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Thermal ecotypes of amphi-Atlantic algae. I. Algae of Arctic to cold-temperate distribution (*Chaetomorpha melagonium, Devaleraea ramentacea* and *Phycodrys rubens*)

I. Novaczek, G. W. Lubbers & A. M. Breeman

Department of Marine Biology, Biological Centre, University of Groningen; P.O. Box 14, NL-9750 AA Haren (Gn), The Netherlands

ABSTRACT: Three species of Arctic to cold-temperate amphi-Atlantic algae, all occurring also in the North Pacific, were tested for growth and/or survival at temperatures of −20 to 30 °C. When isolates from both western and eastern Atlantic shores were tested side-by-side, it was found that thermal ecotypes may occur in such Arctic algae. *Chaetomorpha melagonium* was the most eurythermal of the 3 species. Isolates of this alga were alike in temperature tolerance and growth rate but Icelandic plants were more sensitive to the lethal temperature of 25 °C than were more southerly isolates from both east and west. With regard to *Devaleraea ramentacea*, one Canadian isolate grew extraordinarily well at −2 and 0 °C, and all tolerated temperatures 2–3 °C higher than the lethal limit (18–20 °C) of isolates from Europe. Concerning *Phycodrys rubens*, both eastern and western isolates died at 20 °C but European plants tolerated the lethal high temperature longer, were more sensitive to freezing, and attained more rapid growth at optimal temperatures. The intertidal species, *C. melagonium* and *D. ramentacea*, both survived freezing at −5 and −20 °C, at least for short time periods. *C. melagonium* was more susceptible than *D. ramentacea* to desiccation. Patterns of thermal tolerance may provide insight into the evolutionary history of seaweed species.

INTRODUCTION

Algal species of the North Atlantic Ocean may have had diverse evolutionary origins (Lüning, 1985). Some 165 my ago, the developing ocean basin opened into the tropical Tethys Sea, and algae presumably migrated from there (Smith et al., 1981). After North America separated from South America roughly 140 my ago (Lamb, 1977), and thereafter up until 3–5 my ago (Briggs, 1987), algae could also have entered from the eastern Pacific.

Other algae could have reached the Atlantic from the north. The present Arctic Sea, originally an arm of the Pacific (Smith et al., 1981), was cut off from the North Pacific by Beringia. Initially linked to the Tethys and Pacific Oceans by shallow epicontinental seas, it later may have been virtually landlocked for several million years. Between 40 and 55 my BP (Frakes, 1979), Greenland and Norway separated, allowing the temperate waters and, possibly, a distinct cool-water flora of the polar sea to enter the tropical North Atlantic. During the subsequent period of global cooling (Thunell & Belyea, 1982), there may have been a burst of speciation and extinction as northern populations of Tethyan

and Arctic algae either adapted or perished under the stress (van den Hoek, 1984; Lüning, 1985).

Species from the North Pacific Ocean could also have migrated into the Arctic and North Atlantic after the disruption of the Bering land bridge perhaps 2–3 my ago. Evidence of interoceanic migration of molluscs at this time has been found in fossil deposits (McKenna, 1983).

Over the past 2.5–3 my, recurring glaciations may have caused extinctions on one or both sides of the ocean (van den Hoek, 1984; Lüning, 1985; van den Hoek & Breeman, 1990). Ice fields also separated algal populations occupying eastern and western sides of the Atlantic. For many pan-Arctic species, effective isolation may have occurred only during glaciations. For Arctic and temperate species with poor dispersive ability, populations may have been separated earlier (prior to 10 my BP) by the sinking of the Greenland-Scotland ridge (Thiede & Endholm, 1983). Warm temperate and tropical taxa could have been split up by the initial cooling of the north Atlantic or they may have had sporadic genetic exchange across the northern islands up until the most recent warm period around 20 my BP (Frakes, 1979).

Not only have populations of amphi-Atlantic species been separated to various degrees and for various lengths of time but they have also been subject to different temperature regimes owing to patterns of circulation and upwelling (Breeman, 1988, 1990). The more dramatic thermal fluctuations of the western shores may date back to the development of the Labrador Current system, 3 my BP (Berggren & Hollister, 1977). During glacial periods, however, seasonality was reduced on this coast (CLIMAP-Project Members, 1981). Evidence of upwelling in the eastern Atlantic during the last glaciation has been found (Thiede, 1979; CLIMAP-project members, 1981) and there is no reason to doubt that this process has moderated summer temperatures in the region for a longer time period.

