

Temperature requirements for growth and survival of macroalgae from Antarctica and southern Chile

C. Wiencke¹, I. tom Dieck²

¹ Institute of Polar and Marine Research, Am Handelshafen 12, D-2850 Bremerhaven, Federal Republic of Germany

² Biologische Anstalt Helgoland, Notkestraße 31, D-2000 Hamburg 52, Federal Republic of Germany

ABSTRACT: Optimum and limiting temperature demands for growth and survival were determined in 14 species from the Antarctic/cold-temperate region and in 7 cold-temperate species from southern Chile. The growth response was tested in steps of 5°C from 0 to 25°C. In Antarctic/cold-temperate macroalgae 4 groups with different temperature-growth-ranges could be distinguished. The highest possible growth temperature was 5°C in *Iridaea cordata* (Group 1), 10°C in *Geminocarpus geminatus*, *Ulothrix subflaccida* and the female gametophyte of *Desmarestia menziesii* (Group 2), 15°C in *Adenocystis utricularis*, *Scytothamnus fasciculatus*, *Urospora penicilliformis* and *Acrosiphonia arcta* (Group 3) and 20°C in *Prasiola crispa* ssp. *antarctica* f. *antarctica*, *Ulothrix implexa* and *Enteromorpha bulbosa* (Group 4). Maximum survival temperatures of 14 to 19 (up to 25)°C were found in those species growing up to 10 or 15°C. Species growing up to 20°C tolerated 24 to 28°C. Maximum survival temperature in *Gigartina skottsbergii* was 15°C, and in *Leptonematella falklandica* (nov. comb., formerly *Leptonema falklandicum*) and *Pilayella littoralis* 22 to 24°C (growth not determined in these 3 species). Species with exclusively temperate distribution can be divided into 2 groups: The more stenotherm species *Iridaea laminarioides*, *I. undulosa* and a ligulate *Desmarestia* sp. grew between (0 or) 5 and 15 (or 20)°C (Group 1). The more eurytherm species *Chordaria magellanica*, *Ectocarpus siliculosus*, *Enteromorpha clathrata* and *Scytosiphon lomentaria* (Group 2) had an extended growth range from 0°C up to 20 (or 25)°C. Growth at 0°C was very reduced or not possible in all cold-temperate species except for *C. magellanica* and *E. siliculosus*. The maximum survival temperatures of these species were 17 to 24°C. The evolution of cold water macroalgae in Antarctica from cold-temperate species probably started after opening of the Drake Passage and the concomitant temperature lowering in Antarctica some 25 to 30 million yr ago. It is still in process today as indicated in *A. utricularis*. In macrothalli of this species from Antarctica and southern Chile ecotypes were demonstrated exhibiting different temperature optima for growth (at 10 and 15°C) and different upper survival temperatures (at 18 and 19°C).

INTRODUCTION

Endemic Antarctic macroalgae show a temperature requirement for growth between 0 and 10 (or 15)°C, optimum growth values at 0 to 5 (or 10)°C and maximum survival temperatures of 11 to 18°C (Ohno 1984, Wiencke & tom Dieck 1989). These low temperature demands were inferred to be dependent on the long cold water history (25 to 30 million yr) of Antarctica triggering the development of cold water taxa (Wiencke & tom Dieck 1989). Macroalgae distributed in Antarctic and/or cold temperate regions may still be in the process of adaptation to low temperatures. So it is of particular interest to compare the temperature demands of species with Antarctic/cold-temperate and

exclusively temperate distribution. Data on the temperature demands of such macroalgae are available for *Pilayella littoralis* (Müller & Stache 1989) and *Durvillaea antarctica* (Délépine & Asensi 1976). The aim of this study was to describe the temperature requirements for growth of 21 red, brown and green algal species from Antarctica and southern Chile.

MATERIAL AND METHODS

The macroalgae investigated were isolated as spores during 2 expeditions to King George Island (Antarctica; Clayton & Wiencke 1986, Wiencke 1988) and to southern Chile and subsequently cultivated in home

laboratories. The algae are listed in Table 1. Cultivation methods, growth rates and upper survival temperatures were obtained as described elsewhere (Wiencke & tom Dieck 1989).

RESULTS

The investigated Antarctic/cold-temperate species can be classified into 4 groups according to their temperature-growth characteristics.

Group 1: The gametophyte of *Iridaea cordata* was able to grow at up to 5°C (Fig. 1). At 10°C positive growth rates were recorded in the first 3 wk of the experiment, but later turned to negative values accompanied by bleaching of the upper thallus parts. The upper survival temperature of *I. cordata* gametophytes was 14 to 16°C (Table 2).

Group 2: *Geminocarpus geminatus* (Fig. 2), *Desmarestia menziesii* (female gametophyte; Fig. 3) and *Ulothrix subflaccida* (Fig. 4) grew between 0 and 10°C with peak growth rates at 5°C (*G. geminatus*, *D. menziesii*) or 10°C (*U. subflaccida*). The upper temperature tolerance of all subtidal and lower sublittoral species and of *Gigartina skottsbergii* was 14 to 17°C. The only alga of this group from the upper intertidal, *U. subflaccida*, survived up to 23 to 25°C (Table 2).

Group 3: The temperature demands of the isolates of *Adenocystis utricularis* from Antarctica and southern Chile were slightly different. Macrothalli of both isolates grew between 0 and 15°C. The temperature growth optimum in the Antarctic isolate was 10°C (Fig. 5), but 15°C was optimal in the south Chilean isolate (Fig. 6). The maximum survival temperature of Antarctic *A. utricularis* was 18°C and that from south Chile was 19°C (Table 2). *Scytothamnus fasciculatus* (Fig. 7), *Urospora penicilliformis* (Fig. 8) and *Acrosiphonia arcta* (Fig. 9) grew between 0 and 15°C. *S. fasciculatus* showed very uniform growth rates at all temperatures tested, which were maintained over an experimental period of 3 mo; *U. penicilliformis* and *A. arcta* grew optimally at 5°C. The maximum survival temperatures were 19°C for *U. penicilliformis* and *A. arcta* and 22 to 24°C for *S. fasciculatus*, *Leptonematella falklandica* and *Pilayella littoralis* (Table 2) (growth rates were not determined for these 3 species).

Group 4: *Prasiola crispa* ssp. *antarctica* (Fig. 10), *Ulothrix implexa* (Fig. 11) and *Enteromorpha bulbosa* (Fig. 12) grew between 0 and 20°C. The maximum survival temperatures of these species were 24 to 28°C (Table 2).

Macroalgae with exclusively temperate distribution can be divided into 2 groups with different temperature demands for growth, one with more stenothermal, the second with more eurythermal characteristics. Group 1

consists of a ligulate *Desmarestia* sp., *Iridaea undulosa* and *I. laminarioides*. Gametophytes of the ligulate *Desmarestia* sp. grew from 0 to 20°C with very low rates at 0°C and a pronounced optimum at 15°C (Fig. 13). The sporophyte of this species grew only from 5 to 20°C, with a growth peak at 15°C (Fig. 14). *I. laminarioides* gametophytes grew between 0 and 15°C with low rates at 0°C and a maximum between 10 and 15°C (Fig. 15). The temperature growth limits for *I. undulosa* gametophytes were 5 and 15°C (Fig. 16).

