoan colonies by quantifying the production of antioxidant enzymes under the invaded situation. Finally, the third objective was a first approximation to the different carbon sources that may contribute to the *R. grimaldii* food web and the modification of its trophic structure.

Materials and methods

Sampling and study locations

The study area was located in the vicinities of the Dragonera Natural Park (SW off Mallorca Island, W Mediterranean; 39°34′N–2°20′E). Sa Dragonera Island was declared a protected area in 1995 in consideration of its biodiversity, natural, and pristine characteristics. The sampling design was set by choosing three sites over *Posidonia oceanica* meadows and over *P. oceanica* seagrass meadows epiphyted by the algae *Lophocladia lallemandii*. There were invaded and noninvaded seagrass meadows within each of the three sites. At each site eight linear transects (20 m length × 1 m wide) were laid down by scuba diving, and at each transect ten plots of 40 × 40 cm polyvinylchloride (PVC) were randomly displayed in order to quantify total abundances of *Reteporella grimaldii* colonies; therefore a total 480 plots were quantified for bryozoan densities determination. The sites were separated by hundreds of meters and the distance among noninvaded and invaded seagrass beds was tens of meters. All transects were laid over seagrass beds at 6–7 m depth and sand patches were also present.

Seagrass densities, expressed as number of shoots of *Posidonia oceanica*, were calculated at each transect by deploying 40 × 40 cm plots (Prado et al. 2007; González-Correa et al. 2008). Moreover, the cover of *Lophocladia lallemandii* was quantified within 20 × 20 cm plots on the epiphyted *Posidonia* leaves and shoots, and both *P. oceanica* and *L. lallemandii* samples were collected within 20 × 20 cm for algal biomass determination (Piazzi and Balata 2008a). Plots sample size was chosen applied following *Lophocladia lallemandii* natural patchiness (Cebrian and Ballesteros 2007) not larger than 400–500 cm^2.

Oxygen measurements were performed by means of a portable oxygen/temperature meter DO300 and galvanic probe (Eutech Instruments Pte Ltd/Oakton Instruments). Five replicate measurements were performed at the rhizomes of the *Posidonia oceanica* meadow and five more replicate measurements within the *P. oceanica* meadow invaded by *Lophocladia lallemandii* to test for differences in oxygen saturation linked with the possible oxygen changes induced by the macroalga.

Several bryozoan colonies ($n = 8$) were also collected by hand at the invaded and noninvaded seagrass beds to evaluate physiological effects of the presence of *Lophocladia* on the bryozoans. Samples were carried to the surface and immediately frozen in liquid nitrogen once onboard. Then, bryozoans were maintained at −80°C until further biochemical analysis.

Sample processing of bryozoans for enzymatic activities

Biochemical assays were performed on single colonies of *Reteporella grimaldii* without epiphytes. *R. grimaldii* colonies ($n = 8$) were carefully homogenized in five volumes (w/v) of 100 mM Tris–HCl buffer pH 7.5, containing 100 μM of phenylmethylsulfonyl fluoride (PMSF). Homogenates were centrifuged at 9,000 × g for 15 min at 4°C and supernatants were recovered and stored at −80°C until biochemical analysis. Antioxidant enzyme activities and MDA concentration were determined in the supernatants. Total protein content was determined by colorimetric method (Biorad® Protein Assay) using bovine serum albumin (BSA) as standard. All results were referred to the protein content in the samples.

Enzymatic activities

Enzymatic measurements were carried out by specific spectrophotometric assays at constant temperature of 25°C in a Shimadzu UV-2100 spectrophotometer. CAT activity was determined through the method described by Aebi (1984) by measuring the decrease in the absorbance of H_2O_2 at 240 nm. GPx activity was measured using an adaptation of the spectrophotometric method of Flohe and Gunzler (1984). This activity was determined in a coupled system with H_2O_2 and GSH as substrates and glutathione reductase (GR) and nicotinamide adenine dinucleotide phosphate reduced form (NADPH) as enzyme and nonenzymatic indicators, respectively. SOD activity was determined by monitoring the decrease in the rate of reduction of cytochrome C at 550 nm by superoxide anion generated by the reaction of xanthine oxidase with xanthine (McCord and Fridovich 1969).

