Temperature requirements for growth and survival of macroalgae from Disko Island (Greenland)

B. Bischoff & C. Wiencke

Institute for Polar and Marine Research; Am Handelshafen 12, D-27570 Bremerhaven, Federal Republic of Germany

ABSTRACT: The temperature requirements for growth and upper temperature tolerance were determined in 16 macroalgal species collected on Disko Island (Greenland). The upper survival temperatures were examined in 1°C steps, and growth measured at 5°C intervals between 0 and 20°C using a refined method, where the fresh weight was determined weekly or fortnightly over a period of 5 or 6 weeks. To express temperature-growth responses, growth rates of temperature-acclimated plants were taken. Two groups with different temperature requirements were identified: (1) A stenothermal group including *Acrosiphonia arcta*, *Acrosiphonia sonderi*, *Urospora penicilliformis*, *Devaleraea ramentacea*, *Desmarestia aculeata*, *Pilayella littoralis*, growing between 0 and (10 to) 15 (or 20)°C with optima between 0 and 10°C. The upper survival temperatures in these species and in *Chromastrum secundatum*, *Chromastrum virgatulum*, *Chordaria flagelliformis* were between 17 and 23°C (duration of experiment: 2 weeks). (2) A eurythermal group including *Enteromorpha clathrata*, *Enteromorpha intestinalis* and *Polysiphonia urceolata* growing between 0 and 20°C with growth optima at 10 or 15°C. The upper survival temperatures in these species and in *Chaetomorpha tortuosa*, *Bangia atropurpurea* and *Eudesme virescens* were between 24 and 31°C. These algal species showed little adaptation to the Arctic temperatures. In contrast, algae from the first group exhibited a relatively high adaptation to low temperatures – approaching the low temperature requirements of Antarctic algae. The results are discussed in relation to the geographic distribution of individual species.

INTRODUCTION

The development of the cold-water marine algal floras in the Northern and Southern Hemisphere are a result of the great glaciations since the Tertiary (Lüning & tom Dieck, 1989). A characteristic cold water environment has existed in Antarctica for 25–30 million years (= 25–30 Ma), a first glacial peak occurring at approx. 14 Ma (Grant-Meckie, 1979). This development began much later in the North Polar Sea, at approx. 2 Ma (Thiede, 1986). The four great Pleistocene glaciations displaced the terrestial and marine flora and fauna in the Northern Hemisphere towards the south, and during the interglacials, again towards the north. 18,000 years ago, during the last glaciation maximum (Würm-/Wisconsin), the temperature of the upper seawater layer in the North Atlantic was ca. 10°C lower than today (Lüning, 1990). During the glaciations, the North Atlantic region (northwards of a line from New York to southern England) was covered with an ice-layer and was re-colonised during the interglaciation (postglacial colonisation, Hempel, 1987). It is therefore assumed that the Arctic region is an extension of the cold-temperate region of the North Atlantic (Lüning, 1990).

Because of the earlier glaciation of Antarctica, there was a longer period available for the development of cold-water biota in the Southern Ocean, compared to that in the Northern Hemisphere (Hempel, 1987; Lüning & tom Dieck, 1989). Hence, a stenothermal flora and fauna developed in the Antarctica, with a high growth efficiency at low temperatures and a correspondingly low tolerance to high temperatures (Hempel, 1987; Wiencke & tom Dieck, 1989, 1990). In contrast, Arctic and cold-temperate species from the Northern Hemisphere are relatively eurythermal (Bolton & Lüning, 1982; Bolton, 1983; Egan et al., 1990; tom Dieck, 1989, 1992b, 1993).

Experimental data on temperature requirements of Arctic macroalgae are rare (Breeman, 1988). In this study, the temperature requirements for growth and survival of Arctic macroalgae from Disko Island, Greenland, were determined. The method for determination of growth rates at different temperatures has been refined, and, using this technique, it was possible to demonstrate a higher acclimation potential, as well as adaptation to the Arctic temperature regime, than was previously recorded. These results are discussed in relation to the temperature requirements of the same or other species from cold-temperate regions and from the Southern Ocean. Finally, the temperature data obtained are used to explain the biogeographic boundaries of the investigated species.

MATERIALS AND METHODS

The macroalgae investigated were isolated as spores or thallus fragments by C. Wiencke during an expedition to Disko Island (Greenland), using the methods described by Clayton & Wiencke (1986). The species are listed in Table 1. Algae were subsequently cultivated in the laboratory at a temperature of 10 °C. Cultivation methods, determination of growth rates and upper survival temperatures (duration of experiments: 2 weeks) were carried out as described by Wiencke & tom Dieck (1989). The growth experiments, however, were partly modified; growth was followed over a period of 5 weeks. Fresh weight was measured weekly or fortnightly and the algal biomass was reduced to initial weight, in order to exclude the effects of low light conditions resulting from self-shading. Between repetitive experiments the same initial weight was taken. For each interval, the specific growth rates, expressed in % increase d^{-1}, were calculated by use of the following equation from Lüning (1985):

$$\text{Specific growth rate} = 100 \ (\ln W_t / \ln W_j) \ t^{-1};$$

where W_j = initial size or fresh weight; W_t = size or fresh weight on day t; t = time interval.

In *Devaleraea ramentacea* and in the sporophytes of *Desmarestia aculeata* growth was determined once during a period of 6 weeks. In *D. aculeata* gametophytes growth was investigated over a period of 3 days, following 5 days where the algae had been maintained at the experimental temperature and light conditions. The experimental period could not be extended, because of the high growth rates (Fig. 6), making a planimetric evaluation impossible.

RESULTS

The change of growth rates in *Acrosiphonia sonderi* with time after exposure to various temperatures is shown in Figures 1a–e. During the second week the growth rates

Table 1. Investigated species, location, isolator and culture-number

Algal species	Location	Isolator/ Cultivator	Culture No.
Chlorophyta			
Acrosiphonia arcta (Dillw.) J. Ag. Acrosiphonales	Disko Island, Nipisat	Pedersen/ Wiencke/ Bischoff	1120
Acrosiphonia sonderi (Kütz.) Kornm. Acrosiphonales	Disko Island, Godhavn	Wiencke/ Bischoff	1096
Urospora penicilliformis Roth (Areschoug) Acrosiphonales	Disko Island, Godhavn	Wiencke/ Bischoff	1104
Chaetomorpha tortuosa (Dillw.) Kütz. Cladophorales	Disko Island, Godhavn	Wiencke/ Bischoff	1091
Enteromorpha clathrata (Roth) Grev. Ulvales	Disko Island, Godhavn	Wiencke/ Bischoff	1086
Enteromorpha intestinalis (L.) Link Ulvales	Disko Island, Godhavn	Wiencke/ Bischoff	1088
Ulva lactuca L. Ulvales	Disko Island, Godhavn	Wiencke/ Bischoff	1128
Rhodophyta			
Bangia atropurpurea (Roth) C. Ag. Bangiales	Disko Island, Godhavn	Wiencke/ Bischoff	2089
Devaleraea ramentacea (L.) Guiry male gametophyte, Palmariales	Disko Island, Godhavn	Wiencke/ Bischoff	2094
Polysiphonia urceolata (Lightf. ex Dillw.) Grev. Ceramiales	Disko Island, Godhavn	Wiencke/ Bischoff	2093
Chromastrum secundatum (Lyngb.) Papenfuss Nemaliales	Disko Island, Godhavn	Wiencke/ Bischoff	2092
Chromastrum virgatulum (Harvey) Papenfuss Nemaliales	Disko Island, Nipisat	Pedersen/ Wiencke/ Bischoff	2091
Phaeophyta			
Chordaria flagelliformis (O. F. Müller) C. Ag. Chordariales	Disko Island, Godhavn	Wiencke/ Bischoff	
Eudesme virescens (Carm. ex. Harv. Hook) J. Ag. Chordariales	Disko Island, Godhavn	Wiencke/ Bischoff	3107
Desmarestia aculeata (L.) Lamour. male & female gametophyte, Desmarestiales	Disko Island, Godhavn	Wiencke/ Bischoff	3108/ 3109
Pilayella littoralis (L.) Kjellm. Ectocarpales	Disko Island, Godhavn	Wiencke/ Bischoff	3100

