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Distribution and morphological variation of low-shore algal turfs

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Abstract The distribution of three functional groups of algae (filamentous, corticated terete and calcareous articulated) was investigated in low-shore, turf-forming assemblages from rocky shores in the western Mediterranean Sea (Italy). Algae were sampled along shores from three different stations. Shores were either exposed to wave action or sheltered and were characterised by various inclinations of the rocky substratum (horizontal, sloping and vertical). The hypotheses tested were: that the relative abundance of the three functional groups of algae (1) varies between sheltered and exposed shores, (2) is influenced by substratum inclination and (3) that these distributions are consistent across stations. There was no clear relationship between the morphology of turf-forming algae and shore characteristics. Covers of filamentous, corticated terete and calcareous articulated algae differed among shores and stations, but patterns were not consistent across shores with similar exposure to waves and substratum inclination. Turfs often comprised algae with different morphologies, in a combination of anchor and epiphytic species. It is suggested that functional groups of algae, as currently identified, are not effective in describing changes in distribution of algae between sheltered and exposed shores, when turf morphologies are considered. Future research on relationships between morphology and ecology of algae should consider the potential importance of positive interactions among associated species, which could override responses of individual functional groups.

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Introduction

Studies have shown that algal morphology is often related to several important functional traits, including productivity, respiration, growth rate, reproductive output, longevity, resistance to physical stress, susceptibility to herbivores and competitive ability (Littler 1980; Littler and Littler 1980; Littler and Arnold 1982, but see Dudgeon et al. 1995). Based on these observations, morphologically similar algae are usually classed into six to eight polyphyletic functional groups, which have been suggested to differ in various ecological characteristics and to respond differently to perturbations such as herbivory, desiccation and wave force (Littler and Littler 1980; Steneck and Watling 1982; Littler and Littler 1984; Hay 1994; Steneck and Dethier 1994, but see Padilla and Allen 2000).

Macroalgal assemblages dominated by turf-forming algae are abundant worldwide in tropical and temperate, intertidal and subtidal habitats (Airoidi et al. 1995 and references therein). In the most common interpretation, turfs are assemblages of densely packed, small macroalgae which are often associated with trapped sediment (Stewart 1983; Kendrick 1991; Airoidi and Virgilio 1998). Despite this similar structural arrangement, turf-forming algae display remarkable variation in morphology of the thallus (Hay 1981). Most turf-forming algae can be classed as filamentous, calcareous articulated or corticated terete [sensu Steneck and Dethier (1994), where corticated terete is equivalent to coarsely branched in Littler and Littler (1984), and include branched, corticated upright forms]. Algae with different morphologies generally occur intermixed in the same turf; often, however, one morphology is quantitatively dominant over the others. Differences can occur not only from shore to shore and over large geographical scales (Murray and Bray 1993), but also locally over small spatial scales (Stewart 1982; Airoidi 1998). These variable distributions may reflect different responses to physical and/or biological factors. Despite the worldwide abundance of

algal turfs, however, relationships between different morphologies of turf-forming algae and environmental variables have remained largely unexplored [but see Hay (1981) and Taylor and Hay (1984)].