Given the genetic isolation and differing environments of many amphi-Atlantic algal populations, one might expect to find that they have diverged in terms of thermal response. A further hypothesis is that ecotypic variation might be more common in species that have totally disjunct distributions, as opposed to pan-Arctic species that have some possibility of genetic interchange. Furthermore, among those species having a southerly distribution, ecotypic variation might be most prevalent in those that have been in the Atlantic Ocean for the longest time, i.e. those of Tethyan origin.

To determine to what extent ecotypic variation in thermal response occurs in amphi-Atlantic species, we have brought into culture isolates of species of various distributional types from both sides of the ocean and tested them side-by-side for the ability to survive and grow in different temperatures. In this paper we report on three pan-Arctic species, *Chaetomorpha melagonium* (Web. et Mohr) Kütz., *Devaleraea ramentacea* (L.) Guiry and *Phycodrys rubens* (L.) Batt.

MATERIALS AND METHODS

Isolates of all 3 species were collected from both eastern and western shores of the North Atlantic Ocean (Table 1). Unialgal clones of all isolates were propagated from vegetative tissue or occasionally from spores (see Table 1) at 5° and/or 10 °C, in long (16 h) days. To test for growth and survival, each isolate was incubated in growth

Table 1. Place and year of collection of algal isolates. (t) = tetrasporophyte, (m) = male, (f) = female

Species/Code	Location	Year
Chaetomorpha melagonium		
CMASS	Woods Hole, Mass., USA	1971
CBRIT	Roscoff, Brittany, France	1986
CHELG	Helgoland, FRG	1987
CICE1	Iceland	1987
CICE2	Iceland	1987
Devaleraea ramentacea		
DCAN1 (t)	NW Cove, N.S., Canada	1986
DCAN2 (t)	Peggys Cove, N.S., Canada	1986
DCAN2 (m)	Peggys Cove, N.S., Canada (from tetraspores)	1986
DCAN3 (t)	Peggys Cove, N.S., Canada	1986
DJM (m)	Jan Mayen Is.	1978
DNOR1	Tromsø, Norway	1982
DNOR2	Tromsø, Norway	1987
DICE (t)	Iceland	1987
Phycodrys rubens		
PCAN1	Wolf Is., Bay of Fundy, N.B., Canada (from tetraspores)	1986
PCAN2	Anglo, P.E.I., Canada	1986
PEUR1	Plougarneau, Brittany, France	1987
PEUR2	Plougarneau, Brittany, France	1987
PEUR3	Plougarneau, Brittany, France	1987

chambers (± 1–2 °C) at temperatures ranging from 5 to 30 °C and in water baths (± 0.5 °C) at temperatures of 0 and −2 °C (i.e. −1.8 °C in unfrozen seawater at 33 ‰). All cultures received cool white fluorescent light of 10, 20 or 40 µmol m^{-2} s^{-1}. Sterile PES medium (McLachlan, 1973) was made from 33 ‰ salinity, North Sea water.

Prior to either growth or survival trials, all material was moved from the stock condition towards the experimental temperature in stages of no more than 5 °C wk^{-1}, and then trimmed and acclimated at the experimental temperature for at least 5 days before growth trials began. All isolates of any one species were tested concurrently.

For each growth trial, 5 healthy plants (*Chaetomorpha melagonium*) or plant segments (other species) from each clone were incubated separately in sterile plastic Petri dishes (10 cm ∅) containing 50 ml of medium and sealed with parafilm. For trials conducted in water baths, the plant material was incubated in test tubes containing 20 ml of medium. Whole juvenile plants of *Chaetomorpha melagonium*, all generated from spores in culture and at least 2 mm in length, were used for growth trials. In the case of *Devaleraea ramentacea*, apices 5–10 mm long were used and in the case of *Phycodrys rubens*, small leaflets were employed. For each species, the average initial size of experimental subjects was similar in all trials. Using a camera lucida on a dissecting microscope, the lengths of the former two species and the surface area of the latter (after flattening under a glass cover slip) were traced at 7× magnification. The tracings were later measured using a computer digitiser to give the length or, in the case of *P. rubens*, the surface area. Measurements were made at intervals of 2 to 10 days, depending upon the rate of growth, until a straight line on semi-log paper, indicating steady logarithmic

increase, could be drawn between at least three consecutive data points. The relative growth rate (Kain, 1987), expressed as % increase d^{-1}, was computed for the period of exponential growth. Experiments were conducted at 10 and/or 40 μmol m^{-2} s^{-1} at temperatures of −2, 0, 5, 10, 15, 18, 20, 22, and 25 °C. Separate growth trials on *C. melagonium* were conducted as above, using 1-cm fragments of young plants incubated in test tubes. In this case, the increase in cell numbers was monitored.