The more eurythermal second group consists of *Chordaria magellanica*, *Ectocarpus siliculosus*, *Enteromorpha clathrata* and *Scytosiphon lomentaria*. *C. magellanica* grew from 0 to 20°C showing a slight maximum at 5 to 10°C (Fig. 17). *E. siliculosus* grew at all temperatures from 0 to 20°C with a broad maximum between 5 and 15°C (Fig. 18). *E. clathrata* was also able to grow from 0 to 20°C, with a growth plateau between 5 and 15°C and with very reduced growth rates at 0 and 20°C (Fig. 19). A similar growth pattern was shown by *S. lomentaria* with a broad maximum between 5 and 20°C and reduced growth rates at 0 and 25°C (Fig. 20).

The maximum survival temperatures of most temperate algae were between 21 and 24°C (Table 2). The blades of *Iridaea undulosa* and *I. laminarioides* had a somewhat lower temperature tolerance of 17°C, but the holdfasts of *I. undulosa* survived 22°C (Table 2).

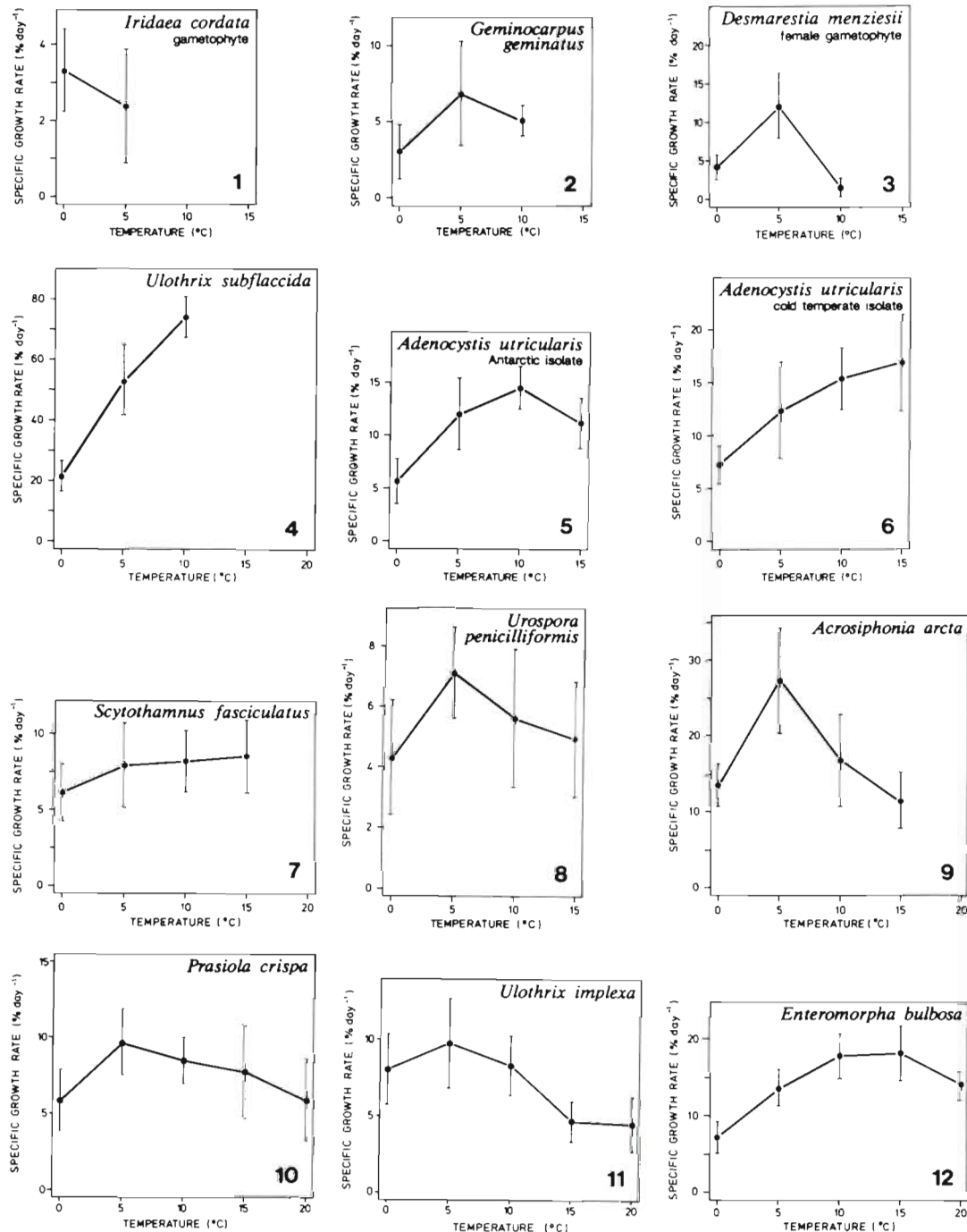
DISCUSSION

The Antarctic/cold-temperate species grow between 0 and 5, 10 or 15°C exhibiting relatively uniform optima at 5 or 10°C and maximum survival temperatures of 14 to 19 (up to 25)°C. Only the supratidal species *Prasiola crispa* ssp. *antarctica* and the intertidal species *Enteromorpha bulbosa* and *Ulothrix implexa* show higher temperature limits for growth ($\leq 20^\circ\text{C}$) and survival (24 to 28°C). Another intertidal species, *Pilayella littoralis*, from Diego Ramirez Island grows between 2 and 20°C with an optimum at 12°C (Müller & Stache 1989) and has an upper survival temperature of 23 to 24°C (Table 2). Thus, most of the Antarctic/cold-temperate algae have higher temperature demands than endemic Antarctic species (Wiencke & tom Dieck 1989), but similar growth (Adey 1970, Fortes & Lüning 1980, Bolton & Lüning 1982, Rueness & Tanager 1984) and survival limits (Sundene 1962, Munda & Lüning 1977, Bolton & Lüning 1982, Lüning 1984, Lüning & Freshwater 1988) to those of endemic Arctic and Arctic/cold-temperate species.

