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Effect of algal architecture on associated fauna: some evidence from phytal molluscs

Abstract In the southern Mediterranean Sea, replicate samples of six common upper-infralittoral algae (*Cystoseira barbatula*, *Cystoseira spinosa*, *Sargassum vulgare*, *Halopteris scoparia*, *Dictyota fasciola*, and *Dictyota dichotoma*) were collected with the major goal of investigating the composition and structure of molluscan assemblages between the algal species. In order to measure the habitat architecture of the six algal species and relate this to the molluscan assemblages, several structural attributes were calculated on each individual plant. There were differences in architectural attributes between the six algal species, with data recorded for *S. vulgare* and *H. scoparia* more similar to data for *C. barbatula* and *C. spinosa* (which grouped closely), than for the two species belonging to the genus *Dictyota*, which had a less complex structure. A total of 1,914 specimens and 57 species of molluscs were found on the collected algae. The abundance and diversity of the molluscan assemblages were significantly different between different macroalgae. In general *S. vulgare*, *C. barbatula* and *C. spinosa* supported a higher abundance, greater number of species, Shannon–Wiener diversity, and Margalef's index than the remaining three algal species. Both multivariate analyses (i.e. cluster and multidimensional scaling) and a posteriori tests (Student–Neuman–Keuls' test) demonstrated that samples collected on *D. dichotoma* were well separated, reflecting the lowest values of abundance and diversity. The molluscan assemblage data were also correlated to the attributes of algal architecture revealing that the combination of degree of branching, algal width and the log of the stem width provides a good explanation for molluscan structure. Differences in the molluscan assemblages of these six common Mediterranean algae can be attributed to different algal architectures, and, consequently, these could be related to the supposed variations in food availability and predation rate.

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Introduction

A major goal in ecology is to determine the causes of spatio-temporal variation in community structure (e.g. specific composition and richness, relative abundance, trophism, size structure). The forces driving these variations can be biological (e.g. predation, competition, recruitment, disturbance) and/or physical (e.g. light intensity, nutrient availability, hydrodynamic features, habitat structure). The problem is to quantify the relative importance of each factor in influencing community structure (Dunson and Travis 1991; but see Menge and Sutherland 1987 for review).

It is well known that composition and structure of benthic communities in temperate seas are generally affected by water depth (Dahl 1948), light intensity (Ercegovic 1958), hydrodynamic features (Norton 1971; Riedl 1971; Fenwick 1976), seasonality (Mukai 1971), water temperature (Hagerman 1966; Mukai 1971), pollution (Jones 1973; Sheppard et al. 1980) and salinity (Dahl 1948). Presently, very little attention has been devoted to the role of habitat structure (see Bell et al. 1994) in modifying and influencing the structure and distribution of benthic invertebrates.

At a small spatial scale of observation (10^{-2}–10^{-3} m), marine algae provide a suitable habitat for a wide range of animal species and can also be deemed as biological "formers" of habitat structure (Jones and Andrew 1992; but see García-Charton et al. 2000 for further reading).

There is evidence that different macroalgae do not support benthic fauna in the same way (see review by Williams and Seed 1992), and this may depend on

several factors such as life cycles, algal architecture, or the exhibition of chemical defences (e.g. like many red algal species) (Duffy and Hay 1994).

Very few papers have dealt with the role of marine algae in structuring faunal communities. Different algal shapes are important in determining patterns of abundance and size structure of associated animal species (Edgar 1983a). The current study revealed that amphipods were more present on finely branched algae than on plants with wide thalli that showed proportionately higher abundances of larger animals. Similarly the structure of the harpacticoid copepod community associated with different macroalgae differed significantly in relation to algal complexity (Gibbons 1988).

Other authors have highlighted the importance of the fractal dimension of the algal substratum in giving a clue to relationships with the abundance and species richness of the associated small epifauna (Gee and Warwick 1994). More recently, seasonal changes in the diversity and abundance of ostracods were investigated on four intertidal algal species with different structural complexities, measured as the number of branches per centimetre (Hull 1997). The results revealed that these variables were positively correlated with algal structural complexity, demonstrating also a pronounced seasonal variation.

At present, in the Mediterranean Sea very few studies have been aimed to highlight the importance of marine algae as biological formers of habitat complexity. Chemello and Russo (1997) and Chemello et al. (1997), by means of a comparison between structural changes in space of the algal assemblages and their associated malacofauna, pointed out two main structural patterns, respectively depth-related and alga-related, at two different Mediterranean sites. Other authors suggested that faunal distribution along a vertical cliff could be influenced by algal cover rather than direct physical factors (Abbiati et al. 1987; Giangrande 1988). More recently, Russo (1997) compared the epifauna living on four algal species in the eastern Mediterranean, revealing that the abundance of epifauna (mainly amphipods, polychaetes and molluscs) per gram of macroalga was significantly lower on *Cystoseira barbata* than on the other algal species (e.g. *Laurencia obtusa*, *Padina pavonica* and *Jania rubens*).

