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The effect of wave exposure on the foraminifera of *Gelidium pristoides*

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The foraminifera of *Gelidium pristoides* were examined on exposed and sheltered shores around False Bay, South Africa, during the summer and winter of 1998/1999. Twenty-five species were recognized, seven are potentially new. Multivariate statistics indicated that the assemblages on plants from exposed shores were distinct from those on sheltered shores, and two species of foraminifera were confined to exposed shores. Plant size and the quantity of trapped sediment were positively correlated, and plants on exposed shores were significantly bigger than those on sheltered shores. Plant size and sediment weight were linked to assemblage diversity and abundance; assemblages on exposed shores were generally more diverse and abundant than those of sheltered shores. Different species dominated on the two shore types, and larger foraminifera tended to be more common on exposed shores.

INTRODUCTION

Foraminifera form a conspicuous component of the meiofauna in both intertidal sediments (Boltovskoy, 1970), and amongst intertidal algae (Hedley et al., 1967). This study focuses on the intertidal foraminifera associated with *Gelidium pristoides* which is endemic to South Africa and is found from Sea Point in the Western Cape to Port Edward on the east coast (Day, 1969). The alga is tuft-like, consists of many fronds and is approximately 30 mm in height (Carter & Anderson, 1986). *Gelidium pristoides* appears to provide an ideal microenvironment for intertidal fauna (Gibbons, 1988).

Gibbons (1988) demonstrated that the meiofauna of *G. pristoides* varied with shore exposure; small meiofauna were generally more abundant and diverse on sheltered shores. These observations were based on studies of broad taxa (e.g. copepods, nematodes), and lacked the detail inherent in studies of individual species.

MATERIALS AND METHODS

Sampling

Sampling took place on 10–11 August 1998 (austral winter) and 1–2 February 1999 (austral summer) at low tide, ~0.8 m above Chart Datum. Five of the largest *Gelidium pristoides* plants were collected from two exposed shores [St James (18.45°E–34.11°S) and Dalebrook (18.45°E–34.12°S)] and from two sheltered shores [Froggy Pond (18.45°E–34.19°S) and Miller's Point (18.45°E–34.22°S)] around False Bay. To investigate the effect of algal size on foraminiferal assemblages, an additional five plants of variable size were collected from each shore in February 1999. All plants were collected on limpets to minimize the disturbance and loss of phytal fauna (Gibbons, 1988). Samples were preserved in 70% ethanol.

Laboratory analysis

The alga was scraped off the limpet and agitated to remove sediment. The alga was wet-weighed and then dried at 60°C to constant mass. Sediments and meiofauna were sieved through a 63-μm mesh and stained in rose Bengal. Carbon tetrachloride was used for isolating foraminifera (Cushman, 1959), and the sediments were visually inspected. All live foraminifera were identified and counted at 80× magnification. A representative of each species was measured using scanning electron microscopy. The mean individual size of foraminifera per plant was calculated by multiplying the number of individuals of a species by the size of the measured representative of that species, the measurements were totalled for the plant and divided by the total number of individuals. Sediments from each sample were then dried at 60°C and weighed.

Statistical analysis

Analysis of variance was used to determine if algal or sediment weight and the abundance and diversity of foraminifera varied with season or shore type. Species diversity was calculated using the Shannon–Wiener index (H′) (Krebs, 1999). Linear relationships between the physical environment and the abundance and diversity of foraminifera were determined using correlation analyses. Analysis of variance was used to compare the individual size of foraminifera on the two shore types during summer and winter. A significance level of $P<0.05$ was used in all tests.

The structure of the foraminifera communities on the different shores was investigated using descriptive multivariate statistics. The numerical composition of samples was root–root transformed and a similarity matrix was constructed using the Bray–Curtis similarity index (Clarke & Warwick, 1997). All species from all samples were included in the analysis. Cluster analysis of the samples was undertaken using the Plymouth Routines in Multivariate Ecological Research (PRIMER) software using group average sorting (Clarke & Warwick, 1997).

