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Fatty acid composition of Arctic and Antarctic macroalgae: indicator of phylogenetic and trophic relationships

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ABSTRACT: The fatty acid composition of 6 Arctic and 14 Antarctic macroalgae species (Rhodophyta, Phaeophyta and Chlorophyta) from Kongsfjorden (west Spitsbergen, Arctic) and King George Island (Antarctic Peninsula) was investigated. The macroalgae were cultivated in nutrient-enriched seawater at low temperatures (0 to 5°C) and light conditions similar to natural irradiance. The most abundant fatty acids in the Arctic and Antarctic Rhodophyta were generally 20:5(n-3) and 16:0. The Arctic *Palmaria palmata* and the Antarctic *Audouinella purpurea* were characterised by very high proportions of 20:5(n-3) (67.3 and 60.3%, respectively). Other important fatty acids were 16:1(n-7) and 20:4(n-6). Two species were dominated by 20:4(n-6) (*Phycodrys rubens*, 35.3% and *Delesseria lancifolia*, 31.1%). In *Ptilota gunneri* and *Rhodymenia subantarctica*, 16:1(n-7) accounted for 39.9 and 32.7%, respectively. In the Phaeophyta, the major polyunsaturated fatty acids were 18:4(n-3), 20:5(n-3) and 20:4(n-6) followed by 18:3(n-3) and 18:2(n-6). The principal saturated fatty acid was 16:0. A high percentage of the uncommon monounsaturated fatty acid 16:1(n-5) (11.1%) was found in *Desmarestia muelleri* sporophytes. Their gametophytes exhibited only traces of this component, but instead had double the amount of 18:2(n-6) and 18:3(n-3). The Arctic chlorophyte *Prasiola crispa* and the Antarctic *Lambia antarctica* had fatty acid compositions dominated by the polyunsaturated fatty acids 18:3(n-3) and 18:2(n-6). In *L. antarctica*, 18:1(n-7) was present at higher levels than 18:2(n-6). The clear differences in fatty acid compositions of these 3 taxa are probably due to their different evolutionary position. The high proportions of 20:5(n-3) in the Rhodophyta reflect a 'marine'-like character and hence the phylogenetically oldest lineage. The Chlorophyta comprise the most 'modern' group and this is supported by primarily C_{18} unsaturated fatty acids typical of the vegetative tissue of higher plants. The fatty acid composition of the Phaeophyta support their intermediate position. The clear differences between the macroalgal taxa, and also variations between species, make fatty acids a potential tracer for studies of food-web interactions.

KEY WORDS: Macroalgae · Arctic · Antarctic · Fatty acids · Polyunsaturates · Biosynthesis

INTRODUCTION

Although they are restricted to continental shelves and coastal areas, benthic macroalgae play an important role in marine primary production. They serve as a food source for herbivores and detritivores, as well as nursery areas for fishes, crustaceans and other invertebrates (Smith 1981, Duggins et al. 1989). While these ecological functions are well-documented for temperate and tropical waters (Gaines & Lubchenco 1982, Hawkins & Hartnoll 1983), appropriate studies for polar regions are still rare (Iken et al. 1997, Iken 1999).

As reported for temperate and tropical habitats, the macrophytobenthos in the Antarctic often serves as a hard substratum for numerous, mainly sessile, organisms

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supporting the development of complex benthic communities (Klöser et al. 1996). Some of the few observations on the trophodynamics of Antarctic macroalgal forests demonstrate a high abundance of herbivores grazing directly on the plants. A small number of predators such as fishes hunt for vagile invertebrates associated with macroalgae and for sessile animals (Amsler et al. 1998, Iken 1999). These studies indicate manifold ecological interactions between the underwater flora and fauna in Antarctica, but little information is available, for example, on the fate of benthic primary production and on the trophic relationships (Iken et al. 1997, Iken 1999, Graeve et al. 2001). While few ecological investigations have been carried out in Antarctic waters, similar data on trophic relationships of Arctic macroalgae are lacking.