Differences among isolates were tested using a posteriori Student-Neuman-Keuls (SNK) and Scheffe multiple range tests, using subprogram "oneway" from the Statistical Package for the Social Sciences (SPSS).

To determine lethal limits, whole plants (including holdfasts) were incubated in 500-ml flasks at extreme temperatures for a period of 3 months, to simulate a winter or summer time span. The medium was changed every 2–3 weeks, after being warmed or cooled to the experimental temperature so as to avoid thermal shocks. Temperatures of −2, 0, 18, 20, 23, 25, 27 and 30 °C were tested. A photon fluence rate of 10 μmol m^{-2} s^{-1} was used because of the tendency of algae to be sensitive to light at sublethal temperatures. At 0 °C, incubations were also performed in total darkness. In the case of *Chaetomorpha melagonium,* both juvenile and full-sized adult plants were tested for thermal tolerance. At the end of the test period, plants were returned to stock culture conditions and monitored for up to 3 months for signs of regrowth. Trials were repeated on at least 2 separate occasions.

Response to high temperatures was also investigated by two other procedures for *Chaetomorpha melagonium* and *Devaleraea ramentacea.* Firstly, growth rates over 6–8 weeks were monitored at sub-lethal high temperatures. Secondly, to test for short-term lethal effects, plant apices, each in a test tube of medium, were incubated in a cryostat (± 0.5 °C) for a two-wk period. Tests were performed on 10 replicates at each of the following temperatures: 16, 18, 20, 22, 24, 26, 28 and 30 °C. Following the test period, plant material was returned to 10 °C and monitored for regrowth.

Resistances to freezing and/or desiccation were also tested. Plant segments were taken from long-term culture at 5 °C and held at 0 °C for at least 1 week before being incubated in the dark at −5 and −20 °C, either in ice or in air. Tissues were cooled to −5 °C at a rate of 1.1 °C min^{-1} and to −20 °C at a rate of 2.3 °C min^{-1}. For some tests, plants were pre-dried to various extents at 4 °C; otherwise all tissues were fully hydrated. After test periods ranging from 1 hour to 14 days, the plant material was thawed in seawater at 0 °C and then transferred to 5 or 10 °C and monitored for regrowth.

RESULTS

Chaetomorpha melagonium

Growth. The two growth experiments, in which either length (Fig. 1a–c) or cell number (Fig. 1d–i) of isolates CMASS, CBRIT and CHELG were measured, gave similar results. When lengths were measured, CBRIT had significantly higher rates of elongation than the other isolates at 5–15 °C but no such differences were apparent in the trial in which cells were counted. All isolates grew slowly at −2 and 0 °C, in both long days (Fig. 1a–f) and short days (Fig. 1g–i). Maximum rates of growth generally occurred at 10–15 °C, although growth at the sublethal temperature of 22 °C could be rapid for a short period of