The species most responsible for determining similarities between and within the groups were determined using the similarity percentage analysis (SIMPER) routine in PRIMER. The BIOENV procedure in

Table 1. *Species of foraminifera identified from samples of* Gelidium pristoides *on exposed and sheltered shores in False Bay, South Africa.*

Sub-order	Super-family	Genus	Species
Miliolina	Miliolacea	*Quinqueloculina*	*Quinqueloculina* cf. *undulata* d'Orbigny
			Quinqueloculina vulgaris d'Orbigny
			Quinqueloculina dunkerquiana (Heron-Allen & Earland)
			Quinqueloculina isabellei d'Orbigny
			Quinqueloculina seminulum (Linné)
		Miliolinella	*Miliolinella subrotunda* (Montagu)
Rotalina	Nodosariacea	*Lagena*	*Lagena semilineata* Wright
			Lagenosolenia sp. A
			Lagena sp. A
		Oolina	*Oolina* sp. A
			Oolina cf. *melo* d'Orbigny
		Fissurina	*Fissurina* sp. A
		Glandulina	*Glandulina* sp. A
	Buliminacea	*Bolivina*	*Bolivina fossa* McMillan, 1987
			Bolivina pseudoplicata Heron-Allen & Earland
		Brizalina	*Brizalina rocklandsensis* McMillan, 1987
	Rotaliacea	*Elphidium*	*Elphidium macellum* (Fichtel & Moll)
			Elphidium cf. *advenum* (Cushman)
	Discorbacea	*Rosalina*	*Rosalina* cf. *globularis* (Heron-Allen & Earland)
		Glabratella	*Glabratella australensis* (Heron-Allen & Earland)
			Glabratella sp. A
	Orbitoidacea	*Cibicides*	*Cibicides* sp. A
		Planorbulina	*Planorbulina mediterranensis* d'Orbigny
		Lobatula	*Lobatula lobatula* (Walker & Jacob)
	Spirillinacea	*Patellina*	*Patellina corrugata* Williamson

PRIMER was used to determine which of the investigated environmental parameters (algal weight and sediment weight) could best explain the structure of the identified foraminiferal assemblages (Clarke & Warwick, 1997).

RESULTS

Two sub-orders, seven superfamilies and 25 species of foraminifera were present in the samples. Of these, some were difficult to separate consistently and further analyses were confined to 20 species (Table 1). The identification of seven of the species was uncertain. These included *Glabratella* sp. A, *Cibicides* sp. A, *Glandulina* sp. A, *Lagenosolenia* sp. A, *Lagena* sp. A, *Oolina* sp. A and *Fissurina* sp. A.

Only two species of foraminifera (*Lagena semilineata* Wright and *Planorbulina mediterranensis* d'Orbigny) were confined to one shore type (exposed). However, species that dominated on exposed shores were different to those that dominated on sheltered shores. *Glabratella australensis* (Heron-Allen & Earland), *Rosalina* cf. *globularis* d'Orbigny and *Lobatula lobatula* (Walker & Jacob) were dominant on *Gelidium pristoides* from exposed shores. *Patellina corrugata* Williamson, *Miliolinella subrotunda* (Montagu) and *Bolivina pseudoplicata* Heron-Allen & Earland were dominant on *G. pristoides* from sheltered shores. Patterns of dominance appeared independent of plant size. Foraminifera on exposed shores were significantly larger than those on sheltered shores during both summer ($292.18 \pm 4.25\,\mu$m vs $213.98 \pm 10.94\,\mu$m) and winter ($308.59 \pm 3.55\,\mu$m vs $254.69 \pm 8.31\,\mu$m).

