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Stable carbon isotope composition, depth distribution and fate of macroalgae from the Antarctic Peninsula region

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Summary. Stable carbon isotope composition of macroalgae collected at King George Island (Antarctica) ranged from about −8‰ to −34‰. We hypothesize that the $\delta^{13}C$ values are related to the depth distribution: species inhabiting greater depth had much lower values (around −30‰) compared to species from shallower waters (around −17‰). Isotopic studies on sediment trap samples from the King George Basin (2,000 m deep) revealed that benthic macroalgae contributed strongly to the total organic carbon pool of the deeper basin waters during austral spring and summer. Fragments of brown macroalgae (Desmarestiales) were detected in microscopical analyses of semi-thin sections of sediment samples from the Bransfield Strait. Possible mechanisms regarding the erosion of benthic macroalgae and their transport to the deeper waters and to the sediment are summarized.

Introduction

Only sparse information is available today on the depth zonation of benthic marine macroalgae in Antarctica, especially in greater water depths. Zaneveld (1966a, b) and Zielinski (1981) carried out a high number of dredging investigations. Diving observations were made by Neushul (1961, 1965), Delepine et al. (1966), Lamb and Zimmermann (1975), Moe and DeLaca (1976) and DeLaca and Lipps (1976). On King George Island (South Shetland Islands), Zielinski (1981) differentiated three communities: 1. An association dominated by *Adenocystis utricularis* and *Monostroma hariotii* in the intertidal, 2. A community with *Desmarestia menziesii* and *Phycodrys antarctica* in the subtidal down to 15–30 m, 3. A community with *Cystosphaera jaquinotii*, *Plocamium cartilagineum*, *Himantothallus grandifolius* and another *Desmarestia* species from 10–15 m to 70–90 m (revealed by dredging). These data on the occurrence of Antarctic macroalgae in relative deep waters are supported by diving observations by Lamb and Zimmermann (1975) and DeLaca and Lipps (1976) who showed that the algal vegetation is still abundant below 20–40 m.

Indirect information on the depth zonation of Antarctic macroalgae comes from the culture experiments of Wiencke (1990a, b) in which the minimum light requirements for completion of the life-cycle were determined. His values predict a lower distribution limit of endemic Antarctic Desmarestiales of 53 ± 23 m in clear offshore waters and of 28 ± 5 m in inshore fjords of the Antarctic Peninsula region. In another culture study, Wiencke and Fischer (1990) demonstrated a trend towards more negative stable carbon isotope ratios with decreasing photon fluence rates. The latter results are used here to interprete the stable carbon isotope ratios determined in macroalgae collected in Antarctica.

Benthic macroalgae are important contributors to primary production in coastal areas (Mann 1973) and must be considered as an energy source for benthic organisms that depend on the detrital food chain (Stephenson et al. 1986; Duggins et al. 1989). Relatively little is known about the transport of macroalgal debris to the deep water column and to the deep-sea benthos community (Menzies et al. 1967; Menzies and Rowe 1969; Reichardt 1987). Large amounts of macroalgae may be eroded and transported by landslides and turbidity currents (Anikouchine and Ling 1967), sea-ice, storm events and surface currents (Zielinski 1981). Tegner and Dayton (1987) and Seymour et al. (1989) reported the influx of kelp detritus into the Santa Barbara Basin (California) as a result of storm and strong El Niño-Southern Oscillation events. Schimmelmann and Tegner (19(1) correlated changes in the local historical kelp abundance with an isotopic time-series of organic carbon from varved sediment in the Santa Barbara Basin.

Dieckmann et al. (1985) emphasized that the coastal ecosystem of the Antarctic depends at least partly on a detritus food chain comparable to temperate and subtropical regions. Liebezeit and von Bodungen (1987) measured the chemical composition of sediment trap samples taken in November and December 1983, and estimated

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that macroalgae contribute up to 71% to the organic material in the deeper waters of the King George Basin.

In the present study the stable carbon isotope composition of benthic macroalgae will be discussed in relation to their depth zonation. We demonstrate that macroalgal fragments are transported to the deeper water column of the King George Basin and are embedded into the underlying sediments.

Material and methods

The investigated species are listed in Table 1. For stable carbon isotope analysis, adult individuals of species of macroalgae were collected mostly as drift material at different sites of the Fildes Peninsula (King George Island, South Shetland Islands) in January and February 1986 and 1987 (Clayton and Wiencke 1986; Wiencke 1988). Some supralitoral and intertidal algae as well as two *Himantothallus grandifolius* plants were collected in situ.