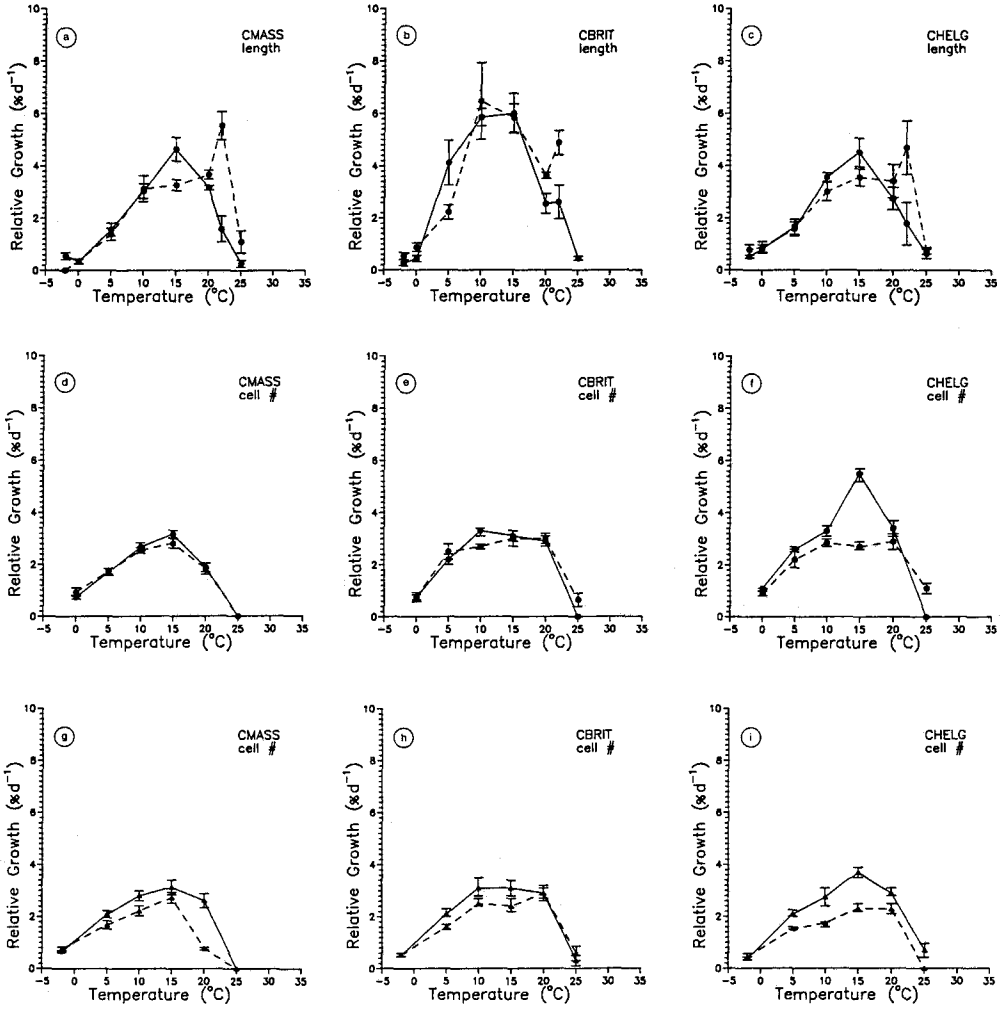

Fig. 1. Relative growth rates (mean ± standard error) of isolates of *Chaetomorpha melagonium* at various temperatures and at photon fluence rates of 10 μmol m^{-2} s^{-1} (dashed line) and 40 μmol m^{-2} s^{-1} (solid line). a–c Increase in filament length in 16-h days. d–f Increase in cell number in 16-h days. g–i Increase in cell number in 8-h days. Isolate indicated in upper right hand corner of each graph

time. When monitored over weeks, it was found that growth rates at 22 °C declined steadily, stabilizing near zero after 3–4 weeks (Fig. 2). At 25 °C, growth approached zero within the 5-day acclimation period. In most cases there was no significant difference between growth rates at high and low photon fluence rates. With the exception of CHELG at 15 °C, rates of cell division were also comparable in long- versus short-day conditions.

High-temperature tolerance. When tested for 2-wk periods at high temperatures, juvenile plants of isolates CMASS, CBRIT and CHELG survived at tem-

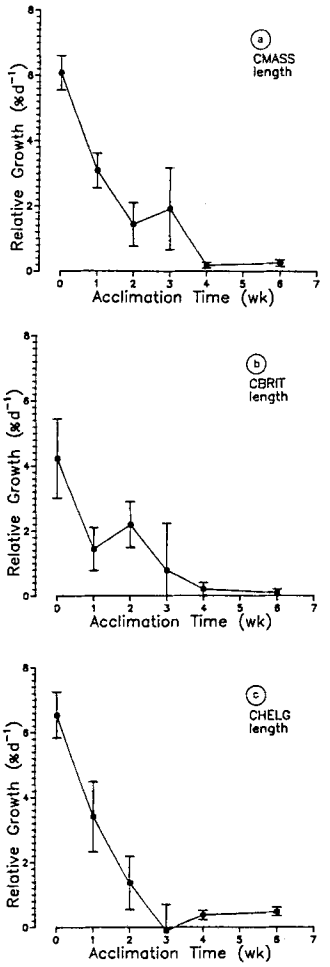

Fig. 2. Decline in relative growth rates (mean ± standard error) of isolates of *Chaetomorpha melagonium* over time at 22 °C in 16-h days. Isolate indicated in upper right hand corner of each graph

peratures up to and including 26 °C, but all died at 28 °C (Table 2). In trials lasting 3 months, however, both juvenile and mature plants of the above isolates and of isolates CICE1 and CICE2, were damaged or died at 23 and 25 °C, and died after 2–6 weeks at 27 and 30 °C (Table 3). Only the Icelandic isolates (CICE1 and CICE2) consistently died at 25 °C; a few replicates of all 3 more southerly isolates survived this temperature (with damage). Mature plants tended to persist longer at high lethal temperatures than did the juveniles, and the smaller juveniles were the most sensitive.

