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CONTENTS

Algae as hosts for epifaunal bryozoans: Role of functional groups and taxonomic relatedness

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ABSTRACT

Macroalgae build biogenic habitats which give shelter and provide a suitable physical environment for a great variety of organisms. Structural complexity of algal substrates may influence the composition of their attached epifauna. The aim of this study is to test whether the taxonomic relatedness of the algal hosts and the functional groups to which they belong influence the species richness and composition of their epifaunal bryozoans. We analysed 36 algal genera from the Atlantic coast of South America between 42°S and Cape Horn. Changes in bryozoan species richness (number of species) among different algal functional groups (filamentous algae, foliose algae, corticated foliose algae, corticated macrophytes) were non-significant. The composition of the epifaunal assemblages differed significantly only between filamentous and foliose algae. Sheet-like bryozoans (i.e. encrusting, pluriserial colonies) were more frequent on foliose than on filamentous algae, while runner-like species (i.e. uniserial stolons) were characteristic epibionts on filamentous thallii. Similarity of bryozoan assemblages increased with increasing taxonomic relatedness of their hosts. As most filamentous seaweeds analysed in this study are members of the Order Ceramiales, the influence of algal taxonomic relatedness and functional groups on the composition of their bryozoan assemblages can be viewed as two different aspects of the same phenomenon.

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1. Introduction

Many macroalgae build biogenic habitats which give shelter and provide a suitable physical environment for a great variety of organisms (e.g. Kelaher, 2002; Roberts et al., 2008). However, the influence of algal structural complexity on abundance and diversity of their associated fauna is complex. Attributes of algal architecture such as stem width and the degree of branching provide a good explanation for differences in molluscan assemblages associated with different algal taxa (Chemello and Milazzo, 2002). Likewise, metazoan community structure and frequency distribution of body size were found to be related to the fractal dimensions of their algal hosts (Gee and Warwick, 1994a, b). In coralline algal turf, increasing structural complexity decreased richness and abundance of gastropod assemblages at different tidal heights of a rocky shore (Kelaher, 2003). On the contrary, the distribution and abundance of epiphytal amphipods showed no consistent relationship with the complexity of their seaweed hosts (Russo, 1990).

Marine macroalgae can be categorized according to the morphology of their thallii and photosynthetic performance (functional-form groups; Littler, 1980; Littler and Arnold, 1982). Patterns in algal biomass, diversity and dominance are also strikingly convergent when examined at a functional group level. This polyphyletic approach stresses similarities among unrelated species that share critical organismal features (Steneck and Watling, 1982; Steneck and Dethier, 1994). Other authors have recommended that functional groupings be based on specific functions such as nutrient uptake, photosynthesis rates, or resistance to herbivores, rather than gross morphology (Padilla and Allen, 2000). Assemblage structure of mobile epifaunal invertebrates, however, is not influenced by changes in algal species richness and functional groups in the Pacific coast of Canada (Bates and DeWreede, 2007). Internal features of seaweeds tend to be conserved within taxonomic lineages. Consequently, species that are closely related are more likely to share traits and thus perform similarly in ecological scenarios (Bates, 2009).

Bryozoans are encrusting, colonial invertebrates usually attached to subtidal macroalgae (reviewed by Seed and O'Connor, 1981). Interactions between bryozoans and algae are complex and may result in disadvantages (defoliation: Saunders and Metaxas, 2008; reduction of incident light reaching the thallus: Muñoz et al., 1991) or benefits (source of CO_2 for photosynthesis: Mercado et al., 1998) for the basibionts. Some algae have developed chemical or mechanical defenses to deter the settlement and growth of fouling organisms (Dworjanyn et al., 1999, 2006; Nylund and Pavia, 2005). Bryozoan-algal associations have been studied in several coastal regions in the Northern Hemisphere (Rogick and Croasdale, 1949; Ryland, 1962; Pinter, 1969; Winston and Eiseman, 1980), but this relationship has yet to be further explored by the application of multivariate techniques. Therefore, our aim is to analyse whether the composition of epifaunal bryozoan assemblages is influenced by the taxonomic relatedness of their algal substrates as well as by the functional groups to which they belong. In this study, the following hypotheses will be tested: (1) species richness of epifaunal

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bryozoans increases with increasing algal structural complexity, (2) epifaunal assemblages associated with different algal functional groups are significantly different, and (3) similarity of bryozoan assemblages is higher on closely related than on unrelated algal genera.