Freshly collected plants were fixed for light microscopical studies. Fixation and initial dehydration was carried out in Antarctica, and the further procedures were completed 3–6 weeks later in Germany. As fixatives, 4% glutaraldehyde with 4% paraformaldehyde or 1% glutaraldehyde with 1% paraformaldehyde in 50 mM sodium cacodylate buffered seawater (pH 7.2) were used (Fixation times 4–7 h; Temperature 0°–8°C). Specimens were then rinsed in four changes of buffered seawater and postfixed for 3 h in 1% osmium tetroxide prepared in buffered seawater. Dehydration was made in 10% acetone steps, ultimately to 100% in 15 min intervals. Samples were then washed in 6 changes of 100% water-free acetone and embedded in Spurr's low viscosity resin (Spurr 1969). Semi-thin sections were prepared by use of a Reichardt OM U3 microtome and stained with toluidene blue.

For stable carbon isotope analysis, fresh plants without obvious epibionts were dried at room temperature in Antarctica. In the home laboratory, they were rinsed briefly with cold distilled water to remove surface salt and, subsequently, vacuum-dried at 30°C. A few milligrams from the main branches or blades of each specimen were then analyzed in a Heraeus-CHN elemental analyzer for organic carbon and organic nitrogen. The combustion was carried out at 1050°C using pure oxygen and helium as carrier gases. For $\delta^{13}C$ analysis, the CO_2 leaving the conductivity cell of the CHN analyzer was trapped at $-196°C$ in glass ampoules, using a manual trapping device described by Fischer (1989). Subsequently, the purified carbon dioxide was transferred to a Finnigan MAT 251 mass spectrometer for stable carbon isotope composition. The $^{13}C/^{12}C$ values are expressed in the δ-notation and refer to the limestone standard PDB (Craig 1957). They are defined as:

$$\delta^{13}C\,(‰)=\frac{^{13}C/^{12}C_{\mathrm{Sample}}-{}^{13}C/^{12}C_{\mathrm{Standard}}}{^{13}C/^{12}C_{\mathrm{Standard}}}\times 1000.$$

The total reproducibility of the preparation and the measuring procedure was better than 0.15‰ (1 sd).

Sediment trap samples (Table 2) were obtained using two moored arrays described in detail by von Bodungen et al. (1987). Before processing in the laboratory, a small portion of each sample containing detritus from phytoplankton and macroalgae was removed for light microscopy. Portions of vacuum-dried and homogenized 1/4 aliquots of the total sample were decalcified with 2N HCL in silver foil crucibles and combusted as described above.

Sediments from the Bransfield Strait (Table 2) were recovered with a giant box corer (Wuttke, Hamburg; 50 × 50 cm in cross-section, 50 cm in length). Subsamples were taken from the sediments using plastic tubes 7 cm in diameter. The sediments were wet-sieved through 250 and 1,000 μm screens and macroalgal fragments were collected using a forceps. Samples were rinsed twice with about 5 ml of distilled water and subsequently prepared for light microscopy and isotopic analysis in the same way as freshly collected plants.

Results

The stable carbon isotope data are given in Table 1. From most macroalgae, different parts of the same thallus were analyzed. They showed only small isotopic variations. The only exceptions were *Kallymenia antarctica* and *Adenocystis utricularis.* Differences in the isotopic composition of intact and decomposed thallus parts were around 2‰. Intraspecific isotopic variation was around 1–2‰. Differences between cystocarpic plants and tetraporophytes in the red algae *Iridaea cordata* and *Gigartina skottsbergii* were between 2 and 4‰.

Figure 1 shows the isotope values of total organic carbon collected with sediment traps in November and December 1983, 1984, 1985 in the King George Basin. A detailed description of the trapped particles is given by von Bodungen et al. (1987). Detritus derived from depths of 180–700 m in 1983 and 1985 had a $\delta^{13}C$ ratio close to -29.5‰. In the deeper waters of the basin (below 1,000 m), a distinct change to more positive values (maximum value -26‰) occurred.

