THE INVASIBILITY OF MARINE ALGAL ASSEMBLAGES: ROLE OF FUNCTIONAL DIVERSITY AND IDENTITY

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Abstract. The emergence of the biodiversity–ecosystem functioning debate in the last decade has renewed interest in understanding why some communities are more easily invaded than others and how the impact of invasion on recipient communities and ecosystems varies. To date most of the research on invasibility has focused on taxonomic diversity, i.e., species richness. However, functional diversity of the communities should be more relevant for the resistance of the community to invasions, as the extent of functional differences among the species in an assemblage is a major determinant of ecosystem processes.

Although coastal marine habitats are among the most heavily invaded ecosystems, studies on community invasibility and vulnerability in these habitats are scarce. We carried out a manipulative field experiment in tide pools of the rocky intertidal to test the hypothesis that increasing functional richness reduces the susceptibility of macroalgal communities to invasion. We selected a priori four functional groups on the basis of previous knowledge of local species characteristics: encrusting, turf, subcanopy, and canopy species. Synthetic assemblages containing one, two, three, or four different functional groups of seaweeds were created, and invasion by native species was monitored over an eight-month period. Cover and resource availability in the assemblages with only one functional group showed different patterns in the use of space and light, confirming true functional differences among our groups. Experimental results showed that the identity of functional groups was more important than functional richness in determining the ability of macroalgal communities to resist invasion and that resistance to invasion was resource-mediated.

Key words: algal assemblages; biodiversity; Fucus serratus; *functional diversity; intertidal macroalgal communities; invasibility.*

INTRODUCTION

Biological invasions, whereby a species enters and spreads into areas where it was not previously present, are occurring with increasing frequency in both terrestrial and aquatic ecosystems (Lodge 1993). This is leading to concern over the impact of introductions on population, community, and ecosystem properties and prompted considerable interest in understanding the patterns and mechanisms by which alien species are established in new communities. Although invasions are often context-specific processes, generalities and global patterns have emerged (Lonsdale 1999). One of the earliest generalizations of community invasibility was the concept of "biotic resistance" proposed by Elton (1958). Biotic resistance predicts that highly diverse communities should be less susceptible to invasion because of a more complete utilization of resources.

Despite the intuitive plausibility of Elton's ideas, most observational studies that have attempted to relate the frequency of invasion to community diversity have failed to link high diversity with low invasibility. In fact the opposite has proved to be the case in many studies, with a positive relationship between diversity and some measure or index of invasibility, usually richness of introduced species (e.g., Lonsdale 1999). Debate regarding interpretation of this positive relationship has focused on the likely covariance between the level of native diversity and extrinsic factors such as resource availability and frequency of disturbance. Environmental factors known to promote native species diversity are also likely to favor the occurrence of invasions (Stohlgren et al. 1999).

Such observational approaches may give limited insight into the actual direct effect of diversity on invasibility owing to the numerous confounding factors. In recent years an experimental approach to understanding the relationship between biodiversity and a number of ecosystem properties and processes (functioning) including resistance to invasion has emerged. In

contrast to most observational studies, the majority of experimental work supports Elton's ideas in demonstrating greater resistance to invasion in diverse communities (McGrady-Steed et al. 1997, Naeem et al. 2000, Shurin 2000, Stachowicz et al. 2002, Troumbis et al. 2002), although there are exceptions (Robinson et al. 1995, Dukes 2001). The mechanism driving such a relationship remains unclear. On the one hand resource use complementarity is suggested by proponents of true diversity effects (Naeem et al. 2000) while on the other it is argued that a decline in invasibility with increasing diversity is simply a result of an increasing occurrence of suppressive species in more diverse communities, the sampling effect (Wardle 2001).

The role of individual species or taxa in suppressing invasion has come to the fore, with increasing recognition that idiosyncratic interactions between species can play a major part (Crawley et al. 1999, Law et al. 2000, Meiners et al. 2004). Species richness per se is increasingly disregarded as the driving force in diversity–invasibility relationships (Prieur-Richard and Lavorel 2000, Dunstan and Johnson 2004) with increased interest in the functional roles that species or groups of species play. Functional groups of species are generally defined by the way in which they use and compete for resources. Since resource availability is central to our current understanding of invasion processes, the number and identity of functional groups within a community may dictate the level of invasibility. Studies on the role of functional diversity on the resistance to invasion by communities are limited, and results are inconclusive (Prieur-Richard and Lavorel 2000, Symstad 2000).

In marine systems, the usually irreversible impacts of exotic species have profound consequences on ecological systems. Marine ecosystems differ fundamentally from their terrestrial counterparts. They are relatively open, with fewer limits to organism dispersal and energy flow, while terrestrial systems are relatively closed and material flow is largely local. Surprisingly, experimental studies of community invasibility in marine ecosystems have been scarce (but see Stachowicz et al. 2002, Britton-Simmons 2006).

Here we present the results of an experimental study on invasibility of marine macroalgal communities using synthetic assemblages. We assessed the effect of functional diversity and functional identity in synthetic communities on colonization by native species, used as model invaders. Functional groups of macroalgae that link species traits to resource use strategies were identified (see Lavorel et al. [1997] for a similar approach in plant communities) and incorporated into a replicated combinatorial design (Morin and McGrady-Steed 2004). The effect of functional group diversity and identity on the magnitude and predictability of invasion was determined over an 8-mo period. The mechanism of potential links between community composition and invasibility were assessed by determining the modes of resource exploitation by the different functional groups

and the relationship between resource availability and colonization.