at 0 and 5 °C increased rapidly, levelling off during the next 7 days and increasing slowly up to the end of experiment. At 10 and 15 °C, similar but not as large increases in growth rate were evident, and, later, growth rates were relatively constant. At 20 °C, growth rates decreased during the second week, but then increased slowly.
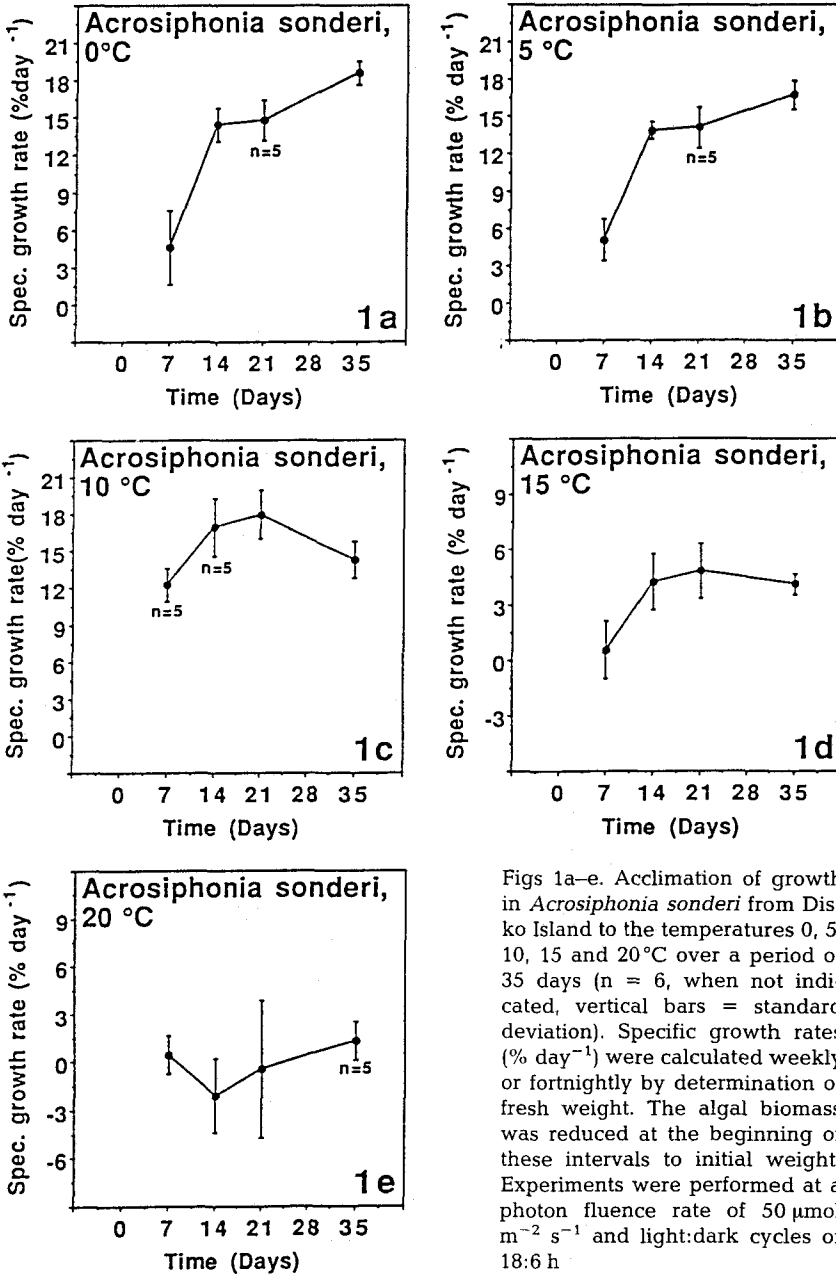
Figs 1a–e. Acclimation of growth in *Acrosiphonia sonderi* from Disko Island to the temperatures 0, 5, 10, 15 and 20 °C over a period of 35 days (n = 6, when not indicated, vertical bars = standard deviation). Specific growth rates (% day^{-1}) were calculated weekly or fortnightly by determination of fresh weight. The algal biomass was reduced at the beginning of these intervals to initial weight. Experiments were performed at a photon fluence rate of 50 μmol m^{-2} s^{-1} and light:dark cycles of 18:6 h

The investigated species can be classified into 2 groups according to their temperature-growth characteristics (Figs. 2–12) and upper survival temperature (USL):

G r o u p 1 , stenothermal species: *Acrosiphonia sonderi* grew between 0 and 20 °C, with an optimum at 0 °C and with very low rates at ≥ 15 °C (Fig. 2). The USL was 23 °C
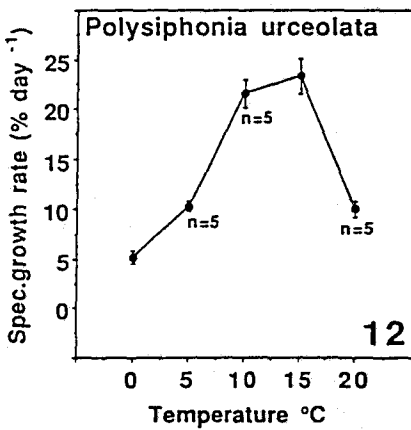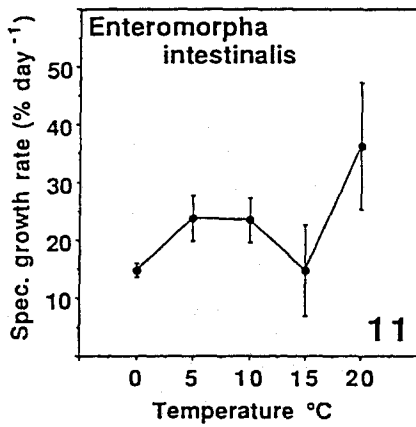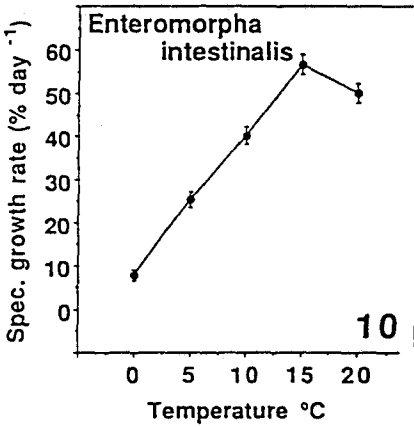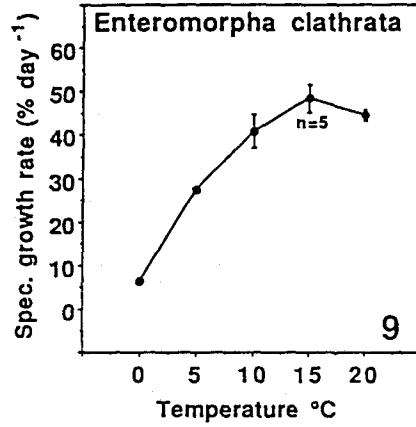
Table 2. Life cycles of the investigated marcroalgae

Algal species	Life-cycle	Literature
Chlorophyta		
Acrosiphonia arcta (Dillw.) J. Ag. Acrosiphonales	isomorphic, monoecious	Kornmann (1964)
Acrosiphonia sonderi (Kütz.) Kornm. Acrosiphonales	asexual	Kornmann & Sahling (1983)
Urospora penicilliformis Roth (Areschoug) Acrosiphonales	heteromorphic, dioecious, anisogameous	Lokhorst & Trask (1981) Kornmann (1966a, b)
Chaetomorpha tortuosa (Dillw.) Kütz. Cladophorales	asexual	Kornmann (1972)
Enteromorpha clathrata (Roth) Grev. Ulvales	isomorphic, dioecious, anisogameous	Bliding (1963)
Enteromorpha intestinalis (L.) Link Ulvales	isomorphic, dioecious, anisogameous	Bliding (1963)
Ulva lactuca L. Ulvales	isomorphic, dioecious, anisogameous	Kornmann & Sahling (1983)
Rhodophyta		
Bangia atropurpurea (Roth) C. Ag. Bangiales	asexual, heteromorphic	Pedersen (1976) Richardson & Dixon (1968)
Devaleraea ramentacea (L.) Guiry Palmariales	heteromorphic, dioecious	van der Meer (1981)
Polysiphonia urceolata (Lightf. ex Dillw.) Grev. Ceramiales	isomorphic, dioecious	van den Hoek (1984)
Chromastrum secundatum (Lyngb) Papenfuss Nemaliales	asexual	Pedersen (1976)
Chromastrum virgatulum (Harvey) Papenfuss Nemaliales	asexual	Pedersen (1976)
Phaeophyta		
Chordaria flagelliformis (O. F. Müller) C. Ag. Chordariales	asexual, heteromorphic	Kornmann (1962)
Eudesme virescens (Carm. ex. Harv. Hook) J. Ag. Chordariales	asexual, heteromorphic	Peters (1987)
Desmarestia aculeata (L.) Lamour., Desmarestiales	heteromorphic, dioecious, oogameous	Schreiber (1932) Müller & Lüthe (1981)
Pilayella littoralis (L.) Kjellm. Ectocarpales	asexual	Müller & Stache (1989)