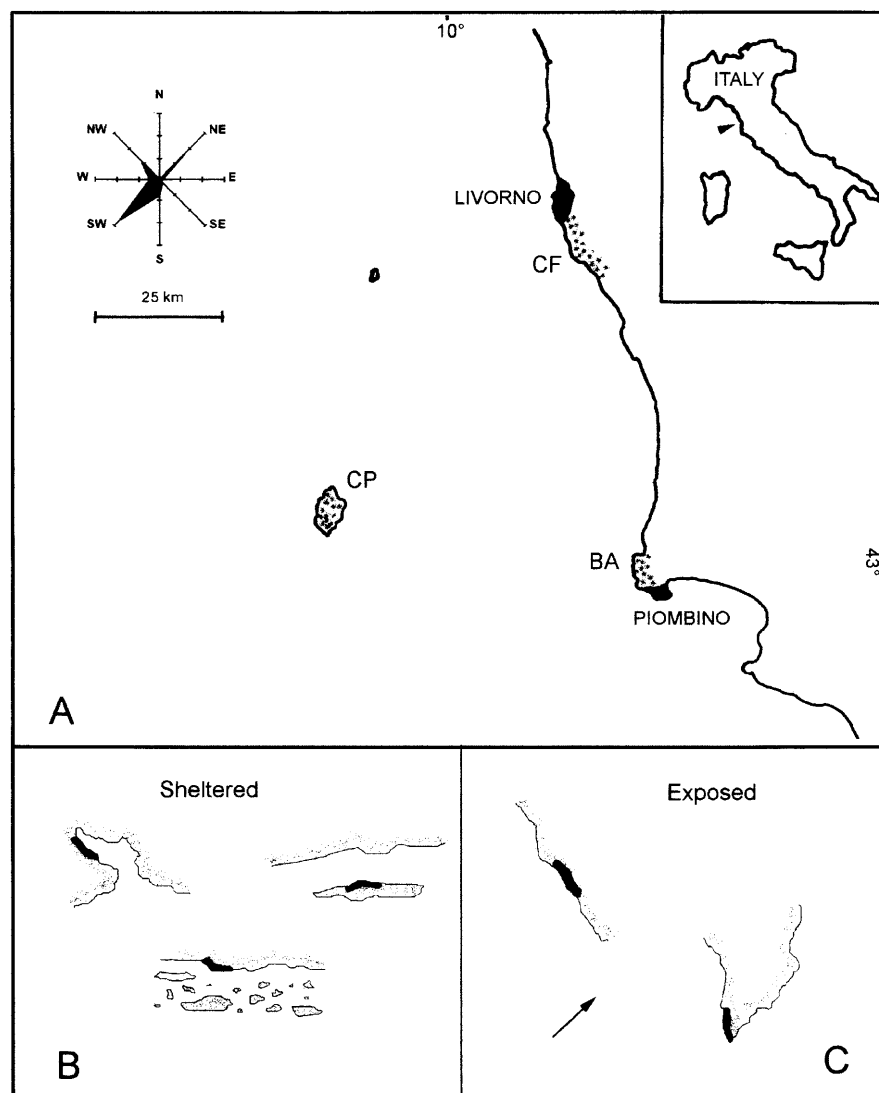
A major environmental gradient exists across low-shore habitats exposed to varying degrees of wave action (Lewis 1968; Denny et al. 1985). Differences in cover, density, morphology and size of macroalgae between exposed and sheltered shores have been reported for many assemblages (Southward 1958; Menge 1976; Norton 1985; Viejo et al. 1995; Kaehler and Williams 1996), including Mediterranean algal assemblages (Boudouresque 1984; Ballesteros 1992). In particular, it has been suggested that algae with greater structural complexity of thallus, including corticated terete and calcareous articulated algae, should be better at resisting wave shear than structurally simple functional groups, such as filamentous algae (Littler and Littler 1980, 1984; Harrold et al. 1988). Nevertheless, little empirical information is available about distribution of functional groups of algae at sheltered and exposed shores. In this

study, I tested the general hypothesis that the morphology of low-shore, turf-forming algae is related to wave exposure or to factors potentially interacting with wave exposure, such as the inclination of the substratum. I predicted that, if greater structural complexity of functional groups of algae effectively reflects greater resistance to wave action, then (1) turf-forming algae that could be classed as corticated terete or as calcareous articulated should be more abundant than those classed as filamentous on exposed shores, whereas the opposite pattern should occur at sheltered shores; (2) differences in the relative abundance of corticated terete, calcareous articulated and filamentous algae should increase from horizontal to vertical substrata; and (3) these distributions should be consistent across stations.

Materials and methods

The study was conducted at three localities (hereafter referred to as stations) in the Ligurian Sea, Italy (Fig. 1A). The island of Capraia

Fig. 1 **A** Map of the study area indicating location of the three stations (*CP* Capraia, *BA* Baratti and *CF* Calafuria) and direction of winds registered at Livorno (frequency distribution of winds over 30 km h^{-1} speed during 1992–1996, data from the *Avvisatore Marittimo* di Livorno). **B** Example of shores assigned the attributes of sheltered and **C** exposed in Capraia (arrow indicates direction of prevailing winds from the south-west)