Low-temperature tolerance. All isolates survived 3 months at 0 and −2 °C, even in total darkness (Table 3). The isolates CMASS, CBRIT and CHELG were compared for resistance to desiccation and freezing (Table 4). In all cases, drying out to 70–80 % of initial fresh weight at 4 °C was in itself lethal. Plants could, however, survive

Table 2. Survival of fragments or apices, respectively, of *Chaetomorpha melagonium* and *Devaleraea ramentacea* after incubation for 2 weeks at temperatures of 16 to 30 °C in long days (16 h) at 20 μmol m^{-2} s^{-1}. In each case n = 10

	% Survival at each temperature (°C)							
	16	18	20	22	24	26	28	30
C. melagonium								
CMASS	100	100	100	100	100	80	0	0
CBRIT	100	100	100	100	100	100	0	0
CHELG	100	100	100	100	100	100	0	0
D. ramentacea								
DCAN1	100	100	100	90	0	0	0	0
DCAN2 (t)	100	100	100	80	0	0	0	0
DCAN3	100	100	100	80	0	0	0	0
DNOR1	100	100	50	50	0	0	0	0
DNOR2	100	100	30	10	0	0	0	0
DJM	100	100	60	0	0	0	0	0
DICE	100	100	20	20	0	0	0	0

Table 3. Thermal tolerance of whole plants of *Chaetomorpha melagonium* in trials of 3 months duration. L = long days (16 h), S = short days (8 h), D = dark; ++ = undamaged, + damaged but recovered, +− = damaged or dead in repeated trials, − = dead; ju = juvenile plants, ad = adult plants, nd = no data

Isolate	Temperature (°C) and Daylength												
	−2S	OL	OD	20L		23L		25L		27L		30L	
	ad	ad	ad	ju	ad	ju	ad	ju	ad	ju	ad	ju	ad
CMASS	++	++	++	++	++	−	+−	+−	+−	−	−	−	−
CBRIT	++	++	++	nd	++	nd	+−	+−	−	−	−	−	−
CHELG	++	++	++	nd	++	+−	+	+−	+−	−	−	−	−
CICE1	++	++	++	++	++	−	+−	−	−	−	−	−	nd
CICE2	++	++	++	++	++	−	+−	−	−	−	−	−	nd

for a week after being quickly frozen in air or in water at −5 °C. Survivorship, after being frozen in water at −20 °C, was good after 1 hour but declined to zero within 24 hours. If frozen to −20 °C in air, some replicates of all isolates survived for 4 or 24 hours. No plant survived a week at −20 °C in any condition.

Devaleraea ramentacea

Growth. In an analysis of variance of growth rates of *Devaleraea ramentacea*, temperature, photon fluence rate and isolate were all highly significant factors ($P < 0.001$). Significantly higher rates of growth were recorded in long days than in short days at 0 °C (Fig. 3). Canadian isolates had growth optima at 0 or 5 °C (Fig. 3), and at least one of these isolates grew significantly faster than all European plants at −2 and 0 °C. In European plants, maximum growth occurred at 5 or 10 °C. In long-day conditions, an enhancement of growth in higher photon fluence rates was often statistically significant

Table 4. Survival of fragments of *Chaetomorpha melagonium* after different periods of time at –5 and –20 °C, either immersed in water (W) or in air (D). nd = no data

Isolate	W/D	Time	% Survival (n = 4–8)	
			–5 °C	–20 °C
CMASS	D	4 h	75	0
		1 d	100	12
		7 d	100	0
	W	1 h	nd	100
		4 h	100	0
		1 d	100	0
		7 d	100	0
CBRIT	D	4 h	100	12
		1 d	nd	25
		7 d	100	0
	W	1 h	nd	100
		4 h	50	0
		1 d	100	0
		7 d	88	0
CHELG	D	4 h	100	25
		1 d	nd	0
		7 d	100	0
	W	1 h	nd	75
		4 h	100	12
		1 d	100	0
		7 d	78	0

in Canadian plants but was rarely observed in European plants. For DCAN2, growth varied significantly with temperature and photon fluence rate but not with phase (tetrasporophyte versus male) or daylength. In most cases, growth rates dropped dramatically at 15 °C, and long-term monitoring revealed that at both 15 and 18 °C, growth rates declined to zero within 2–6 weeks (Fig. 4). DCAN3 was particularly tolerant of high temperatures. It had a significantly higher rate of growth than all others after 1 week at 18 °C and was still growing after 6 weeks at this temperature.

High-temperature tolerance. Isolates from the eastern and western Atlantic differed consistently in their upper tolerance limits. In short-term tests (Table 2), at least 80 % of replicates of Canadian isolates tolerated 22 °C for 2 weeks, while no more than 50 % of European plants tolerated this treatment. Even at 20 °C, all the European clones suffered some mortality after 2 weeks. In 3-month trials (Table 5), it was found that the upper lethal limit for the European isolates lay between 18 and 20 °C, whereas Canadian isolates survived with damage at 20 °C and died at 23 °C.