The $\delta^{13}C$ values of macroalgal detritus isolated from the sediments are given in Table 2. Most of the isolated fragments were too small for both isotopic determinations and microscopic preparations. The $\delta^{13}C$ ratios of algal fragments from the sediments were in the range of those determined for the freshly collected macroalgae (Tables 1, 2).

The microscopical analysis of semi-thin sections of material taken from the sediments and – for comparison – of fresh algal tissue are shown in Figs. 2–7. Two representative sediment examples are shown in Fig. 2 from a depth of 1225 m (site 290, Table 2) and in Fig. 3 from a depth of 823 m (site 302, Table 2). Both samples are parts of Desmarestialean macrothalli. Most protoplasmic components were degraded and leached out. However, the general structure of the pseudoparenchymateous tissue, especially the cell walls were fairly well preserved. The sample in Fig. 2 is characterized by two cell types, palisade-like and more or less isodiametric cells. This morphology most closely corresponds to the outer and inner cortical cells of ultimate branchlets of *Desmarestia menziesii* (Fig. 4). *Desmarestia antarctica* (Fig. 5) has a comparable cortex structure but much shorter outer cortical cells (two times long as broad), and large inner cortical cells often adjacent to the outer cortical cells. Both features were not found in *D. menziesii.* In *Desmarestia anceps* (Fig. 7) and *Himantothallus grandifolius* (Fig. 6) outer cortical cells are always more or less isodiametric. The $\delta^{13}C$ value of -22.9‰ measured in the *D. menziesii* sample taken from the sediment was somewhat lower than the isotope ratio of the fresh specimen (≈ -20‰; Tables 1, 2).

The sample in Fig. 3 shows relatively large, approximately isodiametric cells surrounded by smaller cells resembling the inner cortex of macrothalli of one of the above mentioned Desmarestiales. A cross section through a thallus part of *Desmarestia anceps* is shown in Fig. 7. The inner cortical cells are relatively large and develop small cells called hypha-like cells as they are strongly elongated in longitudinal direction (not shown here). They occur

Table 1. Stable carbon isotopes and sampling dates of macroalgae collected in Antarctica. Place names after Barsch et al. (1985); KGI = King George Island

Species name	Developmental stage	Sample site (depth)	Plants a, b, c	Sampling segment	$\delta^{13}C$ (‰ PDB)
Enteromorpha bulbosa (Suhr) Montagne		KGI, Biologists Bay, intertidal, in situ	a	vegetative part of thallus	−17.33
			a	decomposed part of thallus	−15.13
Monostroma bariotii Gain		KGI, Biologists Bay, drift	a	lower part of thallus	−15.45
		KGI, Biologists Bay, drift	b	lower part of thallus	−17.76
Prasiola crispa subsp. antarctica (Kützing) Knebel *f. antarctica*		KGI, Skuabay, supralitoral, in situ	a	whole plants	−16.40
Acrosiphonia arcta (Dillwyn). Agardh		KGI, Biologists Bay, upper sublitoral, in situ	a	whole plants	−17.55
Gigartina skottsbergii (Bory) Setchell and Gardner	Tetrasporophyte	KGI, Ardley Bay, drift	a	marginal part of blade	−14.42
	Tetrasporophyte	KGI, Skuabay, drift	b	blade	−17.35
	Cystocarpic plant	KGI, Biologists Bay, drift	c	marginal part of blade	−18.33
Iridaea cordata (Turner) Bory	Cystocarpic plant	KGI, Biologists Bay, drift	a	central part of blade	−16.28
	Tetrasporophyte	KGI, Biologists Bay, drift	b	marginal part of blade	−14.72
Curdiaea racovitzae Hariot	Cystocarpic plant	KGI, Ardley Bay, drift	a	central part of blade	−15.99
Palmaria decipiens (Reinsch) Ricker	Tetrasporophyte	KGI, Biologists Bay, drift	a	top part of thallus	−9.69
			a	lower part of thallus	−9.76
Plocamium cartilagineum (L.) Dixon	sterile plant	KGI, Biologists Bay, drift	a	stipe	−34.16
			a	top part of thallus	−32.83
Georgiella confluens (Reinsch) Kylin	sterile plant	KGI, Ardley Bay, drift	a	stipe	−31.04
			a	young thallus parts	−30.79
Kallymenia antarctica Hariot	sterile individual	KGI, Ardley Bay, drift	a	stipe	−21.08
			a	blade	−15.51
Neuroglossum ligulatum (Reinsch) Skottsberg	Cystocarpic plant	KGI, Biologists Bay, drift	a	stipe	−31.89
			a	blade	−33.13
			a	decomposed blade	−32.62
Porphyra endiviifolium (A. et E. Gepp) Chamberlain		KGI, Ardley Bay, upper intertidal, in situ	a	whole plant	−20.86
Phycodrys antarctica (Skottsberg) Skottsberg	sterile plant	KGI, Ardley Bay, drift	a	blade	−31.43
Adenocystis utricularis (Bory) Skottsberg		KGI, Ardley Bay, intertidal, in situ	a	lower part of thallus	−13.82
			b	lower part of thallus	−14.56
			b	middle part of thallus	−9.58
			b	top part of thallus	−8.26
Cystosphaera jacquinotii (Montagne) Skottsberg		KGI, Ardley Bay, drift	a	blade	−27.90
			b	stipe	−27.86
			b	stipe	−27.89
			b	blade	−28.86
			b	blade	−27.17
			b	blade	−27.90
Desmarestia anceps Montagne	Sporophyte	KGI, Ardley Bay, drift	a	holdfast	−28.52
			a	part of top blades	−29.52
		KGI, Ardley Bay, drift	b	stipe	−29.23
			b	part of top blade	−30.68
Desmarestia menziesii J. Agardh	Sporophyte	KGI, Biologists Bay, drift	a	top blades	−19.32
		KGI, Biologists Bay, drift	b	stipe	−20.26
			b	stipe	−21.39
			b	blades	−20.09
			b	blades	−20.51
			b	decomposed top part	−17.88
Desmarestia antarctica Moe and Silva	Sporophyte	KGI, Ardley Bay, drift	a	middle part of thallus	−18.57
Himantothallus ograndifolius (A. et E. Gepp) Zinova	Sporophyte	KGI, Sputnik Island, 6 m in situ	a	stipe	−20.17
			a	blade	−20.46
		KGI, Ardley Bay, 15 m in situ	b	stipe	−19.99
			b	stipe	−20.19
			b	upper decomposed part of blade	−17.59
			b	upper decomposed part of blade	−20.79
			b	growth zone	−18.90