The results of the cluster analysis revealed that samples from exposed shores were distinct from those on sheltered shores, irrespective of season (Figure 1A,B). Although no seasonal variation in abundance or diversity was observed overall ($P > 0.05$), the specific composition of foraminifera on algae from exposed and sheltered shores did change. The species that contributed to differences between exposed and sheltered shores varied seasonally (Table 2). For example, *Fissurina* sp. A was responsible for ~13% of the difference between algae on exposed and sheltered shores during winter, whereas, *Elphidium* cf. *advenum* (Cushman) was responsible for ~11% of the difference between assemblages during summer.

Seasonality had no effect on the weight of algae ($P = 0.096$) or sediments ($P = 0.822$) per shore. However, algae were significantly larger on exposed (8.02 ± 0.86 g), than on sheltered shores (4.54 ± 0.37 g), and also trapped more sediment (2.41 ± 0.35 g vs 1.32 ± 0.29 g, respectively). There was a significant, positive correlation between algal weight and sediment weight ($P < 0.05$).

Correlations between the abundance, richness and diversity of foraminifera and algal (Figure 2A–C) and sediment (Figure 2D–F) weight, were positive and significant. These relationships were asymptotic and tended to level off at ~9 g algal weight and ~3 g sediment weight.

A re-analysis of all data, including the extra samples collected during summer, revealed three distinct clusters, or four if all outliers are grouped together. These clusters show a pattern of similarity that was more strongly linked to algal and sediment weight than to exposure *per se* (Figure 3). The mean algal weights of the four groups were: Group A (3.25 ± 0.59 g), Group B (4.32 ± 0.55 g), Group C (9.17 ± 0.84 g) and Group D (5.54 ± 0.53 g). Group C differed significantly ($P < 0.05$) from the other three groups, and consisted mainly of exposed shore samples of algae weighing between 8 g and 16 g. Groups