The aims of the present study were to: (1) characterise molluscan assemblage structure associated with six different Mediterranean algal species; (2) determine whether, at a small spatial scale of observation, higher levels of habitat architecture (e.g. algal structure) support greater community diversity; and (3) assess to what attribute of habitat architecture (sensu Hacker and Steneck 1990) or characteristic of the algae the molluscan assemblage respond.

Materials and methods

Study site

The study site was a shallow rocky plateau at Capo Madonna, Lampedusa Island (35°30′39″N; 12°35′8″E; Fig. 1), a calcareous
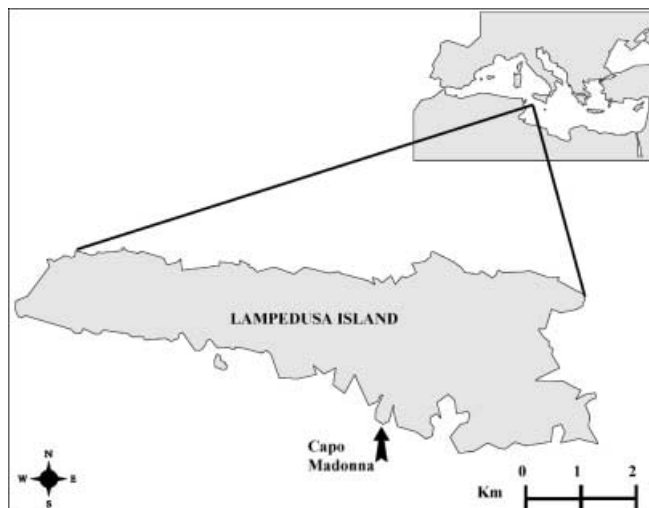

Fig. 1. Lampedusa Island and the location of the study site at Capo Madonna

protrusion of the African shelf belonging to the Pelagian archipelago (Strait of Sicily, southern Mediterranean, Italy).

The seascape of the sampling area was characterised by rocky substrata, mainly covered by brown algae (Chemello 1991; Scamacca et al. 1993), that gently sloped from the intertidal zone to about 12 m depth. Below this depth sandy bottoms were common, with dense *Posidonia oceanica* meadows.

Sampling procedures

An appropriate sampling plan was carried out to minimise the influence of the environmental factors (e.g. hydrodynamism) and to highlight the role of algal architecture in structuring molluscan assemblage. Six different algal species were collected in May 1994, during the period of peak algal biomass in the Mediterranean, as indicated by Sala and Boudouresque (1997). Sampling depths (DE; m) of each individual alga were measured with an electronic gauge (± 0.1 m).

The macroalgae collected were: *Sargassum vulgare* C. Agardh (abbreviation SAR), *Cystoseira barbatula* Kützing (CBA), *Cystoseira spinosa* Sauvageau (CSP), *Dictyota dichotoma* (Hudson) Lamouroux (DID), *Dictyota fasciola* (Roth) Lamouroux (DIF) and *Halopteris scoparia* (L.) Sauvageau (HAL). These canopy-forming brown algae were the most conspicuous species at the study site and may represent a potential gradient of structural complexity (Chemello 1991).

Collection of samples was carried out by SCUBA divers enclosing macroalgae within a 0.45 mm mesh bag. The holdfast of each plant was levered from the substratum with chisel and hammer. Each alga was previously cleaned of vagile fauna, with the use of an airlift sampler (Chess 1978; Benson 1989), to prevent the loss of more motile species. Three replicated samples of each algal species were collected.

In the laboratory, samples were sorted, sieved with 0.5 mm mesh and preserved in a solution of seawater and formalin (4%). After fixation each adult mollusc was identified to species level (according to Van Aartsen et al. 1984; Gofas 1990; Giannuzzi-Savelli et al. 1994, 1996) and counted.

Algal architecture

For benthic invertebrates, not exceeding 2 cm in length, complexity can be considered as the architectural shape of the dominant macroalga. In order to measure the habitat architecture (defined as "the structural and spatial attributes that define a habitat"; see

Table 1. Mean values ($\pm$SD) of the algal attributes and depth of sampling of the six algal species sampled at Capo Madonna, Lampedusa Island (*AH* algal height; *AW* algal width; *DB* degree of branching; *SW* stem width; *NB, NR, NL, NV* number of branches, ramuli, leaflets and vesicules, respectively, of levels 1–3, for further details on attribute measurement see "Materials and methods"; *DE* sampling depth)