interspersed between the much larger inner cortical cells. Both cell types are also evident in the sample shown in Fig. 3. An isotope ratio of this specimen was not determined. Similar material sampled at site 196 (Table 2) is most probably *Desmarestia anceps*. This fragment had a value of −30.19‰ which is slightly lower compared to the fresh specimen (≈ −29.5‰; Tables 1, 2).

Discussion

Brown algae of the order Desmarestiales, in particular *Himantothallus grandifolius*, *Desmarestia anceps* and *Desmarestia menziesii* are the dominating canopy macroalgae in the Antarctic Peninsula region (Neushul 1965). A single macrothallus of *H. grandifolius* can reach a length of 18 m

Table 2. Locations of sediment trap and box-core sites in the Bransfield Strait. Stable carbon isotope ratios of macroalgal fragments isolated from the sediments are also given

Location	Sample type	Site	*RV Polarstern* cruise	Position	Water depth (m)	Isolated macroalgae $\delta^{13}C$ (‰ PDB)	Species order
King George Basin	Sediment trap	KG83	ANT-II/3	62°16′S 57°23′W	1890		Desmarestiales
		KG84	ANT-III/2	62°21′S 57°44′W	1945		Desmarestiales
		KG85	ANT-IV/2	62°22′S 57°26′W	1920		Desmarestiales
Admiralty Bay	Sediment (0–1 cm)	196	ANT-III/2	62°09′S 58°24′W	484	−30.19	*Desmarestia anceps*?
Joinville Shelf	Sediment (0–1 cm)	207	ANT-III/2	63°00′S 57°04′W	70	−22.65	Desmarestiales
King George Island (slope)	Sediment (0–1 cm)	290	ANT-IV/2	62°16′S 58°11′W	1225	−22.90	*Desmarestia menziesii*
King George Basin	Sediment (0–1 cm)	294	ANT-IV/2	62°15′S 57°38′W	1983		Desmarestiales
NW Weddell Sea	Sediment (1–2 cm)	302	ANT-IV/2	62°07′S 53°51′W	823		*Desmarestia anceps*, or *D. antarctica*, *D. menziesii*, *H. grandifolius*