2. Materials and methods

A total of 805 macroalgal samples stored at the herbarium of the Museo Argentino de Ciencias Naturales (MACN) were analysed. Algal specimens came from the coasts of Argentina, the Chilean islands located south of the Beagle Channel and the Malvinas/Falkland Islands, and were collected between 42°S and Cape Horn. Samples from outside this latitudinal range were not analysed, as this study was restricted to the Austral American Atlantic phytogeographical region (*sensu* Kühnemann, 1972). As not all the algal specimens stored at the herbarium were identified to species, this analysis was performed at the generic level. The current status of each genus was verified consulting Algaebase (www.algaebase.org) and Boraso and Zaixso (2008). The genus *Enteromorpha* Link was regarded as a synonym of *Ulva* L. (see Hayden et al., 2003). Bryozoans on herbarium specimens were very well preserved and were identified to the lowest possible taxonomic level. The name *Celleporella hyalina* sensu lato was used in this study to identify an undescribed cryptic species of *Celleporella* within this species complex (see Gómez et al., 2007). *Celleporella tehuelcha* was transferred to *Antarctothoa* following Wright et al. (2007) and Hughes et al. (2008).

2.1. Functional groups

According to their morphological complexity, macroalgal genera were allocated to the following functional groups (see Steneck and Dethier, 1994): filamentous algae, foliose algae, corticated foliose algae, corticated macrophytes, leathery macrophytes, articulated calcareous algae and crustose algae. Only algae with at least one epifaunal bryozoan

were considered in this study. Functional groups represented by less than 4 algal genera (leathery macrophytes, articulated calcareous algae and crustose algae) were not analysed.

The composition of the bryozoan assemblage on different macroalgal functional groups was compared with a one-way Analysis of Similarities (ANOSIM) using the PRIMER package (Clarke and Warwick, 2001). A similarity matrix was obtained applying the Sørensen index based on presence/absence data of bryozoan species on each algal substrate. The relationships of the bryozoan assemblages developed on different algal genera were displayed using non-Metric Multidimensional Scaling (MDS). The stress value shows to which extent the MDS bivariate plot is a reliable representation of the relationships among genera in the similarity matrix (Clarke and Warwick, 2001). The contribution of each bryozoan species to dissimilarity in significant pairwise contrasts between algal functional groups was calculated with the Similarity Percentage routine (SIMPER) of the PRIMER package (Clarke, 1993). Tables were truncated when cumulative percentages reached 50%.

Bryozoan species richness (i.e. number of species) was compared among functional groups with the Kruskal–Wallis non-parametric test (Sokal and Rohlf, 1981).