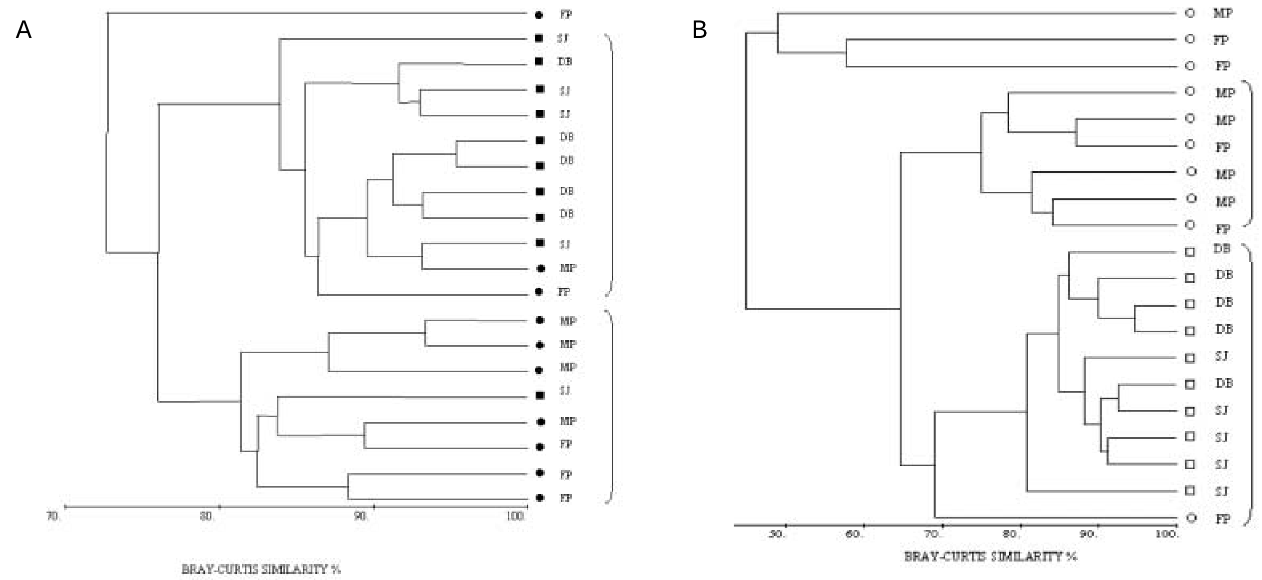


Figure 1. Dendrogram of the percentage similarity amongst the foraminiferal assemblages found on *Gelidium pristoides* on exposed and sheltered shores in (A) winter and (B) summer. Circles, sheltered shores; squares, exposed shores. Shaded symbols, winter months; open symbols, summer months. FP, Froggy Pond; MP, Miller's Point; DB, Dalebrook; SJ, St James.

Table 2. *The species of foraminifera identified by the SIMPER routine in PRIMER as being indicative of the two clusters of samples in Figure 1A & B. The average similarity between samples in each group is indicated in parentheses on the title row. The average abundance of each species in the different groups is indicated in brackets, the second value refers to the mean abundance of that species in the contrasted group. The proportion contributed by each species to the difference between the two groups is also shown.*

Group A (exposed) (87.16%) WINTER	Group A (exposed) (86.39%) SUMMER
Fissurina sp. A (3.27, 0.13) 12.8%	*Elphidium* cf. *advenum* (13, 0.17) 11.13%
Quinqueloculina cf. *undulata* and *Q. vulgaris* (2.91, 0.13) 11.71%	*Oolina* sp. A (4.8, 0) 8.55%
Elphidium macellum (8.09, 2.13) 9.28%	*Rosalina* cf. *Globularis* (44.3, 3.5) 7.92%
Lobatula lobatula and *Cibicides* sp. A (40.64, 11.5) 8.84%	*Lobatula lobatula* and *Cibicides* sp. A (21.6, 1) 7.9%
Quinqueloculina dunkerquiana and *Q. isabellei* and *Q. seminulum* (3.27, 1.13) 8.53%	*Glabratella australensis* (40.7, 4) 7.33%
Glabratella australensis (32.91, 10.13) 7.29%	*Bolivina fossa* (6.4, 3.33) 6.82%
Oolina sp. A (3.36, 0.88) 7.14%	*Planorbulina mediterranensis* (2.4, 0.33) 6.4%

A, B and D did not differ significantly from each other and consisted of algae between 0.1 g and 8 g; these were mainly sheltered shore samples.