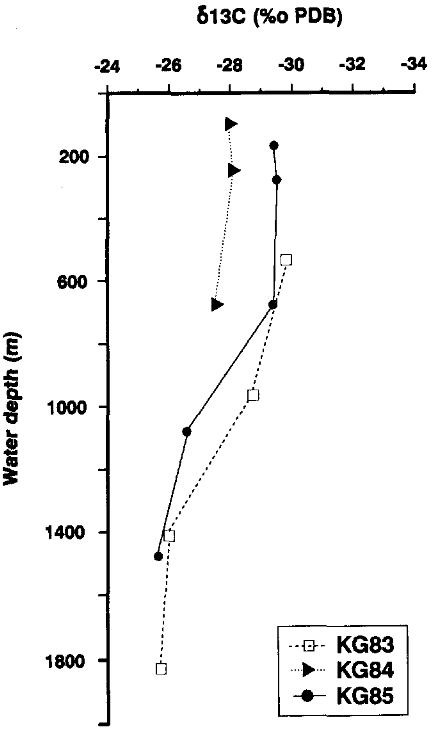


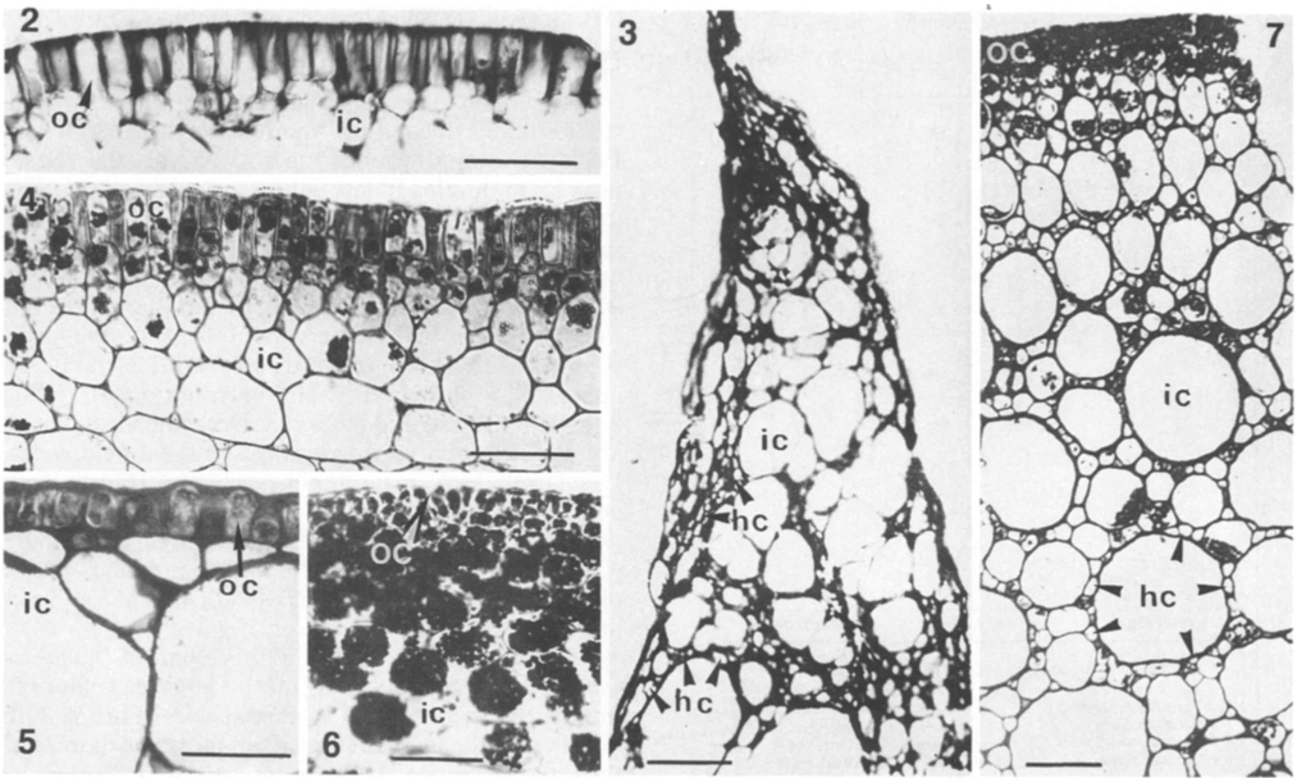
Fig. 1. $\delta^{13}C$ values of particulate organic matter sampled by sediment traps in the King George Basin in November/December 1983, 1984, 1985. For details on the trap system, deployment times etc. see von Bodungen et al. (1987).