	Sargassum vulgare (SAR)	*Cystoseira barbatula* (CBA)	*Cystoseira spinosa* (CSP)	*Halopteris scoparia* (HAL)	*Dictyota fasciola* (DIF)	*Dictyota dichotoma* (DID)
AH (cm)	33 $\pm$ 3.8	24 $\pm$ 3.3	21.3 $\pm$ 0.9	11.4 $\pm$ 0.9	12.3 $\pm$ 0.6	17.5 $\pm$ 1.3
AW (cm)	18.5 $\pm$ 0.7	15.6 $\pm$ 1.5	18.5 $\pm$ 0.7	13.5 $\pm$ 0.6	10 $\pm$ 0.3	18.4 $\pm$ 0.7
DB	7 $\pm$ 0	5 $\pm$ 0	7 $\pm$ 0	3 $\pm$ 0	11.7 $\pm$ 0.5	9 $\pm$ 0
SW1 (cm)	0.52 $\pm$ 0.08	0.5 $\pm$ 0.02	0.36 $\pm$ 0.04	0.53 $\pm$ 0.02	0.42 $\pm$ 0.01	0.81 $\pm$ 0.02
SW2 (cm)	0.32 $\pm$ 0.02	0.24 $\pm$ 0.02	0.19 $\pm$ 0.01	0.21 $\pm$ 0.02	0.26 $\pm$ 0.05	0.60 $\pm$ 0.01
SW3 (cm)	0.14 $\pm$ 0.01	0.13 $\pm$ 0.01	0.12 $\pm$ 0.01	0.11 $\pm$ 0.01	0.11 $\pm$ 0.01	0.42 $\pm$ 0.02
NB1	5.3 $\pm$ 0.6	17 $\pm$ 1	15.3 $\pm$ 1.1	2.3 $\pm$ 0.6	12.3 $\pm$ 1.5	4.7 $\pm$ 1.2
NB2	2.3 $\pm$ 0.6	7.7 $\pm$ 1.2	7.7 $\pm$ 0.6	5 $\pm$ 1	5 $\pm$ 1.5	13 $\pm$ 2
NB3	2 $\pm$ 0	4.7 $\pm$ 0.6	4.3 $\pm$ 0.6	7.3 $\pm$ 0.6	5.7 $\pm$ 0.6	10.3 $\pm$ 1.5
NR1	4 $\pm$ 1	11 $\pm$ 2	11.3 $\pm$ 0.6	13.7 $\pm$ 0.6	11.7 $\pm$ 1.5	13.7 $\pm$ 3.1
NR2	8.7 $\pm$ 1.5	24.7 $\pm$ 2.8	28.3 $\pm$ 4.5	16.7 $\pm$ 1.5	9 $\pm$ 2	6 $\pm$ 1.7
NR3	43 $\pm$ 4.6	31 $\pm$ 2	33.3 $\pm$ 2.5	20.3 $\pm$ 3	21.3 $\pm$ 1.5	14.7 $\pm$ 3.5
NL1	48.7 $\pm$ 16	12 $\pm$ 1.7	12.3 $\pm$ 6.1	134.7 $\pm$ 8.6	–	–
NL2	146.7 $\pm$ 34	104.3 $\pm$ 7.8	112.7 $\pm$ 13.6	149.7 $\pm$ 13	–	–
NL3	128 $\pm$ 27.5	129.3 $\pm$ 14.7	139.3 $\pm$ 13.4	169.7 $\pm$ 8.7	–	–
NV2	37.3 $\pm$ 10	–	–	–	–	–
NV3	42.3 $\pm$ 10.6	–	–	–	–	–
DE (m)	5.8 $\pm$ 0.8	4.1 $\pm$ 1.1	6.8 $\pm$ 0.2	6 $\pm$ 0.1	4.1 $\pm$ 0.2	3.9 $\pm$ 0.1

Hacker and Steneck 1990) of the six algal species, the following attributes were evaluated:

- Algal height (AH; cm), the length from the base of the holdfast to the distal tip of the frond.
- Algal width (AW; cm): the maximum transverse distance across the primary branch (the largest one).
- Degree of branching (DB): counted from the distal branch to the stem. The final branches were classed first order, and whenever two branches of the same order joined, the order of the resultant branch was increased by one (Edgar 1983a).

- Stem width (SW_i; cm): the thickness of the stem at three different levels (upper, intermediate and lower) along the main axis of the individual alga.
- Number of branches (NB_i): the number of branches emerging from the stem. This was also counted at three levels along the stem.

Other structural attributes like number of ramuli (NR_i), number of leaflets (NL_i) and number of vesicules (NV_i) in each level were also recorded.