In recent years, various studies on the ecological interactions within the Arctic and Antarctic pelagic food web have successfully used fatty acids as trophic markers to answer the question 'Who is feeding on whom?' (e.g. Graeve et al. 1994a,b, 1997, Phleger et al. 1998, Nelson et al. 2000, 2001). Some data on the fatty acid composition of macroalgae from temperate and tropical waters have also been reported (Arao & Yamada 1989, Aknin et al. 1992, Banaimoon 1992, Jones & Harwood 1992, Khotimchenko 1998), although similar information on polar species are not available.

Here we determined, for the first time, the fatty acid composition of macroalgae from Antarctic and Arctic waters, to identify specific fatty acids characteristic for different macroalgal taxa and even species. For the first time, fatty acids have been used to reveal ther potential for the identification of phylogenetic relationships. These basic data could serve as trophic markers in studies on polar plant-herbivore interactions.

MATERIALS AND METHODS

Algal material. The locations of and ecological information on the macroalgal species studied are pre-

Table 1. Location and habitat of the investigated Arctic and Antarctic macroalgae. E: endemic; –: not endemic

Species	Arctic/Antarctic	Habitat (depth)	Origin
Rhodophyta			
Ceramiales			
Delesseria lancifolia (J. D. Hooker) J. Agardh	Ant	Sublittoral (5–30 m)	–
Georgiella confluens (Reinsch) Kylin	Ant	Sublittoral (5–25 m)	E
Myriogramme smithii (J. D. Hooker et Harvey) Kylin	Ant	Sublittoral (8–45 m)	–
Neuroglossum ligulatum (Reinsch) Skottsberg	Ant	Sublittoral (0–10 m)	E
Pantoneura plocamioides Kylin & Skottsberg	Ant	Sublittoral (2–45 m)	E
Phycodrys rubens (Linnaeus) Batters	Arc	Sublittoral (12–18 m)	E
Ptilota gunneri Silva, Maggs & L. M. Irvine	Arc	sublittoral (12–15 m)	–
Palmariales			
Devaleraea ramentacea (Linnaeus) Guiry	Arc	Eulittoral to sublittoral (0–7 m)	E
Palmaria decipiens (Reinsch) Ricker	Ant	Eulittoral to sublittoral (0–30 m)	E
Palmaria palmata (Linnaeus) Greville	Arc	Sublittoral (2–10 m)	–
Gigartinales			
Gigartina skottsbergii Setchell & Gardner	Ant	Tide pools, sublittoral (0–30 m)	–
Gymnogongrus turquetii Hariot	Ant	Eulittoral, sublittoral (0–30 m)	–
Acrochaetiales			
A*udouinella purpurea* (Lightfoot) Woelkerling	Ant	Eulittoral, sublittoral	–
Rhodymeniales			
Hymenocladiopsis crustigena Moe	Ant	Sublittoral (2–30 m)	E
Rhodymenia subantarctica Ricker	Ant	Sublittoral (5–25 m)	–
Phaeophyta			
Desmarestiales			
Desmarestia antarctica Moe & Silva	Ant	Sublittoral (2–20 m)	E
Desmarestia muelleri Ramirez & Peters	sub-Ant	Sublittoral (2–20 m)	–
Laminariales			
Laminaria solidungula J. Agardh	Arc	Sublittoral (12–18 m)	E
Chlorophyta			
Halimedales			
Lambia antarctica (Skottsberg) Delépine	Ant	Eulittoral, tide pools	E
Prasiolales			
Prasiola crispa (Lightfoot) Kützing	Arc	Supralittoral	–

sented in Table 1. Macroalgal material was collected in Kongsfjorden (Ny-Ålesund, Spitsbergen, Arctic, 78° 56′ N, 11° 56′ E) between 1996 and 1998, and on King George Island, Antarctica (62° 12′ S, 58° 58′ W), between 1986 and 1994. In the laboratory at Bremerhaven, macroalgae were cultivated at 0 to 5°C in 1 to 5 l glass beakers containing aerated membrane-filtered North Sea water (Sartorius Sartobran II, 0.2 µm) enriched with Provasoli's ES nutrients (Provasoli 1968). The media were replaced every 2 wk to avoid nutrient limitation. The cultures were illuminated with cool-white fluorescent neon tubes (Osram L58/W19) at photon fluence rates of 20 to 50 µmol photons m^{-2} s^{-1} (Wiencke 1990).