(Dieckmann et al. 1985) and a weight of about 15 kg (Zielinski 1981). In Antarctica, the Desmarestiales ecologically replace the Laminariales which dominate in other cold and temperate sublittoral marine floras (Moe and Silva 1977).

The data on the stable carbon isotope composition shown in Table 1 correspond to the average values of macroalgae given by Fry and Sherr (1984). In Fig. 8, the data are plotted versus the depth distribution of the respective species. The depths data were taken from literature and are mostly based on dredging. Therefore there is some uncertainty of the precise depth distribution of these algae, especially for those living in greater depths.

Indirect information concerning the depth distribution of Antarctic macroalgae may be derived from their stable carbon isotope composition. Laboratory experiments indicate a relation between $\delta^{13}C$ values and photon fluence rate (Wiencke and Fischer 1990). In particular, a significant overall trend to more negative values with decreasing irradiance at a constant temperature (0° ± 1°C) and decreasing specific growth rate was shown. Possible reasons for strong isotope vartiations of up to 20‰ observed for some species due to different light supply are discussed in detail by Wiencke and Fischer (1990).

As shown in Fig. 8, it appears to be a relation between the $\delta^{13}C$ values of the Antarctic macroalgae and their depth distribution. Algae from the supralitoral or intertidal such as *Prasiola crispa*, *Enteromorpha bulbosa* and *Adenocystis utricularis* and algae from the upper sublitoral such as *Iridaea cordata* and *Gigartina skottsbergii* grow under relatively high light conditions and have rather high $\delta^{13}C$ ratios of −17‰. In contrast, algae living in the deeper waters show values around −30‰. This applies especially to *Desmarestia anceps*, *Cystosphaera jacquinotii* and *Plocamium cartilagineum*. These findings correspond to those by Wefer and Killengley (1986) who suggested a light-related isotope fractionation for the calcareous benthic algae *Halimeda incrassata*. A strong light effect on the $\delta^{13}C$ values of the seagrass *Posidonia oceanica* has also been reported by Cooper and DeNiro (1989). They found a mean value for leaves growing in water 5 m deep of −11‰ which declined to a minimum mean value of −16.4‰ at 35 m. The same trend has been observed in the above discussed culture experiments (Wiencke and Fischer 1990).



Figs. 2–7. **2** Semi-thin section of a sample taken from the sediment (1,225 m depth; site 290). The sample is identified as a thallus part of *Desmarestia menziesii* and shows outer (*oc*) and inner cortical cells (*ic*). **3** Semi-thin section of a sample taken from the sediment 823 m depth; site 302) showing a cross section through cortical cells of one of the following species: *Desmarestia anceps*, *D. antarctica*, *D. menziesii* or *Himantothallus grandifolius*. In diameter relatively small hypha-like cells (*hc*) occur among large inner cortical cells (*ic*). **4** Semi-thin cross-section of outer (*oc*) and inner cortical cells (*ic*) of freshly collected *Desmarestia menziesii*. Note the similarity in structure with the sediment sample shown in Fig. 2. **5** Semi-thin cross-section of outer (*oc*) and inner cortical cells (*ic*) of a freshly collected ultimate branchlet of *Desmarestia antarctica*. **6** Semi-thin cross-section of outer (*oc*) and inner cortical cells (*ic*) from the middle part of a freshly collected *Himantothallus grandifolius* blade. In contrast to the outer cortical cells of *Desmarestia menziesii* and *D. antarctica* the outer cortical cells of *H. grandifolius* are isodiametrical. **7** Semi-thin cross-section through a penultimate branch of *Desmarestia anceps* showing outer (*oc*), inner cortical cells (*ic*) and hypha-like cells (*hc*). The outer cortical cells are isodiametrical. Inner cortical cells are somewhat (like the hypha-like cells) elongated longitudinally. Note the similarity in structure with the sediment trap sample shown in Fig. 3. Bars = 50 μm

The isotope ratio of *Himantothallus grandifolius* (Fig. 8) apparently does not correspond to the depth distribution of this algae. But its δ^{13}C value of −20‰ is related to the fact that the plants used for the isotope determination originated from depths of only 6 m and 15 m, respectively, i.e. the upper depth ditribution limit of this species. A δ^{13}C value of −20‰ in this species appears to be typical for this water depth.