(Table 3). Macrothalli of *Acrosiphonia arcta* and *Urospora penicilliformis* grew between 0 and 15 °C, with optimum growth at 0 to 10 °C and 0 °C, respectively (Fig. 4). Very low growth rates were measured in *A. arcta* at ≥ 15 °C (Fig. 3). *A. arcta* survived up to 22 °C and *U. penicilliformis* up to 23 °C (Table 3). The male gametophyte of *Devaleraea ramentacea* grew at similar rates between 0 and 10 °C with a slight optimum at 5 °C (Fig. 5). The USL was 19 °C (Table 3). The gametophytes of *Desmarestia aculeata* grew between 0 and 20 °C (Fig. 6). The female gametophyte exhibited a growth plateau
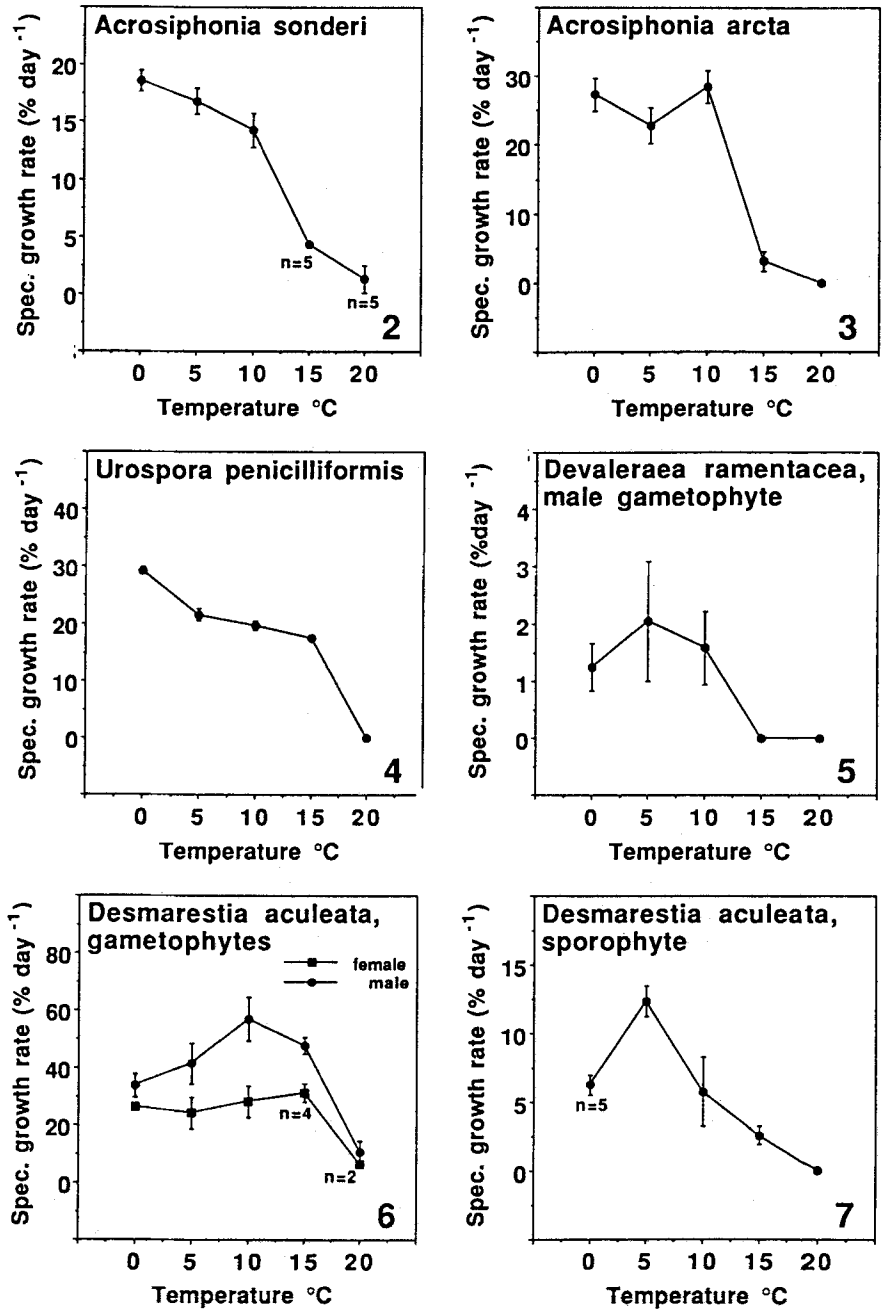
Figs 2–12. Temperature requirements for growth of macroalgae, isolated on Disko Island. Most experiments were performed as described in the legend of Figures 1a–e. Generally, the growth rates obtained in the measurement of the last interval were chosen to describe relationships between growth and temperature. N. B. The scales represent different values. Growth rates in Figure 10 were measured after 14 days. The experiments shown in Figures 5 and 6 were performed in Petri dishes at

Figure 8. Pilayella littoralis — Spec. growth rate (% day^{-1}) vs Temperature °C

Figure 9. Enteromorpha clathrata — Spec. growth rate (% day^{-1}) vs Temperature °C

Figure 10. Enteromorpha intestinalis — Spec. growth rate (% day^{-1}) vs Temperature °C

Figure 11. Enteromorpha intestinalis — Spec. growth rate (% day^{-1}) vs Temperature °C

Figure 12. Polysiphonia urceolata — Spec. growth rate (% day^{-1}) vs Temperature °C

50 or 15 μmol m^{-2} s^{-1}, respectively, and the growth rates were determined in terms of area. Growth rates in Figure 5 were measured after a period of 42 days. Growth rates shown in Figure 6 were determined after 3 days, following a period of 5 days, where the algae had been maintained at the experimental temperature and light conditions (n = 3, when not indicated)

between 0 and 15 °C, whereas the male gametophyte grew optimally at 10 °C, and in both cases the USL was 22 °C (Table 3). The sporophyte of *D. aculeata* only grew between 0 and 15 °C, with maximum rates at 5 °C (Fig. 7). Two out of the three sporophytes survived 20 °C (Table 3). *Pilayella littoralis* grew between 0 and 20 °C with an optimum between 5 and 15 °C. At 20 °C and also at 0 °C, only low growth rates were determined (Fig. 8). The USL was 21 °C (Table 3). *Chromastrum secundatum, Chromastrum virgatulum* and the micro- and macrothalli of *Chordaria flagelliformis* survived up to 17 °C, 21 °C or 23 °C, respectively (Table 3).

G r o u p 2 , eurythermal species: *Enteromorpha clathrata* grew optimally between 10 and 20 °C (Fig. 9), with 10 % of the optimal growth rate at 0 °C. The USL was 31 °C (Table 3). *Enteromorpha intestinalis* sporulated in some cases at 15 and 20 °C, resulting in a simultaneous decline of the growth rate. Figure 10 shows the growth rates from the first two weeks before sporulation, and Figure 11 from the week after sporulation. Ignoring the sporulation, growth was highest between 15 and 20 °C. This species tolerated 28 °C (Table 3). *Polysiphonia urceolata* showed optimum growth between 10 and 15 °C (Fig. 12), and two of the three test plants survived 26 °C (Table 3). *Ulva lactuca* and *Chaetomorpha tortuosa* tolerated 26 °C, macrothalli of *Bangia atropurpurea* tolerated 23–24 °C, and the micro- and macrothalli of *Eudesme virescens* tolerated 30 °C (Table 3). It is not known if gametophytes or (tetra-)sporophytes of *E. clathrata, E. intestinalis, P. urceolata* and *U. lactuca* were used, since these species have isomorphic life-history stages (Table 2).

DISCUSSION

Methodological considerations

In most previous macroalgal growth studies, specific growth rates (% d^{-1}) have been calculated as mean values over whole experimental periods mostly between 24 hours and months (e.g. Fortes & Lüning, 1980; Bolton, 1983; Guiry et al., 1987; tom Dieck, 1989; Wiencke & tom Dieck, 1989, 1990; Novaczek & Breeman, 1990), although some investigations used experimental periods of up to seven months (Rueness & Tanager, 1984; Yarish et al., 1986). In the current study, growth rates were determined weekly or fortnightly over 5 (or 6) weeks (Fig. 1a–e). The values obtained reflect the temperature acclimation of growth during this period. Rates from the last measurement were generally chosen to describe relationships between growth and temperature. If growth rates had been calculated over the whole time, the resulting temperature growth patterns would differ from those described. It is obvious that the growth rates of temperature-acclimated plants give a more precise indication of temperature-growth relationships than results obtained by a more simplified methodology. It must, however, be noted that this refined methodology can be used only with species, which grow consistently over long periods. In algae with internal growth rhythms (Lüning, 1991; tom Dieck, 1992a), this method is probably not applicable.

Changes in temperature have a fundamental influence on algal metabolism, and certain processes such as enzymatic reactions are strongly temperature dependent (Lobban et al., 1985). The balance between single metabolic steps or whole pathways may be altered by temperature changes (Berry & Raison, 1981). After acclimation to a

Table 3. Temperature tolerance of the investigated species determined in two weeks exposures to the given temperatures (x = species alive; - = species dead, no growth during 4-week postculture under favourable conditions. m./f gam. = male/female gametophyte; sporo. = sporophyte; micro./macro. = micro-/macrothalli. Every developmental stage was tested in 3 to 6 series.)