is a nature reserve, relatively unaffected by human activities. The two other stations were at Calafuria and Baratti on the Italian mainland, fairly close to urban areas. Turf-forming algae were common at all stations in low-shore habitats (0–20 cm with respect to the mean low-water level), where they formed extensive turfs intermixed with patches of mussels and, at Capraia, canopy-forming algae. Three major functional groups of turf-forming algae could be recognised according to the schemes proposed by Littler and Littler (1984) and Steneck and Dethier (1994): (1) “filamentous”, including uniseriate, multiseriate, lightly corticated or polysiphonous filamentous algae; (2) “corticated terete”, including branched, upright, extensively corticated, fleshy to wiry algae; and (3) “calcareous articulated”, consisting of calcified, articulated algae. Algae with other morphologies, such as foliose, also occurred in the turf, but they were generally less than 5% of the cover, and were not considered in this study. Intensive experimental work on the structure and dynamics of mid-shore and low-shore algal assemblages at these and other stations in the north-west Mediterranean has shown that, in contrast to mid-shore habitats, limpets and other herbivores were scarce at low levels on the shore, and had negligible effects on low-shore, turf-forming algae (Benedetti-Cecchi et al. 2000).

At each station, six exposed and six sheltered shores of rather homogeneous, unbroken bedrock (hereafter referred to as shores), less than 10 m long and interspersed along 2–4 km of the coast, were selected at random and used in the study. At Calafuria, where the coast is fairly straight and heavily exposed to wave action, only three sheltered shores could be found. Owing to technical difficulties in direct simultaneous measurements of wave force at 36 shores up to 80 km apart, shores were assigned the attributes of sheltered and exposed based on exposure to prevailing winds (Fig. 1A, data relative to years 1992–1996 from the Avvisatore Marittimo di Livorno). All sheltered shores were located either inside small protected bays or creeks, or on the landward side of coastal rocky reefs or were protected by close reefs attenuating the breaking of waves (Fig. 1B); all exposed shores were either on headlands or on straight coasts facing the open sea and were exposed to strong prevailing winds from south to north-west (Fig. 1C). Sampling was done between July and August 1996. During the months immediately preceding the study to the end of the sampling period, the sea was unusually rough compared to typical summer conditions in the area, and a series of storms occurred, with wave heights up to 4–6 m (Fig. 2, data from the Avvisatore Marittimo di Livorno). Shores with different inclinations were included in the sampling design, in order to evaluate the potential interactive effects of inclination and wave exposure on the relative distribution of different morphologies of turf-forming algae. Shores were defined as “horizontal” when the slope of the bedrock ranged between 0° and 10°, as “sloping”, between 40° and 50°, and as “vertical”, between 80° and

90°. At each station, two horizontal, two sloping and two vertical shores, at random, were sampled for each level of exposure to wave action (except at Calafuria, where only one horizontal, one sloping and one vertical sheltered shore were sampled). Percentage covers of filamentous, corticated terete and calcareous articulated algae were estimated in quadrats of 6.5×6.5 cm by means of the visual estimation method (Dethier et al. 1993). Owing to the small size of the algae (generally less than 2 cm high), and to the relative homogeneity of the assemblages within each shore (see Results), this sampling surface was considered large enough to quantify algal cover adequately. Further, larger surfaces would have been difficult to sample at exposed sites. A plastic grid with 25 small quadrats was used, and a score from 0% to 4% was given to each functional group of algae in each small quadrat (Dethier et al. 1993). Since the aim of the study was to test whether the relative abundance of turf-forming algae that could be attributed to the three different functional groups changed in relation to shore characteristics, only algae belonging to one functional group were quantified in each sample, so as to ensure that abundance data for each functional group were statistically independent. Nine quadrats were sampled at random on each shore at low tide, with three replicate samples for each functional group. Samples of intact turf were also collected for taxonomic determination of most-abundant species.

Percentage-cover data were analysed by a five-way, mixed-model analysis of variance (ANOVA). Only data from the two stations where six sheltered shores could be sampled, Capraia and Baratti, were used in this analysis, in order to maintain a balanced design (Underwood 1997). The analysis included the following factors: wave Exposure (exposed and sheltered; fixed factor), substratum Inclination (horizontal, sloping and vertical; fixed factor), Station (two stations; random factor), Shore (two shores; random factor) and functional Group (filamentous, corticated terete and calcareous articulated; fixed factor). Exposure, Inclination, Station and Group were orthogonal, whereas Shore was nested in the interaction of Station × Exposure × Inclination. Percentage-cover values were arcsine-transformed prior to analysis. Cochran's *C* test was performed to check for homogeneity of variances. Results showed no effects of shore Inclination either as main factor ($F_{2,2} = 0.24$, $P > 0.05$) or in combination with other factors ($P > 0.05$ in all tests), and visual inspection of graphs suggested that this was true also at Calafuria (see Results). A second analysis was thus performed, in which shores with different inclinations were considered as replicate shores. Calafuria was also included as a station in this analysis, which increased the power of the test for the interaction Exposure × Group. The design was balanced by randomly choosing three shores among the six available for each exposure at Capraia and Baratti and for exposed shores at Calafuria. A four-way, mixed-model ANOVA was performed, which included Exposure (exposed and sheltered; fixed), Station (three stations; random), Shore (three shores; random) and Group (filamentous, corticated terete and calcareous articulated; fixed) as factors. When possible, pooling procedures were used to increase the power of tests (Underwood 1997).