METHODS

Our experiment was carried out at Wembury Point in the southwest of England (50°19′ N, 04°06′ W). This moderately exposed rocky shore consists of a gently sloping rock platform and abundant rock pools. Emergent substrata support a typical intertidal assemblage with dense barnacle cover and patchy fucoid algae described in detail in early work (e.g., Colman 1933).

Experimental procedure

On the basis of previous knowledge of the species inhabiting rock pools at Wembury, and from grouping systems used extensively in other intertidal studies (e.g., Steneck and Dethier 1994, Benedetti-Cecchi 2000) we selected a priori four morpho-functional groups: (a) encrusting coralline species, a group of red algal species including the genus *Phymatolithon* and *Lithophyllum* with a crustose growth form; (b) turf-forming species, a group of primary space-holders with limited vertical height (usually ~5 cm length) including articulated calcareous species (*Corallina* spp.), other corallinaceas (such as *Mesophyllum liquenoides*), and also other associated small species, mainly Ceramiales; (c) sub-canopy space-holder species, a group of species including *Bifurcaria bifurcata*, *Mastocarpus stellatus*, and *Chondrus crispus* that reach a maximum length of ~20 cm and form a secondary cover in many tide pools; these species produce prostrate axes or extensive encrusting holdfasts from which the erect fronds develop; (d) canopy species, a group of species including *Halidrys siliquosa* and *Cystoseira* spp. that can grow in pools up to 60–80 cm in length and form a true shade-forming canopy. All the major components of these groups are perennial species and belong to the local pool of species present in rock pools at Wembury.

Using these morpho-functional groups we assembled communities of varying morpho-functional diversity. Experimental assemblages consisted of PVC plates (20 × 20 cm) containing an array of 16 pieces of slate rock. Each rock piece was fully covered by one of the selected functional group or in the case of the canopy species group (*Halidrys siliquosa* and *Cystoseira* spp.) held a single adult plant.

To construct our synthetic assemblages, pieces of rock bearing the required species were chipped off from rock pools. Rock pieces were carefully transported to the laboratory and cut into the correct size (4 × 4 cm quadrats) using a commercial tile cutter. Rock pieces with the selected functional group were then randomly arranged on the PVC plate and held in position using underwater setting cement and screws. Sixty-four plates were constructed in this way: 16 plates with only one functional group (four replicates per group), 24 plates with all the combinations of two groups (four replicates per combination), 16 plates with all the combinations of

three groups (four replicates per combination), and 8 plates with all the groups. Additionally four plates with bare rock were also constructed. Our experimental design is therefore a factorial design (Allison 1999) or a replicated combinatorial design as defined by Morin and McGrady-Steed (2004).

Due to logistical restrictions such as the nature of some functional groups and the dearth of species within some functional groups we could not manipulate species number inside the functional groups. Therefore our experiment did not allow us to disentangle the effect of the number of species from the effect of number of functional groups, since assemblages had an increasing number of species with increasing functional diversity. However, although the assemblages were synthetic they resembled quite realistically the patchy "tile-like" pattern of intertidal algal assemblages, in which extremely small spatial scales of variation seem to be among the most important sources of heterogeneity (Archambault and Bourget 1996). In the same way as our synthetic plates, highly diverse natural pools are those with a high structural diversity, containing a mosaic of several species from different functional groups. Conversely, pools with low diversity contain species representing only one or two functional groups.

Prior to the installation of the plates on the shore, initial primary cover of each species and functional group and of bare rock was visually estimated using a sampling frame of 16 quadrats of 4 × 4 cm (i.e., equivalent to the mosaic plate arrangement). Estimates of percent cover of algae were obtained by assigning each taxon a score from 0 to 4 in each quadrat and adding up the 16 estimates (Dethier et al. 1993).

Plates were then transported to Wembury and attached to the substratum of a large rock pool (>100 m^2 area) with a minimum separation between plates of at least 1 m. All plates were attached at a similar depth in the pool of between 20 and 30 cm. Assemblage and installation of the plates was completed between October and November 2003.

In May 2004, plates were carefully detached from the pool and a second estimation of the percent cover of algae was performed in the field. Species used in the assemblages are perennial and slow growing. As a result, original covers were virtually unchanged in May (Bray-Curtis similarity indices for the square-root-transformed data between the same plates in May and June were on average higher than 0.9). Statistical analyses were carried out using only the initial cover data.

Although grazers are reported to play a key role in the formation and maintenance of algal mosaics in tide pools (Metaxas and Scheibling 1993) our aim here was to study pure diversity effects (Schmid and Hector 2004), i.e., how macroalgal functional diversity and identity affected the invasibility of the assemblages by new colonizers. Therefore grazers over and around the plates (mainly limpets and trochids) were removed monthly to reduce grazing pressure and promote

survival of algal propagules. However, no control was implemented to avoid grazing by small swimming grazers such as amphipods.

Our model invaders were native species. We assumed that the potential factors affecting the establishment and growth of native species and introduced species should be similar since there is little taxonomic difference between native and introduced macroalgal species in the area of study. Of the 15 macroalgal species listed as introduced species in U.K. coastal waters (Eno et al. 1997), only three belong to new families for British waters.

