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ORIGINAL PAPER

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Biomass and associations of benthic marine macroalgae from the inner Potter Cove (King George Island, Antarctica) related to depth and substrate

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Abstract The biomass of the benthic marine macroalgae from the inner Potter Cove was studied along a depth profile across different substrates during Antarctic summer. Macroalgal associations were identified by means of cluster analysis. Twenty-two species were found in the study site, approximately half of the species present in the area. This paucity may be explained by the strong preponderance of the brown algae *Desmarestia anceps* and *D. menziesii*, which are able to exclude other species by competition for light. The mean biomass of all macroalgae was 1,390 g DW/m^2 ± 1,787 g DW/m^2. Nine macroalgal associations were identified with different preferences for depth, substrate and the degree of exposure. Overall, there was a tendency for macroalgae to grow on fine substrates with increasing depth. Species richness decreased at 20 m depth, probably due to limiting light conditions. The results are discussed with respect to previous studies in East and West Antarctica.

Introduction

Benthic macroalgae contribute significantly to the Antarctic coastal food web either directly (Iken 1996, 1999) or via the detrital food chain (Reichardt and Dieckmann 1985; Fischer and Wiencke 1992; Amsler et al. 1995; Brouwer 1996). Since the first expeditions in Antarctic waters, a number of phycological studies have been performed (see reviews in Lamb and Zimmerman 1977; Cormaci et al. 1992; Wiencke 1996). With increasing latitudes, a decrease in species richness and an increase in endemism of Antarctic macroalgae are evident (Heywood and Whitaker 1984), and compared to temperate and tropical macroalgal floras, the species richness of the Antarctic marine algal flora is lower (Clayton 1994).

So far, most studies on sublittoral vegetation have been of qualitative nature, while quantitative data are scarce. Several studies were performed by means of video documentation. Although this method allows the analysis of large areas, it is not adequate for the estimation of species abundance, especially that of smaller species. Therefore, a quantitative study was carried out by destructive sampling along a depth profile over different substrates during three consecutive summers in Potter Cove. Macroalgal associations were identified by cluster analysis. The data give new insights into macroalgal community structure, biomass and the ecological preferences of individual species with respect to depth, substrate and the degree of exposure.

Materials and methods

The present study was performed in Potter Cove (62°14′S, 58°40′W), a tributary inlet of Maxwell Bay, one of the two big fjords of the central South Shetland Islands. The study area is situated on the northwestern coast at the mouth of the cove (Fig. 1, Station 2). Compared to the exposed shoreline outside Potter Cove, the study area is relatively sheltered. Detailed descriptions of Potter Cove have been presented earlier (Klöser et al. 1994a, 1994b, 1996).

Sampling was done monthly by scuba-diving from January to April of the years 1992, 1993 and 1994 along transects perpendicular to the shore at 5, 10, 15 and 20 m. At each depth, three quadrats of 0.25 m^2 positioned at a distance of 2 m from each other, from a starting point chosen at random, were sampled. A total of 12 sampling surveys were done and 144 samples taken. All macroalgal individuals within the quadrats were removed from the substrate except crustose coralline rhodophytes. The substrate was visually classified into five types: solid rock (R), boulders >50 cm