Data analysis

To analyse the molluscan assemblage structure the following variables were calculated: total abundance of individuals (*N*), total number of species (*S*), Shannon–Wiener diversity (*H′*), Margalef's index (*d*) and frequency of occurrence (Fr%) (Magurran 1988). Differences of univariate indices with algal types as the source of variation were assessed by analysis of variance (ANOVA). Cochran's test was used to check for the homogeneity of variances (Underwood 1997). Student–Newman–Keuls' (SNK) test was employed to separate means (at $\alpha = 0.05$) following significant effects in the ANOVAs. These analyses were performed using GMAV 5.0 statistical software (University of Sydney).
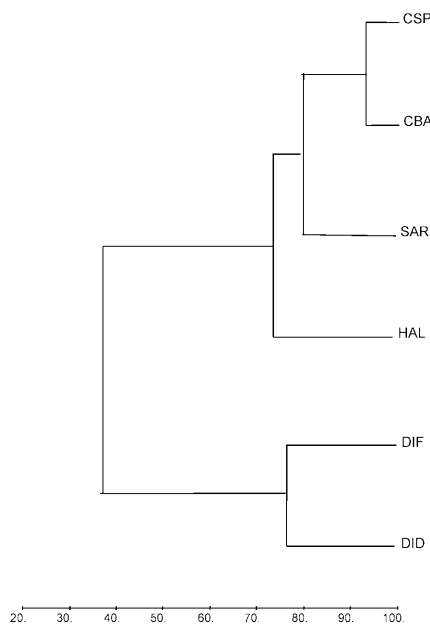
Fig. 2. Bray–Curtis cluster analysis on algal attributes between different types of macroalgae. No transformation. Taxon codes, see Table 1
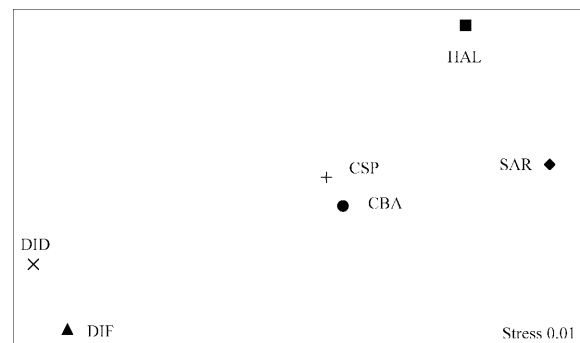
Fig. 3. Multidimensional scaling ordination model of architectural attributes of different algal species. Taxon codes, see Table 1

Table 2. Abundance and frequency of occurrence (*Fr%*) of the molluscan species collected in association with the six algal species (replicates 1–3). Checklist arranged in accordance with Bedulli et al. (1995a,b,c) and Bodon et al. (1995) (*N* number of individuals)

Species	Sargassum vulgare SAR1	SAR2	SAR3	Cystoseira barbatula CBA1	CBA2	CBA3	Cystoseira spinosa CSP1	CSP2	CSP3	Halopteris scoparia HAL1	HAL2	HAL3	Dictyota fasciola DIF1	DIF2	DIF3	Dictyota dichotoma DID1	DID2	DID3	N	Fr%
Bittium latreillii	7	2	9	4	6	6	7	3	5	2	3	2	74	35	12				177	83.3
Mitra cornicula	11	13	1	8	3	33	21	5	13		1	4	2	3	8	1	5	1	133	94.4
Alvania lineata	1	8	7	5	1	2	18	21	23	16	1	9	1		4				117	77.8
Setia ambigua	3	7	1	5	5	1	4	1	1	1			46	32	33	8	3	5	112	66.7
Musculus costulatus	23	36	18	2	3	2	1	1				1	6	9	35				98	61.1
Runcina sp.	20	2	33	6	5	5	1	6	1					1					87	38.9
Alvania oranica	1	4	15	4	6	2	3		5		1		1	1					86	61.1
Gibberula miliaria	1	7	19	8	3	5	1	20	11	2	3	1	3	3	3				69	77.8
Jujubinus gravinae	1	7	8		3	5	4		1		3	1	4	2	3	3			66	88.9
Cerithium sp.	5	2	3	1		25							2	19	7				64	44.4
Rissoa similis		4	1	1	5	1	3	2		20	5	13	1	3	2				61	72.2
Granulina clandestina	4		7	24	19	7													61	27.8
Barleeia unifasciata										1	1	4	20	16	16				58	33.3
Haminoea hydatis	1	2	5	1	2	2	3	8	6	1		1	2	2	22				56	72.2
Eatonina fulgida	21	5	16	3	1	1	1		1				1	1	1				51	55.6
Chauvetia submamillata	7	20	3								2	5	3						41	38.9
Tricolia tenuis	6	5	6	1	2	1		1	1	3	1	3	1	1	2	1	3	2	40	94.4
Columbella rustica	3	1	4	4	3	4	3		4	1	3	3		1	1	1	1		37	83.3
Rissoa variabilis	3		1	7	4	6	1	5	2	1	2	1	1		2				36	72.2
Vexillum savignyi	2	5	4		4		6	9	5	1									33	44.4
Pisinna glabrata	2	1	1		4		16	3	3					1	2				33	50
Alvania cancellata	5	3	5		4	4	1	4	2										28	44.4
Alvania mammillata	3	1	1	3	3	1	6	2	4	4		2							27	55.6
Vexillum tricolor				9	1	4	6	1	3										24	33.3
Chauvetia brunnea	3		1		2	2	4	5	5										22	38.9
Gibbula turbinoides	1	4	4	4	2	2	1	4	2										20	44.4
Chrysallida doliolum			1		1	5	1	1	7				2						20	50
Ammonicera fischeriana		1		1	8	4	2		3										18	27.8
Sinezona cingulata	6	1													5	5		4	17	27.8
Cerithium vulgatum			1	1		1	1		7	1	5	1							17	38.9
Rissoa guerinii	5	1		2	3		4	1		1									16	33.3
Nodulus contortus	1	2	1		7	4													15	27.8
Alvania discors	1		4	1	2	2	3		1										14	38.9
Pusillina interrupta				1	1	1							10						14	27.8
Muricopsis cristata	1		3	4	2	3								1					13	27.8
Rissoa scurra	3	1	9																13	16.7
Mitrella sp.				6	2	4	2				1								12	16.7
Musculus discors													7	1					10	22.2
Odostomia erjaveciana				4	4	1	1	2	1	1		1							9	27.8
Bittium reticulatum	3	1					2	1	1							1	2		8	27.8
Pollia scabra					3			4					3			2	1	1	8	22.2
Aplysia fasciata														1		1	2	2	8	27.8
Conus mediterraneus						1	1			1		1							7	27.8
Marshallora adversa				1	1		1	2	2										7	27.8