In addition to the examination of the relationship between functional diversity and invasibility in our plates, we were particularly interested in examining how invasibility differs depending on the characteristics of the invaders (i.e., on the species' invasiveness). Therefore we examined in detail the patterns of colonization of two groups of species with different ecological strategies: early successional species and the perennial canopy alga *Fucus serratus*. Early successional species are usually the first to colonize and dominate new areas wherever space and light are available and grazers fail to control its growth. *Fucus serratus* is a perennial brown alga, common in sheltered and moderately exposed shores of the Atlantic European coast, where it frequently monopolizes the space at mid and low intertidal levels (Lewis 1964).

To ensure an appropriate propagule pressure by *F. serratus* embryos, fertile plants of *F. serratus* were fixed beside each plate in December 2003. One fertile male and one fertile female plant of similar size (~50 cm length) were attached at each of two diagonal corners of the plates. All *Fucus* plants were removed in March after release of gametes. Early colonizing species, such as *Ulva* spp., largely remain fertile all year around and hence propagules of these species are always abundant in the water column. Lotze et al. (1999) recorded a recruitment rate up to 1.2×10^6 settling spores·m^{-2}·h^{-1} for *Ulva* spp. from April to December in the Baltic Sea. No seeding system was considered necessary for these species.

Colonization of the experimental plates (invasibility) was measured in July as the total biomass of new nonresident species, the biomass of ephemeral species, and the biomass and number of *F. serratus* plants established in experimental plates. Experimental plates were transferred to the laboratory, and, using forceps, newly colonized species were removed. Biomass was measured as dry mass after 48 h in an oven at 60°C.

Light penetration into the plates was also measured in July in the laboratory. Plates were submerged in a 75-L tank and light penetration, measured as the ratio of photosynthetically active radiation under the algal canopy to that above the vegetation, was estimated using a LI-COR-250 (LI-COR, Lincoln, Nebraska, USA) fitted with an underwater sensor. Due to the size of the sensor and its cylindrical shape, it was impossible to take measurements at surface level in the center of the

plates. We therefore placed the plates on a small stand that allowed positioning of the sensor on the plate border under the canopy of all the functional groups with erect fronds (i.e., turf, subcanopy, and canopy species). For each plate we took four measures (one on each side of the plate), and the average of these four measures was considered as an estimation of light penetration inside the plate.

Statistical methods

To test for differences in resource availability (bare rock and light levels) and susceptibility to invasion between plates with only one functional group, we performed an ANOVA. ANOVA tests were also used to test differences in resource levels among functional diversity treatments. Tukey's hsd tests were used to separate means (at $\alpha = 0.05$). Cochran's C tests were used to test the assumption of homogeneity of variance.

Simple linear regression models were used when testing relationships between single resource availability and the different invasion metrics. Multiple linear regression models were used to test the influence of the number and identity of the functional groups on the resistance of the synthetic assemblages to invasion. When appropriate, dependent variables were transformed in order to guarantee linearity in the relationships and to ensure that residual distributions approximated normality. Multi-collinearity between predictors in multiple regression models was tested using variance inflation factor (VIF). In our design the number of plots with dissimilar compositions was enough to get low levels of collinearity among predictors (VIF < 10 for all the cases). The type of regression model fitted (standard ordinary least squares [OLS] multiple regressions or quasi-Poisson regressions) varied among response variables depending on the distribution of the data. We fit standard OLS linear models for all the models involving biomass of invaders (log transformation was applied to total invader biomass and ephemeral biomass and square-root transformation to *F. serratus* biomass). A quasi-Poisson regression model was used in the *F. serratus* recruits model due to underlying distribution of the data and the over-dispersion observed (Quinn and Keough 2002).

We used linear models not to find a single "best" model describing the relationship between predictors and dependent variables but to analyze causality between them. Therefore once each full multiple regression model was set, we proceeded to select those predictors with a truly significant effect on the response variable. Hierarchical partitioning, a method based on the theorem of hierarchies, is particularly suitable for this task (Chevan and Sutherland 1991). Hierarchical partitioning compares all possible models in a multiple regression setting and determines the independent capacities of the predictive variables to explain the patterns of variability in the corresponding response variable. For each predictor, its independent explanato-

ry power on the dependent variable is characterized with an index "I," which reflects the independent contribution of the predictor to the variance explained by the models. A second parameter "J" measures the interaction between each predictor and the others. In our study J values were relatively small ($|I/J|$ ratios > 1). Therefore interactions among predictors were not considered (Mac Nally 2000).

Variables that independently explained a larger proportion of variance than by chance were identified using randomization tests. For each predictor, the observed contribution to the explained variance (I) was compared to the distribution of a population of Is of 1000 randomizations of the data matrix. Significance was accepted at the upper 95% confidence limit (Z score $\geq$ 1.65). Hierarchical partitioning procedures were estimated using the hierarchical partitioning software for the public domain package R (Walsh and Mac Nally 2003). The hierarchical partition approach alleviates one of the major limitations of multiple regressions, namely that the contributions of each predictor variable are dependent upon which other predictor variables happen to be included in the model (Chevan and Sutherland 1991, Mac Nally 2000).

Additionally, we assessed the validity of the hierarchical partitioning procedure in selecting significant predictors by using Crawley (2002) guidelines to identify the minimal adequate model (MAM) for each regression model. A successive backward-forward selection procedure was used starting from the maximal model. The MAMs were identified as those ones that simultaneously minimized Akaike Information Criterion (AIC) of the model and had the smallest number of significant predictors. The quality of fit of the models including the significant predictors was assessed with the R^2 value (OLS models) and the D^2 values (R^2-like statistic for quasi-Poisson linear models; Guisan and Zimmermann 2000), which state how much of the variation in the response variable is explained by the model.