MDA determination

Malondialdehyde (MDA), as a marker of lipid peroxidation, was analyzed by a colorimetric assay kit (Calbiochem, San Diego, CA, USA) following the manufacturer's instructions. Briefly, homogenates or standard were placed in glass tubes containing *n*-methyl-2-phenylindole (10.3 mM) in acetonitrile:methanol (3:1). HCl 12 N was added and samples were incubated 1 h at 45°C. The absorbance was measured at 586 nm. MDA concentration was calculated using standard curve of known concentration.

Sample processing of bryozoans for determination of carbon sources through stable isotopes analysis

All samples were stored at −20°C until they were processed. Each sample was cleaned of epibionts by scratching its surface and then split into two subsamples, one of which was also treated with 1 M HCl for 3 h in order to remove the calcium carbonate from the calcareous structure (Le Loc'h F Hily and Grall 2007; Doi et al. 2008; Pitt et al. 2008). The samples were then rinsed with ultrapure water and dried at 60°C for at least 24 h. (Melville and Connolly 2005; Ince et al. 2007; Doi et al. 2008). $^{15}N/^{14}N$ ratios were measured before acidification because of significant modification of $^{15}N/^{14}N$ after HCl addition (Kang et al. 2008). Each dried sample was ground to homogeneous powder. About 1.9–2.1 mg of the powder was weighed in ultraclean tin capsules and was combusted for C and N isotope compositions using continuous flow isotope ratio mass spectrometry (CF-IRMS) THERMO delta X PLUS mass spectrometer. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were expressed as conventional delta (δ) notation in parts per thousand (‰) deviations relative to the Peach Leave Standard (1547) (PLS) and Bovine Liver Standard (1577b) (BSA) (US Department of Commerce, National Institute of Standards and Technology, Gaitherburg, MD), according to the following equation:

$$\delta X(\text{‰}) = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 10^3$$

where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

To determine which of the potential food sources (i.e., seagrass, *Lophocladia lallemandii*, plant detritus, POM) were assimilated by *Reteporella grimaldii* at each treatment, we estimated the feasible contributions for each source by isotope mixing models using IsoSource version 1.3.1 software (Phillips and Gregg 2003). The model was used to estimate the potential contributions of the primary producer groups to each *R. grimaldii* specimens. For each primary producer, the mean, 1st–99th percentiles, and range of probability contributions to consumer at increments of 1‰ were determined (Decottignies et al. 2007; Ince et al. 2007; Pitt et al. 2008). Tolerance was calculated as half this amount (0.5 × increment × maximum differences between sources; Phillips and Gregg 2001; Decottignies et al. 2007). In the absence of consumer-specific isotope discrimination factors for these two consumers, an assumed discrimination of 0.5‰ was applied for carbon (McCutchan et al. 2003; Pitt et al. 2008). Nitrogen could not be incorporated into the model since the discrimination levels were unknown and applying an assumed 3–4‰ value could not yield results as the values of the consumers lay outside the polygon created by the potential sources (Connolly et al. 2005; Ince et al. 2007; Pitt et al. 2008).

Statistical analysis for bryozoans population

Densities of bryozoans at invaded and noninvaded seagrass beds were compared by nested multifactorial analysis of variance (ANOVA) to test differences in *Reteporella grimaldii* distribution among meadows, sites, and transects (STATISTICA, 7.0). The factors considered were: invasion (two levels: invaded meadows and noninvaded meadows; fixed, orthogonal); site (three levels, random, orthogonal) and transect (eight levels, random, nested in invasion × site). At each transect ten plots were randomly considered. Homogeneity of variances was tested by Cohran's *C*-test and data was $\ln(x + 1)$ transformed when necessary.

Enzymatic activities comparison between bryozoans at noninvaded versus invaded seagrass plots was carried out by one-way analysis of variance (ANOVA).

Results

Structural components of both vegetated systems greatly differed. In this sense, mean *Posidonia oceanica* dry weight biomass 175 ± 15.5 g m^{-2} was significantly higher than *Lophocladia lallemandii* biomass 16 ± 4 g m^{-2}. Similarly, dissolved oxygen saturation was significantly higher in the *P. oceanica* invaded by *L. lallemandii* (92.6 ± 0.6% saturation) than in *P. oceanica* noninvaded plots (90.5 ± 0.3% saturation; ANOVA $P < 0.05$).