Low-temperature tolerance. Both European and Canadian plants remained healthy at 0 and −2 °C in light and at 0 °C in darkness for 3 months (Table 5). All isolates were damaged but survived after being dried to as little as 60 % of original fresh weight at 4 °C. Survival was good when plants were frozen in water or in air for up to a week at −5 °C, but they died if first dried at 4 °C (Table 6). Survivorship declined with time in material frozen to −20 °C, especially if frozen in air. Contrary to the trend at −5 °C, long-term survivorship in air at −20 °C was better after pre-drying at 4 °C.

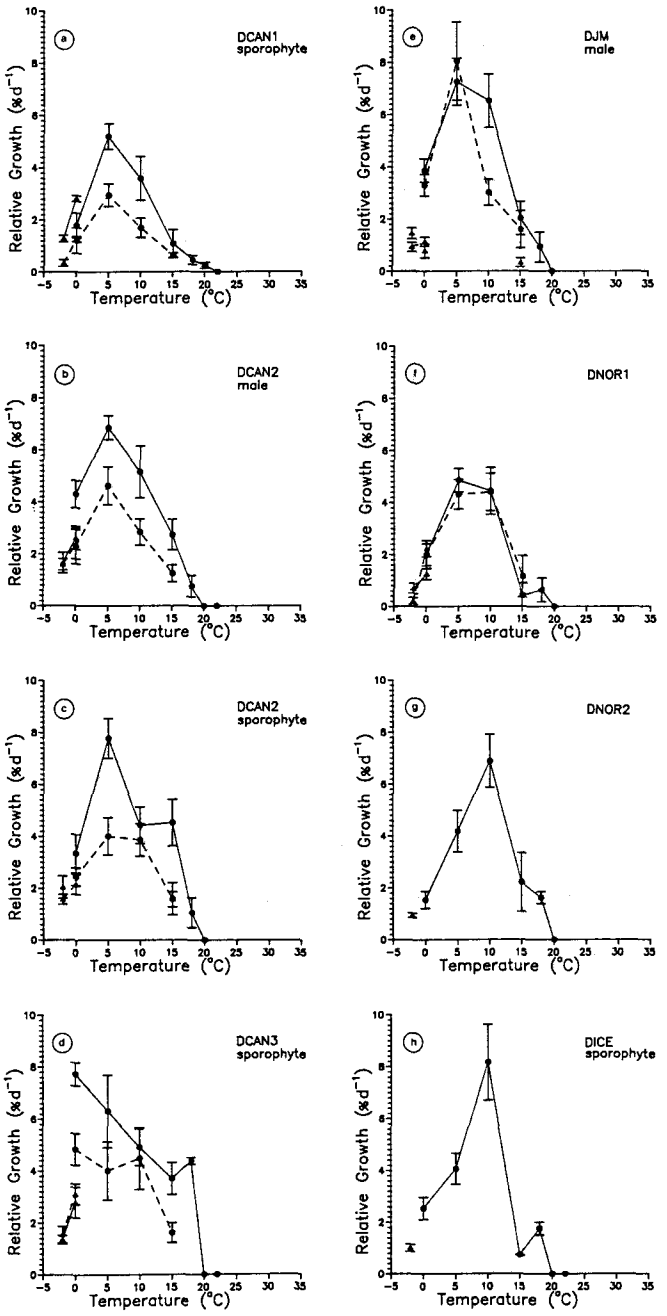

Fig. 3. Relative growth rates (mean ± standard error) of isolates of *Devaleraea ramentacea* at various temperatures at photon fluence rates of 10 μmol m^{-2} s^{-1} (dashed line) and/or 40 μmol m^{-2} s^{-1} (solid line) in 8-h days (triangles) or 16-h days (circles). Isolate indicated in upper right hand corner of each graph. a–d Canadian isolates. e–h European isolates