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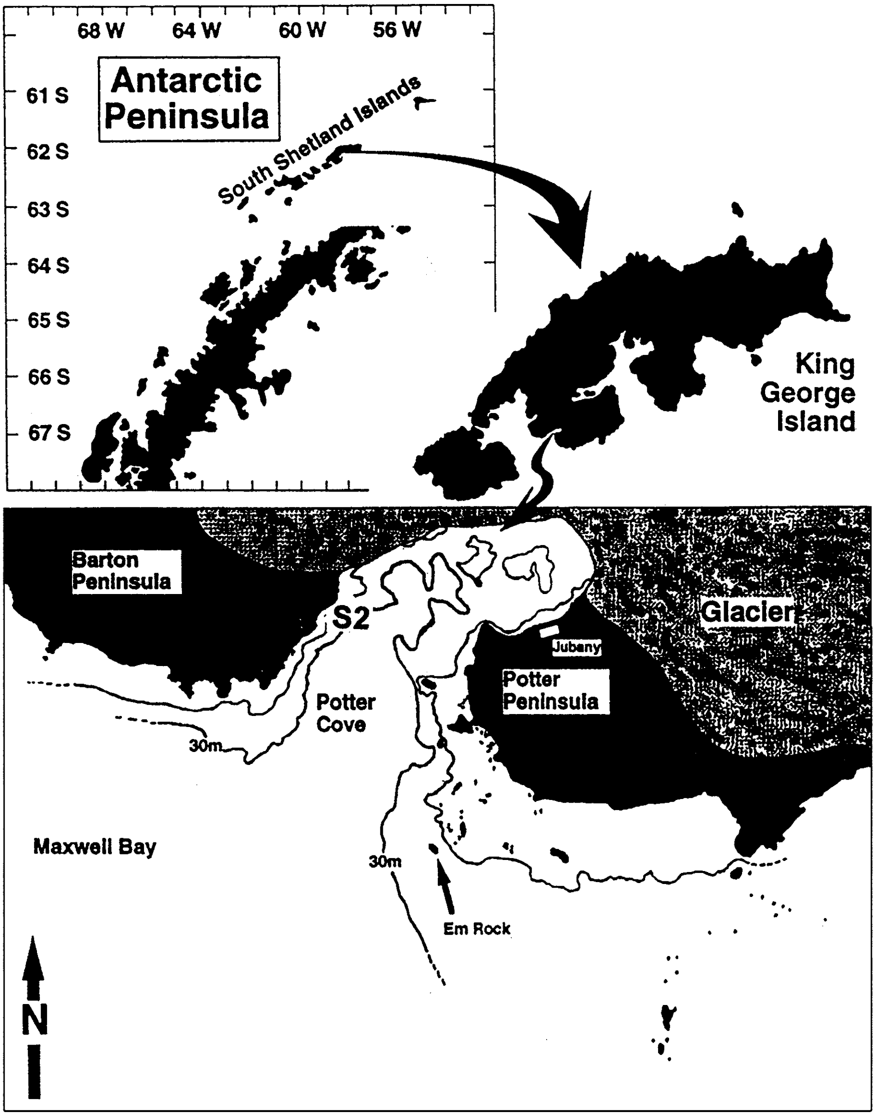

Fig. 1 Map of the investigation area with indication of the sample site station 2 (*S2*)

(B), stones 50–20 cm (S), pebbles 20–5 cm (P), gravel and sand < 5 cm (GS).

Field samples were carried to the Dallmann Laboratory at Jubany Station in large polyethylene bags for identification, counting and weighing. The material was then fixed in 4% formaldehyde made up with seawater and transported to the home laboratory in Buenos Aires, where biomass was determined by drying the specimen at 60°C to constant weight. Voucher specimens are stored in a herbarium.

For each species, total biomass was calculated. In order to identify macroalgal associations, a cluster analysis was performed on the data of specific biomass per square metre. The average values of each depth and each sample ($n = 48$) were used, and the Flexible Response Method and the Bray-Curtis and Curtis (1957) dissimilarity coefficient for quantitative biomass data were applied. The Bray-Curtis index is sensitive to large values, ignores double zero matches and minimises the importance of rare species. This method has been used successfully in several studies (i.e. Galil and Lewinsohn 1981; Bakus 1990) and is regarded as a robust and meaningful measure for ecological applications (Anderson and Clements 2000). The clusters were defined as significant at the 0.7958 cut level as compared to the largest distance between consecutive dichotomies. Diversity (H) and evenness (J) were calculated using Shannon indexes (Shannon 1948). Dominance (D) and frequency (F) were calculated after Bakus (1990). Species richness (d) was calculated after Margaleff (1958). The values of diversity, evenness and species richness for different depths, substrates and biomass were compared by means of a one-way analysis of variance (ANOVA).

Results

Twenty-two taxa were identified (Table 1). Of these, three large, brown algal species (*Desmarestia menziesii*, *D. anceps* and *Himantothallus grandifolius*) exhibited the highest mean biomass values: 307 ± 592–538 ± 1363 g DW/m^{2} (Table 1). In the other species, biomass varied between 0.06 ± 0.40 and 65.18 ± 260.91 g DW/m$^{2\cdot}$ The mean biomass of all species was 1,396 ± 1,787 g DW/m^{2} and ranged from 19 g DW/m^{2} to 7,911 g DW/m^{2} (Table 2). There was no difference in biomass among the years studied. In terms of frequency, several species were important. *Plocamium cartilagineum* was present in almost all the samples, and had the highest frequency value (Table 1). *D. menziesii*, *H. grandifolius*, *D. anceps*,