Results from both approaches were virtually the same. Except for one predictor in one model detected as significant by the hierarchical procedure but not by the Crawley-recommended method, both approaches identified the same variables as significant. Here we present the results obtained through the hierarchical partitioning analysis.

RESULTS

As a result of winter storms, seven of the 64 experimental plates were lost and hence all results refer to the remaining 57 plates.

Patterns of resource availability and invasibility in the plates assembled with only one functional group

Primary space use varied among functional groups. In the plates assembled with only encrusting species (CR), algae only a few millimeters thick covered much of the space and cover of bare rock was only ~9%. In the

plates with only turf (TU) species, erect fronds of *Corallina* spp. covered ~80% of the primary space with the other 20% of cover equally shared by calcareous crust and bare rock. In the plates assembled with the subcanopy (SU) functional group, *Bifurcaria bifurcata*, *Mastocarpus stellatus*, and *Chondrus crispus* used most of the primary space (90%), leaving 10% of bare rock. Finally, in the canopy (CA) species plates, the holdfasts of *Halidris siliquosa* and *Cystoseira* spp. covered ~40% of primary space with ~60% bare rock.

Differences in size and morphology of the different functional groups shaped resource availability on the plates. Statistical analysis showed that the availability of bare space was the greatest for plates assembled entirely of canopy species but there were no significant differences among the other groups (ANOVA, $F_{3,8} = 63.9$, $P < 0.0001$, Tukey's hsd, CA > CR = TU = SU). Light availability was markedly influenced by the identities of species assembled in the plates, with significant differences among functional groups (ANOVA, $F_{3,8} = 17.24$, $P < 0.001$, light levels transformed to $\sin^{-1}(\sqrt{Y})$). Plates assembled entirely with crustose and turf species showed the highest values of light at the substratum surface. On the other hand, canopy species reduced light levels drastically, and assemblages composed of subcanopy species showed intermediate levels of light (Tukey's hsd, CR > TU = SU > CA).

Although bare rock was not included as a functional group in our synthetic assemblages, we did assemble four control plates entirely of bare rock. Patterns of colonization in these bare rock plates and in the monofunctional plates showed that across all invasion metrics crustose plates were on average the most heavily colonized, with bare rock showing similar high levels for total invader biomass and total ephemeral biomass (Fig. 1). Colonization of canopy plates was consistently low. However, differences among groups were only significant for two of the four invasion metrics: total invader biomass (ANOVA, $F_{4,11} = 10.93$, $P < 0.001$, Fig. 1A) and ephemeral biomass (ANOVA, $F_{4,11} = 7.95$, $P < 0.01$, Fig. 1B). Total invader and ephemeral biomass were significantly higher in the plots assembled entirely with rock or crustose species than in the plates assembled entirely with subcanopy or canopy species (Tukey's hsd, ROCK = CR > SU = CA). Plates assembled with turf were not significantly different from any of the other groups for these two metrics of invasibility.

Functional diversity and identity effects on the susceptibility of assemblages to invasion

Patterns of colonization observed did not support the hypothesis that increased diversity reduces invasibility of plant communities. Functional diversity was not a significant predictor for three out of the four invasion metrics examined: total biomass of invaders, ephemeral species biomass, and *Fucus serratus* biomass (Table 1, Fig. 2). Only number of recruits of *F. serratus* was
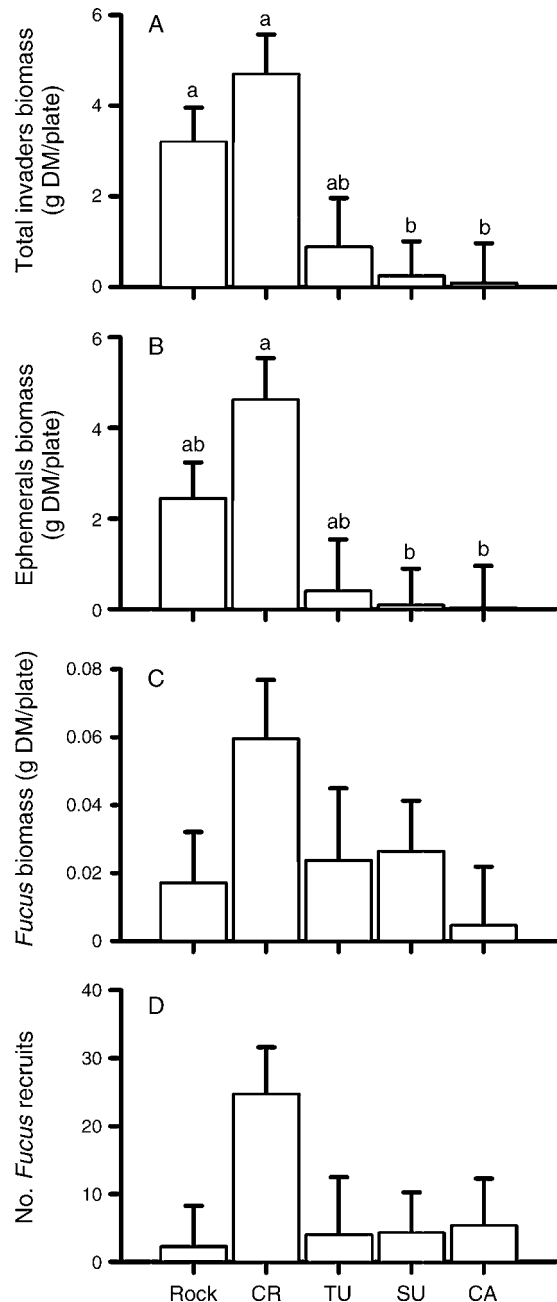