Results

The maximum taxonomic richness of turf-forming algae occurred among filamentous algae (Table 1), which included species from the three major divisions of seaweeds (Chlorophyta, Heterokontophyta class Phaeophyceae, and Rhodophyta). Corticated terete and calcareous articulated algae only included species belonging to the division Rhodophyta. Calcareous articulated algae were entirely articulated corallines, mainly *Corallina elongata* and *Jania rubens* (Table 1), while corticated terete algae included several branched species which could be classed as “non-spongy” according to the subcategories identified within this group by Murray and Bray (1993).

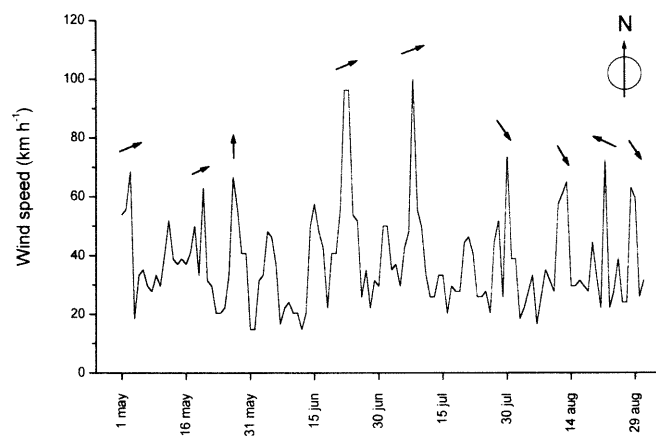


Fig. 2 Average wind speed (km h^{-1}) and direction of winds recorded at Livorno from 1 May to 31 August 1996; data are from the Avvisatore Marittimo di Livorno

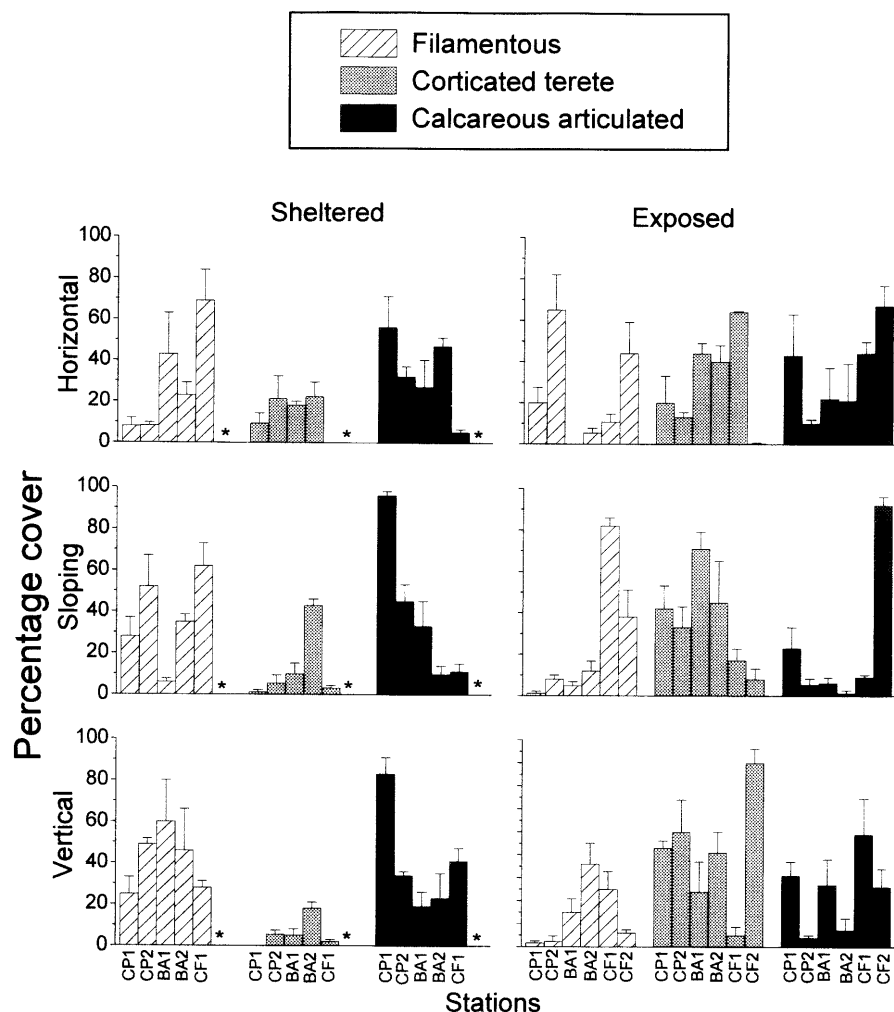
Individual shores were generally dominated by one or two functional groups of algae (Fig. 3), which formed rather homogeneous turfs. The structure of turfs re-