Quantitatively large divergences were encountered in bryozoan density at both invaded and noninvaded conditions. A total of 2261 bryozoans colonies were quantified at transects performed on rhizomes of *Posidonia oceanica* meadows whereas *P. oceanica* invaded by *Lophocladia lallemandii* exhibited only 343 colonies. Comparatively, number of *Reteporella grimaldii* colonies at invaded plots ranged from 0.62 to 25.62 colonies m^{-2}, corresponding to 218.75 shoots m^{-2}, respectively, whereas at noninvaded seagrass beds bryozoans colonies ranged from 38.25 to 111.25 colonies m^{-2} within seagrass plots of 487.5–681.25 shoots m^{-2} (Fig. 1).

Mean bryozoan *Reteporella grimaldii* densities at *Posidonia oceanica* seagrass beds (88.32 colonies m^{-2} ± 3.11; mean ± SE) were significantly

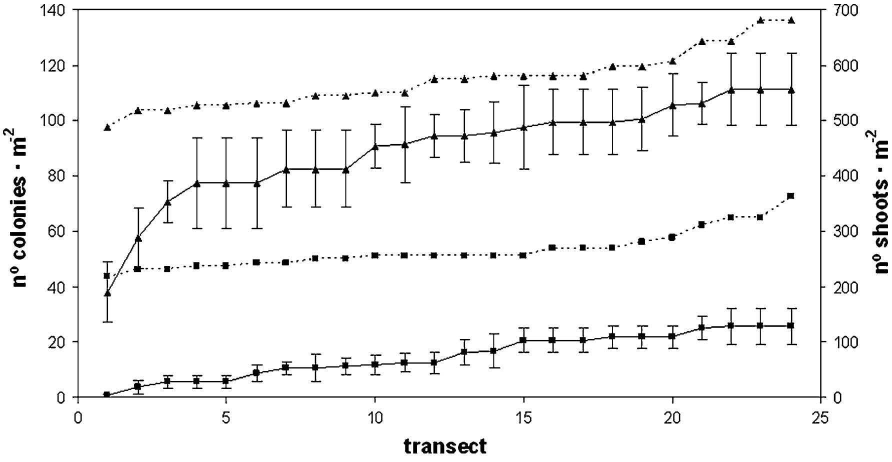

Fig. 1 Mean abundance of *Reteporella grimaldii* colonies (*solid line*) counted at each plot per transect and mean number of *Posidonia oceanica* shoots (*dashed line*); ▲ colonies at *P. oceanica* meadows without algae invasion; ■ colonies at *P. oceanica* meadows invaded by *Lophocladia lallemandii*. *Bars* represent mean ± standard error on the mean (SEM)

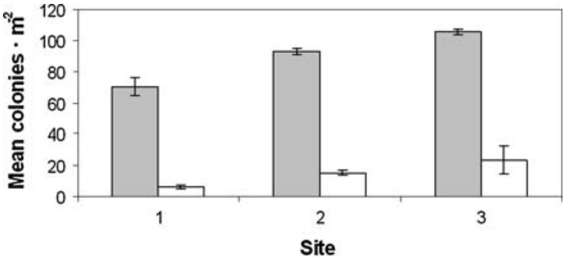

Fig. 2 Mean number of *Reteporella grimaldii* colonies per m^2 at sampling sites 1, 2, and 3 in *Posidonia oceanica* meadows (*grey bars*) and *Posidonia oceanica* meadows invaded by *Lophocladia lallemandii* (*white bars*)

Table 1 Nested multifactorial analysis of variance on mean number of colonies of *Reteporella grimaldii* at noninvaded *Posidonia oceanica* seagrass plots and at plots invaded by *Lophocladia lallemandii*

Source of variation	*df*	MS	*F*	*P*
Invasion	1	17,136.30	790.805	**0.000**
Site	2	33.10	1.527	0.210
Transect (invasion × site)	42	48.05	2.217	**0.000**
Residual	432	21.67		
Cohran's test (*C*)		0.0009		

Significant effects are indicated in bold

higher than those at invaded seagrasses (13.39 colonies m^{-2} ± 1.09; one-way ANOVA; $P < 0.05$; Fig. 2).

The patterns of spatial distribution of *Reteporella grimaldii* at noninvaded versus invaded seagrass beds clearly differ at the invasion level and among sites (ANOVA, $P < 0.01$; Table 1). On the contrary, differences among transects nested in sites were not encountered (Table 1).