The PRIMER package of the Plymouth Marine Laboratory (Clarke and Warwick 1994) was used to perform all the multivariate analyses. Both algal attributes and molluscan samples were compared, using cluster analysis and non-parametric, multidimensional scaling (MDS) ordination technique (Kruskal and Wish 1978) based on Bray–Curtis' similarity index of attribute/species composition among samples. Data on molluscan assemblages were double square-root transformed. The SIMPER procedure (Clarke 1993) was performed in order to determine which molluscan species are most responsible for differences between algal types. Analysis of similarities (ANOSIM) was employed to determine whether molluscan assemblages associated with different macroalgae were significantly different ($P < 0.05$) from each other. To assess to what attribute of habitat architecture the phytal mollusc responds, the BIO-ENV procedure was employed (see Clarke and Ainsworth 1993).

Results

Algae

A varied and structurally complex group of macroalgae was present at the sampling site (Table 1). The algae ranged from elongate, vesiculate (*Sargassum vulgare*) and non-vesiculate forms (*Cystoseira barbatula*, *Cystoseira spinosa* and *Dictyota dichotoma*) to short and non-vesiculate species, such as *Dictyota fasciola* and *Halopteris scoparia*. Another distinction has to be made between openly branched algae (*S. vulgare*, *D. dichotoma* and *D. fasciola*) and finely-branched (*C. barbatula*, *C. spinosa* and *H. scoparia*). Individual plants were collected on the average at 5.1 m (± 1.2 m) depth.

Bray–Curtis cluster analysis and MDS ordination applied to the data on algal attributes defined two main groupings of samples (Fig. 2), providing a good two-dimensional representation between different algal types (stress = 0.01) (Fig. 3). The architectural attribute data recorded for *S. vulgare* and *H. scoparia* revealed a high similarity with the data for both *Cystoseira* species, which grouped closely. By contrast, the species belonging to the genus *Dictyota* were well separated from the other algal samples.

Molluscs

A total of 1,914 specimens belonging to 57 species made up the phytal malacofauna, numerically dominated by Neotaenioglossa (43.86% of the total number of species) and Neogastropoda (24.56%). Vetigastropoda (14.03%), Heterostropha (7.02%), Cephalaspidea (3.51%), Sacoglossa (1.75%) and Anaspidea (1.75%) were less prevalent, while *Musculus costulatus* and *M. discors* were the only bivalve species (3.51%) among the phytal fauna in this set of algae.

Bittium latreillii, *Mitra cornicula*, *Alvania lineata* and *Setia ambigua* were the most abundant species. The most common species were *M. cornicula* (94.4% of all samples), *Tricolia tenuis* (94.4%), *Jujubinus gravinae* (88.9%), *B. latreillii* (83.3%) and *Columbella rustica* (83.3%) (Table 2).

Species								
Vexillum ebenus	1						6	22.2
Mitrella scripta		1			2		6	11.1
Clanculus jussieui	1	4	1			4	6	16.7
Elysia viridis						4	5	11.1
Cerithiopsis tubercularis			2	1	2	1	4	16.7
Tricolia pullus		2	1	1			4	16.7
Rissoella diaphana						3	4	11.1
Cerithiopsis minima			3		3		4	11.1
Megalomphalus azonus				2	1		3	11.1
Rissoa auriscalpium	1	2	1				3	11.1
Alvania beniamina			1	1			2	11.1
Jujubinus striatus			1	1			2	11.1
Gibbula ardens			1				2	11.1

Total number of individuals, total number of species, Shannon–Wiener diversity and Margalef's index were significantly different ($P < 0.001$) between the six algal species (Table 3). SNK tests revealed a general trend in these community variables, with data collected on *S. vulgare*, *C. barbatula* and *C. spinosa* significantly different from those belonging to the other algal species, although some differences between *D. dichotoma*, *D. fasciola* and *H. scoparia* may be evident (Table 3).