In addition to the depth distribution, the period of maximal growth probably influences the isotopic composition of macroalgae. *Palmaria decipiens* grows very rapidly in early spring under favourable light supply (Gain 1912). In culture, high specific growth rates under elevated irradiance resulted in high δ^{13}C values of −13‰ to −16‰ (Wiencke and Fischer 1990) comparable to the value of −10‰ for the plant collected in Antarctica (Table 1). In *Adenocystis utricularis*, one may speculate that the low values found in the lower part of the thallus result from growth in late winter and early spring, whereas the higher values in the middle and top thallus part correspond to the period of optimum growth in summer (Table 1; Wiencke 1990a).

These interpretations are not effected by the status of the algal tissue as no or only small differences between fresh and partly decomposed thalli were detected (Table 1). However, one has to keep in mind that the ideas discussed here are based mostly on drift material and have to be strengthened by measurements of in situ collected samples from different water depths during different times of the year.

The observed changes in the isotopic composition of particles collected with sediment traps from different trap levels (Fig. 1) are due to different carbon sources. The isotopic composition of surface water phytoplankton is discussed in detail by Fischer (1991). Phytodetritus from upper sediment trap samples (180–700 m) had rather low values close to −29.5‰ (Fig. 1). In the deeper waters of the basin (below 1,000 m), a distinct change to more positive values (maximum value −26‰) occurred which is attributed to lateral influx of benthic macroalgae. This

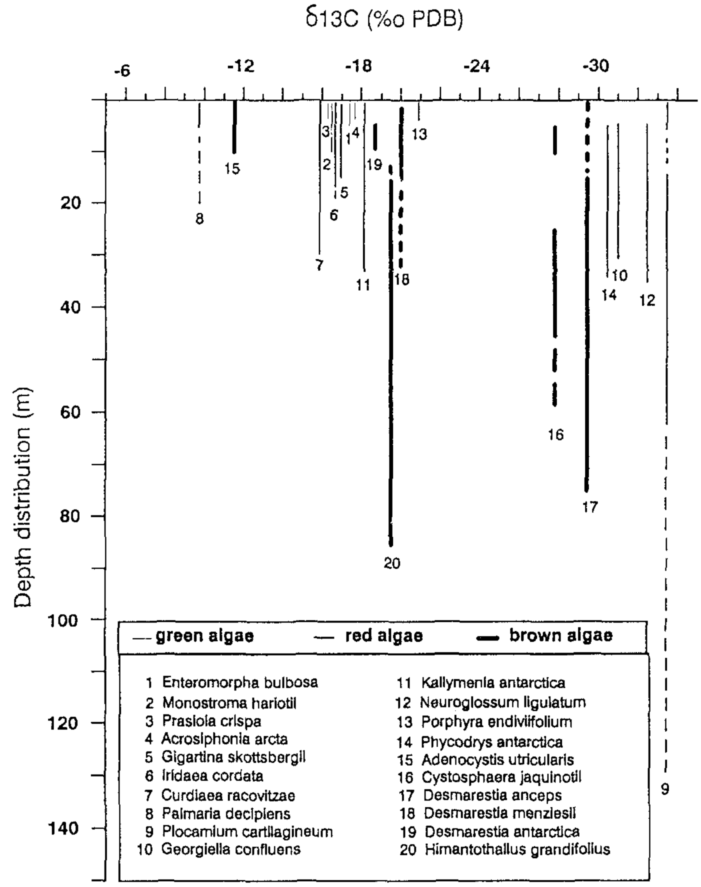


Fig. 8. Mean $\delta^{13}C$ values of macroalgae collected in Antarctica in relation to their depth distribution. Depth informations were taken from Lamb and Zimmermann (1975), DeLaca and Lipps (1976), Zielinski (1981), Moe and Silva (1983) and Moe and Silva (1988) (—— occurring frequently; - - - occurring infrequently)

assumption is supported by our microscopical observations on sediment trap material, showing Desmarestialean fragments of 10–20 μm size (Table 1).