Linear regression on *Posidonia oceanica* shoot densities and *Reteporella grimaldii* abundance (Fig. 3) show a fourfold decrease in the number of colonies in denser seagrass beds. There is an average of 5 colonies corresponding to seagrass densities of 250–350 shoots m^{-2} for invaded plots, increasing to 15–20 colonies in dense meadows of 500–600 shoots m^{-2} corresponding to noninvaded plots (Fig. 3).

Antioxidant enzyme activities and MDA concentration are presented in Table 2. *Reteporella grimaldii* living in *Lophocladia lallemandii* plots presented higher CAT and GPx activities compared with *R. grimaldii* from *Posidonia oceanica* plots.

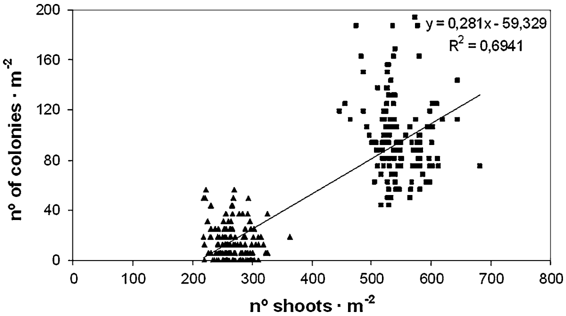

Fig. 3 Linear regression between *Posidonia oceanica* shoot density and *Reteporella grimaldii* abundance. ▲ colonies at noninvaded *Posidonia oceanica* meadows; ■ colonies at *Posidonia oceanica* meadows invaded by *Lophocladia lallemandii*

Table 2 Antioxidant enzyme activities and MDA concentration in *Reteporella grimaldii* ($n = 8$ colonies)

	Reteporella noninvaded	*Reteporella* + *Lophocladia*
Catalase	65.5 ± 7.3	113 ± 9*
SOD	3.61 ± 0.34	4.61 ± 0.51
GPX	4.31 ± 0.15	5.2 ± 0.30*
MDA	0.80 ± 0.06	1.08 ± 0.03*

Catalase (mK/mg prot), SOD (pKat/mg prot), GPX (nKat/mg prot) activities, and MDA concentration (nmol/mg prot) in *Reteporella grimaldii* invaded and noninvaded by *Lophocladia lallemandii*

* Significant differences between plots (one-way ANOVA, $P < 0.05$). Mean ± SEM

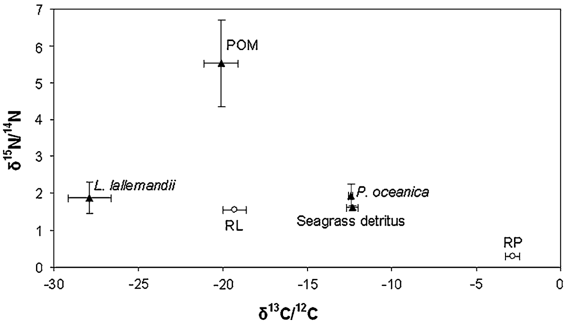

Fig. 4 Relative contributions of carbon and nitrogen sources to *Reteporella grimaldii* at *Posidonia oceanica* seagrass plots and *Lophocladia lallemandii* plots based on mean stable isotope values (±standard deviation). All possible sources were represented: ▲ *POM* particulate organic matter, seagrass detritus = detritus from *Posidonia oceanica*, *L. lallemandii* = *Lophocladia lallemandii* samples, *P. oceanica* = *Posidonia* seagrass samples; ○ for RL = *Reteporella grimaldii* from invaded plots by *Lophocladia lallemandii*, RP = *Reteporella grimaldii* from noninvaded plots

Table 3 Mean carbon contribution (%), 1–99%, and range of feasible contributions (proportion) of distinct food sources to *Reteporella grimaldii* at noninvaded and invaded plots based on δ^{13}C values

	R. grimaldii at noninvaded plots			*R. grimaldii* at invaded plots		
	Mean (%)	1–99%	Range	Mean (%)	1–99%	Range
POM	12.6	0.00–0.37	0.00–0.41	35.5	0.00–0.92	0.00–0.97
Seagrass detritus	40.5	0.00–0.24	0.00–0.89	17.8	0.00–0.47	0.00–0.52
Lophocladia lallemandii	6.5	0.00–0.05	0.00–0.18	30.2	0.02–0.48	0.00–0.48
Posidonia oceanica	40.4	0.00–0.24	0.00–0.89	16.5	0.00–0.47	0.00–0.52

CAT activity significantly increased from 65.3 ± 8.5 to 113 ± 10 nK/mg prot ($P < 0.05$), and GPx activity significantly increased from 4.31 ± 0.18 to 5.28 ± 0.33 nKat/mg prot ($P < 0.05$). SOD activity presented similar values in both plots. MDA concentration significantly increased from 0.80 ± 0.06 nmol/mg prot at the *P. oceanica* plots to 1.08 ± 0.04 nmol/mg prot in the *L. lallemandii* plots ($P < 0.05$).