Algal species	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	Maximum survival temp. (°C)
Chlorophyta																		
Acrosiphonia arcta						xxx	xxx	- -	- -	- -	- -	- -						22
Acrosiphonia sonderi						xxx	xxx	xxx	- -	- -	- -	- -						23
Chaetomorpha tortuosa								xxx	xxx	xxx	xx-	- -	- -					25–26
Enteromorpha clathrata				xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	- -	31
Enteromorpha intestinalis				xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	- -	- -	- -		28
Ulva lactuca							xxx	xxx	xxx	xxx	xxx	- -	- -					26
Urospora penicilliformis			xxx	xxx	xxx	xxx	xxx	xxx	- -	- -	- -	- -						23
Rhodophyta																		
Bangia atropurpurea	xxx	xxx	xxx	xxx	- -	- -	- -	- -	-xx	- -	- -							23–24
Devaleraea ramentacea m. gam.	xxx	xxx	xxx	xxx	xxx	xxx	- -	xxx	- -	- -								19
Polysiphonia urceolata									xxx	xxx	xx-	- -						25–26
Chromastrum secundatum	- -	xxx	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -						17
	xxx	xxx	- -	- -	- -	- -												
Chromastrum virgatulum	xxx	xxx	xxx	xxx	xxx	xx-	- -	- -	- -	- -	- -	- -						21
Phaeophyta																		
Chordaria flagelliformis micro.	xxx	xxx	xxx	xxx	xx-	xxx	xxx	xxx	- -	- -	- -	- -						23
Chordaria flagelliformis macro.	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	- -	- -	- -	- -						23
Desmarestia aculeata m. gam.						xxx	xxx	- -	- -	- -	- -	- -						22
Desmarestia aculeata f. gam.						xxx	xxx	- -	- -									22
Desmarestia aculeata sporo.	xxx	- -	xxx	xxx	xx-	- -	- -	- -	- -	- -	- -	- -						19–20
Eudesme virescens						xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	- -	- -	30
Pilavella littoralis						xxx	- -	- -	- -	- -	- -	- -						21

respective temperature, metabolic processes are adjusted to an appointed rate, and a new balance is restored within an experimental time-span of mostly 5 weeks (Fig. 1).

There was frequently a large increase in growth during the first 2 to 3 weeks (Fig. 1a–d). It is conspicuous that, at 10 °C, a decrease was observed, although the algae had been cultivated at this temperature before experimentation. However during this time the cultures were quite dense. At the start of the growth measurements the density was reduced, and the increases in growth are possibly a reflection of acclimation to higher photon fluence rates, due to less self-shading. Studies on *Scytosiphon lomentaria* (Phaeophyta) and *Bangia atropurpurea* (Rhodophyta) have shown that acclimation to altered photon fluence rates requires a period of approx. 2 weeks (Orfanidis, 1992). This indicates the importance of keeping the amount of algal material relatively constant during a growth experiment, thereby avoiding shelf-shading effects.

General temperature characteristics

The isolated macroalgal species from Disko Island can be divided into two groups. The first group includes species with more stenothermal temperature requirements: *Acrosiphonia arcta*, *Acrosiphonia sonderi*, *Urospora penicilliformis*, *Devaleraea ramentacea*, *Desmarestia aculeata*, *Pilayella littoralis*, *Chromastrum secundatum*, *Chromastrum virgatulum*, *Chordaria flagelliformis*. These algae displayed a high degree of cold adaptation with respect to the growth ranges (mostly 0–15 °C) and optima (0–10 °C). The USL's (17–23 °C) were however – with the exception of *C. secundatum* and *D. ramentacea* – similar to those of algae from the cold-temperate regions (Bolton & Lüning, 1982; Lüning, 1984; Lüning, 1985; Lüning & Freshwater, 1988; tom Dieck, 1992b, 1993; Wiencke & tom Dieck, 1990). The second group includes species with more eurythermal temperature requirements: *Enteromorpha clathrata*, *Enteromorpha intestinalis*, *Polysiphonia urceolata*, *Ulva lactuca*, *Chaetomorpha tortuosa*, *Bangia atropurpurea*, *Eudesme virescens*. The growth range was between 0 and 20 °C with optimum growth between 10 and 15 °C: typical for cold-temperate algae (Bolton & Lüning, 1982; Lüning, 1984; Lüning, 1985; tom Dieck 1992b, 1993; Wiencke & tom Dieck, 1990). These algae survived up to 24 or even 31 °C, similar to warm- and cold-temperate species (Yarish et al., 1987; Cambridge et al., 1987; Lüning, 1990).

These results show that macroalgae from the Arctic region are mostly less adapted to low temperatures than algae from the Antarctic region (Wiencke & tom Dieck, 1989). This applies especially to the eurythermal group, both in regard to growth and temperature-tolerance level. The relatively high USL's of most species of the stenothermal group also indicates this trend. However, in some species from Disko Island unusually low temperature requirements were found.

The low USL of *C. secundatum* (17 °C) is the lowest so far to be determined in Arctic seaweeds, and nearly similar to those of endemic Antarctic macroalgae (Wiencke & tom Dieck, 1989). The temperature-growth ranges are expected to be relatively small with growth optima at low temperatures. The USL of the male gametophyte of the endemic Arctic red alga *D. ramentacea* was, at 19 °C (Table 3), similarly low. The alga grew between 0 and 10 °C, with optimal values at 5 °C (Fig. 5). Novaczek et al. (1990) found a different temperature requirement for optimum growth and survival between isolates from the Canadian Arctic and the European coast (Norway, Jan Mayen, Iceland). The

isolates from both coasts grew between 0 and 10 °C, but the Canadian isolates grew optimally between 0 and 5 °C, and survived up to 20 and 23 °C (experimental period: 2 weeks or 3 months, respectively). The European plants exhibited optimum growth between 5 and 10 °C, and USL's between 18 and 20 °C. The temperature requirements for growth and the USL of *D. ramentacea* are nearly similar to those of the endemic Antarctic species studies so far. For example, the endemic Antarctic alga *Palmaria decipiens,* which belongs to the same order Palmariales (Guiry, 1982), grows between 0 and 10 °C (with an optimum at 5 °C); however, this species only tolerates temperatures of 16 to 17 °C (Wiencke & tom Dieck, 1989).

The growth optima at 0 °C of *A. sonderi* and *U. penicilliformis,* and *A. arcta* between 0 and 10 °C were unexpected (Figs. 2–4). Up to now, growth optima at 0 °C in Arctic to cold-temperate species were found only in the above-discussed *D. ramentacea* (Novaczek et al., 1990). *A. arcta* as well as *U. penicilliformis* grew between 0 and 15 °C and *A. sonderi* between 0 and 20 °C, with very low growth rates at $\geq$ 15 °C. Fortes & Lüning (1980) described a growth range between 0 and 20 °C with an optimum at 10 °C for *A. arcta* from Helgoland. However, the investigation period was only 24 hours, and, hence, the results are not strictly comparable to results obtained in the present study (Fig. 3). Wiencke & tom Dieck (1990) determined growth optima at 5 °C for isolates of *A. arcta* and *U. penicilliformis* from King George Island (Antarctica). These rates were (in contrast to the current study) calculated over the whole investigation period of 28 days (+ 7 days for acclimation). Using the test methods of the present study, a growth optimum at 0 °C can also be expected in the Antarctic isolates of these species. The USL's from the Arctic isolates of *A. arcta* and *U. penicilliformis* were 22 or 23 °C, respectively (Table 3), and from the Antarctic isolates 22 or 19 °C, respectively (Wiencke & tom Dieck, 1990). The available data indicates an ecotypic variation in the temperature requirements for survival, and presumably also for growth, in the different Northern and Southern Hemisphere populations of these two species.

Desmarestia aculeata male and female gametophytes from Disko Island exhibited USL's of 22 °C, which are comparable to gametophytes from Helgoland and Western Canada (Peters & Breeman, 1992), and a growth range between 0 and 20 °C (optimum, male: 10 °C; female: 0 to 15 °C; Fig. 6). In this context, it must be noted that these growth values refer to an investigation time of only 3 days, preceded by 5 days exposure to experimental conditions. The sporophytes showed a lower temperature requirement than the gametophytes, similar to other brown algal species with heteromorphic life-histories (Breeman, 1988, 1990). The growth range of juvenile sporophytes was between 0 and 15 °C, with optimum rates at 5 °C (Fig. 7). Young sporophytes of *D. aculeata* from Helgoland grew between 0 and 25 °C, with optimal values at 10 °C (determined after 24 h exposure; Fortes & Lüning, 1980). The isolate from Disko Island formed sporophytes at 5 °C, but not at 10 °C. This contrasts with isolates from Helgoland in which sporophyte formation was induced at the higher temperature (Lüning, 1981; Müller & Lüthe, 1981), and shows an adaptation to environmental conditions of the Arctic region with respect to growth as well as reproduction. Juvenile sporophytes from Disko Island survived up to 20 °C (Table 3). The USL's in young sporophytes from Helgoland was between 18 and 20 °C (Lüning, 1984). Adult sporophytes from Helgoland and the Northeast Pacific survived up to 20 or 23 °C and up to 23 °C, respectively (Lüning, 1984; Lüning & Freshwater, 1988; incubation period: one

week, photosynthetic evaluation). These results do not point to an ecotypic variation in this species with respect to the USL's.

The isolates of *P. littoralis* from Disko Island grew optimally between 5 and 15 °C (Fig. 8), but with very low growth rates, and with a very reduced zoidangia formation at 20 °C; the USL was 21 °C (Table 3). Isolates from Helgoland, Chile and Diego Ramirez Island (Drake Passage) grew optimally at 12 °C and showed reduced formation of zoidangia at 20 °C (Müller & Stache, 1989). The isolate from Helgoland tolerated 25 °C (Lüning, 1984; one-week test) and that from Diego Ramirez Island 22 to 23 °C (Wiencke & tom Dieck, 1990; two-week test). If the different methods are comparable, it is obvious that the growth optima, temperature requirements for reproduction and survival of the population from Disko Island are broadened towards lower temperatures, compared to cold-temperate isolates. This result is similar to that found in the comparable species *Ectocarpus siliculosus* (Bolton, 1983).