Table 1 List of studied species, their mean biomass ± standard deviation (expressed as dry weight), dominance and frequency in the 48 samples taken in summer 1992, 1993 and 1994

Species	Biomass (g DW/m^2)	Dominance	Frequency
Phaeophyta			
Adenocystis utricularis (Bory) Skottsberg 1907	0.06 ± 0.40	< 0.1	2.1
Ascoseira mirabilis Skottsberg 1907	65.18 ± 260.91	4.7	25.0
Desmarestia anceps Montagne 1942	323.06 ± 978.36	23.1	50.0
D. antarctica Moe et Silva 1989	27.31 ± 88.58	1.9	27.1
D. menziesii j. Agardh 1848	537.77 ± 1362.85	38.5	56.3
Himantothallus grandifolius (Gepp et Gepp) Zinova 1959	306.77 ± 591.85	22.0	54.2
Phaeurus antarcticus Skottsberg 1907	0.74 ± 3.04	0.1	10.4
Rhodophyta			
Ballia callitricha (C. Agardh) Kützing 1843	0.59 ± 1.78	< 0.1	18.8
aff *Callophyllis* sp.	1.04 ± 4.39	0.1	6.3
Curdiaea racovitzae Hariot in De Wildeman 1900	25.83 ± 80.81	1.8	31.3
Georgiella confluens (Reinsch) Kylin 1956	7.88 ± 12.54	0.6	39.6
Gigartina skottsbergii Setchell et Gardner 1936	30.75 ± 55.10	2.2	45.8
Gymnogongrus antarcticus Skottsberg 1953	0.19 ± 0.94	< 0.1	6.3
Gymnogongrus turquetii Hariot 1907	4.65 ± 15.79	0.3	14.6
Hymenocladiopsis crustigena Moe 1986	3.84 ± 10.98	0.3	10.4
Iridaea cordata (Turner) Bory 1826	3.47 ± 7.37	0.2	41.7
Kallymenia antarctica Hariot 1907	11.55 ± 26.77	0.8	35.4
Myriogramme spp. [*M. mangini* (Gain) Skottsberg 1953 and *M. smithii* (Hooker et Harvey) Kylin 1924]	4.66 ± 12.79	0.3	47.9
Palmaria decipiens (Reinsch) Ricker 1987	5.57 ± 20.81	0.4	14.6
Plocamium cartilagineum (Linné) Dixon 1967	29.63 ± 77.89	2.2	81.3
Sarcodia montagneana (Hooker et Harvey) J. Agardh 1872	3.44 ± 9.73	0.2	16.7
Sp. A (O. Cryptonemiales)	2.95 ± 10.45	0.2	8.3

Myriogramme spp. and *Gigartina skottsbergii* were also frequently found in the area. The frequency of the rest of the species was < 45%.

The ANOVA analysis showed no significant differences between diversity and evenness with depth, substrate and biomass. Only species richness decreased significantly at 20 m (ANOVA, F-ratio = 3.813, P = 0.016). Clusters 4, 6 and 8 were characterised by the highest values of diversity. The highest values of evenness were observed in clusters 6 and 8 (Table 2). Most samples contained, on average, six to nine different species (Table 2). The mean number of individuals/m^2 was 14 ± 4.7.

Vertical distribution of species showed a characteristic variation in relation to depth and substrate (Fig. 2). The most abundant species at 5 m were *Ascoseira mirabilis* and *Curdiea racovitzae*, which grew exclusively on boulders or solid rock. Biomass of *D. menziesii* was highest at 5 m and gradually decreased with depth. *D. anceps* and *D. antarctica* were the most abundant species at 10 m, growing, like *D. menziesii*, principally on boulders and stones. *G. skottsbergii* occurred on all