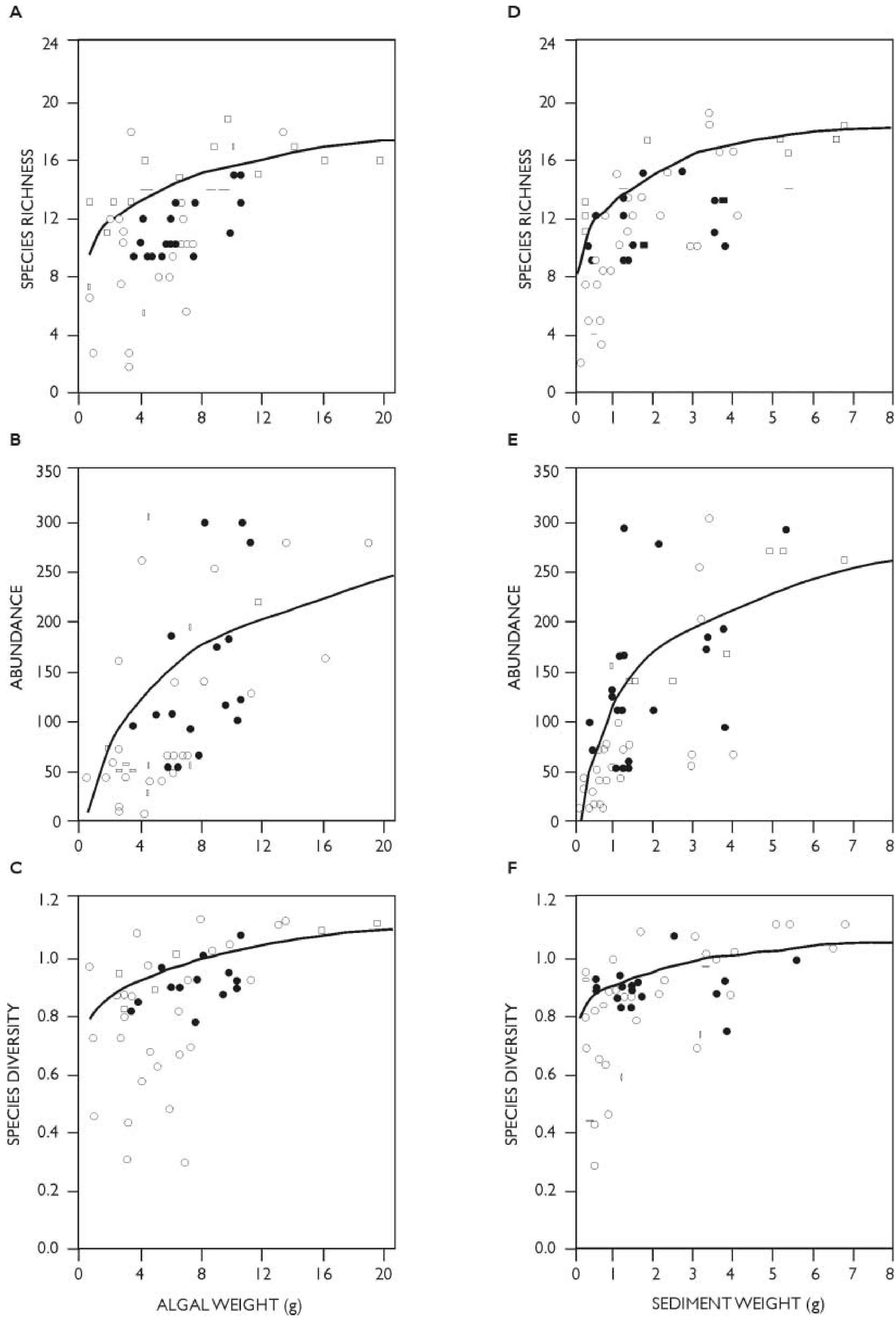
The results of the BIOENV procedure in PRIMER indicated that algal weight accounted for only 12% and sediment weight for only 8% of the pattern in community structure i.e. the measured environmental variables accounted for a total of 20% of the pattern in the biotic assemblages.

DISCUSSION

Glabratella sp. A, *Cibicides* sp. A, *Glandulina* sp. A, *Lagenosolenia* sp. A, *Lagena* sp. A, *Oolina* sp. A and *Fissurina* sp. A may be potentially new species. The relatively high number of potentially new species reflects the lack of taxonomic studies of intertidal foraminifera around southern Africa. With the exception of these species, all the other foraminifera have been reported from intertidal phytal communities elsewhere in the world: Argentina (Boltovskoy et al., 1976), New Zealand (Hedley et al., 1967), Japan (Kitazato, 1988) and Wales (Atkinson, 1969).

The species dominant on exposed shores are commonly reported from coarse sands and gravel, while those dominant on sheltered shores are all typically found in fine sediments and mud (Murray, 1991). The genera found in greatest abundance had flat, concave shells with a large surface area for attachment, e.g. *Glabratella*, *Cibicides* and *Rosalina* (Atkinson, 1969) implying that most foraminifera found were attached to the alga rather than in the trapped sediments. *Elphidium*, *Quinqueloculina*, *Miliolinella*, *Bolivina* and *Brizalina* were also common, and these genera are free-living and are typically found in sediments at the base of algae (Kitazato, 1988) i.e. the foraminifera on *Gelidium pristoides* include phytal as well as psammal species.