The more stenothermal temperate species (*Iridaea laminarioides*, *I. undulosa*, *Desmarestia* sp.) grow between (0 or) 5 and 15 (to 20)°C with optimum rates at 10 and 15°C and maximum survival temperatures

Table 1. Investigated species, location, isolator and date of collection

Algal species Systematic position	Location	Collector Isolator	Date
A. Antarctic/cold-temperate species			
<i>Ulothrix implexa</i> (Kützinger) Kützinger (Ulotrichales, Chlorophyta)	King George Island ^a Ardley Bay	Wiencke	29 Jan 1986
<i>Ulothrix subflaccida</i> Wille (Ulotrichales, Chlorophyta)	King George Island ^a Ardley Bay	Wiencke	28 Jan 1986
<i>Enteromorpha bulbosa</i> (Suhr) Montagne (Ulvales, Chlorophyta)	King George Island ^a Sea Elephant Bay	Wiencke	28 Jan 1986
<i>Prasiola crista</i> subsp. <i>antarctica</i> (Kützinger) Knebel f. <i>antarctica</i> (Prasiolales, Chlorophyta)	King George Island ^a Sea Elephant Bay	Wiencke	27 Jan 1986
<i>Urospora penicilliformis</i> (Roth) Areschoug (Acrosiphoniales, Chlorophyta)	King George Island ^a Ardley Bay	Wiencke	29 Jan 1986
<i>Acrosiphonia arcta</i> (Dillwyn) J. Agardh (Acrosiphoniales, Chlorophyta)	King George Island ^a Sea Elephant Bay	Wiencke	29 Jan 1987
<i>Geminocarpus geminatus</i> (J. D. Hooker et Harvey) Skottsberg (Ectocarpales, Phaeophyta)	King George Island ^a Ardley Bay	Clayton Wiencke	28 Jan 1986
<i>Pilayella littoralis</i> (Linnaeus) Kjellmann (Ectocarpales, Phaeophyta)	Diego Ramirez Island	Westermeier Wiencke	10 Feb 1986
<i>Leptonematella falklandica</i> (Skottsberg) Wiencke nov. comb. ^b (Chordariales, Phaeophyta)	Navarino Island ^c Puerto Williams	Wiencke	10 Feb 1986
<i>Scytothamnus fasciculatus</i> (J. D. Hooker et Harvey) Cotton (Chordariales, Phaeophyta)	Tierra del Fuego Porvenir	Clayton Wiencke	16 Feb 1986
<i>Adenocystis utricularis</i> (Bory) Skottsberg (Dictyosiphonales, Phaeophyta)	King George Island ^a Ardley Bay	Clayton Wiencke	2 Feb 1986
	Diego Ramirez Island	Westermeier Clayton, Wiencke	10 Feb 1986
<i>Desmarestia menziesii</i> J. Agardh (Desmarestiales, Phaeophyta)	King George Island ^a Albatross Island	Clayton Wiencke	27 Jan 1986
<i>Iridaea cordata</i> (Turner) Bory (Gigartinales, Rhodophyta)	King George Island ^a Skua Bay	Wiencke	1 Feb 1987
<i>Gigartina skottsbergii</i> (Bory) Setchell et Gardner (Gigartinales, Rhodophyta)	King George Island ^a Ardley Bay	Wiencke	28 Jan 1986
B. Cold-temperate species			
<i>Enteromorpha clathrata</i> (Roth) J. Agardh (Ulvales, Chlorophyta)	Navarino Island ^c Puerto Williams	Wiencke	11 Feb 1986
<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye (Ectocarpales, Phaeophyta)	Navarino Island ^c Puerto Williams	Wiencke	10 Feb 1986
<i>Chordaria magellanica</i> Kylin (Chordariales, Phaeophyta)	Navarino Island ^c Puerto Williams	Clayton Wiencke	10 Feb 1986
<i>Desmarestia</i> sp. ^d (Desmarestiales, Phaeophyta)	Brunswick Peninsula Fuerte Bulnes	Clayton Wiencke	14 Feb 1986
<i>Petalonia fascia</i> (O. F. Müller) O. Kuntze (Scytosiphonales, Phaeophyta)	Diego Ramirez Island	Wiencke	10 Feb 1986
<i>Scytosiphon lomentaria</i> (Lyngbye) Endlicher (Scytosiphonales, Phaeophyta)	Navarino Island ^c Puerto Williams	Wiencke	11 Feb 1986
<i>Iridaea laminarioides</i> Bory (Gigartinales, Rhodophyta)	Diego Ramirez Island	Westermeier Wiencke	15 Feb 1986
<i>Iridaea undulosa</i> Bory (Gigartinales, Rhodophyta)	Diego Ramirez Island	Westermeier Wiencke	15 Feb 1986
^a King George Island is one of the South Shetlands			
^b Basionym: <i>Leptonema falklandicum</i> Skottsberg 1907 p. 52. This new combination became necessary after Silva (1959) established the genus <i>Leptonematella</i> Silva as substitute for the invalid name <i>Leptonema</i> (Reinke 1888)			
^c Navarino Island is located on the Beagle Channel, opposite Tierra del Fuego			
^d The species is a ligulate member of the genus <i>Desmarestia</i>			



Figs. 1 to 12. Temperature requirements for growth of species from the Antarctic-cold temperate region. Experiments were performed in 5°C intervals. No entries: the alga is unable to grow at that particular temperature. Prior to the experiments algae were adapted for 10 d to the experimental light and temperature conditions. Experiments in Figs. 3, 4 and 9 were performed in Petri dishes at $15 \mu\text{mol m}^{-2} \text{s}^{-1}$, 18:6 h light-dark-cycle for a period of 1 to 2 wk; all other experiments in large glass beakers at $50 \mu\text{mol m}^{-2} \text{s}^{-1}$, 18:6 h light-dark-cycle for a period of 4 wk or 3 mo (Fig. 7)

between 17 and 23°C. More stenothermal characteristics of the same distribution group are only known from the Subantarctic/cold-temperate *Durvillaea antarctica* which dies above 13.5°C (Délépine & Asensi 1976).

With respect to their growth optima and upper survival temperatures, *I. laminarioides*, *I. undulosa* and the *Desmarestia* sp. are comparable with cold-temperate algae from the northern hemisphere (references given

Table 2. Temperature tolerance of the investigated species determined in 2 wk exposures to the given temperatures (x = specimen alive; (x) = parts of the specimen dead, but young parts (buds, meristems) living; – = specimen dead, no growth during 4 wk postculture under favourable conditions). Every developmental stage was tested in 2 to 4 experimental series, indicated in the table on separate lines