FIG. 1. Invasibility levels for the plates assembled with only one functional group, including those made only of bare rock. (A) Total biomass (dry mass, DM) of invaders, (B) ephemeral biomass, (C) *Fucus serratus* biomass, and (D) number of *Fucus* recruits (mean ± SE). Different lowercase letters indicate differences between groups based on Tukey's hsd test. Functional group abbreviations are: CR, encrusting species; TU, turf species; SU, subcanopy species; and CA, canopy species.

affected by functional diversity; surprisingly, this effect was positive and accounted for 24% of the total independent effects (%I). For two of the invasion metrics (total invader biomass and total ephemeral

TABLE 1. Relationships between functional diversity and abundance of the different functional groups with the different metrics of invasibility used in our study (total colonizer biomass, ephemeral biomass, *Fucus* biomass, and *Fucus* recruits) for the whole set of assemblages.

| | a) Hierarchical partitioning analysis: independent contribution (%I), by predictors | | | | | b) Linear model, OLS | | Quasi-Poisson D^2 |
Functional group	Functional diversity	Encrusting	Turf	Subcanopy	Canopy	R^2	P	
Overall colonizers biomass (log)	0.10	(+)48.31***	4.49	6.91	(−)40.19***	0.55	<0.001	
Ephemerals biomass (log)	0.15	(+)45.94***	4.39	9.56	(−)39.95***	0.52	<0.001	
Fucus biomass (sqrt)	12.09	(+)41.87***	9.89	5.82	(−)30.31***	0.24	<0.001	
Fucus recruits	(+)24.06*	(+)31.10**	(−)30.61**	6.95	7.26		n/a	0.33

Notes: (a) Results of the hierarchical partitioning analysis, "%I" indicates the percentage of independent contribution to explained variance. Significant predictors are indicated by asterisks (see *Methods* for the significance determination procedure). Positive and negative symbols reflect the sign of the effect. (b) Linear model R^2 (ordinary least squares, OLS) and P values for the final model using the significant predictors. The last column reports the D^2 statistic (R^2-like statistic for quasi-Poisson linear models; P values are not available for the quasi-Poisson model). P values <0.05 are statistically significant (n/a, test not available).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

biomass), there was an apparent reduction in the overall variability in invasibility of our assemblages with diversity for two of the invasion metrics (Fig. 2A, B).

In contrast to diversity effects, individual effects by the functional groups were quite obvious. Abundance of crustose species was a significant predictor for each invasion metric considered in this study. Crustose species had a positive effect on the arrival of new colonizers (Table 1), accounting for 48%, 46%, 42%, and 31% of the total independent effects (%I) for total biomass of new colonizers, ephemeral biomass, *F. serratus* biomass, and number of recruits, respectively. Meanwhile, canopy species depressed the arrival of invaders except for the number of recruits of *F. serratus*, although its predictive capacity was slightly smaller (Table 1). Finally, abundance of turf was also a significant predictor for the number of *F. serratus* recruits, accounting for 31% of the total independent effects.

The differences in the effects of the various functional groups on our four invasion metrics are summarized in Fig. 3. Total invader biomass and total ephemeral biomass were almost fully suppressed by canopy species irrespective of the canopy density, while crustose species promoted invasibility, with a clear positive relationship between crustose cover and total and ephemeral biomass (Fig. 3A, B). Turf and subcanopy species effects were similar to those of the canopy species but less intense. In the case of *F. serratus* biomass and number of *Fucus* recruits, a different pattern emerged. The presence of crustose species at any relative density allowed the highest values, while canopy species reduced the biomass and recruitment of *F. serratus* in proportion to their relative cover (Fig. 3C, D). Increasing cover of turf and subcanopy species led to a decline in *Fucus* invasibility, although for *Fucus* biomass, at least, the effect was less intense than for canopy species.

Multiple regressions (MR) using the appropriate significant predictors explained an important percentage of the variance in biomass of all the invaders and ephemerals (multiple R^2, 0.55 and 0.52, respectively;

Table 1). *Fucus serratus* biomass and number of *F. serratus* recruits were not so satisfactorily forecasted (multiple R^2, 0.24 and D^2, 0.33, respectively; Table 1), suggesting that other factors could be involved in the success of *F. serratus* colonization.

Resource availability and invasibility

While different functional groups shaped resource availability on plates (described above) there was little relationship between functional diversity and resource availability. No significant differences were found in resource availability among the different levels of functional diversity (ANOVA, $F_{3,53} = 0.57$, $P > 0.05$ for light availability; ANOVA, $F_{3,53} = 0.98$, $P > 0.05$ for bare rock), although there was a slight trend of mean light reduction with increasing diversity (in the lowest diversity treatment, 53.8 ± 8.3; in the highest diversity treatment, 26.1 ± 10.3 [mean ± SE]).