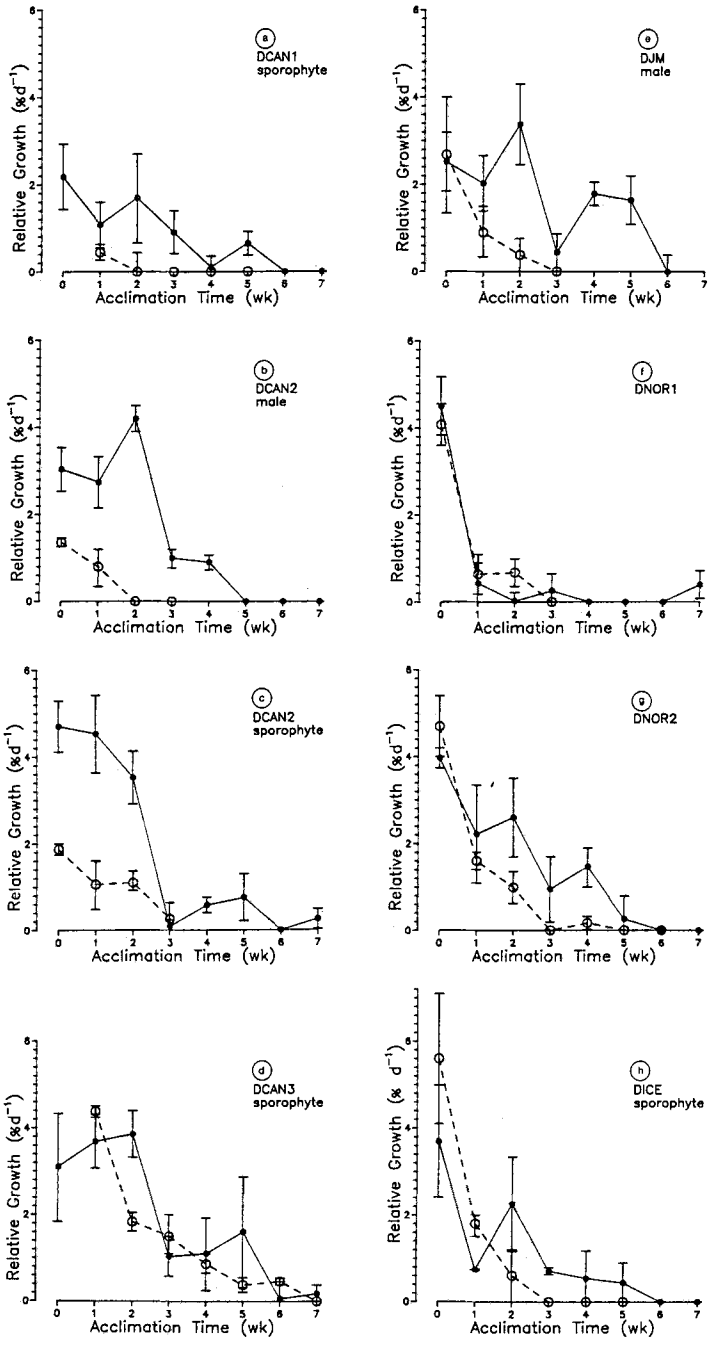

Fig. 4. Decline of relative growth rates (mean ± standard error) of isolates of *Devaleraea ramentacea* over time at 15°C (solid line) and 18°C (dashed line) in 16-h days at 40 μmol m^{-2} s^{-1}.. Isolate indicated in upper right hand corner of each graph. a–d Canadian isolates. e–h European isolates

Table 5. Thermal tolerance of whole plants of *Devaleraea ramentacea* in trials of 3 months duration. L = long days (16 h), S = short days (8 h), D = dark; ++ = undamaged, + = damaged but recovered, – = dead (time to death in brackets), nd = no data

Isolate	Temperature (°C) and Daylength					
	–2S	0L	0D	18L	20L	23L
DCAN1	++	++	nd	++	+	–(6 wk)
DCAN2 (m)	++	++	++	++	+	–(2 wk)
DCAN2 (t)	++	++	++	++	+	–(2 wk)
DCAN3	++	++	++	++	+	–(6 wk)
DJM	++	++	++	+	–(4 wk)	–(1 wk)
DNOR1	++	++	++	+	–(3 wk)	–(2 wk)
DNOR2	++	++	++	+	–(6 wk)	–(2 wk)
DICE	++	++	++	+	–(4 wk)	–(2 wk)

Table 6. Survival of apices of *Devaleraea ramentacea* from the eastern and western Atlantic after different periods of time at –5 and –20 °C (n in brackets). Treatments were: W = immersed in water, D = in air, DD = in air after drying at 4 °C (% fresh weight in brackets). * = Apices damaged

Isolates	Treatment (% FW)			% Survival (n) –5 °C	% Survival (n) –20 °C
DCAN1–3	DD	(70 %)	4 h	nd	25 (16)
		(70 %)	1 d	nd	0 (8)
		(70–80 %)	7 d	0 (8)	12 (16)
	D		1 h	100 (4)	nd
			4 h	100 (4)	100 (8)
			1 d	50 (4)	50 (8)
			7 d	75 (8)	0 (16)
	W		4 h	100 (8)	100 (8)
			1 d	100 (8)	50 (8)
			7 d	100 (8)	6 (16)
DJM/NOR/ICE	DD	(45–55 %)	4 h	nd	14 (16)
		(45–55 %)	1 d	nd	14 (16)
		(35–70 %)	7 d	0 (16)	12 (32)
	D		1 h	100 (4)	nd
			4 h	100 (8)	100 (8)
			1 d	100 (8)	62 (16)
			7 d	100 (16)	0 (16)
	W		4 h	100 (16)	nd
			1 d	100 (16)	74 (16)
			7 d	67 (16)	50* (16)