Table 2 Results of the cluster analysis, indicating macroalgal biomass (expressed as g dry weight/m^2), number of species, diversity (H), evenness (J), density (number individuals/m^2) and species richness (d)

	n		Biomass	Number of species	Diversity (H)	Evenness (J)	Density	Species richness (d)
Cluster 1	10	$\bar{X}$	3012.189	6.90	0.59	0.31	25.69	4.43
		SD	2219.13	1.79	0.35	0.18	18.12	0.65
Cluster 2	3	$\bar{X}$	4270.75	6.00	0.70	0.45	15.47	4.38
		SD	2908.34	2.65	0.44	0.29	10.32	0.93
Cluster 3	5	$\bar{X}$	812.07	7.20	0.84	0.44	20.74	5.02
		SD	474.27	1.10	0.40	0.23	12.06	1.07
Cluster 4	4	$\bar{X}$	335.92	9.25	1.24	0.55	26.00	6.22
		SD	129.44	0.50	0.39	0.20	17.44	0.57
Cluster 5	3	$\bar{X}$	371.73	4.33	0.63	0.39	23.72	2.41
		SD	217.93	2.52	0.54	0.34	20.48	1.32
Cluster 6	3	$\bar{X}$	199.17	7.00	1.31	0.70	16.88	4.96
		SD	78.35	2.65	0.15	0.11	8.67	1.27
Cluster 7	10	$\bar{X}$	219.45	5.60	0.98	0.58	14.12	4.11
		SD	150.38	1.90	0.40	0.21	5.11	1.45
Cluster 8	1	$\bar{X}$	19.03	8.00	1.60	0.77	20.00	5.38
		SD	–	–	–	–	–	–
Cluster 9	9	$\bar{X}$	1640.09	5.67	0.59	0.34	16.25	3.90
		SD	915.13	2.50	0.41	0.21	8.78	1.62

substrate types and at all depths with highest values at 5 and 10 m. *H. grandifolius*, which is also abundant in the area, is more or less evenly present from 10 to 20 m, mostly on pebble and gravel sand. *Georgiella confluens* and *P. cartilagineum* had their highest biomasses at 20 m on gravel sand. *Kallymenia antarctica* grew preferentially at 15 m on stones, pebble and gravel sand.

Eight macroalgal associations were identified by cluster analysis. A ninth cluster (cluster 8) was defined by only one sample (Fig. 3). The results of the cluster analysis and the species composition of each cluster are shown in Tables 2 and 3. Cluster 1 principally contains samples from large boulders, stones and solid rock at