Enteromorpha clathrata from Disko Island grew between 0 and 20 °C with an optimum between 10 and 20 °C (Fig. 9). The upper temperature tolerance was 31 °C (Table 3). An isolate from southernmost Chile showed the same temperature range, but grew optimally between 5 and 15 °C, with lower growth rates at 20 °C than at 0 °C (Wiencke & tom Dieck, 1990). This isolate only tolerated 22 to 23 °C (not shown in Table 3). If the taxonomic status of the two isolates is correct, these data may indicate the presence of temperature ecotypes in this species.

Bangia atropurpurea from Disko Island survived 24 °C (Table 3), a result comparable to the USL of 25 °C for an isolate from Helgoland (Lüning, 1984). The USL of this species from Lake Ontario was between 30 and 35 °C (Graham & Graham, 1987; two to four weeks; photosynthetic evaluation) indicating ecotypic variation. In contrast, isolates of *Polysiphonia urceolata*, *Chaetomorpha tortuosa* and *Ulva lactuca* from Helgoland had an USL at 25 °C, 26 °C or 28 °C, respectively, (Lüning, 1984); this was similar to the temperature tolerance of these species from Disko Island (Table 3).

Many of the investigated species from Disko Island exhibited an adaptation to low temperatures with respect to growth and reproduction, but only two species, *Chromastrum secundatum*, *Devaleraea ramentacea*, showed an adaptation to low temperatures with respect to the USL. This is another indication for the assumption that the temperature tolerance is – in contrast to the temperature requirements for growth and reproduction – a very conservative trait (cf. Breeman, 1988; Novaczek et al., 1989; Lüning, 1990), which probably only changes over long evolutionary periods in macroalgae and other organisms. In molluscs, for example, cold water adaptation is performed in two steps (Scarlato, 1977): firstly, an initial broadening of survival and reproduction ranges towards lower temperatures and secondly, a loss of ability to survive higher temperatures. Similar processes of cold-adaptation may occur in macroalgae (Lüning & tom Dieck, 1989). In this respect, the relatively short cold-water history of only 2 Ma in the Arctic region may not be sufficient to alter the USL's more markedly and in a larger number of species. A higher degree of adaptation to low temperatures has so far only been shown in species from the Antarctic region, where water temperatures have been low for the much longer period of 25 Ma (Grant-Meckie, 1979). This applies not only to endemic Antarctic species (Wiencke & tom Dieck, 1989), but also to *Acrosiphonia arcta*, *Urospora penicilliformis* and other polar-cold temperate species from Antarctica (Wiencke & tom Dieck, 1990).

Phytogeographic analysis

The temperature requirements for growth, reproduction and survival are primarily responsible for determining distribution boundaries of macroalgae: Northern distribution limits of Arctic cold-temperate species are determined by summer temperatures which are too low for growth and/or reproduction, whereas southern boundaries are set by either lethally high summer temperatures, or extreme winter temperatures (van den Hoek, 1982a, b; Breeman, 1988, 1990). In this connection, it is important to take into consideration that the temperatures of near-shore coastal waters may in fact be different from temperatures in the open ocean (van den Hoek, 1982b; van den Hoek & Breeman, 1989). The geographical distributions (in relation to described temperature demands) of the species investigated in this study are discussed below.

Acrosiphonia sonderi is found on both coasts of the N Atlantic, but is absent in the Canadian Arctic. It has only been recorded from one site in the Pacific – an indication of incomplete collecting (Fig. 13). The southern distribution boundary in the NW Atlantic extends along the 20 °C August isotherm (20° S). If the temperature requirement of the Disko Island isolate is extrapolated, this boundary is probably set by the upper growth (20 °C) and/or survival (23 °C) limit. The southern distribution boundary in the NE Atlantic corresponds with the 8 °C February isotherm (8° W). It is presumed that the distribution on this coast is limited by the formation of asexual propagules (Table 2), which were not observed at ≤ 10 °C.

Acrosiphonia sonderi
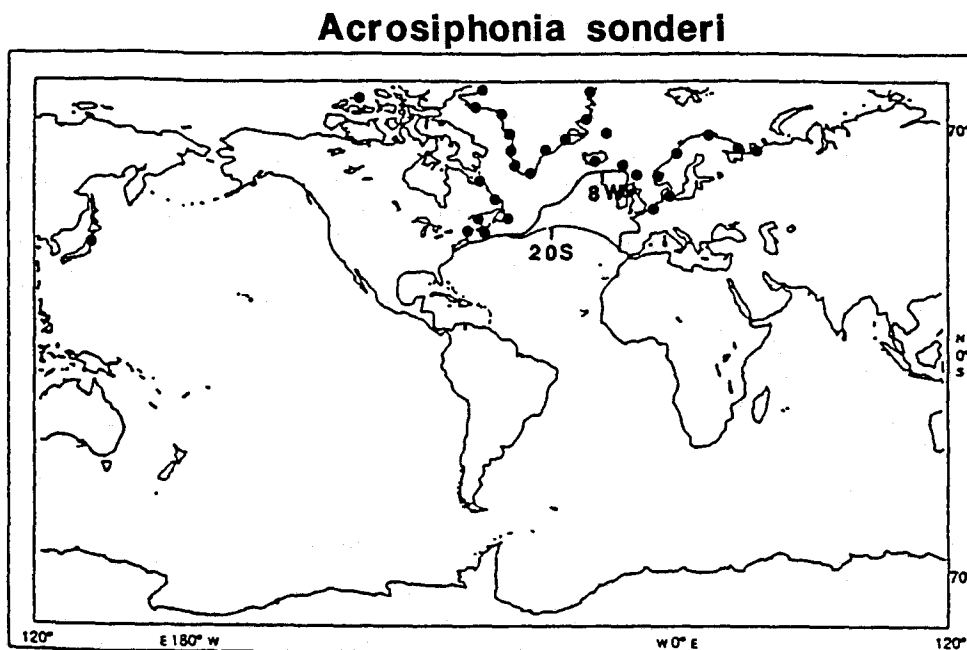
Fig. 13. Distribution of *Acrosiphonia sonderi*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Pedersen, 1976; South, 1984; South & Tittley, 1986; van den Hoek [pers. comm.].)
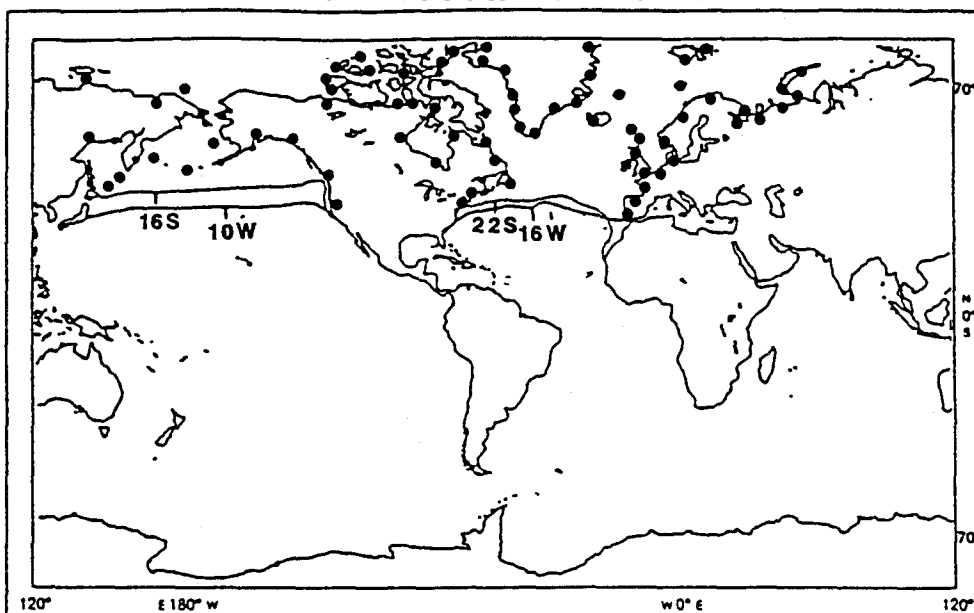
Devaleraea ramentacea
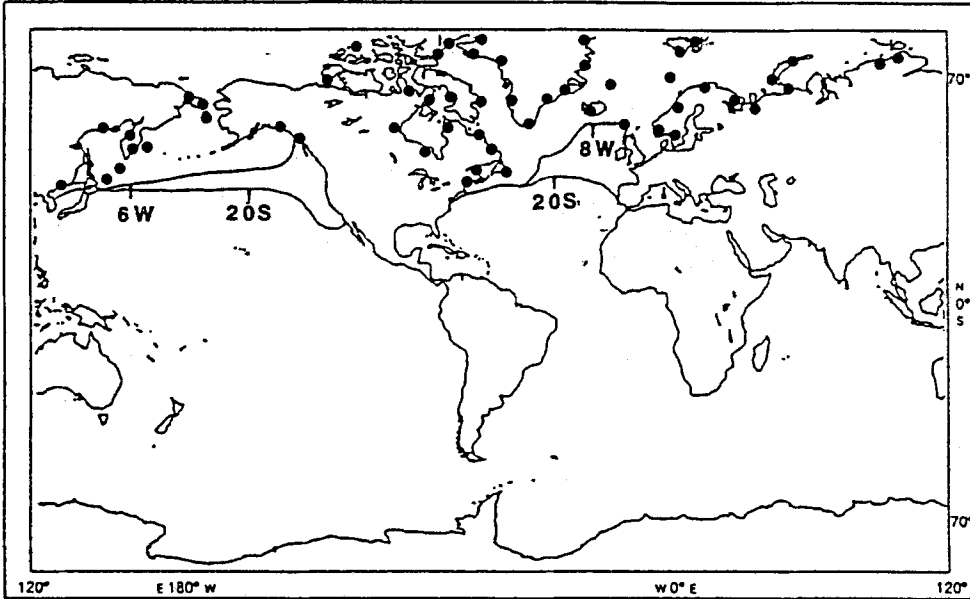
Fig. 14. Distribution of *Devaleraea ramentacea*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Kjellman, 1883; Pedersen, 1976; Scagel et al., 1989; South, 1984; South & Tittley, 1986.)