All Rhodophyta samples were from tetrasporophytic plants. For the Phaeophyta, *Laminaria solidungula* samples were taken from young, mid-aged and old sporophytic tissues, and sporophytes and gametophytes were analysed from *Desmarestia muelleri*. As the life histories of the studied chlorophytes were unknown, the samples could not be further specified.

Fatty acid analysis. Samples were analysed in duplicate or triplicate. The macroalgal tissues were homogenised and extracted in dichloromethane/methanol (2:1; v:v) according to Folch et al. (1957). For gas liquid chromatographic analysis of the fatty acid composition, aliquots of the extracted samples were taken. Methyl esters of the fatty acids were prepared by transesterification with 3% concentrated sulphuric acid in methanol for 4 h at 80°C. After their extraction with hexane, their composition was analysed with a Chrompack gas liquid chromatograph (Chrompack 9000) on a capillary column (30 m × 0.25 mm; film thickness: 0.25 µm; liquid phase: DB-FFAP) using temperature programming according to the method of Kattner & Fricke (1986). Fatty acids were identified with commercially available standard mixtures and also by using a HP 5973 GC-MSD-System. Averaged data of the individual fatty acids are expressed as a mass percentage of total fatty acids.

RESULTS

Rhodophyta

The fatty acid composition of the Arctic and Antarctic Rhodophyta are summarised in Tables 2 & 3. The individual species belong to 5 orders. All species were dominated by only a few fatty acids. They were all rich in 16:0 (16.9 to 37.7%), and most of the species were also rich in 20:5(n-3) (24.2 to 67.3%). Extraordinarily high levels of 20:5(n-3) were determined in the Arctic *Palmaria palmata* (Palmariales) (67.3%) and the Ant-

Table 2. Fatty acid composition (mass %) of Arctic (Arc) and Antarctic (Ant) Rhodophyta (Ceramiales). SAFA: sum of saturated fatty acids; MUFA: sum of monounsaturated fatty acids; PUFA: sum of polyunsaturated fatty acids; –: not detected

Fatty acids	*Phycodrys rubens* (Arc)	*Ptilota gunneri* (Arc)	*Delesseria lancifolia* (Ant)	*Georgiella confluens* (Ant)	*Myriogramme smithii* (Ant)	*Neuroglossum ligulatum* (Ant)	*Pantoneura plocamioides* (Ant)
14:0	3.4	4.9	3.3	2.7	1.3	2.4	1.0
15:0	0.5	0.4	0.5	–	0.2	0.2	0.6
16:0	28.0	27.9	37.7	16.9	27.5	27.8	33.7
16:1(n-7)	17.9	39.9	13.5	10.6	0.6	6.5	1.7
16:1(n-5)	0.4	0.3	–	–	–	–	2.5
16:2(n-4)	0.3	1.0	–	3.2	–	–	–
16:3(n-4)	0.5	0.6	–	5.9	–	–	–
16:4(n-1)	0.7	0.7	–	5.0	–	0.6	13.1
18:0	0.6	1.1	0.8	–	0.3	0.3	–
18:1(n-9)	3.6	5.3	5.3	3.2	1.4	4.3	5.7
18:1(n-7)	3.2	2.0	2.2	3.9	5.6	11.6	2.6
18:2(n-6)	0.5	2.6	0.3	0.7	1.7	1.7	0.6
18:3(n-3)	–	0.4	–	1.2	–	–	–
18:4(n-3)	–	1.9	–	2.6	–	–	–
20:4(n-6)	35.3	0.9	31.1	1.9	13.0	7.7	12.6
20:4(n-3)	–	–	–	–	–	–	–
20:5(n-3)	4.8	9.4	4.4	40.9	48.3	35.3	25.9
22:6(n-3)	0.3	0.6	1.0	1.3	–	1.5	–
SAFA	31.9	33.2	41.6	19.7	29.1	30.4	35.3
MUFA	25.1	47.5	20.9	17.7	7.6	22.4	12.6
PUFA	42.4	18.1	36.8	62.6	63.0	46.8	52.2
(n-6) FA	35.8	3.5	31.4	2.6	14.7	9.4	13.2
(n-3) FA	5.1	12.3	5.4	46.0	48.3	36.8	25.9
(n-3)/(n-6)	0.1	3.5	0.2	17.6	3.3	3.9	2.0