The number of molluscan species (S) ranged on the average from 30.7 (± 3.5) on *C. barbatula* to 8.7 (± 1.5) on *D. dichotoma*, while the total number of individuals (N) ranged from 161 (± 23.3) on *S. vulgare* samples to 20.7 (± 5.7) on *D. dichotoma* (Fig. 4). Shannon–Wiener diversity (H') and species richness (Margalef's index, d) showed similar trends, with higher values in CBA, CSP and SAR with respect to the other algal species (Fig. 5). The highest values on the average of both indices were recorded in *C. barbatula* samples ($H' = 2.97 \pm 0.13$; $d = 6.16 \pm 0.60$), while the lowest values were recorded in *D. dichotoma* ($H' = 1.93 \pm 0.15$; $d = 2.54 \pm 0.32$).

The results of ANOSIM and Bray–Curtis cluster analysis showed that the molluscan assemblages associated with different macroalgae were significantly different from one another ($P < 0.001$) and that replicates of each algal species grouped together, separate from the other species (Fig. 6). Similarly, non-parametric MDS defined several groups of malacofauna associated with the different species of algae. Three main groups can be highlighted: (1) the molluscan assemblage associated with the most complex macroalgae (CBA, CSP and SAR); (2) an intermediate group between complex and less complex algae (HAL and DIF); and (3) the malacofauna of the least complex macroalga (DID), which was well separated from the other samples (Figs. 6, 7).

The species having the greatest contribution to dissimilarity between the three main groups of macroalgae (SIMPER, cut off 40%) were the 13 most abundant species (with the exclusion of *Mitra cornicula* and *Jujubinus gravinae*, which were equally distributed on the six algal species and were not a source of dissimilarity among samples) and eight other species: *Rissoa variabilis*, *Gibbula turbinoides*, *Conus mediterraneus*, *Alvania mammillata*, *Alvania cancellata*, *Alvania discors*, *Chauvetia brunnea* and *Vexillum tricolor* (Table 4).

Relationships between algal architecture and molluscan assemblage

The physical attributes of the different algae were correlated to the distribution of the epiphytic malacofauna by the BIO-ENV procedure. Not all the physical data were included in the analysis, because some data added nothing extra to explaining variations of faunal composition among different algae. No significant correlation was found between the biotic data and the following structural parameters: number of branches (NB), num-ber of ramuli (NR), number of leaves (NL) or number of vesicles (NV).

The results of the analysis have indicated that degree of branching (DB) on its own provides a very good explanation for the molluscan assemblage distribution (Spearman's rank correlation: $r_S = 0.626$). The overall best combination was: degree of branching, algal width and the log of stem width ($r_S = 0.685$).

Discussion

The six macroalgae collected were the most common species in the upper infralittoral of Lampedusa Island (Scamacca et al. 1993). On the basis of the shape and physical attributes calculated for each algal type, the species having the highest values of structural complexity were *Cystoseira barbatula* and *C. spinosa*; both show high similarity values with *Sargassum vulgare* and *Halopteris scoparia*. By contrast, *Dictyota dichotoma* and *D. fasciola* were the least complex macroalgae. These results represented the first attempt to quantify algal architecture of Mediterranean upper-infralittoral algal species using different structural attributes. Previous studies have focussed on algal biomass to assess the structural complexity of four Mediterranean species (Russo 1997) and correlate this to their epifauna; this approach, however, did not distinguish between algae that may have similar biomass, but different architectural attributes.

The molluscan assemblages associated with the six algae collected showed high values of total abundance and species richness. The abundance and diversity of the molluscan assemblages were on the average significantly different between the six algal species. In general *S. vulgare*, *C. barbatula* and *C. spinosa* supported a higher abundance and greater number of species (Shannon–Wiener diversity and Margalef's index) than the three remaining algal species.

Both multivariate analyses (i.e. cluster and MDS) and a posteriori tests (SNK test) demonstrated that samples collected on *D. dichotoma* were well separated, reflecting the lowest values of abundance and diversity.

On average the abundance of phytal molluscs living on *H. scoparia* was significant lower than the other most complex species. Similarly, the same results were found when taking into consideration diversity variables, although *H. scoparia* demonstrated a high similarity with architectural attributes recorded for *S. vulgare* and *Cystoseira* species. This could be related to the body-size-dependent habitat selection proposed by Hacker and Steneck (1990). Heck and Orth (1980) showed a positive correlation between faunal abundance and plant surface per unit bottom area (density): "increases in surface-area lead to increases of animal abundance". But they also identified a "threshold" value of structural complexity beyond which animal abundance declines because of physical and environmental constraints (i.e. dense vegetation). In the

Table 3. Analysis of variance on molluscan assemblages variables (*N* number of individuals; *S* number of species; *H'* Shannon-Wiener diversity; *d* Margalef's index; ***$P < 0.001$). In the Student–Neuman–Keuls' (*SNK*) test the names of each algal species are coded as in Table 1