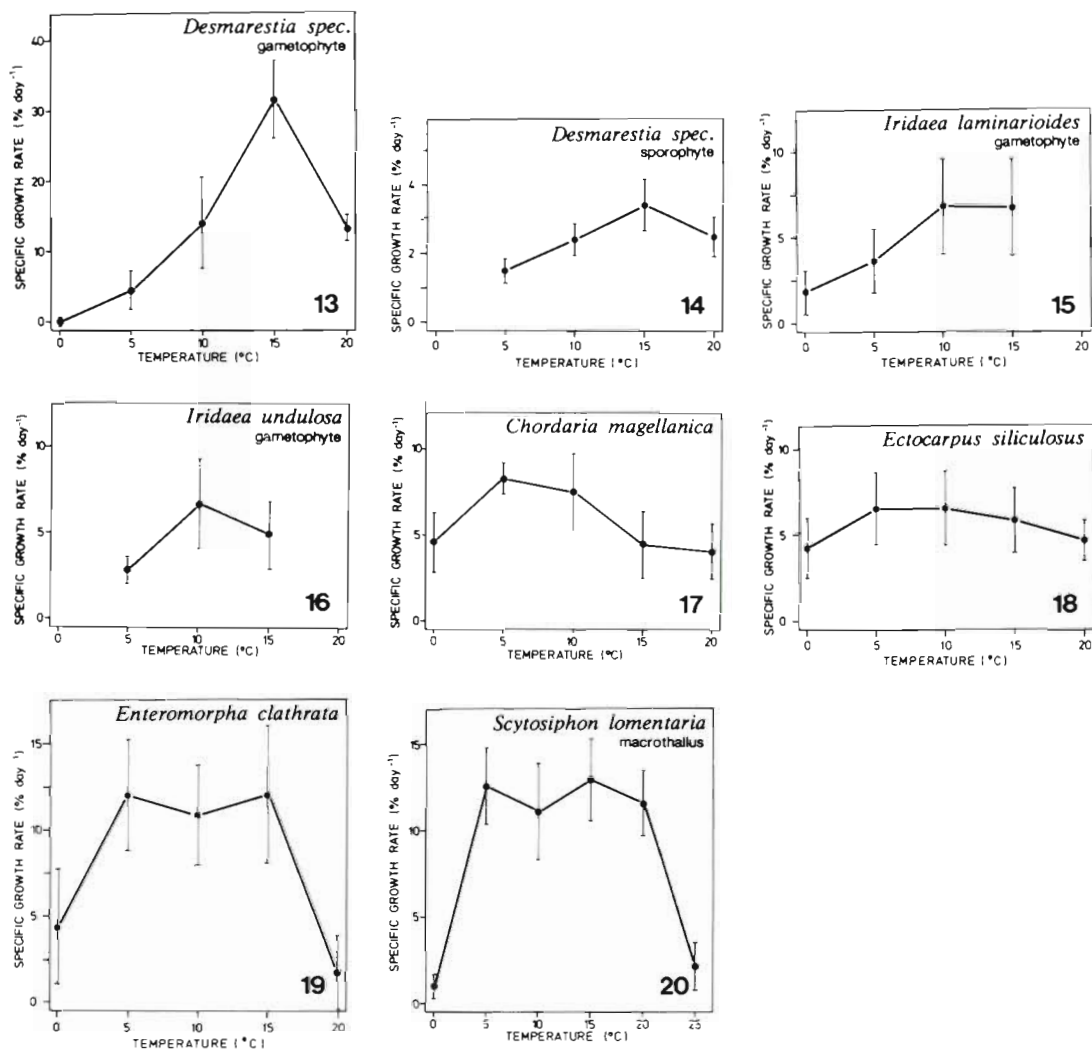
Species Developmental stage tested	Temperature (°C)																		Maximum survival temp. (°C)
	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
A. Antarctic/cold-temperate species																			
<i>Geminocarpus geminatus</i>		x		–			–		–			–		–					14 (15)
		x	x	(x)	–	–	–	–											
		x	x	–	–	–	–	–	–										
<i>Gigartina skottsbergii</i>		x	x	–	–	–	–	–	–										15
Tetrasporophytes, germlings	x	x	x	x	–	–													
			x	–	–	–	–	–	–	–									
<i>Iridaea cordata</i>	x	x	x																15 (16)
Gametophytes, germlings			x	x	(x)														
<i>Desmarestia menziesii</i>			x	x	x	–	–	–	–	–	–	–	–	–	–				16 (17)
Female microthalli			x	x	x	(x)	–	–	–	–									
			x	x	x	(x)	–	–	–	–									
			x	x	(x)	–	–	–											
<i>Adenocystis utricularis</i>				x	x	x	x	–	–	–									18
Antarctic isolate				x	x	x	x	–	–	–									
Young macrothalli																			
<i>Adenocystis utricularis</i>		x		x			x	–				–		–					19
Cold-temperate isolate			x	x	x	x	x	x											
Young macrothalli			x	x	x	x	x	x	–	–									
<i>Urospora penicilliformis</i>			x	x	x	x	x	x	–	–									19
						x	x	x	–	–	–	–	–	–					
								x											
<i>Acrosiphonia arcta</i>							x	x	x	x	(x)	–	–	–					21 (22)
							x	x	x	x	(x)	–							
<i>Scytothamnus fasciculatus</i>									x	x	x	x	x	–	–	–	–	–	22 (24)
1 cm large macrothalli									x		x	–	–	–	–	–	–	–	
<i>Leptonematella falklandica</i>				x			x		x		x	–		–					22 (24)
Juvenile microthalli									x	(x)	x	(x)							
									x	x	x	–	x	–	–	–			
<i>Pilayella littoralis</i>		x		x			x	x	x	x	x	x	–	–					23 (24)
							x	x	x	x	x	x	–	–					
									x	x	x	x	x	–					
									x	x	x	x	(x)	–	–	–			
<i>Ulothrix subflaccida</i>								x	x	x	x	x	x	(x)	–	–	–	–	23 (25)
									x		x	x		–	–	–	–	–	
													–	–	–				
<i>Prasiola crispa</i> ssp. <i>antarctica</i> f. <i>antarctica</i>																			
8 mm large plants							x	x	x	x	x	x	x	–	–				24 (28)
															(x)	(x)	(x)	–	
														x	–				
<i>Enteromorpha bulbosa</i>								x	x	x	x	x	x	x	–	–	–	–	25
Several cm long, vegetative plants								x		x	x	x	x	x	–	–	–	–	
<i>Ulothrix implexa</i>								x	x	x	x	x	(x)	x	–	–	–	–	25 (26)
												x		x	(x)	–	–	–	
B. Cold-temperate species																			
<i>Iridaea undulosa</i>					x	(x)	(x)	(x)	(x)	(x)	(x)	–	–	–					17 (22)
Gametophytes											(x)	–	–	–	–	–	–	–	
					x	x	(x)												
<i>Iridaea laminarioides</i>					x	x	–	–	–	–									17
Gametophytic blades					x	x	–	–	–	–									
Ligulate <i>Desmarestia</i> sp.										x	–	–							21
Filamentous sporophytes										x	(x)	–	–						
Ligulate <i>Desmarestia</i> sp.										x	x	(x)	(x)	–					22 (23)
Gametophytes														–	–	–	–	–	
										x	x	x	(x)						
<i>Chordaria magellanica</i>								x	x	x	x	x	–	–	–	–	–	–	23 (24)
Up to 2 cm large macrothalli									x		(x)	x	(x)						
											(x)	–	–	–	–	–	–		
<i>Ectocarpus siliculosus</i>							x		x			x	–						24
							x	x	x	x	x	x	(x)	–					
									x	x	x	x	x	–					

above). The more eurythermal temperate species (*Enteromorpha clathrata*, *Chordaria magellanica*, *Scytosiphon lomentaria*, *Ectocarpus siliculosus*) grow between 0 and 20 (to 25) °C with optimum values between 5 and 15 °C. They also exhibit an extended upper survival range. These temperature requirements are intermediate between cold- and warm-temperate algae (Akiyama 1965, Branch 1974, Norton 1977, Kapraun 1978, Ohno 1979, Novacek 1984). All temperate species studied here (except *C. magellanica* and *E. siliculosus*) show reduced or zero growth rates at 0 °C. This might be an adaptation to the temperature regime in the cold temperate region of South America. They differ in this respect from North Atlantic cold-temperate/Arctic species, which show relatively high growth rates at 0 °C (Bolton & Lüning 1982, tom Dieck 1989).