Table 3. Fatty acid composition (mass %) of Arctic (Arc) and Antarctic (Ant) Rhodophyta. SAFA: sum of saturated fatty acids; MUFA: sum of monounsaturated fatty acids; PUFA: sum of polyunsaturated fatty acids; – not detected

Fatty acids	Palmariales			Gigartinales		Acrochaetiales	Rhodymeniales	
	Devaleraea ramentacea (Arc)	*Palmaria palmata* (Arc)	*Palmaria decipiens* (Ant)	*Gymnogongrus turquetii* (Ant)	*Gigartina skottsbergii* (Ant)	*Audouinella purpurea* (Ant)	*Rhodymenia subantarctica* (Ant)	*Hymenocladiopsis crustigena* (Ant)
14:0	9.8	5.7	9.4	1.9	2.2	1.5	7.5	3.5
15:0	0.6	–	0.5	0.2	0.4	–	–	0.5
16:0	25.5	19.4	20.9	29.4	28.4	23.6	20.5	30.4
16:1(n-7)	9.0	0.3	2.8	3.1	5.5	0.9	32.7	4.4
16:1(n-5)	–	–	–	–	–	–	–	0.3
16:2(n-4)	0.4	–	–	–	0.4	–	1.8	0.6
16:3(n-4)	–	–	–	0.1	0.5	–	–	0.5
16:4(n-1)	0.4	–	–	–	0.5	–	0.7	1.4
18:0	1.1	0.4	0.9	0.5	0.8	–	1.6	0.6
18:1(n-9)	7.5	2.1	7.0	3.3	10.7	2.0	12.5	3.9
18:1(n-7)	3.1	3.2	4.8	1.5	2.5	1.6	4.8	1.7
18:2(n-6)	3.4	0.5	0.4	3.6	0.7	0.6	0.9	3.4
18:3(n-3)	4.1	–	0.2	–	–	–	1.1	0.8
18:4(n-3)	6.7	–	0.4	–	–	–	4.1	1.8
20:4(n-6)	1.9	1.1	2.2	11.5	22.2	9.4	1.0	8.5
20:4(n-3)	0.6	–	–	–	–	–	–	–
20:5(n-3)	24.2	67.3	49.8	44.3	25.2	60.3	10.8	37.3
22:6(n-3)	1.6	–	0.7	0.5	–	–	–	0.5
SAFA	35.9	25.1	30.7	31.5	31.0	25.1	28.0	34.3
MUFA	19.5	5.6	14.7	8.0	18.7	4.5	50.0	10.3
PUFA	43.3	68.9	53.7	60.0	49.4	70.4	20.4	54.8
(n-6) FA	5.3	1.6	2.6	15.1	22.9	10.1	1.9	11.9
(n-3) FA	37.2	67.3	51.1	44.8	25.2	60.3	15.9	40.3
(n-3)/(n-6)	7.0	42.2	19.9	3.0	1.1	6.0	8.3	3.4

arctic *Audouinella purpurea* (Acrochaetiales) (60.3%). Low percentages of 20:5(n-3) were found in the Antarctic *Rhodymenia subantarctica* and in 3 species of the order Ceramiales (2 species were from the Arctic [*Phycodrys rubens* and *Ptilota gunneri*] and 1 was from Antarctica [*Delesseria lancifolia*]). These 4 species were richer in 16:1(n-7), with the highest levels of 39.9% in *P. gunneri* and 32.7% in *R. subantarctica*. The fatty acid compositions of the 2 species with lower levels of 20:5(n-3) and 16:1(n-7) were dominated by 20:4(n-6), which accounted for 35.3% in the Arctic *Phycodrys rubens* and 31.1% in the Antarctic *D. lancifolia*, both belonging to the order Ceramiales. A higher percentage of 20:4(n-6) was also found in *Gigartina skottsbergii* [22.2%: similar to the percentage of 20:5(n-3)]. A special feature of the Antarctic *Pantoneura plocamioides* was the high level of 16:4(n-1). Generalising, mainly 4 major fatty acids were detected in the Rhodophyta: 16:0, 20:5(n-3), 16:1(n-7) and 20:4(n-6). In addition, the fatty acids 14:0, 18:1(n-9), 18:1(n-7) and 18:4(n-3) were found in proportions of 5 to 10%. The ratios of the sums of the (n-3) and (n-6) fatty acids [i.e. (n-3) and (n-6) families] covered a wide range. The ratio of the 20:5(n-3)-dominated species varied between 3 and 42.2, whereas those species with a major contribution of 20:4(n-6) had ratios between 0.1 and 1.1.