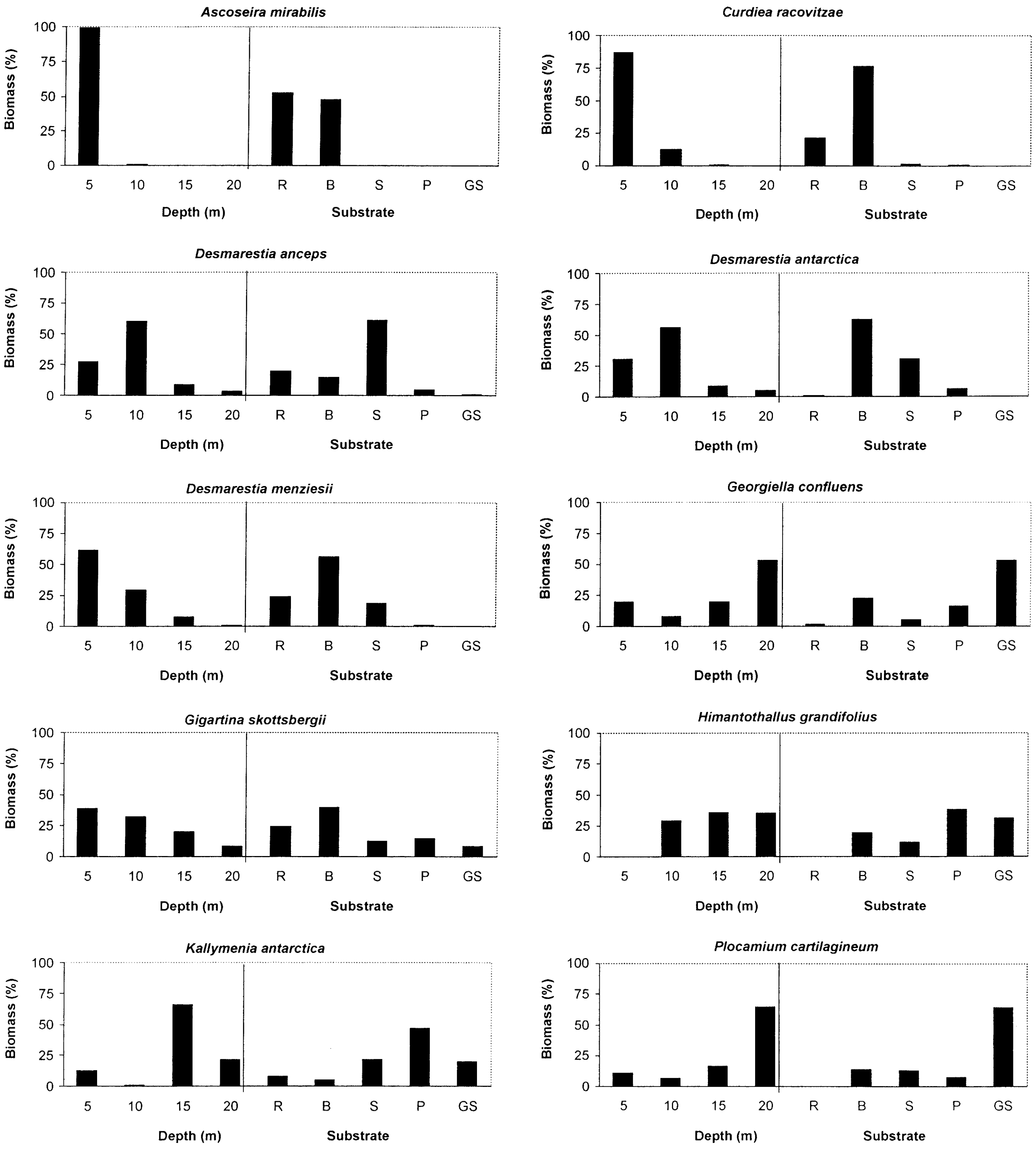

Fig. 2 Percentage of biomass (%) of the most abundant macroalgal species at different depths (5, 10, 15 and 20 m) and on different substrates (*R* solid rocks, *B* boulders, *S* stones, *P* pebbles, *GS* gravel sand)

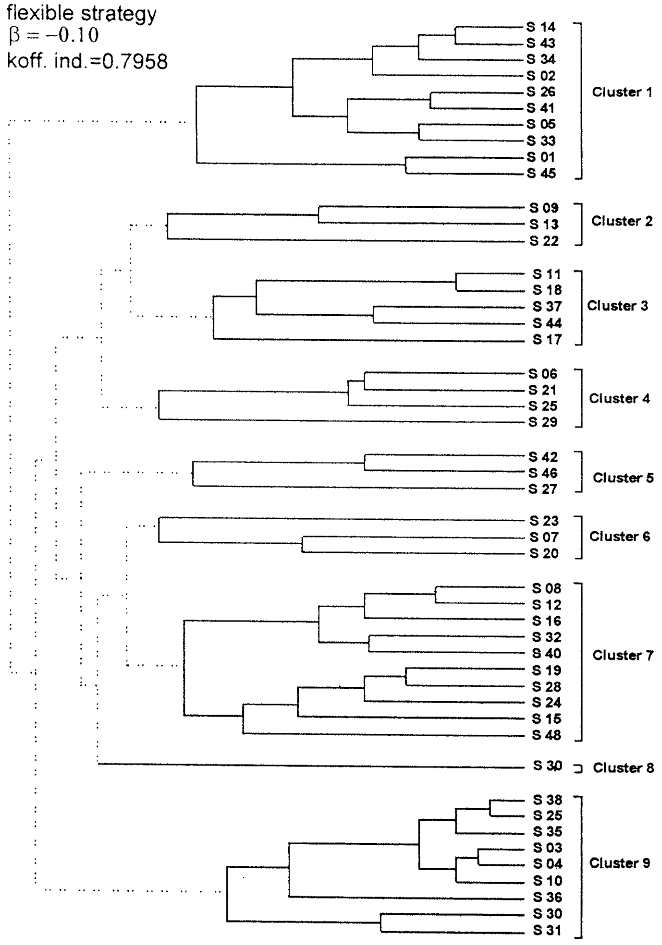

Fig. 3 Dendrogram of the cluster analysis showing nine clusters (flexible strategy: $\beta = -0.10$; coffenetical index = 0.7958)