Van den Hoek (1982a, b) and Breeman (1988)

showed that the geographic distribution of macroalgae depends on the temperature tolerance and the temperature requirement for growth and reproduction of the different stages in the life cycle of a given alga. Additionally the photoperiod triggering the induction of different phases in the algal life cycle and other factors such as interaction with animals and other plants (Hay 1981, Gaines & Lubchenco 1982) or incomplete propagation may limit the distribution of macroalgae.

In the following section the geographic distributions of the studied species are analysed in relation to the described temperature demands. The northern distribution of *Iridaea cordata* is limited by winter temperatures just low enough to allow sufficient growth (Fig. 1; Tables 3 and 4; Fig. 21). The populations from the Aucklands and the west coast of South America at 41°S are – with respect to the temperature regime at these locations –



Figs. 13 to 20. Temperature requirements for growth of cold-temperate species from southern Chile. The experiment in Fig. 13 was performed at $15 \mu\text{mol m}^{-2} \text{s}^{-1}$, 18:6 h light-dark-cycle for a period of 2 wk; all other experiments at $50 \mu\text{mol m}^{-2} \text{s}^{-1}$, 18:6 h light-dark-cycle for a period of 4 wk. For further information see legend to Figs. 1 to 12

Table 3. Geographic distribution of the investigated species. Sources: Skottsberg (1907, 1921, 1923, 1941), Laing (1909), Knebel (1935), May (1939), Taylor (1939), Papenfuss (1940), Levring (1944, 1945, 1960), Chapman (1956), Scagel (1957), Lindauer et al. (1961), Pujals (1963), Papenfuss (1964), Asensi (1966), Neushul (1968), Zaneveld (1968), Asensi (1975), Abbott & Hollenberg (1976), Hansen & Doyle (1976), Pedersen (1976), Simons (1976), Lamb & Zimmermann (1977), Santelices & Abott (1978), Müller (1979), Santelices (1980), Lokhorst & Trask (1981), Tseng (1983), Seagrief (1984), South (1984), Womersley (1984, 1987), Hay et al. (1985), Wynne (1986), Ramirez et al. (1986), South & Tittley (1986), tom Dieck (1987), Fletcher (1987), Ricker (1987), Wagner & Zaneveld (1988). Locations arranged after their temperature regimes shown in Table 4. Question marks indicate uncertain records

Algal species	Geographic distribution
A. Antarctic/cold-temperate species	
<i>Ulothrix implexa</i>	Ross Island, Antarctic Peninsula, South Shetlands, Falklands, Tierra del Fuego, South America (east coast). Northern hemisphere: Cold-temperate regions in the Northeast Atlantic and North Pacific
<i>Ulothrix subflaccida</i>	South Shetlands, South Australia. Northern hemisphere: Widely distributed in the North Atlantic
<i>Enteromorpha bulbosa</i>	Antarctic Peninsula, South Shetlands, Bouvet, South Georgia, Kerguelen, Macquarie Island, Falklands, Crozet, Tierra del Fuego, Campbell Island, Auckland, New Zealand, Chatham Island, South America (west coast, 20°S), South Africa, South America (east coast, 35°S)
<i>Prasiola crispa</i> subsp. <i>antarctica</i> f. <i>antarctica</i>	Antarctic Peninsula, Victoria Land, Possession Island and other islands in the Ross Sea, George V Coast, Adelie Coast, Wilkes Land, Queen Mary Coast, Ingrid Christensen Coast, Prince Olav Coast, South Shetlands, South Orkneys, South Sandwich Islands, Bouvet, South Georgia, Kerguelen, Macquarie Island, Falklands, Tierra del Fuego, Southeast Tasmania, New Zealand. On the northern hemisphere the other subspecies occurs: <i>Prasiola crispa</i> ssp. <i>eucrispa</i> (Kützing) Knebel
<i>Urospora penicilliformis</i>	Antarctic Peninsula, Victoria Land, Ross Island and other islands in the Ross Sea, Wilkes Land, Ingrid Christensen Coast, Mac Robertson Coast, South Shetlands, Heard Island, Kerguelen, Macquarie Island, Falklands, Crozet, Tierra del Fuego, Tasmania. Northern hemisphere: Arctic Ocean and temperate regions of Atlantic and Pacific Ocean
<i>Acrosiphonia arcta</i> . Synonyms: <i>Spongomorpha arcta</i> (Dillwyn) Kützing, <i>Cladophora arcta</i> (Dillwyn) Kützing	South Shetlands, South Georgia, Kerguelen, Falklands, Tierra del Fuego, Campbell Island, Auckland. Northern hemisphere: Arctic Ocean and cold-temperate regions of the Atlantic and Pacific Ocean
<i>Geminocarpus geminatus</i>	Antarctic Peninsula, Victoria Land, Wilkes Land, South Shetlands, South Georgia, Kerguelen, Macquarie Island, Falklands, Crozet, Tierra del Fuego, South America (west coast, 52°S), Campbell Island, New Zealand (east coast, 43°S), Juan Fernandez Island
<i>Pilayella littoralis</i>	Antarctic Peninsula, South Shetlands, South Georgia, Kerguelen, Macquarie Island, Falklands, Diego Ramirez Island, Tierra del Fuego, Campbell Island, Tasmania, South Australia (140°E), South America (west coast, 30°S). Northern hemisphere: Arctic Ocean and temperate regions of Atlantic and Pacific Ocean
<i>Leptonematella falklandica</i>	Wilkes Land, Falklands, Navarino Island
<i>Scytothamnus fasciculatus</i>	Victoria Land (?), Possession Island, South Shetlands, South Georgia, Kerguelen, Macquarie Island, Falklands, Tierra del Fuego, Campbell Island, Auckland, South America (east coast, 48°S), South America (west coast, 41°S), Southeast Tasmania, New Zealand (east coast, 43°S)
<i>Adenocystis utricularis</i>	Antarctic Peninsula, Victoria Land (?), South Shetlands, South Orkneys, South Georgia, Kerguelen, Marion Island (?), Macquarie Island, Falklands, Diego Ramirez Island, Crozet, Tierra del Fuego, Campbell Island, Auckland, Antipodes, Snares, South America (east coast, 48°S), Stewart Island, Southeast Tasmania, New Zealand, Chatham Island, South America (west coast, 17°S)
<i>Desmarestia menziesii</i>	Antarctic Peninsula, Victoria Land, Possession Island, Adelie Coast, Wilkes Land, Enderby Land, Balleny Islands, South Shetlands, South Georgia, Kerguelen, Falklands
<i>Iridaea cordata</i> (Turner) Bory	
Entity from the Southern Ocean: Synonyms: <i>I. obovata</i> <i>I. micans</i> (Bory)	Antarctic Peninsula, Victoria Land, Adelie Coast, Possession Island, Ross Island, Wilkes Land, Ingrid Christensen Coast, Balleny Islands, South Shetlands, South Georgia, Heard Island, Kerguelen, Macquarie Island, Falklands, Diego Ramirez Island, Crozet, Tierra del Fuego
Entity from the Northern hemisphere:	Pacific Ocean from Honshu (Japan) to Northern Mexico
<i>Gigartina skottsbergii</i>	Antarctic Peninsula, South Shetlands, Falklands, Tierra del Fuego, South America (west coast, 32°S)