Phaeophyta

The fatty acid composition of the Arctic and Antarctic Phaeophyta are presented in Table 4. The major fatty acids were 20:5(n-3) (20% on average) and 18:4(n-3) (19%), followed by 16:0 (13%) and 18:3(n-3) (13%). The fatty acids 18:2(n-6), 18:1(n-9) and 14:0 varied between 4 and 10%. The fatty acids 20:4(n-6) and 16:1(n-7), which exhibited high levels in some Rhodophyta species, occurred only in small amounts in the Phaeophyta. The fatty acids 16:0 and 20:5(n-3) were also less dominant compared to most of the Rhodophyta species. The ratios of the (n-3) and (n-6) fatty acid families were 2.1 to 4.0, reflecting the dominance of 20:5(n-3) and 18:4(n-3). The comparison of young, mid-aged and old sporophytic tissue of the Arctic *Laminaria solidungula* showed a similar percentage for most fatty acids except 18:4(n-3), the relative abundance of which decreased with age and was mostly compensated by an increase in 20:5(n-3) (Table 4).

The sporophytes and gametophytes of the Antarctic *Desmarestia muelleri* exhibited almost similar fatty acid composition, but some conspicuous differences were found. Sporophytes contained 11.1% of 16:1 (n-5), but gametophytes contained only trace amounts

Table 4. Fatty acid composition (mass %) of Arctic (Arc) and Antarctic (Ant) Phaeophyta and Chlorophyta. SAFA: sum of saturated fatty acids; MUFA: sum of monounsaturated fatty acids; PUFA: sum of polyunsaturated fatty acids; –: not detected

Fatty acids	Phaeophyta						Chlorophyta	
	Laminariales			Desmarestiales			Halimedales	Prasiolales
	Laminaria solidungula (Arc)			*Desmarestia muelleri* (Ant)		*Desmarestia antarctica* (Ant)	*Lambia antarctica* (Ant)	*Prasiola crispa* (Arc)
	Young	Mid	Old	Sporophytes	Gametophytes	Sporophytes		
14:0	5.3	6.3	5.2	5.9	3.7	4.8	5.0	1.5
15:0	–	0.2	0.6	–	0.1	0.1	0.1	–
16:0	12.4	12.1	15.5	11.3	12.5	11.5	19.8	28.6
16:1(n-7)	0.9	0.9	2.3	0.9	0.7	0.6	0.6	1.5
16:1(n-5)	–	–	–	11.1	0.5	1.6	–	–
16:2(n-4)	–	–	–	–	0.1	–	–	–
16:3(n-4)	–	–	–	–	–	–	–	–
16:4(n-1)	–	–	–	–	–	0.1	–	–
18:0	–	0.2	0.3	0.3	0.5	0.1	0.7	0.1
18:1(n-9)	5.3	4.8	5.1	6.7	4.7	7.0	10.7	1.7
18:1(n-7)	–	–	0.7	0.5	0.3	0.1	2.1	20.9
18:2(n-6)	7.3	8.8	5.7	5.2	10.1	3.6	22.3	6.3
18:3(n-3)	9.8	10.5	11.3	11.4	24.8	8.0	23.7	26.1
18:4(n-3)	26.8	23.7	15.7	13.3	13.4	21.2	2.8	2.1
20:4(n-6)	10.8	12.5	8.1	10.4	14.6	14.6	5.2	2.4
20:4(n-3)	1.1	1.2	3.0	1.2	0.7	0.7	0.7	0.4
20:5(n-3)	19.3	17.6	25.0	21.8	13.2	25.4	5.0	8.4
22:6(n-3)	–	–	–	–	–	–	0.9	–
SAFA	17.7	18.6	21.2	17.2	16.3	16.4	24.9	30.1
MUFA	6.2	5.7	8.1	19.2	6.3	9.3	13.5	24.1
PUFA	75.1	74.3	68.6	63.3	76.9	74.3	60.8	45.7
(n-6) FA	18.1	21.3	13.7	15.6	24.7	18.2	27.6	8.7
(n-3) FA	57.0	53.0	54.9	47.7	52.1	55.2	33.3	37.1
(n-3)/(n-6)	3.2	2.5	4.0	3.1	2.1	3.0	1.2	4.3