Source of variation	df	N		S		H'		d	
		MS	F	MS	F	MS	F	MS	F
Algal species	5	10,261.87	33.51***	257.02	51.98***	0.62	19.64***	6.98	40.38***
Residuals	12	306.22		4.94		0.03		0.17	
Cochran's test		$C = 0.36$, $P > 0.05$		$C = 0.42$, $P > 0.05$		$C = 0.53$, $P > 0.05$		$C = 0.35$, $P > 0.05$	
Transformation		None		None		None		None	
SNK test algal species		SAR = CBA = CSP = DIF > HAL = DID		SAR = CBA = CSP > HAL = DIF > DID		SAR = CBA = CSP > HAL = DIF = DID		SAR = CBA = CSP > HAL = DIF > DID	

absence of predation, for example, prey densities would be expected to increase with increased physical complexity. However, prey abundances will be in balance between refuge from predation and the availability of increased space and/or food. It is noteworthy, however, that the combination of algal shape and architectural attributes may alternatively enhance and/or depress the abundance and diversity of associated invertebrate fauna (i.e. molluscs, amphipods, polychaetes) (Edgar 1983a; Hacker and Steneck 1990).

H. scoparia is a finely branched alga with a reduced interstitial volume and a low degree of branching (Cabioc'h et al. 1992). These characteristics may represent a physical constraint to large-sized malacofauna, as has been indicated by analysis with the BIO-ENV procedure. The correlation between molluscan assemblage data and the attributes of algal architecture revealed that the combination of degree of branching, algal width and the log of stem width provides a good explanation for molluscan structure.

The relationship we observed between marine algae and benthic molluscs may be a general pattern, in which complex macroalgae encourage a more abundant and well-diversified associated invertebrate fauna than simple and flat-thalloid algae (Gunnill 1982; Edgar 1983a,b,c; Gibbons 1988; Gee and Warwick 1994), although Dean and Connell (1987a) asserted that a general, functioning model could only be hypothesised after taking into consideration data from an entire faunal group.

Many authors have proposed mechanisms by which variations of habitat architecture may influence the composition and distribution of the associated assemblages (Dean and Connell 1987b): (1) decrement of mortality rate due to predation ("refuge effect"); (2) decrease of hydrodynamic features ("shelter effect"); and (3) collectors of species ("filter effect"), strictly related to hydrodynamic processes and the larval supply (Morse 1992).

At a small spatial scale of observation (e.g. 10^{-2}–10^{-3} m), marine algae promote complexity of coastal rocky bottoms, providing additional resources such as surface area for attachment, shelter, sediment or POM traps, and food items to invertebrate species (Hayward 1980).
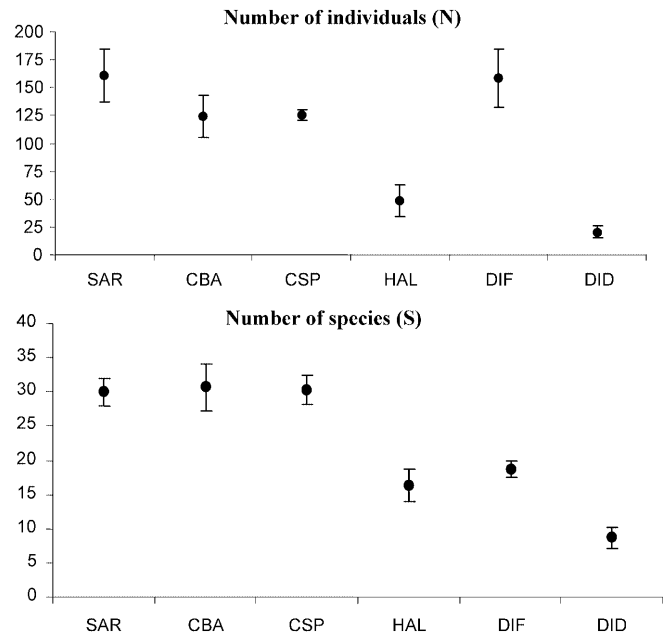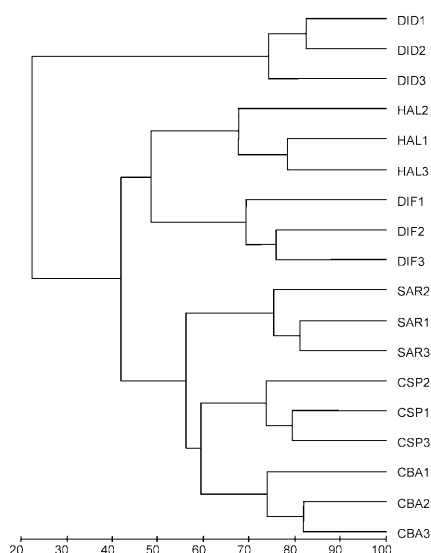

Fig. 4. Mean values ($\pm$ SD) of total number of individuals (*N*) and total number of species (*S*) among different algal species. Taxon codes, see Table 1

In the present study differences in the molluscan assemblages of these six common Mediterranean algae can be attributed to different algal architectures, and, consequently, these could be related to the supposed variations in food availability and predation rate.