(Table continued overleaf)

Table 3 (continued)

Algal species	Geographic distribution
B. Cold-temperate species	
<i>Enteromorpha clathrata</i>	Falklands, Tierra del Fuego, Aucklands, Antipodes, Snares, New Zealand, South Africa (?), South, East and West Australia, Northern hemisphere: Arctic to temperate regions of the Atlantic and Pacific Oceans
<i>Ectocarpus siliculosus</i>	South Georgia, Macquarie Island, Falklands, Tierra del Fuego, Aucklands, Snares, South America (east coast, 48°S), New Zealand, Tasmania, South Australia (140°E), South America (west coast, 20°S), South Africa, Juan Fernandez Island, South Australia (129°E), East Australia (27°S). Northern hemisphere: Greenland, temperate to tropic regions of Atlantic and Pacific Ocean, Mediterranean Sea
<i>Chordaria magellanica</i>	Tierra del Fuego, Chile 37°S (?)
Ligulate <i>Desmarestia</i> sp.	Antarctic Peninsula, South Shetlands, South Orkneys, South Georgia
Antarctic entity:	
Cold-temperate entities:	Falklands, Crozet, Tierra del Fuego, Campbell Island, Aucklands, Antipodes, Bounties, Snares, Tasmania, South Australia (140°E), South America (west coast, 30°S), South Africa (18°30' E). Northern hemisphere: temperate regions of the Atlantic and Pacific Ocean
<i>Scytosiphon lomentaria</i>	South Georgia, Kerguelen, Macquarie Island, Falklands, Diego Ramirez Island, Tierra del Fuego, Campbell Island, Aucklands, Antipodes, South America (east coast, 48°S), New Zealand, Tristan da Cunha, South America (west coast, 30°S), Southwest Africa (26°S), Juan Fernandez Island, West Australia (28°S), East Australia (26°S). Northern hemisphere: temperate regions of Atlantic and Pacific Ocean
<i>Iridaea laminarioides</i>	Kerguelen, Falklands, Diego Ramirez Island, Tierra del Fuego, Aucklands, South America (west coast 37°S, 32°S)
<i>Iridaea undulosa</i>	Falklands, Diego Ramirez Island, Tierra del Fuego, South America (west coast, 37°S)
records under:	
<i>Iridaea ciliata</i> Kützting	Tierra del Fuego, South America (west coast, 42°S)
and	
<i>Iridaea crispata</i> Bory	Falklands, Tierra del Fuego, South America (west coast, 41°S), South America (west coast 37°S)

probably ecotypes. *I. cordata* from the northern hemisphere, however, is a different species (Papenfuss 1964, Leister, cited in Ricker 1987). This alga shows a maximum survival temperature of 20°C (next temperature tested: 23°C) determined after an exposure time of 1 wk and the photosynthetic evolution of oxygen as criterion for survival (Lüning & Freshwater 1988). In contrast, southern hemisphere *I. cordata* shows an upper survival temperature of 14 to 16°C (Table 2).

The northern boundary of *Gigartina skottsbergii* remains obscure as summer surface water temperatures at its northernmost location (17.8°C; Tables 3 and 4) are above the upper survival temperature of 15°C (Table 2). One explanation might be that the record on the west coast of South America (32°S) is out of the distributional range of the species as stated by Setchell & Gardner (1937).

Geminocarpus geminatus should occur in areas with winter temperatures of $\leq 10^\circ\text{C}$ allowing growth of the alga (Fig. 2) and summer temperatures below 15°C

allowing its survival (Table 2). The material of Juan Fernandez Island (Levring 1941, cited in Ricker 1987) presumably represents a physiological strain as the summer surface water temperature of 20.3°C considerably exceeds the maximum survival temperature of 14 to 15°C of the studied Antarctic isolate (Tables 2, 3 and 4). Ecocline variation is also known from another member of the order Ectocarpales, *Ectocarpus siliculosus* (Bolton 1983).

Desmarestia menziesii is found from Antarctica to the Falklands with surface water temperatures between 4.2 and 8.5°C (Tables 3 and 4). The temperature demands of the female gametophyte (Fig. 3; Table 2) should not be used for the explanation of the phylogeographic distribution since the sporophytes are expected to exhibit a narrower, and thus crucial, temperature range for growth and survival than the gametophytes, as has been shown in Antarctic Desmarestiales. The northern distribution of these species is determined by the low temperature demands

Table 4. Variation of mean monthly seawater temperatures during the course of the year at the locations listed in Table 3. Source: Gorshkov (1985a, b). Classification of biogeographic regions after South (1979) and Lüning (1985)

Location	Temperature (°C)
Antarctic Region:	
Antarctic Peninsula (east coast), Victoria Land, Possession Island, Ross Island and other islands in the Ross Sea, George V Coast, Adèle Coast, Wilkes Land, Queen Mary Coast, Ingrid Christensen Coast, Mac Robertson Coast, Enderby Land, Prince Olav Coast	≤ -1.8 throughout the year
Antarctic Peninsula (west coast, polar circle), Balleny Islands	≤ -1.8 to -0.2
South Shetlands	≈ -1.8 to $+1.2$
South Orkneys	≈ -1.8 to $+1.4$
South Sandwich Islands	≈ -1.8 to $+2.1$
Bouvet	-1.5 to $+3.0$
South Georgia	-0.6 to $+4.8$
Heard Island	$+1.5$ to $+5.2$
Cold-temperate (incl. Subantarctic) Region:	
Kerguelen	3.2 to 7.0
Macquarie Island	5.0 to 8.0
Marion Island	4.8 to 8.4
Falklands	4.2 to 8.5
Diego Ramirez Island	4.3 to 8.5
Crozet	5.0 to 9.0
Tierra del Fuego (Strait of Magellan), Navarino Island	6.0 to 9.4
South America (west coast, 52°S)	6.5 to 10.4
Campbell Island	8.0 to 10.8
Aucklands	8.0 to 11.0
Bounties	7.5 to 12.0
Antipodes	7.5 to 12.0
Snares	9.7 to 13.0
South America (east coast, 48°S)	7.5 to 14.0
Stewart Island	10.2 to 14.0
South America (west coast, 41°S)	10.0 to 14.8
Southeast Tasmania	11.6 to 15.2
New Zealand (east coast, 43°S)	11.5 to 16.5
Chatham Island	11.6 to 16.6
St. Paul	12.0 to 16.2
Tristan da Cunha	12.0 to 18.5
New Zealand (west coast, 40°S)	13.0 to 18.8
South Australia (140°E)	15.0 to 18.8
Warm-temperate Region	
South America (west coast, 37°S)	11.7 to 15.5
South America (west coast, 32°S)	12.4 to 17.8
South America (west coast, 30°S)	13.0 to 18.0
South America (west coast, 20°S)	14.0 to 19.0
South America (west coast, 17°S)	14.8 to 19.8
Southwest Africa (26°S)	12.5 to 19.5
South America (east coast, 35°S)	12.5 to 20.0
South Africa (18° 30' E)	15.5 to 20.0
Juan Fernandez Island	14.6 to 20.3
South America (west coast, 12°S)	15.5 to 20.9
South Australia (129°E)	16.5 to 21.8
West Australia (28°S)	17.3 to 22.2
East Australia (26°S)	17.1 to 22.8
Tropical Region	
South East Africa (31°S)	19.6 to 24.5
East Australia (27°S)	19.8 to 26.0

of the sporophytes (Wiencke & tom Dieck 1989). Thus, in *D. menziesii* a northern boundary with inhibiting high winter temperatures for sporophytic growth is to be expected.