sulted from a combination of anchor and epiphytic species. Filamentous algae often occurred as epiphytes of calcareous articulated and corticated terete algae,

Table 1 Most common species of turf-forming algae found at the study area and brief description of morphological attributes which justify their attribution to filamentous, corticated terete and calcareous functional groups

Filamentous	
<i>Chaetomorpha aerea</i> (Dillwin) Kützing	Uniseriate
<i>Cladophora</i> spp.	Uniseriate
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	Multiseriate
<i>Ceramium ciliatum</i> (Ellis) Ducluzeau	Lightly corticated
<i>Ceramium</i> spp.	Lightly corticated
<i>Herposiphonia secunda</i> (C. Agardh) Ambrogn	Polysiphonous
<i>Lophosiphonia cristata</i> Falkenberg	Polysiphonous
<i>Polysiphonia opaca</i> (C. Agardh) Moris and De Notaris	Polysiphonous
<i>Polysiphonia</i> spp.	Polysiphonous
Corticated terete	
<i>Callithamnion granulatum</i> (Ducluzeau) C. Agardh	Collected specimens were large, rather extensively corticated plants, with a wiry texture
<i>Chondria capillaris</i> (Hudson) M. Wynne	Tufted, terete, pseudoparenchymatous, corticated, fleshy
<i>Gelidiella pinnosa</i> (Bornet) J. Feldman and Hamel	Tufted, terete, corticated, fleshy
<i>Hypnea musciformis</i> (Wulfen) Lamouroux	Tufted, terete, pseudoparenchymatous, corticated, fleshy
<i>Laurencia</i> sp.	Branched, upright, terete, extensively corticated, tough
<i>Polysiphonia flocculosa</i> (Agardh) Kützing	Collected specimens were large, rather extensively corticated plants, with a wiry texture
Calcareous articulated	
<i>Corallina elongata</i> Ellis and Solander	Calcified, articulated
<i>Jania rubens</i> (Linnaeus) Lamouroux	Calcified, articulated

Fig. 3 Covers of filamentous, corticated terete and calcareous articulated turf-forming algae at shores with different exposure to wave action (sheltered and exposed) and substratum inclination (horizontal, sloping and vertical). Data are average percentage covers (\pm SE, $n=3$) for each shore at each station (Capraia, Baratti and Calafuria). At Calafuria, only one sheltered shore could be sampled for each substratum inclination. Stations are coded as in Fig. 1



whereas thalli of *C. elongata* always attached directly to the rock. Corticated terete algae were either attached to the rock or anchored to branches of *C. elongata*.