2.2. Taxonomic relatedness

The taxonomic classification of algal genera (Fig. 1) follows Algaebase. Taxonomic distances for all pairwise combinations of algal genera were calculated by counting the number of steps (i.e. levels) through a dendrogram of the Linnean taxonomic hierarchy from genus to kingdom until a match was found (Fig. 1). For instance, the distance between *Phycodrys* and *Cladodonta* was scored as 1, as both genera belong to the same tribe. On the other hand, the distance between *Hymenena* and *Ulva* was given a value of 8, since they belong to different phyla within the same kingdom. The taxonomic levels subkingdom, infrakingdom and subphylum were not taken into account. The
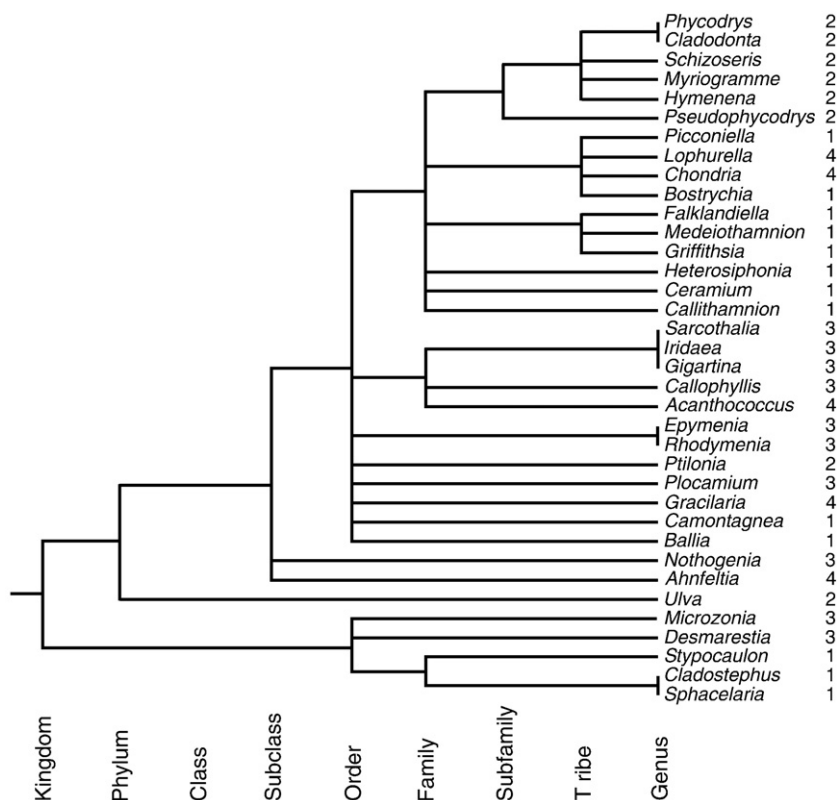

Fig. 1. Dendrogram showing taxonomic relatedness and functional groups of 36 algal genera analysed in this study. Algal taxonomic classification follows Algaebase. Functional groups: 1, filamentous; 2, foliose; 3, corticated foliose; 4, corticated macrophytes.

Table 1
Bryozoans found on different algal functional groups.

Species	Functional groups			
	Filamentous algae	Foliose algae	Corticated foliose algae	Corticated macrophytes
Aetea anguina (Linnaeus, 1758)	X	X	X	X
Amastigia nuda Busk, 1852	X			
Antarctothoa anneae Wright et al., 2007	X		X	X
Antarctothoa bougainvillei (d'Orbigny, 1847)	X	X	X	X
Antarctothoa cancinoi Wright et al., 2007			X	
Antarctothoa sp.	X		X	
Antarctothoa tehuelcha (López Gappa, 1985)	X	X	X	X
Austrothoa yagana (Moyano & Gordon, 1980)	X	X	X	X
Beania costata (Busk, 1876)	X	X	X	X
Beania inermis (Busk, 1852)		X	X	
Beania magellanica (Busk, 1852)		X		
Bicrisia spp.	X	X	X	X
Caberea darwinii Busk, 1884	X	X	X	
Callopora deseadensis López Gappa, 1981			X	X
Cellaria malvinensis (Busk, 1852)	X			
Cellaria scoresbyi Hastings, 1946	X			
Celleporella hyalina (Linnaeus, 1767) sensu lato	X	X	X	X
Chaperia acanthina (Lamouroux, 1825)		X		
Crisia spp.	X			
Electra longispina (Calvet, 1904)	X			
Electra monostachys (Busk, 1854)		X		
Fenestrulina cf. *dupla* Hayward & Ryland, 1990		X		
Membranipora isabelleana (d'Orbigny, 1847)			X	
Menipea patagonica Busk, 1852	X	X	X	
Metroperiella galeata (Busk, 1854)	X			
Neothoa patagonica (Busk, 1852)	X	X	X	X
Osthimosia bicornis (Busk, 1881)	X			
Osthimosia eatonensis (Busk, 1881)				X
Plesiothoa australis Moyano & Gordon, 1980	X		X	
Porella hyadesi Jullien, 1888		X		
Romancheina labiosa (Busk, 1854)		X		
Scruparia ambigua (d'Orbigny, 1847)	X	X	X	X
Smittina monacha (Jullien, 1888)		X		X
Tricellaria aculeata (d'Orbigny, 1847)	X	X	X	X
Tubulipora spp.	X	X	X	X
Umbonula alvareziana (d'Orbigny, 1847)		X	X	