The southern distribution of the endemic Arctic alga *Devaleraea ramentacea* is limited in the N Atlantic through the 20° S and 8° W isotherms (Fig. 14). The southern boundary in the NW Atlantic seems to be a lethal boundary. In support of this, *D. ramentacea* from the Canadian Arctic had USL's between 20 and 23 °C (Novaczek et al., 1990), but the survival temperature of the Disko Island isolate (19 °C; Table 3) does not explain this. Novaczek et al. (1990) showed different temperature requirements for optimum growth and survival between isolates from the Canadian Arctic and the European coast. The temperature requirement of the isolate from Greenland, studied here, is similar to that of the European isolates (see Section B). It can therefore be hypothesised that this species recolonised Greenland from the European coast after the last Pleistocene glaciation. The distribution boundary in the NE Atlantic correlates with the 8° W isotherm. This area is probably limited through the temperature requirement for growth and reproduction, since this species only grew between 0 and 10 °C, and fertilisation has been observed between −2 and 8 °C with optima at 5 °C (A. M. Breeman, pers. comm.). The distribution boundary in the NW Pacific extends along the 20° S isotherm, suggesting a lethal boundary similar to that in the NW Atlantic. On the NE Pacific coast, the boundary (6° W) is lower than in the NE Atlantic. This implies differences in the temperature requirement for growth and/or reproduction in the Pacific and Atlantic populations.

The southern distribution boundary of *Desmarestia aculeata* in the N Atlantic extends along the 22° S and 16° W isotherms (Fig. 15). This species grows in the sublit-
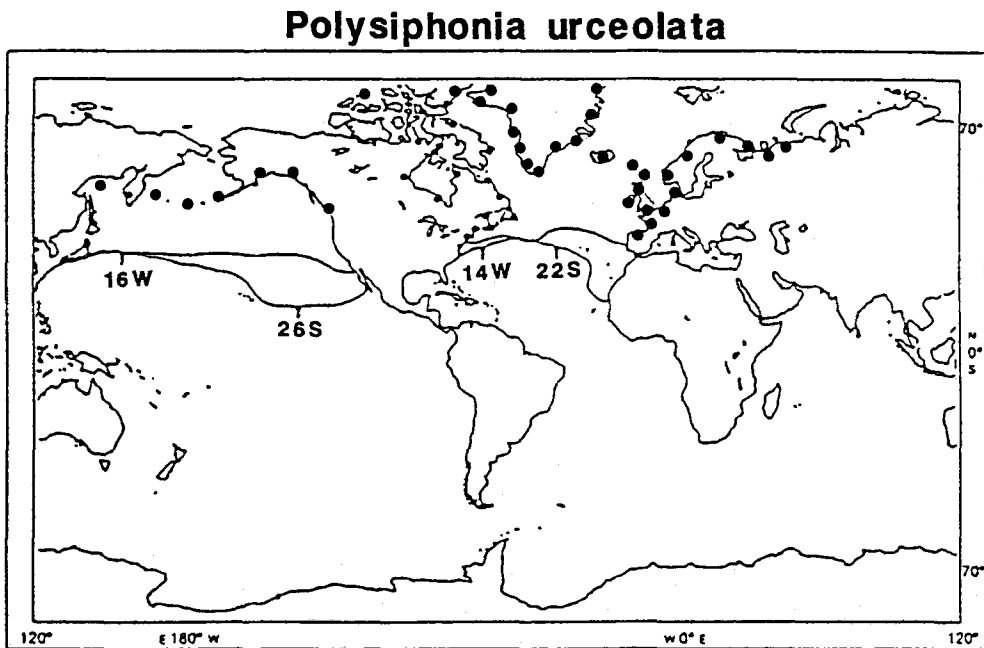
Desmarestia aculeata

Fig. 15. Distribution of *Desmarestia aculeata*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Kjellman, 1883; Pedersen, 1976; Scagel, 1957; Scagel et al., 1989; South, 1984; South & Tittley, 1986.)

toral, where temperatures are lower than at the surface. The distribution on the NW Atlantic coast, described by the 22° S isotherm, can be explained by the USL of gametophytes and/or sporophytes (22 or 20–23 °C, respectively, Table 3; Section B). The southern distribution on the NE Atlantic coast (16° W) is evidently limited by the temperature requirement for reproduction, since the gametophyte USL's would permit a more southerly distribution. On the other hand, the temperature requirement for reproduction of the Disko Island isolate (≤ 5 °C) and the Helgoland isolate (≤ 10 °C) is not sufficient to explain this boundary. It is foreseeable that further ecotypic differentiation has occured. The distribution on the NE Pacific coast is limited by the 16° S and 10° W isotherms (Fig. 15). In all probability, the 16° S isotherm does not represent the southern boundary, because the USL of sporophytes from this coast was 23 °C (Lüning & Freshwater, 1988; Section B). Therefore it is to be expected that the southern boundary is set by the 10° W isotherm. It appears that the information about the distribution in the NW Pacific is incomplete (16° S), since it would be expected that this species could occur at least down to the 10° W isotherm (Fig. 15). Based on the USL of the gametophytes, it is probable that *D. aculeata* could be found even further south.

The distributions of *Chromastrum secundatum* and *Chromastrum virgatulum* are unknown. The southern distribution in the NW Atlantic could be limited through the USL's (21 or 17 °C, respectively). During cultivation at 10 °C, growth and monospore formation (Table 2) was observed, therefore in the NE Atlantic this species could extend at least down to the 10° W isotherm.

The southern distribution of *Polysiphonia urceolata* on the NW Atlantic coast is limited by the 22° S isotherm. The USL (26 °C; Table 3) of the Disko Island isolate points to a lethal boundary. The southern boundary in the NE Atlantic (14° W) is probably limited by the temperature requirement for reproduction. Because of the growth range (0 to 20 °C) and the USL (26 °C), this species could potentially occur on the NW African coast (Fig. 16). The southern distribution in the NW Pacific can be characterised by the 26° S and 16° W isotherm. It could be a combination between a lethal and reproduction boundary. The southern distribution in the NE Pacific reaches North Washington (16° S, 8° W). The distribution potential of this species would appear to be underexploited on this uninterrupted rocky coast.

Polysiphonia urceolata

Fig. 16. Distribution of *Polysiphonia urceolata*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Kjellman, 1883; Lindauer et al., 1961; Papenfuss, 1964; Pedersen, 1976; Scagel, 1957; Scagel et al., 1989; South, 1984; South & Tittley, 1986.)

The southern distribution of *Acrosiphonia arcta* in the NW Atlantic correlates with the 22° S isotherm (Fig. 17). The USL of the Disko Island isolate (22 °C; Table 3) explains this boundary. On the NE Atlantic coast this species is found up to the 14° W isotherm. This boundary can be set by growth, since this isolate had negative growth rates at 20 °C and very low rates at 15 °C (Fig. 3). Moreover, low temperature requirements for spore formation can explain this boundary (cf. van den Hoek, 1982b). The southern distribution boundary in the N Pacific extends along the 26° S isotherm in the West and along the 12° W isotherm in the East (Fig. 17). Based on the one available record, the 26° S isotherm is a southern lethal boundary. Possibly, this species occurs in this region during limited periods, surviving the warm summers as crusts. The distribution on the NE Pacific coast
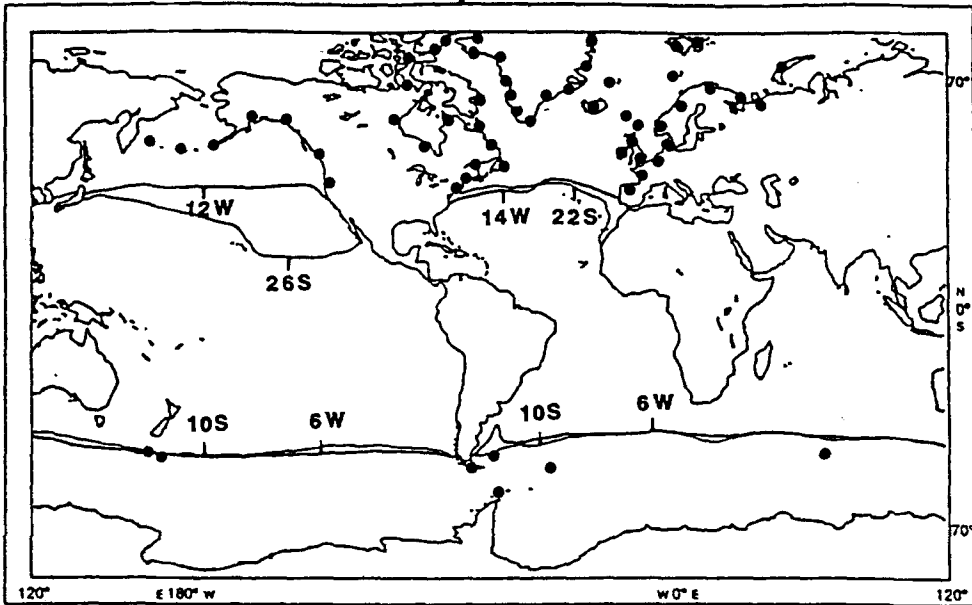
Acrosiphonia arcta