Light availability showed a positive relationship with three of the four metrics used to measure invasibility in our experiment. Total invader biomass, ephemeral biomass, and *F. serratus* biomass were positively correlated with light measured in the plates (OLS simple regression, $R^2 = 0.41$, $R^2 = 0.46$, and $R^2 = 0.10$, respectively; $P < 0.05$ for all the cases). Only the number of *F. serratus* on the plates was not correlated with light levels. There was a negative relationship between bare rock availability and total invaders and ephemerals biomass (OLS simple regression, $R^2 = 0.19$, $R^2 = 0.16$, respectively; $P < 0.05$ for both cases). The reason for this unexpected result was that bare rock presence was associated with canopy species, which strongly suppressed invasion through light reduction. Therefore bare rock was a resource present but was mostly not available for new colonizers. However, when we consider substratum availability as the cover of bare rock and encrusting species simultaneously, this predictor showed a positive and significant relationship with all the invasion metrics used in the study, i.e., total invader biomass, ephemeral biomass, and biomass and number of *F. serratus* (OLS simple regression, $R^2 = 0.14$,
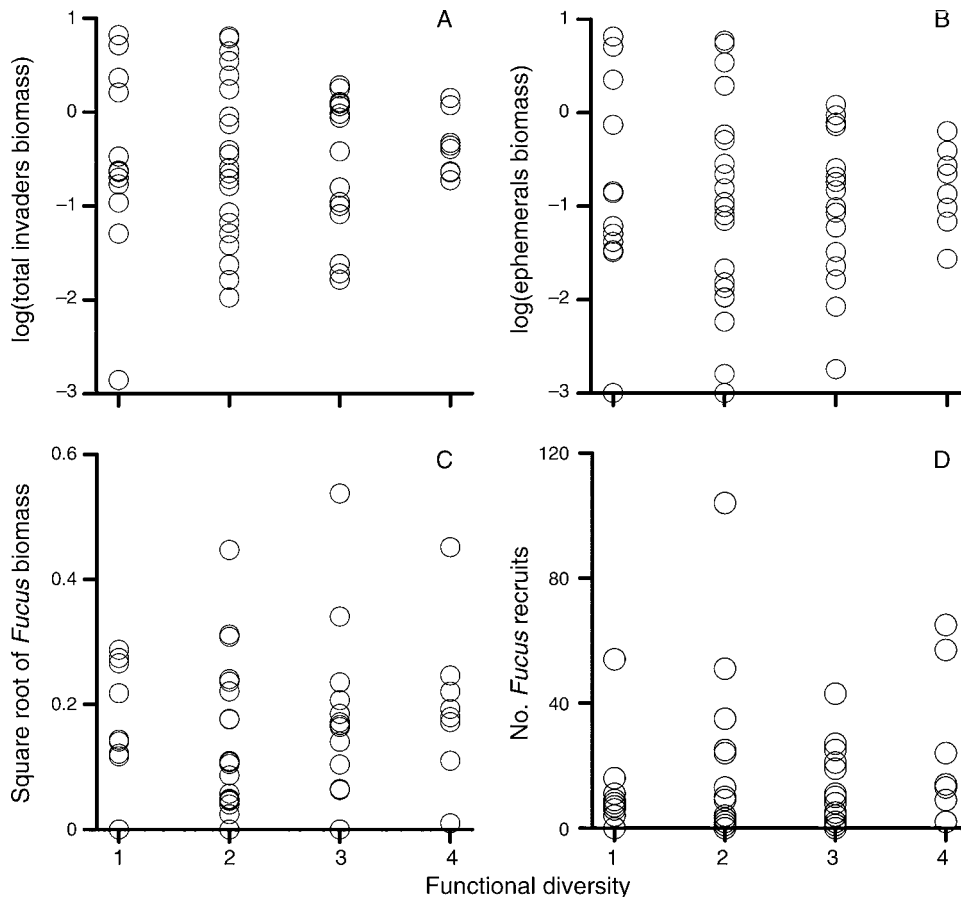
FIG. 2. Relationship between functional diversity and the invasion metrics used in this study: (A) total biomass of invaders (log-transformed); (B) biomass of ephemeral species (log-transformed); (C) biomass of *Fucus serratus* (square-root-transformed); and (D) number of recruits of *F. serratus*. Each circle represents a single plate. Biomass is given as transformed grams dry mass per plate.

$R^2 = 0.16$, $R^2 = 0.10$, and $R^2 = 0.15$, respectively; $P < 0.05$ for all the cases).

DISCUSSION

Our work on intertidal macroalgal communities aimed to determine the role of functional group diversity and identity in determining the invasibility of tide pool communities by two model invaders and to establish the role of resource availability in any such relationship. Results did not support the hypothesis that increased functional diversity leads to a reduction in invasibility but did provide clear evidence of the importance of functional group identity. Thus, idiosyncratic effects of the functional groups were identified as the dominant process in determining invasion success. This important role appeared to be mediated by the effects of functional group identity on the availability of the key resources, suitable settlement substrate and light, for potential colonizers. We showed, as in previous studies (Airoldi 2000), that the functional group of encrusting species acted as a suitable settlement substrate for new colonizers with equivalent or higher colonization levels

on encrusting species than on bare rock. Hence in the following discussion suitable settlement substrate refers to the combination of bare rock and encrusting species.

Elton's concept of biotic resistance implies a negative relationship between diversity and invasibility through a more efficient use of resources by native species in more diverse communities, the so-called complementary resource use hypothesis (Hooper 1998). Our experiment based on functional attributes of species provided little support for the complementary resource use hypothesis. The predictive capacity of functional diversity on resource availability was statistically undetectable. In contrast individual functional group identity had a much greater predictive capacity, indicating that the functional attributes of a few species may govern the ecosystem use of resources. Compositional effects have been widely described in terrestrial studies in which identity was more decisive than diversity effects in the resource–diversity relationship (Naeem et al. 1994, Symstad 2000).