(0.5%). The percentage of 18:2(n-6) and 18:3(n-3) were 2 times higher in the gametophytes (10.1 and 24.8%, respectively) than in the sporophytic plants. The latter contained 22.8% of 20:5(n-3), whereas gametophytes contained only 13.2%. The fatty acid composition of sporophytes of *D. muelleri* and *D. antarctica* were similar, except for 16:1(n-5), which was low in *D. antarctica* (Table 4).

Chlorophyta

The major fatty acids of the 2 Chlorophyta, *Prasiola crispa* from the Arctic and *Lambia antarctica* from Antarctica were 18:3(n-3) (23.7 and 26.1%, respectively) and 16:0 (19.8 and 28.6%) in both species. In *P. crispa*, 18:2(n-6) was of similar abundance with 22.3%, whereas in *L. antarctica* 18:1(n-7) accounted for 20.9%. The (n-3) to (n-6) ratios were low (1.2 and 4.3: Table 4). In the Phaeophyta and Rhodophyta these C_{18} unsaturated fatty acids represented less than 10% on average or were only minor components. The high proportion of C_{18} polyunsaturates in the Chlorophyta was unique for all macroalgae studied.

DISCUSSION

The amount of polyunsaturated fatty acids in marine macroalgae from Arctic and Antarctic regions was extremely high, in some cases 60 to 80% of the total fatty acids. These levels are much higher than those reported for macroalgae from lower latitudes (Khotimchenko & Vaskovsky 1990, Aknin et al. 1992, Banaimoon 1992, Fleurence et al. 1994, Khotimchenko 1998). The principal unsaturated fatty acids were C_{18} and C_{20} polyunsaturates, whereas C_{22} polyunsaturates, which are abundant in many phytoplankton species (e.g. Harrington et al. 1970), were only trace components or even nonexistent in the macroalgae.

Within the main taxonomic classes, Rhodophyta, Phaeophyta and Chlorophyta, we found clear differences in the fatty acid composition. The major polyunsaturated fatty acids of the Rhodophyta were 20:5(n-3) and partly 20:4(n-6), and those of the Phaeophyta 20:5(n-3) and 18:4(n-3), while 18:3(n-3) was dominant in the Chlorophyta. These results correspond well with the fatty acid composition of macroalgae from temperate and tropical regions (Khotimchenko & Vaskovsky 1990, Banaimoon 1992, Fleurence et al. 1994). In the

Rhodophyta from Arctic and Antarctic regions we found some exceptions from the general fatty acid composition of this class. Although 20:5(n-3) is a major component in many Rhodophyta (Banaimoon 1992, Fleurence et al. 1994), the values (50 to 70%) found in *Palmaria palmata*, *Audouinella purpurea*, *Palmaria decipiens* and *Myriogramme smithii* were extremely high. The Arctic *Phycodrys rubens* and the Antarctic *Delesseria lancifolia* contained exceptionally high levels of 20:4(n-6) (>30%), whereas Rhodophyta from other regions contain only 2 to 15% of this fatty acid (Khotimchenko & Vaskovsky 1990). Some Arctic and Antarctic species were also rich in 16:1(n-7), a component that usually contributes only 0.3 to 4% of the total fatty acids in red macroalgae (Fleurence et al. 1994). In addition, the elevated occurrence of 16:4(n-1) in 2 Antarctic Rhodophyta, particularly in *Pantoneura plocamioides* (13.1%), is striking, since this fatty acid is missing from temperate and tropical taxa (Arao & Yamada 1989, Khotimchenko & Vaskovsky 1990, Banaimoon 1992, Fleurence et al. 1994).