Lagena sp. A and *Planorbulina mediterranensis* were found only on exposed shores. *Lagena* is unicameral and flask-shaped and is rarely as a phytal (Boltovskoy et al., 1976). The greater sediment loads carried by the algae on these shores could explain its presence on exposed shores. By contrast, *Planorbulina mediterranensis* is an attached species, which clings to hard substrata. It is a passive suspension feeder (Murray, 1991), which might explain why it would


A
B
C
D
E
F
SPECIES RICHNESS
ABUNDANCE
SPECIES DIVERSITY
ALGAL WEIGHT (g)
SEDIMENT WEIGHT (g)

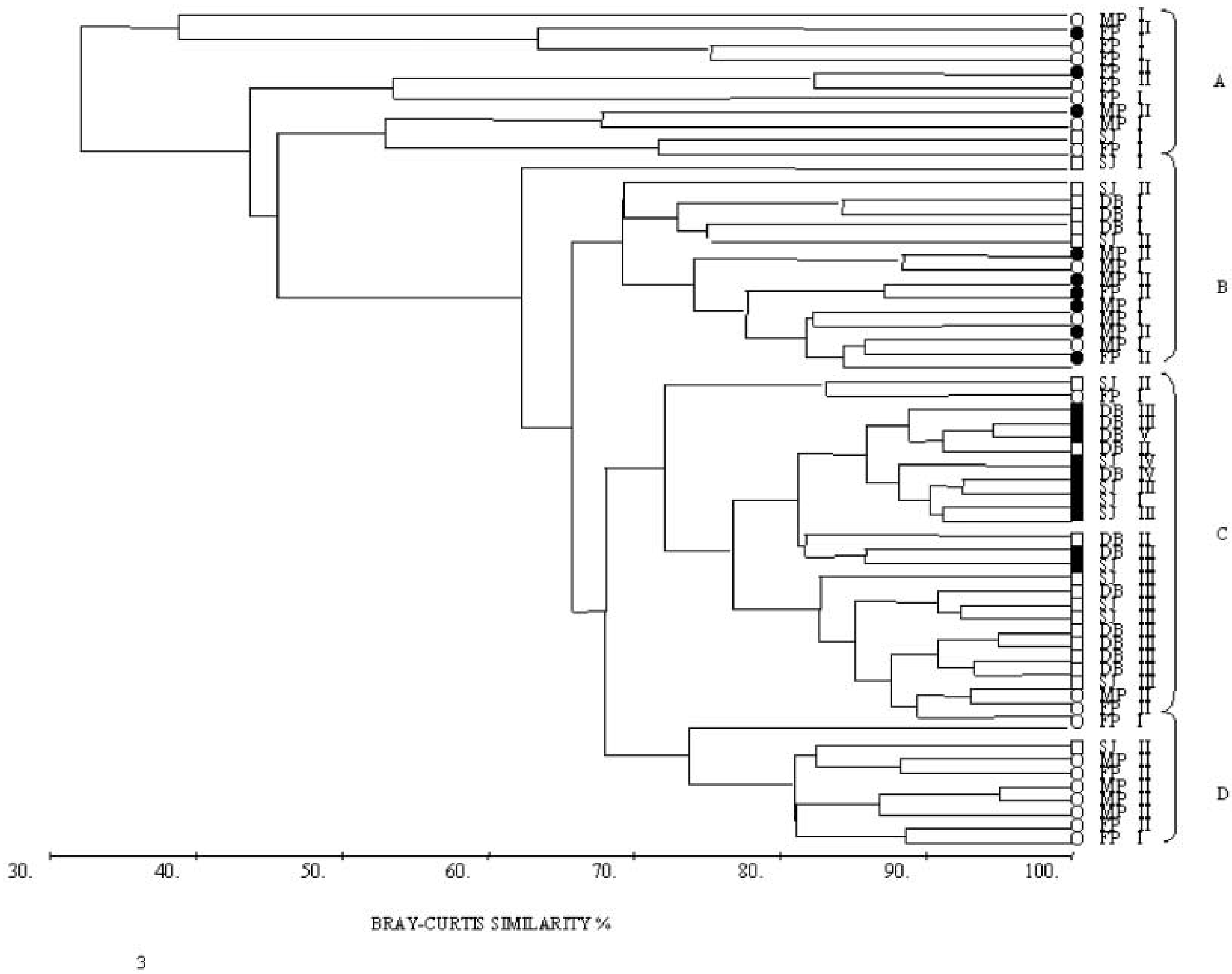


Figure 3. Dendrogram of the percentage similarity amongst the foraminiferal assemblages found on all *Gelidium pristoides* samples. Circles, sheltered shores; squares, exposed shores. Shaded symbols represent winter months and open symbols represent summer months. The algal weight classes are I, <4 g; II, 4–8 g; III, 8–12 g; IV, 12–16 g; V, >16 g.

'prefer' an exposed shore. Alternatively, plants from exposed shores were significantly larger and supported a greater number of foraminifera than those from sheltered shores. Given the rarity of *Lagena* sp. A and *Planorbulina mediterranensis* even on exposed shores, it is possible that their absence from sheltered shores is a reflection of a reduced habitat size.

Although seasonality did not have an effect on the overall abundance and diversity of foraminifera on *G. pristoides*, different species dominated during the two seasons. Similar results were recorded by Steinker (1976), who reported seasonal changes in the presence of *Glabratella ornatissima* and *Protelphidium*. Murray & Alve (2000) also reported seasonal changes in species dominance.

The numbers of foraminifera per plant were significantly higher on exposed than sheltered shores (Figure 2).

Figure 2. (*opposite*) Relationships between the weight of *Gelidium pristoides* plants and (A) the richness, (B) abundance and (C) diversity of foraminifera. Relationships between the weight of sediment trapped by *Gelidium pristoides* and (D) the richness, (E) abundance and (F) diversity of foraminifera. Circles, sheltered shores; squares, exposed shores. Shaded symbols, winter months; open symbols, summer months.