Elton's hypothesis also means that potential invaders respond when resource opportunities arise. This was
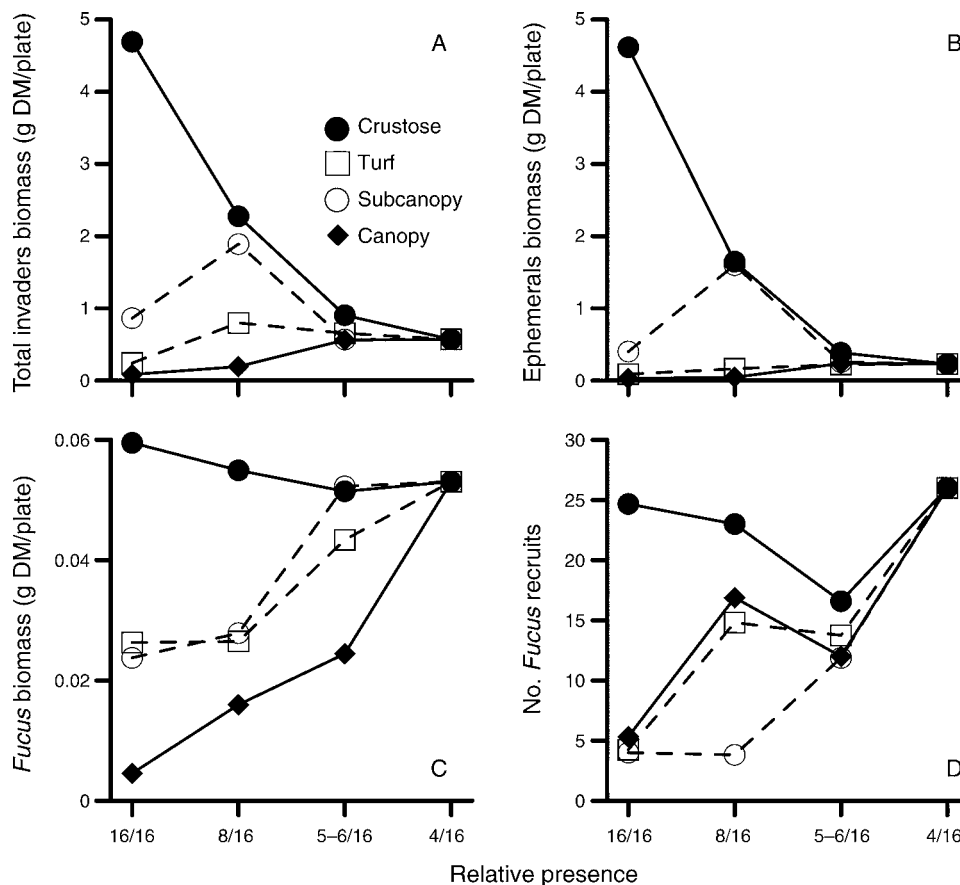
FIG. 3.   Mean effects of the different functional groups (symbols) on the invasion metrics in relation to their relative presence in the plates: (A) total biomass of invaders; (B) biomass of ephemeral species; (C) biomass of *Fucus serratus*; (D) number of recruits of *F. serratus*. Relative presence is the number of pieces of rock in the plate containing the corresponding functional group (i.e., 16/16 means that the entire plate was built with the same functional group, 8/16 means that half of the plate was built with that species). Mean values were calculated using only the plates that included the corresponding functional group. Error bars have been omitted for clarity.

clearly the case in our experimental assemblages, where abundance of colonizers was noticeably related to resource levels (both light and substratum availability). Successful colonization by macroalgae requires a suitable substratum for settlement and early growth and access to sufficient light and nutrient levels for continued development. The idiosyncratic effects of different functional groups on invasion success can be related to a large extent to their effect on the primary resource requirements of space and light. The presence of both canopy-forming macroalgae and crustose species in the synthetic communities had clear consequences for resource levels and consequently were good predictors of invasion success. Crustose species are very efficient in procuring and holding primary substrate and can tolerate overgrowth (Airoldi 2000) and high grazing intensity (Steneck 1983). Communities dominated by this group offered the highest levels of both resources (light and substrate availability) to potential colonizers. Assemblages consisting only of encrusting species held a similar or even higher biomass of colonizers than

equivalent bare rock assemblages, suggesting that at least in the reduced herbivory conditions present in our experiment, encrusting species were invasion "promoters." In some way they may be seen as the marine equivalent of biological soil crusts in terrestrial systems. These crusts, composed mainly of algae, fungi, and lichens, cover the soil surface in arid and semiarid ecosystems and have positive effects on the germination of terrestrial plants (Hawkes 2004). Canopy-forming macroalgae are habitat-forming species with strong effects on the presence and abundance of other taxa (Connell 2003). In our experiment the canopy species group had very strong negative effects on new colonizers. These inhibitory effects were probably produced by the efficiency of this group in altering the quality and quantity of light reaching the substratum (Middelboe and Binzer 2004).

While the crustose and canopy groups were good predictors of resource levels and invasion success in artificial communities, the other two groups showed less clear responses. Turf-forming algae, with *Corallina* spp.

as the main structural species, are a long-lived and highly persistent component of intertidal assemblages that can inhibit the recruitment of large macroalgae (Britton-Simmons 2006). Light levels were high and substrate availability moderately low in turf-dominated synthetic communities. As a result perhaps of these conflicting resource trends, the only significant effect of turf presence was a negative impact on *Fucus serratus* recruitment. Meanwhile, opportunistic species were probably able to partially colonize turf-dominated plots. Similarly the subcanopy group had no significant effect on any of the invasion metrics, although the graphs showed a similar but weaker effect than that of the canopy group.