5 and 10 m at wave-exposed sites, with medium to high biomasses and a dominance of *D. menziesii*. Cluster 2, also high in biomass, is formed by samples from rocks, boulders and stones at 5 and 10 m in a sheltered site dominated by *A. mirabilis*, *D. anceps* and, to a smaller degree, by *C. racovitzae*. Cluster 3 is characterised by medium biomasses and is dominated by *D. anceps*. It occurs between 5 and 20 m on all substrates except gravel sand. Cluster 4 represents samples from rocks and boulders in shallow water, with the opportunistic species *C. racovitzae* and *Gigartina skottsbergii*. Cluster 5 shows a dominance of the annual *D. antarctica* on boulders and stones at 10 and 15 m depth. Cluster 6 is mainly characterised by *K. antarctica*, *Gymnogongrus turquetii* and *P. cartilagineum* on stones and gravel sand in 15 and 20 m. Clusters 4, 5 and 6 are comparatively poor in biomass. Clusters 7, 8 and 9 are characterised by *H. grandifolius*, which mostly dominates over a variety of accompanying species. While biomass is low in clusters 7 and 8, it is relatively high in cluster 9 in which *H. grandifolius* attains its highest dominance. In cluster 8, *Ballia callitricha* and *Sarcodia montagneana* attain exceptionally high biomass values. Only one sample of cluster 7 comes from stones at 15 m while the others are from pebbles and gravel sand at 20 m. The association of cluster 8 occurs at 15 m on pebbles. Cluster 9 contains samples from all substrates except solid rock at 10–20 m.

Discussion

Macroalgal biomass in Potter Cove is relatively high, compared to other areas in the Antarctic Peninsula region and especially in the Ross Sea (DeLaca and Lipps 1976; Miller and Pearse 1991; Amsler et al. 1995;

Table 3 Species composition in each cluster expressed as percentage

Species	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7	Cluster 8	Cluster 9
Adenocystis utricularis	0.00	0.00	0.00	0.43	0.00	0.00	0.00	0.00	0.00
Ascoseira mirabilis	1.03	34.43	4.43	7.84	0.50	0.00	0.00	0.00	0.00
Desmarestia anceps	10.10	51.61	74.03	2.27	0.33	0.00	3.13	1.14	2.97
D. antarctica	0.57	0.00	0.58	0.42	67.04	1.16	2.06	0.00	0.22
D. menziesii	78.43	1.23	5.60	11.27	8.15	0.47	1.45	0.00	3.97
Himantothallus grandifolius	3.81	0.00	1.96	0.17	2.07	3.62	61.12	21.64	82.43
Phaeurus antarcticus	0.00	0.00	0.33	1.21	0.13	0.00	0.02	0.00	0.00
Ballia callitricha	0.04	0.00	0.02	0.09	0.00	0.00	0.00	37.90	0.09
aff Callophyllis sp.	0.02	0.00	0.42	0.00	0.00	0.00	0.60	0.00	0.00
Curdiea racovitzae	1.46	9.40	0.00	22.28	0.00	0.03	0.00	0.00	0.77
Georgiella confluens	0.18	0.30	0.47	2.43	1.72	0.00	0.14	0.70	1.35
Gigartina skottsbergii	2.09	0.77	3.66	45.26	0.00	0.85	1.89	0.00	1.67
Gymnogongrus antarcticus	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gymnogongrus turquetii	0.00	0.38	0.52	0.00	0.00	29.88	1.65	7.15	0.00
Hymenocladiopsis crustigena	0.00	0.06	0.00	0.00	0.00	10.70	2.34	0.00	0.48
Iridaea cordata	0.45	0.28	0.29	3.20	1.23	0.28	0.00	0.00	0.05
Kallymenia antarctica	0.22	0.00	2.14	0.00	0.00	21.84	7.50	0.00	2.49
Myriogramme spp.	0.28	1.47	0.29	2.55	0.03	1.76	3.27	5.60	0.00
Palmaria decipiens	0.19	0.00	3.56	0.00	0.07	0.04	1.74	0.00	0.24
Plocamium cartilagineum	1.17	0.04	0.60	0.51	18.47	14.27	9.90	4.53	2.60
Sarcodia montagneana	0.00	0.00	0.58	0.00	0.00	12.81	2.44	21.16	0.01
Sp. A (O. Cryptonemiales)	0.00	0.00	0.51	0.00	0.00	2.30	1.71	0.00	0.56

Brouwer et al. 1995; Cormaci et al. 1996, 1998). It must be noted, however, that in cases where individual species, such as *D. anceps* and *D. menziesii*, showed a high biomass, the combined effect of the large size of the algae with the size of the sampling quadrat (0.25 m^2) may have caused an overestimation of the biomass of these species when extrapolating data to 1 m^2. A similar problem was discussed by Amsler et al. (1995) using an even smaller sampling quadrat. Moreover, interannual variability and long-term changes have to be considered for an explanation of the differences in biomass, at least in the Antarctic Peninsula region.