The different temperature demands for growth and survival of *Adenocystis utricularis* isolates from both sides of the Antarctic convergence (Figs. 5 and 6; Table 2) indicate the development of temperature ecotypes. The northernmost distributional location of the species on the west coast of South America is characterized by the 19.8°C summer isotherm (Tables 3 and 4). This does not coincide with the upper survival temperature of the macrothallus (19°C, south Chilean isolate; Table 2). With the supposition that microthalli of this species might exhibit a higher survival temperature than their macrothalli – a generally known phenomenon in algae (Breeman 1988) – a northern lethal boundary determined by the microthallus is most probable.

Lethal boundaries seem to limit the northern distribution of the supralittoral and intertidal species *Urospora penicilliformis*, *Ulothrix implexa*, *U. subflaccida*, *Enteromorpha bulbosa*, *Prasiola crispa* ssp. *antarctica*, *Leptonematella falklandica* and *Pilayella littoralis*. The considerable differences between the highest possible summer temperatures in the distribution area of some species and their upper survival temperatures, e.g. 20°C versus 25°C in *Enteromorpha bulbosa*, may reflect a reasonable safety limit. According to van den Hoek (1982b) a 20°C summer isotherm corresponds with an extreme temperature of 23°C at the same location. Moreover water temperatures in the supralittoral and intertidal zone may considerably exceed those in open coastal waters (Biebl & Mc Roy 1971) thereby shifting the northern distribution boundary of the considered species southwards. Finally the mentioned discrepancy may arise from incomplete dispersal or insufficient collecting.

The maximum survival temperature of *Acrosiphonia arcta* from both hemispheres is probably the same. An isolate from Heligoland (North Sea) survives 20 to <23°C (Lüning 1984), whereas the Antarctic isolate tolerates 21 to 22°C (Table 2). The northern boundary of this species in the southern hemisphere is not determined by the temperature limits for growth and survival (Fig. 9; Tables 2, 3 and 4; cf. also van den Hoek 1982b). In the Northeast Atlantic the southern boundary is probably determined by the temperature demands for reproduction of the unicellular sporophyte (van den Hoek 1982b). This developmental stage is, however, lacking in the Antarctic (Wiencke unpubl.) and Heligoland (Kornmann 1964) populations.

Scytothamnus fasciculatus grows at temperatures $\leq 15^\circ\text{C}$ (Fig. 7) but is geographically limited to areas with winter temperatures $\leq 11.6^\circ\text{C}$ (Tables 3 and 4). This suggests a northern reproductive boundary. In

support of this view, formation of gametangia took place at 10°C and 7 h light but not at 11°C and 9.5 h light (Clayton 1986). In culture this species develops haploid sporophytes directly from gametophytes at temperatures up to 15°C and daylengths up to 12.5 h. But this feature might be of no importance in the field as shown for *Scytothamnus australis*: chromosome counts of wild specimens revealed a chromosome number approximately double that of cultured gametophytes (Clayton 1986).

The temperature demands for growth and survival of ligulate *Desmarestia* sp. from Antarctica (Wiencke & tom Dieck 1989) and southern Chile (this study) differ considerably. The gametophytes of the Antarctic isolate grow at temperatures up to 10°C, those of the cold temperate isolate up to 20°C (Fig. 15). In sporophytes of the Antarctic material growth is possible at temperatures between 0 and 5°C, whereas the sporophytic growth range in the cold temperate isolate is shifted to temperatures between 5 and 20°C with no capacity to grow at 0°C (Fig. 14). The maximum survival temperature of the sporophyte from the Antarctic isolate is 13°C, and is 21°C for that from the cold temperate isolate (Table 2). These differences as well as certain

morphological features (e.g. sporangium morphology; Moe & Silva 1977, Anderson 1985) support the hypothesis that ligulate *Desmarestia* sp. on both sides of the Antarctic convergence most probably belong to different species as pointed out earlier (Wiencke & tom Dieck 1989). The Antarctic isolate is phytogeographically limited to areas with winter surface water temperatures sufficiently low ($\leq 5^\circ\text{C}$) to allow growth of the sporophyte, the most sensitive stage in the life cycle of this alga. The cold temperate isolate is restricted to areas with winter temperatures $\geq 5^\circ\text{C}$ enabling growth of the sporophyte. The northern distribution limit of this entity cannot be a growth boundary as the winter surface water temperatures (13 to 15.5°C; Tables 3 and 4) of the northernmost locations of ligulate *Desmarestia* sp. are considerably below the upper temperature limits for growth (20°C; Figs. 13 and 14). The northern boundary may be a composite lethal and reproductive boundary given by the maximum survival temperature of the gametophyte (22 to 23°C; Table 2) and the (unknown) upper temperature limit for reproduction. In support of this view Ramirez et al. (1986) induced gametophyte fertility at temperatures between 5 and 14°C (next temperature tested: 20°C) in another ligu-