Compositional effects from the recipient assemblages were partially matched by similar compositional effects from the invaders point of view. In our experiment we simultaneously examined the invasion patterns by early ephemeral species and the late-colonizing species *F. serratus*. Analysis of the factors influencing the general patterns of invasion revealed some differences in the effects of resource availability on the abundance of invaders. Abundance of early successional opportunistic species was mainly affected by light. This group included green algae like *Ulva* spp., *Cladophora* spp., brown species like *Scytosiphon lomentaria*, and some red filamentous species such as Ceramiales. *Ulva* spp. are responsible for "green blooms" that occur frequently in coastal ecosystems affected by eutrophication (Lotze et al. 1999). On the other hand, *F. serratus* is a canopy-forming species with a very effective short-distance dispersal capacity. Although it has been described as able to colonize spatially saturated communities (Arrontes 2002), the abundance of this species in our plates was mainly promoted by substratum availability.

In addition to assessment of the magnitude of invasion, we also found a reduction in the overall variability in the invasibility of our assemblages with diversity, which supported the similarity hypothesis (Fukami et al. 2001), i.e., an increase in predictability with diversity. Although the similarity hypothesis was interpreted as an artifact of some experimental designs (Wardle 1998), it is now considered as a widely extended phenomenon and as one of the mechanisms that could explain how biodiversity loss influences variability in ecosystem functioning (Fukami et al. 2001).

Our study is one of the first experimental studies on invasibility of macroalgal assemblages using synthetic communities, a procedure already used with sessile marine animals (Stachowicz et al. 2002). Results from studies in marine benthic communities are scarce and conflicting. Stachowicz et al. (2002) showed that increasing diversity reduced the survival and abundance of invaders in marine sessile invertebrate communities. The underlying mechanism was a negative relationship between diversity and resource availability (space) within the experimental assemblages. Conversely in an observational study, Dunstan and Johnson (2004) found

positive relationships between diversity and the abundance of invaders using similar communities. There, opportunistic invaders colonized species-rich communities more effectively because of a higher mortality of native species in high-diversity assemblages and facilitative interactions between native species and new colonizers. Similarly, our experiment did not support the negative relationships between functional diversity and invasibility. We suggest that the lack of an obvious enhancement in the use of resources with increasing functional diversity would explain this lack of relationship between functional diversity and invasibility. The only experiment that to date has explored the relationship between functional diversity and invasibility in marine algal communities also drew attention to the role of resource availability in the success of the invasion (Britton-Simmons 2006).

Niche complementarity (i.e., complementary resource use) has been widely advocated as the underlying mechanism for the relationships found between diversity and many community properties, including invasion resistance. However, species coexistence may be based on numerous different mechanisms (Chesson 2000), and hence a simple relationship between diversity and ecosystem functioning may not occur, especially in nonequilibrium situations (Mouquet et al. 2002). Moore et al. (2001) demonstrated by modeling that positive relationships between diversity and invasion resistance will occur only when there is niche complementarity between species. In intertidal systems, mosaic-like macroalgal assemblages are maintained by a range of different processes such as physical disturbance, predation, spatial heterogeneity, recruitment limitations, and differential life histories (Benedetti-Cecchi and Cinelli 1996, Airoldi 2000, Menge et al. 2005). These diversity-promoting processes may not promote complementarity in resource use, especially where diverse assemblages are maintained as a mosaic of patches in differing stages of succession. Rock pools, where physical factors and grazing interact with intra- and interspecific competition to shape the structure of the macroalgal communities (Chapman 1990, Benedetti-Cecchi and Cinelli 1996), may be a good example of a system in which processes maintaining diversity are not driven by niche complementarity among species and therefore diversity and complementarity resource use are decoupled. In our experiment evidence of complementarity in resource use was very weak and trivial in comparison to compositional effects.

The output of this work clearly shows that in intertidal macroalgal communities the number of functional groups per se does not dictate the magnitude of invasion by potential colonizers. Instead the identity of functional groups determines invasibility, with crustose species promoting and canopy-forming species inhibiting colonization. Marine algal assemblages provide an exceptional model system for ecological research (Olson and Lubchenco 1990). However to date few

experimental studies have focused on the functional consequences of biodiversity in macroalgal communities. The evidence available suggests strong similarities between benthic macroalgal communities and terrestrial and wetland systems with weak diversity effects and strong compositional effects (Middelboe and Binzer 2004, Bruno et al. 2005). This correspondence in the findings may be a consequence of the similar resource requirements that marine and terrestrial plant populations and communities face (Carpenter 1990).

In focusing on functional rather than species-level diversity, an assumption implicit in our work is that invasibility of coastal habitat will only be promoted through loss of a whole functional group rather than one or a few members of that group. While loss of a whole group may seem unlikely, recent work has suggested that human activity in coastal habitats resulting in reductions in water quality is causing widespread loss of canopy-forming macroalgae (Benedetti-Cecchi et al. 2001, Gorgula and Connell 2004). Given the clear role of canopy algae in limiting invasion of our artificial communities, it is straightforward to venture that anthropogenic impact could increase the invasibility of coastal habitats through the reduction of the abundance of native canopy species.

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