Presumably, due to refuge and shelter effects, some vagile species may actively select their host on the basis of its architectural complexity instead of direct feeding preferences, taking into consideration that, generally, phytal fauna do not feed on the host-plant tissues (Gee and Warwick 1994). None of the molluscan species sampled in our study revealed a feeding preference for the host algae (according to the radular model proposed by Steneck and Watling 1982). Microherbivore–detritivore species, such as *Alvania* spp. and other rissoid species that feed mainly on diatom film (Graham 1988), seemed to prefer finely branched algal species; the same was noted for the carnivore *Vexillum tricolor*, which feeds on Demo-
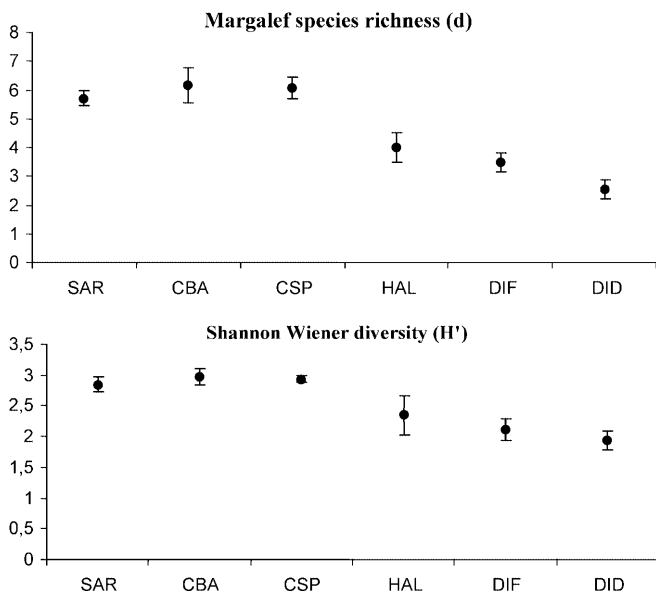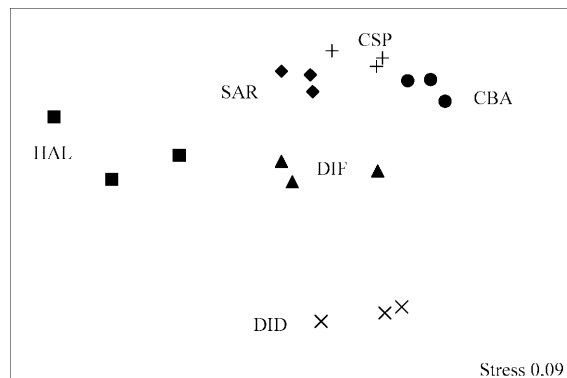
Fig. 5. Mean values ($\pm$SD) of Margalef's index (d) and Shannon–Wiener diversity (H') among different algal species. Taxon codes, see Table 1

Fig. 7. Multidimensional scaling ordination model of molluscan assemblages associated with different algal species. Taxon codes, see Table 1

Table 4. Average abundance of species which contribute to dissimilarity between groups of macroalgae (SIMPER, cut-off 40%)

Species	Group 1 CBA+CSP+ SAR	Group 2 DIF+HAL	Group 3 DID
Bittium latreillii	5.44	21.33	–
Runcina sp.	9.67	–	–
Musculus costulatus	1	12.17	5.33
Barleeia unifasciata	–	9.67	–
Alvania oranica	9.33	0.33	–
Alvania lineata	9.56	5.17	–
Alvania cancellata	3.11	–	–
Gibbula turbinoides	2.22	–	–
Chauvetia brunnea	2.44	–	–
Granulina clandestina	6.78	–	–
Eatonina fulgida	5.44	0.33	–
Alvania discors	1.56	–	–
Vexillum tricolor	2.67	–	–
Cerithium sp.	4	4.67	–
Gibberula miliaria	6.44	1.83	–
Haminoea hydatis	3.33	4.33	–
Rissoa variabilis	3.22	0.5	–
Conus mediterraneus	–	0.33	1.67
Alvania mammillata	2.33	1	–
Rissoa similis	1.88	7.33	–
Setia ambigua	2.44	15	–

Fig. 6. Bray–Curtis cluster analysis on molluscan assemblages of different algal samples. Double square-root transformation of data. Taxon codes, see Table 1

spongiae that form a muff along the stem of *Cystoseira* species (Bellan-Santini et al. 1994). By contrast, openly branched algal species are homes to suspension feeders (i.e. *Musculus costulatus*).

On the other hand, structural complexity of marine algae may stabilise predator–prey interactions by creating physical refuges when predators are on patrol (Menge and Sutherland 1976; Orth 1992; Moreno 1995). In the study area, Mediterranean labrids (i.e. *Thalassoma pavo* and *Coris julis*), blennids and trypterigids are very common and highly related with macroalgal-dominated communities (Mazzoldi and

De Girolamo 1997). There is some evidence that these species feed directly on small-sized invertebrates like phytal polychaetes, amphipods and molluscs (Tortonese 1975). Consequently, it is also presumable that the molluscan assemblages of the most complex algae may be numerically more abundant in individuals and species, due to a lower predation rate, in comparison with those supported by lower levels of algal complexity.

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