Fig. 17. Distribution of *Acrosiphonia arcta*. Thick line (W) limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Gabrielson et al., 1989; Kjellman, 1883; Levring, 1960; Papenfuss, 1964; Pedersen, 1976; Scagel, 1957; Scagel et al., 1989; South, 1984; South & Tittley, 1986; Taylor, 1939; Tseng, 1983.)

reaches the 12° W isotherm indicating a growth and/or reproduction boundary. The northern distribution in both oceans of the Southern Hemisphere is limited by the 10° S and 6° W isotherms (Fig. 17). The temperature requirement for growth (range 0 to 15 °C), and the USL (22 °C) of an isolate from Antarctica (Wiencke & tom Dieck, 1990) infer that *A. arcta* should be found even further north.

The southern distribution in the Northern Hemisphere of *Urospora penicilliformis* extends along the 26° S and 16° W isotherms (Fig. 18). It is expected that the distribution on the west coasts (26° S) of the oceans is limited by a lethal boundary. Nevertheless, the USL of the Disko Island isolate (23 °C) is not sufficient to explain this boundary. This may indicate a seasonal occurrence in areas with high summer temperatures, or ecotypic variation between populations. The distribution on the east coasts of the oceans, which is limited by the 14° W isotherm, is a growth and/or reproduction boundary. The Disko Island isolate grew between 0 and 15 °C (Fig. 4), and fertilisation was recorded in isolates from Helgoland at 15 °C (Kornmann, 1966a). In the Southern Hemisphere the northern distribution is limited in the Pacific along the 16° S and 12° W isotherms. The northern distribution in the Atlantic is characterised by the 12° S and 8° W isotherm (Fig. 18). *U. penicilliformis* from Antarctica grows between 0 and 15 °C, and survives up to 19 °C (Wiencke & tom Dieck, 1990; Section B), certainly indicating incomplete collections.
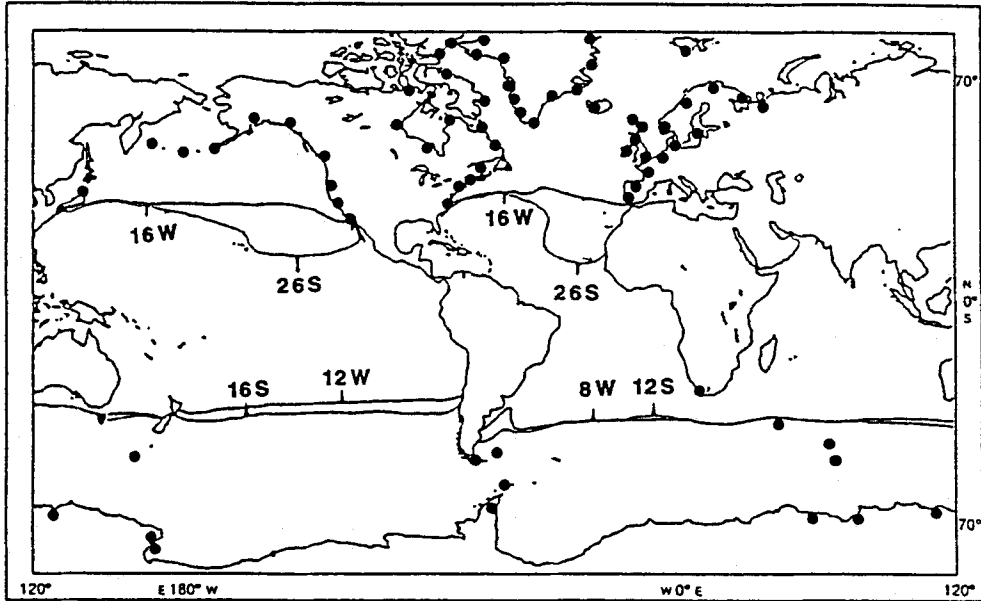
Urospora penicilliformis

Fig. 18. Distribution of *Urospora penicilliformis*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Chapman, 1956; Gabrielson et al., 1989; Kjellman, 1883; Lamb & Zimmerman, 1977; Papenfuss, 1964; Pedersen, 1976; Ricker, 1987; Scagel, 1957; Scagel et al., 1989; Seagrief, 1984; South, 1984; South & Tittley, 1986; Tseng, 1983; Wagner & Zaneveld, 1988; Womersley, 1984.)

The southern distribution boundary of *Pilayella littoralis* in the Northern Hemisphere is correlated with the 26° S and 16° W isotherms (Fig. 19), which extend to almost identical positions in the W Atlantic and W Pacific. Its southern distribution may be limited by both the temperature requirements for growth/reproduction, and survival. However, the available data on USL's of the Disko Island isolate (21 °C; Table 3) and of an isolate from Helgoland (25 °C; Lüning, 1984; Section B) cannot explain a lethal boundary. The distribution on both east coasts extends along the 16° W isotherm. The very low growth rates and the strongly reduced formation of zoidangia at 20 °C of the Disko Island isolate indicates a growth and/or reproduction boundary. The northern distribution in the S Pacific is limited by the 18° S and 14° W isotherms, and in the Atlantic by the 10° S and 6° W isotherms (Fig. 19). Isolates from South Chile grew optimally at 12 °C (Müller & Stache, 1989), and survived up to 22 or 23 °C (Wiencke & tom Dieck, 1990), indicating that *P. littoralis* should be found even further north.

In the N Atlantic, the southern distribution of *Chordaria flagelliformis* is limited by the 18° S and 10° W isotherms (Fig. 20). The distribution boundary on the NW Atlantic coast is characterised by the 18° S isotherm, inferring a lethal boundary, since micro- and macrothalli of the Disko Island isolate survived up to 23 °C (Table 3). The southern distribution on the NE Atlantic coast is limited by both isotherms (Fig. 20). In microthalli,
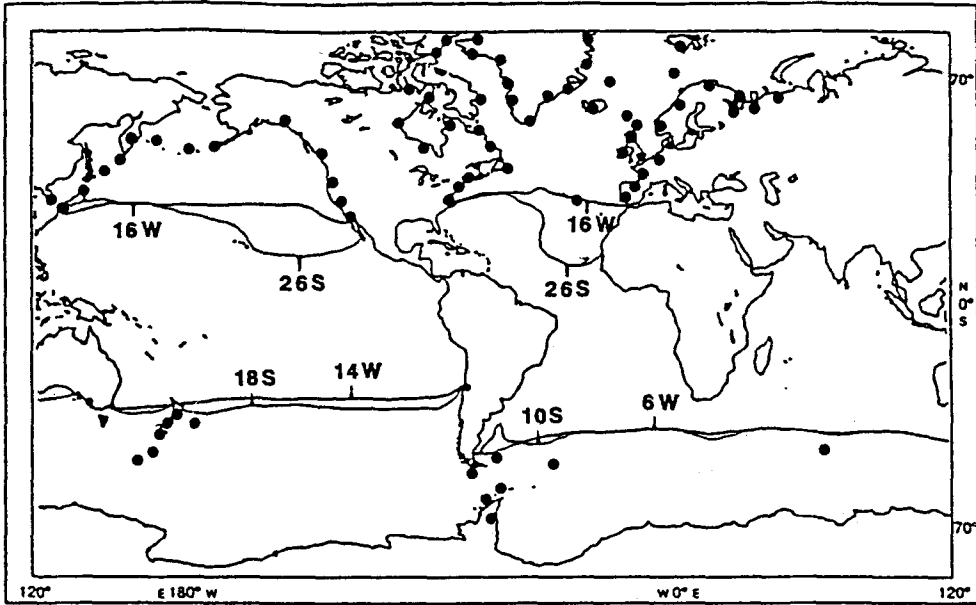
Pilayella littoralis