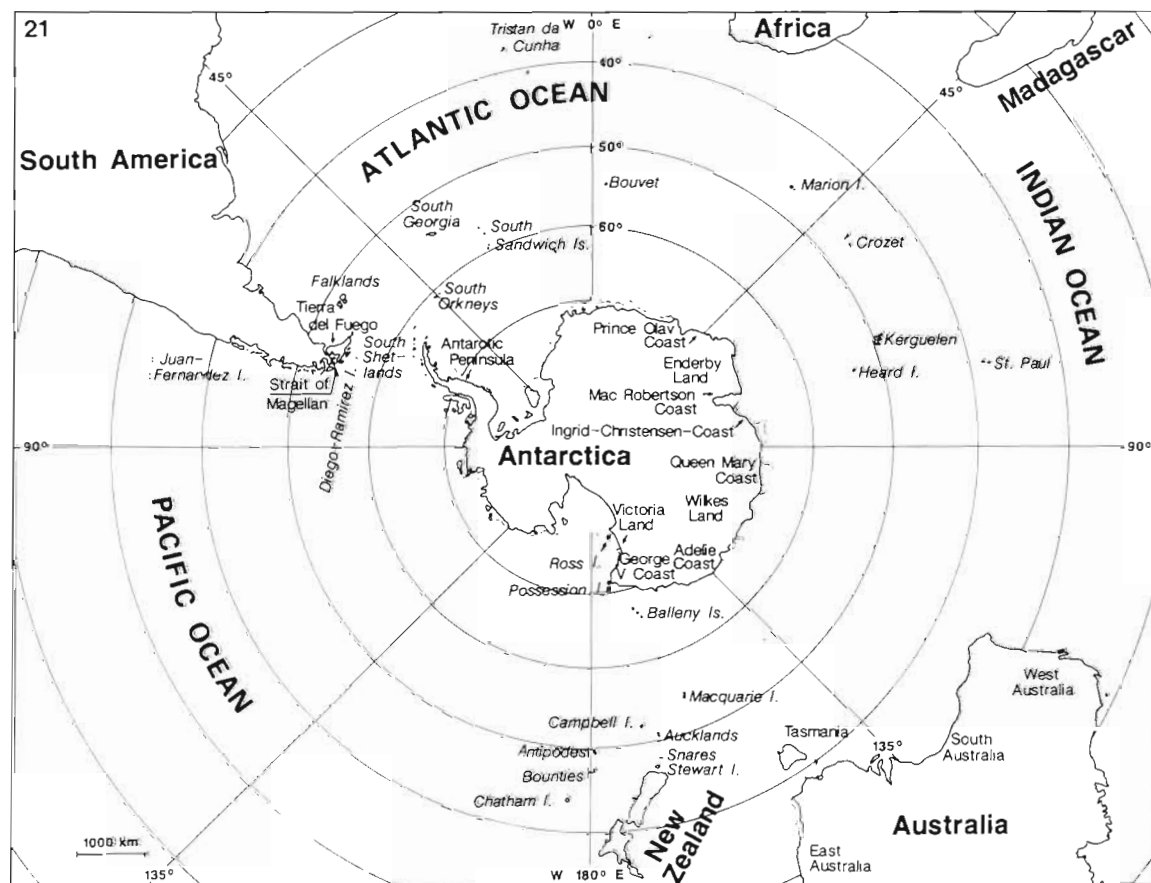


Fig. 21. Map redrawn after Iffereen et al. (1972) showing the locations listed in Tables 3 and 4

late *Desmarestia* sp. from central Chile. The same factors determine the southern boundary of North Atlantic *Desmarestia* sp. (van den Hoek 1982b).

The development of species with different degrees of adaptation to the temperature regime south and north of the Antarctic convergence is also evident in the genus *Iridaea*. The Antarctic/cold-temperate *I. cordata* grows at temperatures $\leq 5^{\circ}\text{C}$ (Fig. 1), whereas the species from southern Chile, *I. undulosa* and *I. laminarioides*, grow between 5 and 15°C or 0 and 15°C , respectively. Thus, as temperatures remain below 5°C in Antarctica, *I. undulosa* is totally excluded from this region. *I. laminarioides* on the other hand occurs on the Kerguelen Islands with lower temperatures compared to the Falkland Islands, the coldest location where *I. undulosa* can exist (Tables 3 and 4). The reduced rate at 0°C may explain why *I. laminarioides* has not yet been found in the Antarctic region. The upper survival temperature of the gametophytic blade (17°C ; Table 2), but not of the holdfasts (22°C ; Table 2) of *I. undulosa* coincides with the 15°C summer isotherm at the northern boundary of this species (Tables 3 and 4). In contrast, the northern distribution limit of *I. laminarioides* on the west coast of South America (18°C summer isotherm; Tables 3 and 4) does not coincide with the temperature limit for growth (15°C ; Fig. 15) nor with the maximum survival temperature of the gametophytic blade (Table 2). This points to the development of temperature ecotypes in the populations of *I. laminarioides* from Diego Ramirez Island (this investigation) and central Chile. Luxoro & Santelices (1989) obtained high growth rates in gametophytic and tetrasporophytic sporelings at 20°C from a central Chilean population ($33^{\circ}29'\text{S}$), supporting this hypothesis.

Chordaria magellanica shows a broad temperature range for growth and survival. Its absence from Antarctica and from localities north of Tierra del Fuego is not in accordance with the experimental results. A related species from Heligoland, *C. flagelliformis*, has a heteromorphic life-cycle with a microthallus probably present throughout the year becoming fertile only in winter (Kornmann 1962). If *C. magellanica* behaves similarly, its northern distribution limit could be a reproductive boundary.

A similar situation is also evident in *Scytosiphon lomentaria*. The seasonal development of this species is controlled by photoperiod and temperature, inducing the formation of macrothalli from crusts in spring (Clayton 1976, Lüning 1980). So low winter temperatures allowing induction of macrothalli from microthalli rather than temperature growth data (Fig. 20) and maximum survival temperatures (tom Dieck 1987) limit the northern distribution of this alga in the southern hemisphere (cf. also van den Hoek 1982b).

In *Ectocarpus siliculosus* the development of temperature ecotypes was shown in northern hemisphere isolates from the Arctic to the warm temperate region and in an isolate from Victoria, Australia (Bolton 1983). The Australian isolate grows between 5 and 26°C (higher and lower temperatures not tested) with a maximum growth rate at 20°C . Its maximum survival temperature is 25°C (next temperature tested: 28°C). The isolate from southern Chile seems to be another not yet described ecotype of the species as the temperature growth range extends from 0 to 20°C with optimum values between 5 and 15°C (Fig. 18) and a maximum survival temperature of 24°C (Table 2). On the west coast of South America (including Juan Fernandez Island), the northern distribution limit (20.3°C summer isotherm; Tables 3 and 4) is determined by the upper survival temperature. Another example of ecotypic variation in relation to temperature may be evident in *Enteromorpha clathrata*. The studied isolate differed from the European *E. clathrata* in its capability to grow at 0°C (Fig. 7), whereas the Netherlands isolate failed to grow below 12°C (Koeman 1985). It should be noted, however, that the taxonomic status on the species level may be uncertain in the genus *Enteromorpha*.

CONCLUSIONS

The data presented give an idea of the time periods necessary to develop temperature ecotypes or species with different temperature demands. *Acrosiphonia arcta* has occurred in 2 disjunct areas in the northern and southern hemisphere at least since the Pleistocene, i.e. for 2 million yr (van den Hoek 1982b) and has not changed its temperature demands for survival since then (see above). The same applies to *Desmarestia aculeata*, *D. viridis*, *Plocamium cartilagineum* and *Ahnfeltia plicata* from the Northeast Pacific, still showing the same upper survival temperatures as their North Atlantic conspecifics (Lüning & Freshwater 1988). The proposed dispersal took place after opening of the Bering Strait some 3.5 million yr ago. On the other hand ligulate *Desmarestia* sp. from both sides of the Antarctic convergence and members of the genus *Iridaea* from Antarctica, southern Chile and the northern hemisphere differ considerably in their temperature demands for growth and survival (see above). For the development of the considered species differing in their temperature demands long divergence times are to be expected. In particular, taxa with a disjunct Antarctic/cold-temperate distribution are thought to have developed after opening of the Drake Passage and the concomitant temperature lowering in Antarctica 25 to 30 million yr ago (Thenius 1977, Hempel 1987). The evolution of cold water macroalgae is still in

process today as indicated by the development of temperature ecotypes in *Adenocystis utricularis* from Antarctica and Southern Chile (see above).

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NOTE ADDED IN PROOF

R. J. Anderson and J. J. Bolton recently published a pertinent paper on another ligulate *Desmarestia* species: 'Growth and fertility, in relation to temperature and photoperiod, in South African *Desmarestia firma* (Phaeophyta).' *Botanica mar.* 32: 149–158 (1989). Their findings are in close accordance to the results reported here.

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