In contrast to the low variability observed within shores, the distribution of filamentous, corticated terete and calcareous articulated algae was very heterogeneous among neighbouring shores and stations (Fig. 3 and Table 2, significant Group \times Shore and Group \times Station interactions). Average covers measured at each shore varied from 0% to 82%, 0% to 80% and 1.3% to 96% for filamentous, corticated terete and calcareous articulated algae, respectively. At exposed shores at Capraia and Baratti, cover of corticated terete algae was generally greater than covers of calcareous articulated and filamentous algae, and the opposite trend was observed at sheltered shores, independently of shore inclination (Fig. 3). Differences in average covers of the three groups of algae between sheltered and exposed shores were, however, less than 20%, and they were not detected as significant (Table 2). Since no differences in the relative abundance of the three groups of algae were observed in relation to shore inclination (Table 2), and visual inspection of the graphs (Fig. 3) suggested this was true also at Calafuria, an additional, more powerful analysis was performed, in which the factor Inclination was eliminated and Calafuria was included as a station, after balancing the number of shores (see Materials and methods). The analysis showed that patterns of abundance of filamentous, corticated terete and calcareous articulated algae were not significantly influenced by shore exposure (Table 3). At Calafuria, filamentous and

calcareous articulated algae were generally more abundant than corticated terete algae at exposed shores, in contrast to the opposite trend frequently observed at shores in Capraia and Baratti (Fig. 3). Filamentous algae were also more abundant than either corticated terete or calcareous articulated algae at sheltered shores at Calafuria, while at Capraia and Baratti, filamentous algae were often as abundant or even less abundant than calcareous articulated algae at sheltered shores (Fig. 3).

Discussion

No clear relationship was found between the morphology of turf-forming algae and shore exposure or inclination. Covers of filamentous, corticated terete and calcareous articulated algae varied among shores and stations, but patterns were not consistent across shores with similar exposure to waves and substratum inclination. Sea conditions were particularly rough during the study, which suggests that the similar distribution of functional groups of algae observed at sheltered and exposed shores was not related to short-term favourable conditions at exposed sites. At low levels on these shores, limpets and desiccation also have negligible effects on the distribution of functional groups of turf-forming algae (Benedetti-Cecchi et al. 2000). A possible interpretation of the results is that functional groups, as currently identified, might not effectively reflect responses of algae to wave action, as suggested by Phillips et al. (1997). Further, association of algae with different morphology in turfs might override responses predicted from the morphology of individual species.

Phillips et al. (1997) have discussed problems associated with the current definition of functional groups,

Table 2 ANOVA of percentage cover of functional groups of turf-forming algae at different stations and shores and in relation to exposure to wave action and substratum inclination. Factors are: Exposure (exposed vs sheltered; fixed), Inclination (horizontal vs sloping vs vertical; fixed), Station (two stations, Capraia and Baratti; random), Group (filamentous vs corticated terete vs calcareous articulated; fixed) and Shore (two shores; random, nested in the interaction Station \times Exposure \times Inclination). Data are arcsine-transformed (Cochran's test $C = 0.088$, n.s.). Only sources of variation involving interactions with Group are relevant to the hypotheses tested and are, therefore, reported. *MS* Mean square; *n.s.* not significant, $**P < 0.01$, $***P < 0.001$

Source of variation	<i>df</i>	<i>MS</i>	<i>F</i>	Denominator <i>MS</i> for <i>F</i> ratio
Exposure (E)	1			
Inclination (I)	2			
Station (S)	1			
Group (G)	2	486.9	0.18 n.s.	S \times G
Shore (S \times E \times I)	12			
(Sh (S \times E \times I))				
E \times G	2	8537.9	11.2 n.s.	S \times E \times G
I \times G	4	314.8	0.34 n.s.	S \times I \times G
S \times G	2	2731.3	5.38 **	G \times Sh (S \times E \times I)
G \times Sh (S \times E \times I)	24	507.8	3.29 ***	Residual
S \times E \times G	2	756.0	1.49 n.s.	G \times Sh (S \times E \times I)
S \times I \times G	4	913.7	1.79 n.s.	G \times Sh (S \times E \times I)
E \times I \times G	4	1029.2	0.90 n.s.	S \times E \times I \times G
S \times E \times I \times G	4	1143.9	2.25 n.s.	G \times Sh (S \times E \times I)
Residual	144	154.2		

Table 3 ANOVA of percentage cover of functional groups of turf-forming algae at different stations and shores and in relation to exposure to wave action. Factors are: Exposure (exposed vs sheltered; fixed), Station (three stations, Capraia, Baratti and Calafuria; random), Group (filamentous vs corticated terete vs calcareous articulated; fixed) and Shore (three shores; random, nested in the interaction Station \times Exposure). Data are arcsine-transformed (Cochran's test $C = 0.13$, n.s.). Only sources of variation involving interactions with Group are relevant to the hypotheses tested and are, therefore, reported. *MS* Mean square; *n.s.* not significant, $**P < 0.01$, $***P < 0.001$