There were also considerable differences in the fatty acid composition of the closely related Arctic species *Phycodrys rubens* and *Ptilota gunneri*, which often grow in close association at depths of <12 m the in Arctic Kongsfjord. The predominant fatty acid in *P. rubens* was 20:4(n-6) and in *P. gunneri* 16:1(n-7). Clear compositional differences were also found between the Arctic Palmariales *Devaleraea ramentacea* and *Palmaria palmata*, also growing at similar locations in shallow waters of the Kongsfjord. We therefore conclude that these conspicuous differences in fatty acid compositions between species within the same order and growing in the same habitat are species-specific rather than being related to environmental factors or depth distribution. Thus, it seems possible to distinguish closely related Rhodophyta species by their fatty acid composition.

Despite their different distribution, the Phaeophyta from the Arctic, Antarctica and sub-Antarctica had a similar fatty acid composition, dominated by 18:4(n-3), 20:5(n-3) and 20:4(n-6). The same fatty acids, but in varying proportions, have been determined in many species of this class from other regions (Fleurence et al. 1994, Khotimchenko 1995b, 1998, Herbreteau et al. 1997). In addition, the gametophytes of *Desmarestia muelleri* had high amounts of 18:3(n-3), whereas the sporophytes were characterised by a considerable proportion of 16:1(n-5). In contrast, sporophytes of *D. antarctica* had only low levels of this fatty acid. 16:1(n-5) is considered an uncommon fatty acid in macroalgae, although it occurs in small amounts of 3% in the closely related *Desmarestia ligulata* from temperate waters, and in amounts up to 14% in *Dictyota ciliata* from the tropics (Aknin et al. 1992, Khotimchenko 1995b, 1998). This is the first report of such striking biochemical differences in the fatty acid composition of different life-history stages of one macroalgal species.

The fatty acid composition of macroalgae is known to be influenced by environmental factors such as light intensity, salinity and temperature (Levy et al. 1992, Floreto & Teshima 1998). Ecophysiological parameters, such as sensitivity of photosynthetic performance under light stress, or pigment content, also differ significantly between gametophytes and sporophytes of *Laminaria saccharina* (Hanelt et al. 1997) and *Desmarestia menziesii* (Gómez & Wiencke 1996). The different fatty acid content of sporophytes and gametophytes of *D. muelleri* is another example of different metabolic characteristics at different life history stages.

The fatty acid composition of the Arctic Chlorophyta *Prasiola crispa* and the Antarctic *Lambia antarctica* differed significantly from that of the other taxa in their high abundance of C_{18} unsaturated fatty acids and relatively low levels of 20:5(n-3). The fatty acid composition found here corresponds to the composition of temperate and tropical Chlorophyta (Banaimoon 1992, Herbreteau et al. 1997), but their proportions are clearly different. The chlorophytes of the genus *Caulerpa*, and the species *Enteromorpha intestinalis* and *Ulva rotundata* (Fleurence et al. 1994, Khotimchenko 1995a), contain lower proportions of 18:1(n-7) than *L. antarctica*, and the proportions in *P. crispa* are also low. In addition, *P. crispa* has higher levels of the fatty acid 18:2(n-6) than *L. antarctica* and the other Chlorophyta. The data for these quantitative differences are probably too fragmentary to distinguish between polar Chlorophyta or between polar species and species from other regions on the basis of fatty acids.

The reason for the distinct differences in fatty acid composition between the 3 taxa Rhodophyta, Phaeophyta and Chlorophyta may be their different evolution. There has been a tendency over the past 30 yr to consider Rhodophyta as the most 'primitive' eukaryotes (Taylor 1978) because of the presence of phycobiliprotein pigments and their arrangement in phycobilisomes, which are typical features of ancient cyanobacteria. Chlorophyta are undoubtedly the closest relatives of higher plants, and hence the most 'modern' macroalgae. The Phaeophyta were thought to have a phylogenetic position between Rhodophyta and Chlorophyta. However, modern molecular approaches indicate a closer relationship between Rhodophyta and Chlorophyta (van den Hoek et al. 1995). Although the phylogenetic relationship between Rhodophyta, Phaeophyta and Chlorophyta is still under debate, the data presented here point to taxa-specific biosynthetic pathways for fatty acids (Fig. 1) that may help to clarify the open questions.