The dominance of brown algae in West Antarctica appears as a general result. In contrast, in the Ross Sea area macroalgal communities are dominated by the red algae *Iridaea cordata* and *Phyllophora antarctica* (Miller and Pearse 1991; Cormaci et al. 1996, 1998). One of the species, *I. cordata*, occurs also in Potter Cove, but it is never dominant.

The mean number of individuals/m^2 of 14 ± 4.7 is relatively low. Concerning species richness, the species collected in the study site include only approximately half of the species present in the whole of Potter Cove and its vicinities (Chung et al. 1994; Klöser et al. 1994a, 1996; Clayton et al. 1997). This relative paucity may be explained by the strong preponderance of *D. anceps* and *D. menziesii*, which are able to exclude other species by competition for light (Klöser et al. 1994a, 1996). However, small macroalgae, especially rhodophytes, appeared at higher frequencies than previously reported (Klöser et al. 1996).

The results from this study complement the published data on latitudinal biodiversity patterns. On a smaller scale, factors determining the abundance of individual species and macroalgal associations have to be regarded as a function of local environmental characteristics. A tendency of macroalgae to grow on fine substrate with increasing depth was observed in Potter Cove (Fig. 2) in accordance with findings in the South Orkney Islands (Richardson 1979). This is probably due to the fact that turbulence is low in deep waters, allowing macroalgae to colonise substrata which would not provide sufficient anchorage in shallower, more turbulent, sites.

Individual species may react to different factors in a different way, e.g. *D. anceps* and *D. antarctica* exhibit the same preference with regard to depth. However, the perennial *D. anceps* outcompetes all other species at moderately exposed sites, while the annual *D. antarctica* is a poor competitor, proliferating on terrain denuded, for example, by ice impact (cf. Chung et al. 1994; Klöser et al. 1994b; Amsler et al. 1995). Thus, despite similar depth preferences, the two species are found in different vegetation types, *D. anceps* in cluster 2, and *D. antarctica* in cluster 5.

D. menziesii is a species characteristic for wave-exposed sites on solid rock and boulders in the upper and central sublittoral (Fig. 2). This species has been shown by Klöser et al. (1996) and in this study (cluster 4) to be associated with *A. mirabilis*. However, we found *A. mirabilis* also associated with *D. anceps*, especially in cluster 2. This is regarded as an effect of the low turbulence at this particular site. Under such conditions, *D. anceps*, which is sensible to turbulence, may well replace *D. menziesii*.

H. grandifolius is a species often occurring at great depth on fine-grained substrates, as also shown by other authors (Neushul 1965; Delépine 1966; DeLaca and Lipps 1976; Zielinski 1990; Klöser et al. 1994a, 1996; Brouwer et al. 1995). Obviously, this species becomes dominant in places where *Desmarestia* spp. cannot grow due to the absence of suitable substrate, solid rock or boulders. Moreover, low light conditions are a major limiting factor for macroalgae at great depths, as demonstrated in ecophysiological studies. Gómez et al. (1997) showed that the lower depth distribution limit of an individual species is determined by the metabolic C balance. *Palmaria decipiens* or *D. anceps* from Potter Cove, for example, achieve in early summer positive C balances close to 3 mg C g^{-1} FW day^{-1} at 20 m depth. At 30 m depth, daily light availability decreases, but C balance is still positive in four of five studied species (Gómez et al. 1997). Only in the case of *D. anceps* from 30 m was a negative C balance determined, indicating that the alga is, at this depth, at its lower distribution limit. In contrast, *Palmaria decipiens*, *Gigartina skottsbergii*, *K. antarctica* and especially *H. grandifolius* are able to grow metabolically, even in deeper waters.

The upper distribution limit of an algal species is, in contrast, determined physiologically by its ability for dynamic photoinhibition, i.e. by the ability to withstand high light stress (Hanelt et al. 1997). UV radiation has also to be considered in this context. According to Bischof et al. (1998), photosynthesis in species occurring exclusively in deep waters is inhibited more and recovers after UV exposure much more slowly than in species from the upper sublittoral, thereby excluding the UV-sensitive species from shallow waters. So the physiological constitution of individual species has also to be taken into account for an explanation of macroalgal zonation patterns.

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