Sørensen index was applied to construct a similarity matrix based on presence/absence data of epifaunal bryozoans with the PRIMER package. The correlation between the similarity of bryozoan assemblages and the taxonomic distance for all pairwise combinations of algal genera (n = 630) was calculated with the Spearman rank index (Sokal and Rohlf, 1981).

3. Results

From a total of around 105 marine macroalgal genera from the SW Atlantic and Antarctica represented in the MACN herbarium, only 36 were basibionts of bryozoans between 42°S and 55°S. Most of these algae were filamentous (n = 13), while the foliose algae, corticated foliose algae and corticated macrophytes were represented by 8, 10 and 5 genera, respectively (Fig. 1).

A total of 36 bryozoan taxa were found (Table 1). Changes in bryozoan species richness among different algal functional groups were non-significant (Fig. 2; Kruskal–Wallis test, n = 36, H = 1.21, P = 0.75).

The ANOSIM test showed that differences in bryozoan assemblage composition among different algal functional groups were statistically significant (Global R: 0.199, P = 0.002). Only pairwise contrasts between filamentous algae and both types of foliose algae were significant (Table 2). These were the only functional groups relatively well separated from each other in the bivariate MDS plot (Fig. 3).

The SIMPER routine (Table 3) showed that the bryozoans that best discriminate between filamentous and foliose algae were not entirely restricted to one functional group. *Austrothoa yagana* and *Antarctothoa bougainvillei*, two encrusting bryozoans with pluriserial colonies, were more frequent on foliose than on filamentous algae. *Scruparia ambigua*

and *Aetea anguina*, two anascans with uniserial stolons, and *Bicrisia* spp., an erect cyclostome genus, were characteristic epibionts on filamentous thallii. *Antarctothoa tehuelcha* was the exception, since the encrusting pluriserial colonies of this hippothoid were more frequent on filamentous than on foliose algae. *Beania costata*, whose reticulated
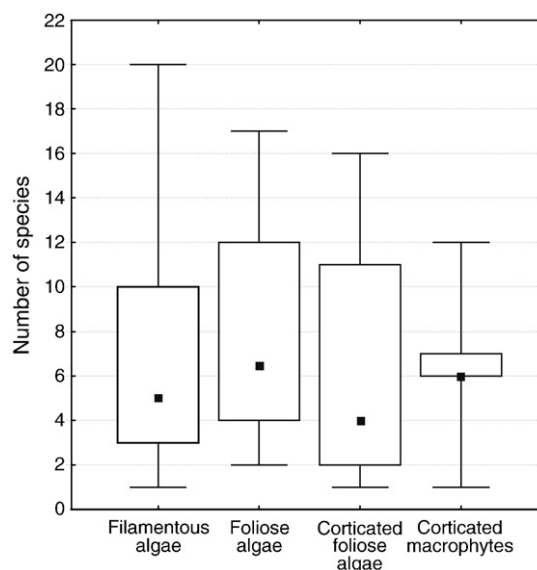

Fig. 2. Species richness of epifaunal bryozoan assemblages on different algal functional groups. Black squares: median, rectangles: first and third quartiles, segments: range.

Table 2
ANOSIM paired contrasts between bryozoan assemblages developed on different algal functional groups.

Contrast	R	P
Filamentous vs. foliose	**0.350**	**0.003**
Filamentous vs. corticated foliose	**0.315**	**0.001**
Filamentous vs. corticated macrophytes	0.168	0.143
Foliose vs. corticated foliose	−0.044	0.682
Foliose vs. corticated macrophytes	0.100	0.223
Corticated foliose vs. corticated macrophytes	0.040	0.336

Significant results in bold.

colonies are loosely attached to the substrate by rhizoids, was more frequent on foliose than on filamentous thallii (Table 3).