The differences could be attributed to individual plant weight, which was much greater on exposed than on sheltered shores around False Bay. Algal weight is thought to be higher on exposed shores because wave action decreases the effect of herbivory, and the plant channels less energy on chemical defence and more on nutrient uptake and growth (Leigh et al., 1987). The level of exposure could thus contribute to the abundance of foraminifera by its effect on algal growth.

The diversity of foraminifera, as in other meiofauna (Gunnill, 1982; Gibbons, 1988), increased with increasing algal weight. Algal size can be equated to area (Harrod & Hall, 1962; but see Hicks, 1976), and so the relationship between diversity and plant size is subject to the various arguments of the species–area relationship: viz the habitat diversity theory, the area-*per se* theory and the passive sampling theory (Connor & McCoy, 1979; McGuinness, 1984). *Gelidium pristoides* increases in size by growth of distal branches and loss of basal branches (Carter & Anderson, 1986), smaller compact plants trap more sediments and support more meiofauna per unit area than larger plants (Gibbons, 1991). Foraminifera can also attach to the alga itself, therefore an increase in the length of distal branches could mean that more phytal foraminifera are able to inhabit the plant. The difference in foraminiferal assemblages on exposed and sheltered shores may be due to the fact that sheltered shores have smaller plants. The chances of a high abundance or species richness are thus lower due to fewer habitats being available on smaller plants.

It is concluded that foraminiferal assemblages differ between the two shore types, and these differences can be attributed (in part) to both algal, and trapped sediment, weight. Foraminifera are more abundant and have a higher diversity on exposed shores. Foraminifera are less mobile than most of the taxa studied by Gibbons (1988), and some have the ability to attach themselves firmly to substrata, and clearly flourish in the face of wave exposure.

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