Fig. 19. Distribution of *Pilayella littoralis*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Asensi, 1966; Etcheverry, 1983; Hay et al., 1985; Kjellman, 1983; Levring, 1945, 1960; Lindauer et al., 1961; Pedersen, 1976; Ricker, 1987; Santelices & Abbott, 1978; Scagel, 1957; Scagel et al., 1989; Skottsberg, 1907; South, 1984; South & Tittley, 1986; Taylor, 1939.)
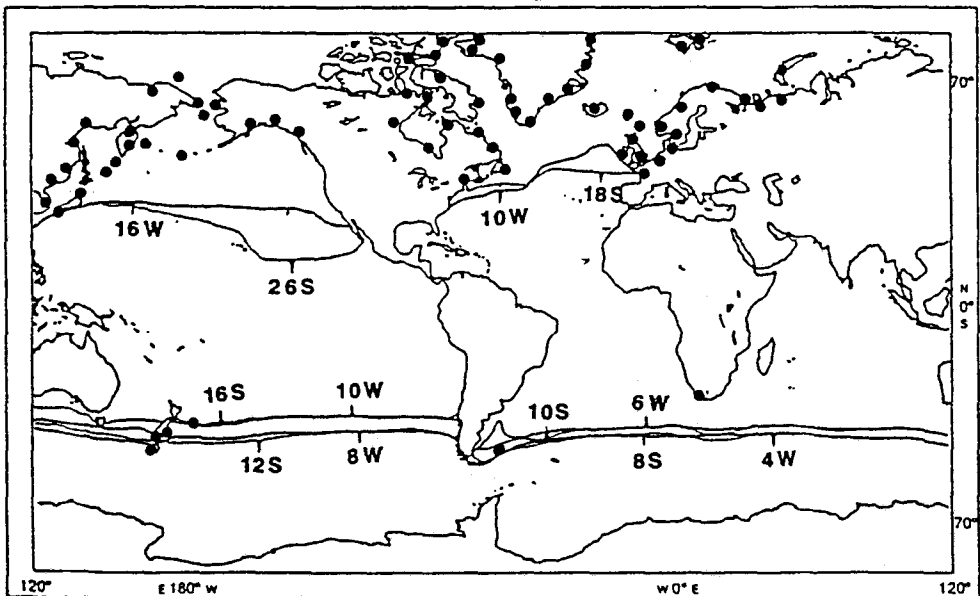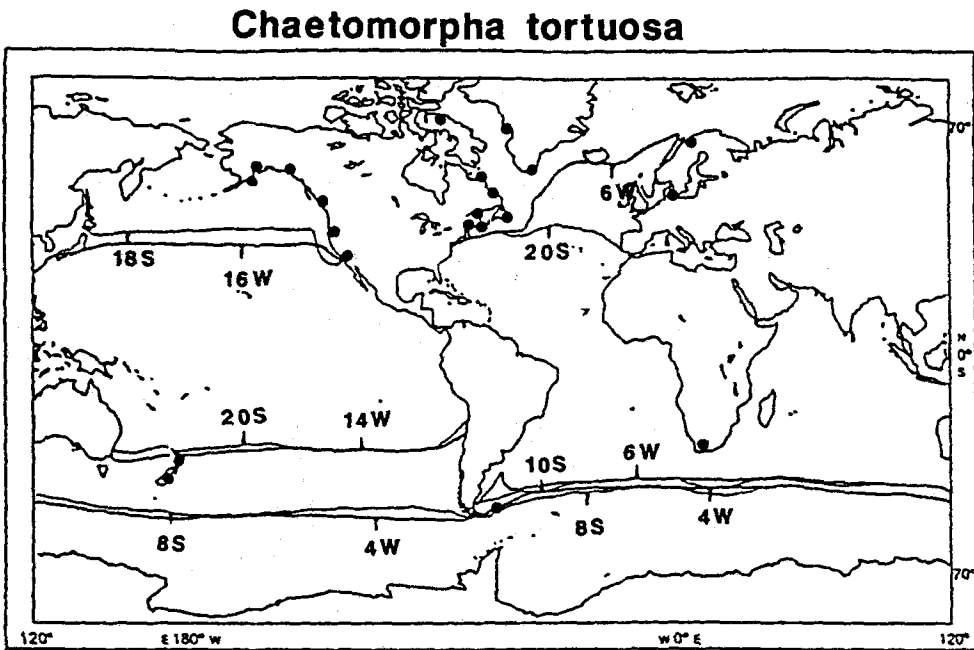
Chordaria flagelliformis

Fig. 20. Distribution of *Chordaria flagelliformis*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Gabrielson et al., 1989; Kjellman, 1883; Lindauer et al., 1961; Papenfuss, 1964; Pedersen, 1976; Scagel et al., 1989; Seagrief, 1984; Skottsberg, 1921; South, 1984; South & Tittley, 1986.)

growth was observed at 5, 10 and 15°C (data not shown). Therefore the distribution cannot be limited by the temperature-growth characteristics of this species. Rather, the distribution is limited by the temperature requirement for formation of macrothalli as the induction of macrothalli was observed at 5 and 10°C only. This is supported by the observations of Kornmann (1962), who only found macrothalli between spring and autumn.

The southern distribution of *Chaetomorpha tortuosa* in the N Atlantic is described in Figure 21. As the USL of 26°C (Table 3) is the only experimental information available on the temperature demands of this species, it is impossible to explain the nature of these boundaries.

Chaetomorpha tortuosa

Fig. 21. Distribution of *Chaetomorpha tortuosa*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Chapman, 1956; Kjellman, 1883; Papenfuss, 1964; Pedersen, 1976; Scagel, 1957; Scagel et al., 1989; South, 1984.)

The southern distribution of *Ulva lactuca* on the NW coasts in the N Atlantic and N Pacific is limited by the 26° S isotherms (Fig. 22), certainly representing a lethal boundary, as the USL of the Disko Island isolate is 26°C (Table 3). The occurrence in W Florida (Dawes, 1974), where the temperature of surface coastal waterscan reaches 30°C, points to a seasonal appearance at this site or to a misidentification (Schneider & Searles, 1991). The distribution on the east coasts is characterised by the 16° W isotherm (Fig. 22). The Disko Island isolate grew well, with sporulation taking place during cultivation at 10 and 15°C. This may indicate that the distribution is limited by the temperature requirement
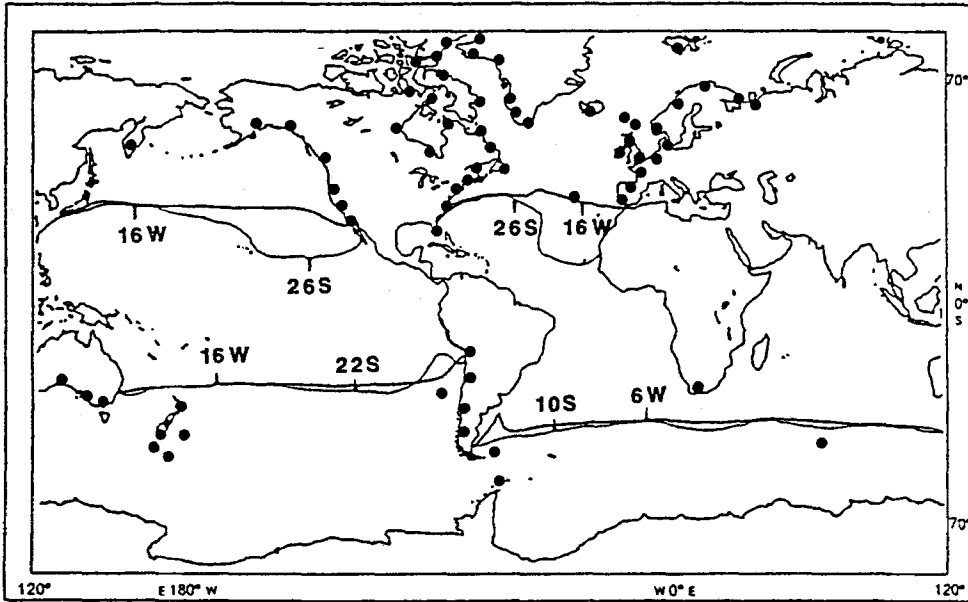
Ulva lactuca

Fig. 22. Distribution of *Ulva lactuca*. Thick line (W): limiting winter isotherm. Thin line (S): limiting summer isotherm. (Distribution according to Chapman, 1956; Etcheverry, 1983; Hay et al., 1985; Kjellman, 1883; Levring, 1960; Papenfuss, 1964; Pedersen, 1976; Scagel, 1957; Scagel et al., 1989; Seagrief, 1984; South, 1984; South & Tittley, 1986; Taylor, 1939; Womersley, 1984.)

for reproduction. The distribution in the Southern Hemisphere cannot be explained by the available experimental data.

Bangia atropurpurea, Enteromorpha clathrata, Enteromorpha intestinalis and *Eudesme virescens* are cosmopolitan species. The distribution pattern of each of these species (not shown) and the high USL's (24, 31, 28 and 30 °C, respectively), indicate that these species may have recently crossed the tropical region. The relatively low USL of *Bangia atropurpurea* (24 °C), seems contradictory, yet the distribution of this species is described for tropical coasts of America (Scagel, 1957; Scagel et al., 1989; Wynne, 1986).

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