The correlation between algal taxonomic relatedness and the similarity of bryozoan assemblage composition was negative and highly significant (Fig. 4; Spearman rank correlation, n = 630, Rs = −0.33, $P < 1 \times 10^{-6}$), meaning that closely related basibionts shared relatively more bryozoan species than unrelated algal genera.

4. Discussion

The abundance, species richness and diversity of mobile epifaunal organisms are positively correlated to the architectural attributes of their macroalgal hosts (Gee and Warwick, 1994a; Chemello and

Fig. 3. MDS showing the relationships among bryozoan assemblages developed on 36 algal genera. The name of each genus was replaced by the functional group to which it belongs. Functional group codes as in Fig. 1.

Milazzo, 2002). Therefore, we expected that species richness of sessile colonial invertebrates such as bryozoans would also increase with increasing structural complexity of the substrate. In the present study we found no support for this hypothesis, as the number of bryozoan species was not higher on more complex than on relatively simpler algae. This conclusion, however, cannot be extrapolated to other morphological groups not examined in this study. Genera of leathery macrophytes were too scarce in the MACN herbarium, preventing a meaningful comparison against filamentous, foliose or corticated seaweeds. In the Magellan region, leathery macrophytes are represented by the native genera *Macrocystis*, *Lessonia* and *Durvillaea*, as well as by the invasive kelp *Undaria*, found for the first time in Patagonia in 1992 (Piriz and Casas, 1994). Kelps are attached to the substrate by complex and often intricate structures called holdfasts, which in the case of *Macrocystis* were found to support 46 bryozoan species in just one Patagonian locality (López Gappa et al., 1982). This extreme biodiversity, however, was observed after an intensive survey involving the thorough examination of 36 holdfasts. The influence of algal structural complexity on epifaunal biodiversity is not always straightforward, as there seems to be an upper threshold beyond which an increase in frond density of coralline turf is associated with a decrease in abundance and richness of the gastropod assemblage (Kelaher, 2003). In the present study, changes observed among algal functional groups were not related to the number of epifaunal species but to their identity.

Changes in assemblage structure of Magellan epifaunal bryozoans showed significant differences only when we compared filamentous algae against two groups of foliose algae. Studies on seaweeds from the Pacific coast of Canada also showed that foliose algae serve as hosts for different associations of mobile invertebrates than those present on other functional groups (Bates and DeWreede, 2007; Bates, 2009). Encrusting, rounded bryozoan colonies with continuous growth margins ('sheets'; see Jackson, 1979) were more frequent on foliose than on filamentous algae. The latter are not a suitable substrate for roughly circular colonies. Most filamentous seaweeds are basibionts of uniserial bryozoans ('runners'; see Jackson, 1979) characterised by ramified stolons such as those of *Aetea anguina* or *Scruparia ambigua*. Thus, a structural similarity occurs between epibionts and basibionts. Although *Antarctothoa tehuelcha* buds encrusting, pluriserial colonies, it usually builds tubular structures around filamentous thallii.

Bates (2009) showed that the similarity in assemblage structure of mobile invertebrates does not decrease with increasing taxonomic distance of host macroalgae. He found that closely related seaweeds shared on average similar numbers of epifaunal organisms as seaweeds belonging to different kingdoms. It can be expected that sessile organisms which live attached to the substrate be more strongly associated with
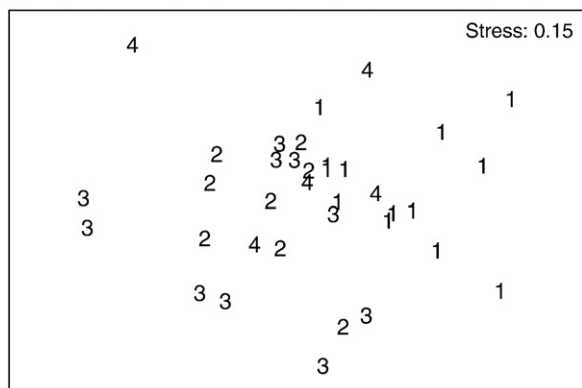
Table 3
Results of the SIMPER test for significant contrasts between bryozoan assemblages developed on different algal functional groups.