Reteporella grimaldii colonies at *Posidonia oceanica* plots presented a more enriched signal of ^{13}C (−2‰) as compared with *Lophocladia lallemandii* plots (−19‰) (Fig. 4). Instead, carbon and nitrogen stable isotope ratios from *P. oceanica* and seagrass detritus are almost identical. Bryozoan colonies on plots invaded by *L. lallemandii* presented a similar nitrogen signature (0.3–1.5‰) (Fig. 4).

Contributions of food sources from IsoSource routine showed differences in the carbon sources at the sessile bryozoans. In this sense, *Lophocladia lallemandii* could contribute up to 48% of the total carbon sources to the bryozoans colonies at invaded plots, followed by particulate organic matter (POM), *Posidonia oceanica* detritus, and *P. oceanica* (Table 3; Fig. 5). Conversely, noninvaded *Reteporella grimaldii* colonies presented a mean contribution of seagrass and seagrass detritus of approximately 40%, while *L. lallemandii* contribution decreased to 6.5%.

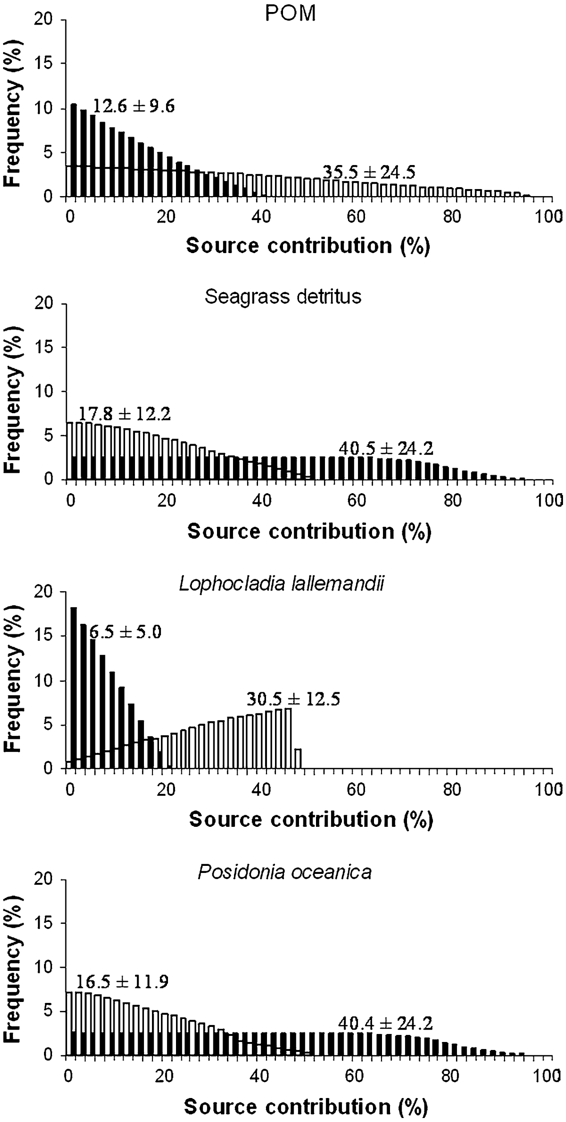

Fig. 5 Distribution of feasible carbon contributions (based on δ^{13}C values) of available sources to the diet of *Reteporella grimaldii* at noninvaded *Posidonia oceanica* plots (*black bars*) and at invaded plots by *Lophocladia lallemandii* (*white bars*). Mean (%, ±SD) carbon contributions are indicated

Discussion

Biotic interactions of *Lophocladia lallemandii* epiphytism and *Reteporella grimaldii* colonies were exhibited by the large differences in bryozoan densities at invaded seagrass plots when compared with those at noninvaded seagrass beds. Accordingly, the patterns of spatial distribution of *R. grimaldii* clearly differed at the invasion level and among sites, although no differences among transects nested in sites were encountered, maybe reflecting rather homogeneous communities at each site. In the present study, the coexistence of two epiphytes on the *Posidonia oceanica* rhizomes (*R. grimaldii* and *L. lallemandii*) can lead to the competitive displacement or exclusion of the native species *R. grimaldii* by the nonnative macroalgae *L. lallemandii*. Previous studies have already registered major alterations in the community structure or exclusion of organisms by invasive species (Boudouresque and Verlaque 2002; Scheibling and Gagnon 2006; Piazzi and Balata 2008b).