Source of variation	<i>df</i>	<i>MS</i>	<i>F</i>	Denominator <i>MS</i> for <i>F</i> ratio
Exposure (E)	1			
Station (S)	2			
Group (G)	2	550.4	0.12 n.s.	S \times G
Shore (S \times E) (Sh (S \times E))	12			
E \times G	2	2254.2	3.18 n.s.	Pooled term
S \times G	4	4522.3	6.76 **	G \times Sh (S \times E)
G \times Sh (S \times E)	24	668.8	4.79 ***	Residual
S \times E \times G	4	940.9	1.41 n.s.	G \times Sh (S \times E)
Residual	108	139.5		
Pooled term = (S \times E \times G) + [G \times Sh (S \times E)]	28	707.7		

including the large variability of physiological responses within each group, and difficulties in assigning species to functional groups. Overall, a major difficulty is identifying morphological traits that separate ecologically meaningful groups, i.e. groups with predictive values in terms of broad responses to various environmental factors (Hay 1994; Lavorel et al 1997). The morphological traits which are presently used to identify functional groups of algae have been chosen mostly based on studies of relationships between seaweed form and productivity and of responses of algae to disturbance by herbivores and desiccation stress (Littler 1980; Littler and Littler 1980; Lubchenco and Gaines 1981; Littler and Arnold 1982; Steneck and Watling 1982; Hawkins and Hartnoll 1983). Those traits mostly refer to components such as thallus cortication, calcification and thickness and complexity of branching. Nevertheless, while structural complexity and calcification of the thallus can confer resistance to tissue loss by herbivores at the cost of decreased growth rates (Littler and Littler 1980, but see Padilla 1989), other morphological traits could be more relevant in terms of response to wave action. Size, for example, has been suggested as a primary factor in determining survival of algae on wave-swept shores (Carrington 1990; Gaylord et al. 1994), and Carpenter and Williams (1993) have shown that flow speed and thickness of the boundary layer of water experienced by algal turfs vary according to their canopy height. Algae growing in turfs with similar sizes might thus respond similarly to wave forces independently of the structural complexity of their thallus. Further, because of the generally smaller sizes and greater compactness attained by algae when aggregated into turfs than when isolated (Hay 1981; Taylor and Hay 1984), turf-forming algae could be relatively little affected by wave exposure, and might face greater constraints on their morphology and distribution from competition or variable dispersal potential (Airoldi 1998; Benedetti-Cecchi et al 2000).

It has been observed that structurally complex algae can protect morphologically simple algae from herbivores or desiccation under their canopies (Littler and Littler 1984), and that dense assemblages can buffer group members from various physical stresses, including wave stress (Bertness and Leonard 1997 and references therein). The potential importance of interactions among algae with different morphologies, however, has been largely overlooked. Positive interactions among closely associated species are common in marine and terrestrial assemblages, especially in severely disturbed or stressed habitats (Brooker and Callaghan 1998), and can play a major role in maintaining coexistence of species (Bertness and Leonard 1997). As in other assemblages (Dahl 1972; Hay 1981; Stewart 1982), the algal turfs observed in this study result from the association of algae of different morphologies, some of which would occur in other habitats more sparsely or as discrete thalli. Often, structurally complex algae, such as *Corallina elongata*, provide anchorage for structurally

simpler filamentous epiphytes, allowing their persistence at exposed or otherwise severely disturbed sites (Stewart 1982, 1983; present study). Aggregation of algae into turfs seems to be advantageous under a variety of environmental conditions, which might explain the extensive abundance of turfs in many tropical and temperate intertidal and subtidal habitats (Hay 1981; Taylor and Hay 1984; Stewart 1989; Airoldi and Cinelli 1997; Airoldi 1998). Identifying ecologically relevant functional groups may, therefore, require consideration not only of individual responses of algae with different morphologies but also of interdependent responses within associations of morphologically heterogeneous algae.

Understanding and predicting the distribution and variability of organisms across the broadest possible range of species and habitats is a major goal for ecologists (Beck 1997; Lavorel et al. 1997). The results of this study suggest that more research is necessary, either to verify or to invalidate the general applicability of the concept of functional groups of algae and to improve the identification of ecologically relevant, functional categories. It seems important that further studies on relationships between morphology and ecology of algae take into account the potential role of interactions among associated species.

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