Species	Average abundance	Average abundance	Average dissimilarity	Contribution (%)	Cumulative%	Growth type
Average dissimilarity = 68.91						
	Filamentous algae	Foliose algae				
Austrothoa yagana	0.08	0.88	6.80	9.86	9.86	Encrusting pluriserial
Scruparia ambigua	0.85	0.38	5.83	8.46	18.32	Encrusting uniserial
Antarctothoa tehuelcha	0.77	0.38	5.31	7.70	26.02	Encrusting pluriserial
Aetea anguina	0.77	0.38	5.15	7.47	33.49	Encrusting uniserial
Antarctothoa bougainvillei	0.62	1.00	4.90	7.12	40.61	Encrusting pluriserial
Bicrisia spp.	0.62	0.50	4.59	6.67	47.27	Erect
Beania costata	0.23	0.63	4.38	6.35	53.63	Prostrated pluriserial
Average dissimilarity = 73.59						
	Filamentous algae	Corticated foliose algae				
Scruparia ambigua	0.85	0.40	7.49	10.18	10.18	Encrusting uniserial
Austrothoa yagana	0.08	0.70	7.46	10.14	20.33	Encrusting pluriserial
Antarctothoa tehuelcha	0.77	0.20	6.87	9.34	29.67	Encrusting pluriserial
Aetea anguina	0.77	0.40	6.23	8.47	38.14	Encrusting uniserial
Antarctothoa bougainvillei	0.62	0.80	5.71	7.76	45.90	Encrusting pluriserial
Bicrisia spp.	0.62	0.30	4.82	6.54	52.44	Erect

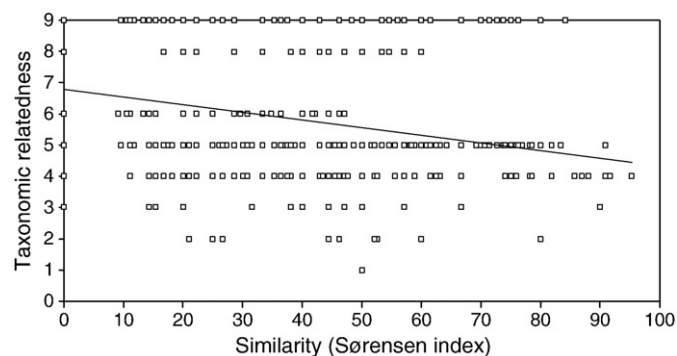The lists were truncated when cumulative percentages reached 50%.

Fig. 4. Relationship between similarity (Sørensen index) of bryozoan assemblages and taxonomic relatedness for all pairwise combinations of 36 algal genera.

their basibionts than mobile invertebrates that use algal thallii mainly as a refuge. Present results show that similarity of bryozoan assemblages was higher on closely related than on unrelated algal genera. An examination of Fig. 1, however, shows that the influence of taxonomic relatedness on the composition of bryozoan assemblages is not independent from the possible effect of functional groups, since most members of the Order Ceramiales have filamentous thallii. Therefore, the significant influence of algal taxonomic relatedness and functional groups on the composition of bryozoan assemblages can be viewed as two different aspects of the same phenomenon.

5. Conclusions

The present study has shown that closely related algae share relatively more epifaunal bryozoan species than unrelated algal genera. Changes in assemblage structure of Magellan bryozoans show significant differences only between filamentous and foliose algae. A structural similarity was found between epifaunal bryozoans and their algal substrates. No support was found for the hypothesis that bryozoan species richness is higher on more complex than on relatively simpler algae. As most filamentous seaweeds belong to the Order Ceramiales, the significant influence of algal taxonomic relatedness and functional groups on the composition of bryozoan assemblages may be regarded as two different aspects of the same phenomenon.

Acknowledgements

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