Variability in bryozoan epiphytes at the scale of meters has been assigned to be mostly influenced by differences in seagrass shoot density and in the canopy, which affect light intensity and water movement (Gambi et al. 1989). Relations of the bryozoan *Reteporella grimaldii* densities with respect to seagrass shoot density clearly appeared in this study, as reported by the fourfold decrease in the number of colonies at the invaded plots that corresponded to 300 shoots m^{-2}. Similarly, previous citations have reported significant densities of *R. grimaldii* at dense meadows with 525–600 shoots m^{-2} while no bryozoans appeared at seagrass densities ranging from 250 to 350 shoots m^{-2} (Ben Mustapha et al. 2002). Regarding the chronology of the invasion pattern of *Lophocladia lallemandii* and concerning the observed densities of *R. grimaldii* at *Posidonia oceanica* invaded by *L. lallemandii* versus noninvaded plots, the present study cannot determine whether the decrease in *P. oceanica* shoots was a cause–effect relationship due to *L. lallemandii* epiphytism inducing direct shoot mortality (Ballesteros et al. 2007) and consequent habitat loss for bryozoans, or conversely if macroalga epiphytism on bryozoan induced direct loss of colonies. Further manipulative experiments will be needed to address the facilitative interactions between invaders and native species (Parker et al. 2006). Nevertheless, in the present study, evidence of physiological responses of the bryozoans at the invaded plots has been demonstrated, pointing out that the nonnative *L. lallemandii* represents an alteration of the natural conditions.

Bryozoan densities obtained in this study also reflected microspatial variability in colonial distribution, which seems to be a triggering factor for recruitment pulses and competitive exclusion by the invasive algae. In addition, substrate typology (rhizomes at different shoot densities) would be expected to determine bryozoan recruitment success. The majority of cheilostomate bryozoans release coronate larvae capable of active swimming and positive reaction to light. Such swimming abilities may allow *Reteporella grimaldii* larvae actively to select the substrate on which to settle and to avoid unsuitable substrates such as the *Lophocladia lallemandii* dense algal turf of the invaded seagrass plots observed in the present study. Accordingly, a possible explanation for the low *R. grimaldii* densities observed at the invaded plots might be high post-recruitment mortality due to competition with the red algae *L. lallemandii*, as has already been pointed out by Mariani et al. (2005) with fast-growing brown algae relevant in determining the adult distributions.

Although bryozoans are quite sensitive to anthropogenic disturbances, such as sewage loads (Piazzi et al. 2004), they are also efficient organisms in terms of filtration and clearance rates. Lisbjerg and Petersen (2000) calculated clearance rates of bryozoans at seagrass beds and concluded that 49% of the total colony area had active zooids. The three-dimensional structure of the invasive macroalgae *Lophocladia lallemandii* could modify the particle flux and filtration rates of encrusting organisms. The interaction between *Reteporella grimaldii* and *L. lallemandii* represents a competition for space and a shift towards sciaphile conditions (Lloret et al. 2006) that can be envisaged in terms of a decrease of clearance rates of *R. grimaldii* at seagrasses rhizomes invaded by *L. lallemandii*. Recent studies on particle trapping at seagrass systems have confirmed the existence of two dynamically different environments: the below-canopy habitat, with low shear stress and reduced turbulence, and the canopy–water interface region, characterized by high shear stress and turbulence intensity where vertical transport of momentum is enhanced (Hendriks et al. 2008). In this sense, modification of particle flow mediated by differences in shoot and leaves densities at invaded and noninvaded seagrass plots will produce differential conditions at the rhizome level, leading to exclusion to bryozoan post-recruits, reduced sestonic particles to zooids, or to anoxic levels. Moreover, since patterns of adult bryozoan distribution did not vary substantially over several years (Mariani et al. 2005), densities of bryozoans should reflect externalities such as invasive effects of macroalgae. On the other hand, partial mortality in colonies can be due to overgrowth by algae and siltation (Cocito et al. 1998).