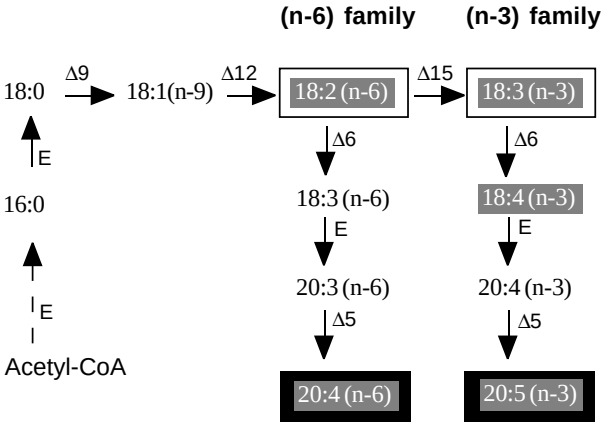

Fig. 1. Major pathways and accumulation of polyunsaturated fatty acids in plants (Gurr & Harwood 1991). Grey: Rhodophyta; black: Phaeophyta; white: Chlorophyta; E: elongation; Δ: desaturases

Rhodophyta and Phaeophyta exhibit the highest amounts of the C_{20} polyunsaturated fatty acids, and Rhodophyta the highest proportions of 20:5(n-3) and partially of 20:4(n-6). We therefore conclude that their presence reflect a more 'marine'-like and hence more ancestral character. This hypothesis is well supported by the fact that, according to fossil records and molecular data, Rhodophyta are the phylogenetically oldest lineage within the macroalgae (van den Hoek et al. 1995). In the Phaeophyta, the fatty acid 18:4(n-3) is as dominant as 20:5(n-3), supporting the intermediate position of this taxon between Rhodophyta and Chlorophyta. It is noteworthy that the intermediate products, 20:3(n-6) and 20:4(n-3), which result from chain elongation, are only minor components or are lacking. They are immediately converted by the delta-5 desaturase to the major end products (Fig. 1). In contrast to Rhodophyta and Phaeophyta, Chlorophyta contain primarily C_{18} unsaturated fatty acids typical of vegetative tissue of higher plants. In Rhodophyta and Phaeophyta, competition between fatty acids of the (n-6) and (n-3) family may occur. As 18:3(n-3) represents the better substrate for the delta-6 desaturase than 18:2(n-6), it can therefore effectively decrease the formation of 20:4(n-6) from 18:2(n-6) (Cook 1991), resulting in higher proportions of 20:5(n-3). Chlorophyta probably lost the general ability to convert C_{18} polyunsaturated fatty acids to C_{20} polyunsaturated fatty acids during evolution to avoid competition between (n-6) and (n-3) fatty acids. This reduction may be regarded as an 'advanced' phylogenetic character.

Comparing the Arctic and Antarctic marcoalgae we found no unequivocal differences in their fatty acid composition, although both regions differ markedly in their cold-water history. While continental glaciation in the Arctic started in the Pliocene 3 to 5 Ma, in Antarctica the first glaciers at sea level appeared in the Oligocene 14 Ma (reviewed by Lüning 1990). In addition, specific oceanographic conditions cause a more pronounced geographical isolation of Antarctica than the Arctic, resulting in a macroalgal flora of which one-third is composed of endemic species. In contrast, the Arctic macroalgal flora consists mainly of a reduced North Atlantic flora with few endemic species. The lipid composition is quite similar in endemic and non-endemic macroalgae of both polar regions. However, many polar macroalgae differ in their fatty acid composition from those of temperate and tropical species. Whether these differences are attributable to latitudinal and/or habitat-specific adaptations, e.g. to guarantee the fluidity of membranes at low temperatures, is still unresolved.

Information on the benthic food web structure of polar regions is essential for understanding the food-web structures and functions (e.g. algal productivity, fate of biomass, grazing pressure and anti-grazing strategies) under extreme environmental conditions. In studies on trophic relationships, microscopical gut-content analysis of herbivores were carried out to identify the macroalgal species consumed (Iken et al. 1997, Iken 1999, Ojeda & Munoz 1999), but this is only possible during the early stages of digestion. Another approach is multiple stable-isotope analysis (Loneragan et al. 1997). While this technique allows differentiation between the main groups of primary producers, all macroalgal species exhibit a very similar isotopic signature. Fatty acids, on the other hand, seem to be a promising tool for studying trophic relationships in polar waters, since the lipid composition of macroalgae is made up largely of characteristic polyunsaturated fatty acids.

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