The above interpretation is strengthened by the opal/C_{org} ratios of the sediment trap particulates. Under the assumption that the opal fluxes were relatively constant in the water column, the much lower ratios below 1,000 m (Fischer 1989) indicate a second carbon source, probably from the near-by shelf areas. The erosion of benthic macroalgae and their transport to the deeper basins and to the sediment are discussed below. Using a mean value of $-22‰$ for members of the Desmarestiales, $-29.5‰$ for phytodetritus in the upper 700 m, and $-26.5‰$ for the organic detritus below 1,000 m (Fig. 1; KG85), the lateral input of macroalgal carbon is very high. Investigations on the chemical composition of the sedimented organic material by Liebezeit and von Bodungen (1987) also indicated a very high macroalgal input (71%) during November and December.

Information on the seasonal carbon influx from benthic macroalgae is provided by time-series sediment traps deployed for one-year periods in the King George Basin (Wefer et al. 1990). The seasonal stable carbon isotope distributions lead to the assumption that the macroalgal influx mostly occurs during the spring and summer season (Fischer 1989). These findings are supported by culture studies under fluctuating Antarctic daylengths (Wiencke 1990a) showing young macrothalli of the Desmarestiales to develop in late winter with a growth optimum from September to November or December. This type of seasonal development correlates with the seasonal frequency of brown algae in drift material at Admiralty Bay (King George Island, South Shetland Islands; Zielinski 1981): whereas in October about 85% of the drift is composed of brown seaweeds this value is reduced to approx. 22% in February. However, not only large algal fragments are lost into the water. Decaying algal parts are also derived from very early stages in the development of Desmarestialean macrothalli such as *Himantothallus grandifolius* (Wiencke and Clayton 1990), *Desmarestia antarctica* (Wiencke et al. 1991) and *Phaeurus antarcticus* (Clayton and Wiencke 1990). Similar processes are also observed in culture in *D. anceps* and *D. menziesii* (Wiencke, unpublished).

The sediment sample in Fig. 2 is a part of *Desmarestia menziesii* due to its strong morphological similarity to freshly collected sample of this species (Fig. 3). Other members of the Desmarestiales can be excluded mostly as their outer cortical cells do not show a palisade-like structure in cross section (Figs. 5–7). The only exception from this rule are the cylindrical sporangia of *D. antarctica* (Moe and Silva 1989; Wiencke et al. 1991), *D. anceps* (Moe and Silva 1981) and *H. grandifolius* (Moe and Silva 1983; Wiencke and Clayton 1990). They are borne terminally on one or two celled stalks and occur interspersed with two to four-celled paraphyses, a cortex structure different from that of the sample shown in Fig. 2.

The sample shown in Fig. 3 is a part of either *Desmarestia anceps*, *D. antarctica* or *Himantothallus grandifolius* by reason of a tissue architecture similar to those species. It should, however, be noted that the cell pattern also resembles that of *Phaeurus antarcticus*, another Antarctic member of the Desmarestiales (Clayton and Wiencke 1990). But due to the small cell sizes found in *P. antarcticus* this species can be excluded.

Finally, possible mechanisms and processes for the erosion of benthic algae and their transport to the deeper waters are summarized:

- erosion due to waves, tidal waves and storms (deLaca and Lipps 1976; Tegner and Dayton 1987)
- erosion due to the occurrence of sea-ice on the coast (Moe and deLaca 1976; Neushul 1965)
- mechanical erosion due to floating icebergs (Zielinski 1981; Heine 1989)
- microbial decay of filamentous parts from juvenile stages of members of the Desmarestiales during early spring/summer (Wiencke and Clayton 1990; Clayton and Wiencke 1990; Wiencke et al. 1991)
- maceration by grazers such as amphipods (Reichardt and Dieckmann 1985)
- transport of fragments washed ashore by waves and wind (Zielinski 1981)

- transport of detritus by wind to the sea (Zielinski 1981)
- transport of thalli or detritus by sea-ice and icebergs to the open ocean (Skottsberg and Neushul 1960; Neushul 1965)
- downslope transport of detritus in suspension (Reichardt 1987)
- transport due to strong currents and turbidity currents (Anikouchine and Ling 1967)

In conclusion, we hypothesize that the stable carbon isotope ratios of Antarctic macroalgae are related to their depth distribution (i.e. light environment) and that macroalgae contribute to the organic carbon pool in certain regions of the Antarctic seafloor. However, further studies will be required to substantiate our statements.

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