Cellular antioxidant status is used to evaluate the ability of organisms to resist an environmental stress (Frenzilli et al. 2004). Correlations between the efficiency of ROS detoxification and the stress tolerance have been reported by several authors (Porte et al. 2002; Cavas et al. 2005). However, there is little published data related to bryozoan and antioxidants (Elia et al. 2007). In the present study, the invasive alga *Lophocladia lallemandii* induced an antioxidant response in the bryozoan *Reteporella grimaldii*, as shown by increased activities of CAT and GPx, whereas SOD presented similar activities in both invaded and noninvaded areas. CAT is involved in the cellular defense system through the detoxification of H_2O_2, whereas GPx catalyses the reduction of GSH and organic hydroperoxides. The similar SOD activity in noninvaded and invaded plots suggests that the main reactive specie participating in *L. lallemandii* toxicity was H_2O_2 and not superoxide anion. The increase in GPx activity could indicate the existence of damage in cellular lipids as result of the environmental stress induced by the invasion of *L. lallemandii*. Accordingly, lipid peroxidation is a well-known mechanism of cellular injury and an indicator of oxidative damage (Ahmad et al. 2006; Monteiro et al. 2006). MDA is the main product resulting from lipid peroxidation and is frequently used as a marker of lipid oxidation. MDA concentration was significantly higher in *R. grimaldii* living in presence of the invasive alga *L. lallemandii*. These results indicate that the reported antioxidant enzyme response was not enough to avoid the lipid damage.

Isotopic values can provide information related to the shifts in food sources (Van Zander et al. 1999) of the *Reteporella grimaldii* at invaded plots. The isotopic composition of the bryozoan differed among seagrass and *Lophocladia lallemandii* plots in the present work. δ^{13}C covered a broad range of values (from -19.30‰ at invaded to -2.84‰ at noninvaded plots), suggesting modification of food sources towards phytoplankton-derived carbon linked to the highly enriched carbon signature (Dubois et al. 2007). Seagrass *Posidonia oceanica* δ^{13}C (-12.34 and -12.51‰) values match previous studies (Hemminga and Mateo 1996; Lepoint et al. 2000; Papadimitriou et al. 2005; Fourqurean et al. 2007). However, the *Reteporella grimaldii* δ^{13}C values in this study exceed the established trophic enrichment value of 1‰ observed elsewhere (Davenport and Bax 2002; Smit et al. 2006; Le Loc'h F Hily and Grall 2007). For filtering bivalves species, trophic enrichment has been demonstrated as being twice as high as commonly assumed (Dubois et al. 2007), which can also be applied in the studied bryozoans. Moreover, the main expected food carbon source for the *R. grimaldii* bryozoans colonies at invaded seagrass plots seems to be the particulate organic matter (POM) surrounding the canopy, as observed from the δ^{13}C values (i.e., bryozoan -19.30‰ and POM -20.1‰). Conversely, bryozoan nitrogen isotopic signatures at both invaded and noninvaded plots were rather low when compared with the observed POM values. However, mean δ^{15}N values of POM (5.52 ± 1.18‰) at *R. grimaldii* were within the range of previous studies (Davenport and Bax 2002; Smit et al. 2006; Le Loc'h F Hily and Grall 2007). The low nitrogen ratio at *R. grimaldii* can be interpreted as a result of the bryozoan filter feeder strategy, mainly feeding from detritus particles, undigested microbes, and symbiotic microbes. Thus, the bryozoans in the present study can be considered as primary consumers at low trophic levels, ingesting small particles that have been modified by benthic recycling, selective ingestion or assimilation of their own food source (Davenport and Bax 2002; Smit et al. 2006; Le Loc'h F Hily and Grall 2007).

The habitat alteration from a pristine seagrass bed to a dominated macroalgae bottom generated a loss of habitat for the bryozoans, as envisaged by the sharp decline in *Reteporella grimaldii* densities at invaded seagrasses. Moreover, activation of enzymatic activities was demonstrated as result of the invasion, together with shifts in carbon sources at the bryozoan colonies. The present results highlight the need to further address interaction across natural communities and alien species invaded systems before further cascade effects are driven.

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