Phycodrys rubens

Growth. No significant differences in growth rate were found among either eastern or western Atlantic isolates of *Phycodrys rubens* but the two groups of isolates did vary significantly from one other. Growth rates of all isolates were comparable at low temperatures but over the optimum range of 10–15 °C, the European plants grew much

faster (Fig. 5). Blades from European plants were also able to grow for at least 2 weeks at 20 °C, whereas Canadian isolates died within days at this temperature (Fig. 5). European isolates did not grow at 22 °C, but neither did they die within 4 weeks. There were no significant differences in growth with photon fluence rate (all temperatures) or with daylength (0 °C only).

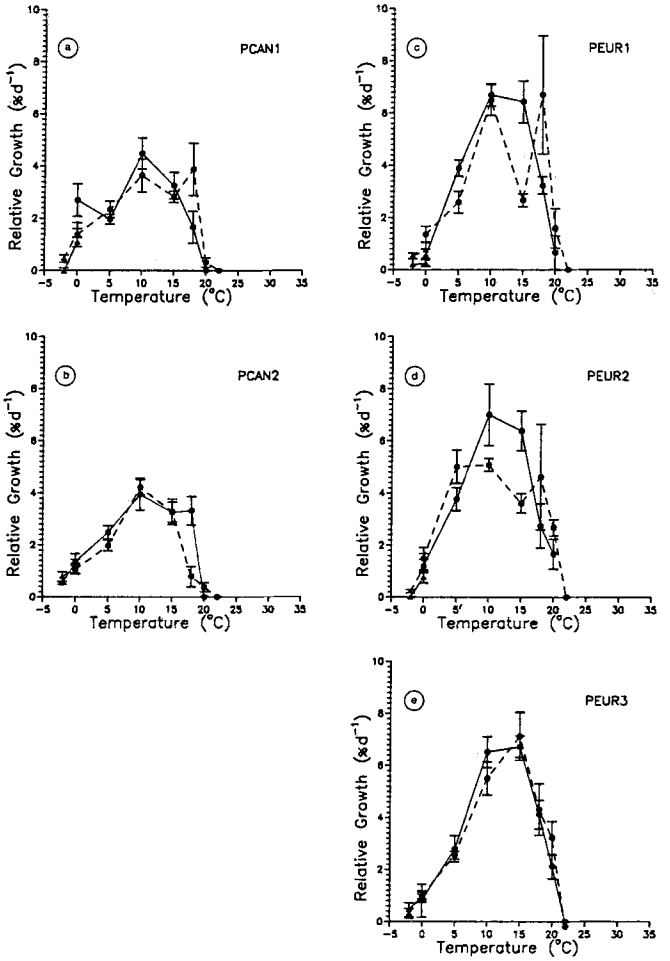

Fig. 5. Relative growth rates (mean ± standard error) of isolates of *Phycodrys rubens* at various temperatures at photon fluence rates of 10 μmol m^{-2} s^{-1} (dashed line) and 40 μmol m^{-2} s^{-1} (solid line) in 8-h days (triangles) or 16-h days (circles). Isolate indicated in upper right hand corner of each graph. a–b Canadian isolates. c–e European isolates

High-temperature tolerance. In long-term (3 months) exposures to high temperatures (Table 7), both Canadian and European isolates died at 20 °C. The two Canadian isolates and one European (PEUR1) sustained damage at 18 °C.

Low-temperature tolerance. All isolates tolerated −2 °C in the light and 0 °C in light or darkness for 3 months (Table 7). When frozen in water to −5 °C, the

Table 7. Thermal tolerance of whole plants of *Phycodrys rubens* in trials of 3 months duration. L = long days (16 h), S = short days (8 h), D = dark; ++ = undamaged, + = damaged but recovered, – = dead, nd = no data

Isolate	Temperature (°C) and Daylength						
	–2S	0L	0D	18L	20L	23L	25L
PCAN1	++	++	++	+	–	–	–
PCAN2	++	++	++	+	–	–	–
PEUR1	++	++	nd	+	–	–	–
PEUR3	++	++	++	++	–	–	–

Table 8. Tolerance of laminae of *Phycodrys rubens* to freezing in ice at –5 °C for up to 2 weeks. + = alive, – = dead, +– = some replicates alive and some dead. N = 4 for each combination of isolate and condition

Isolate	Duration of Freezing (days)				
	1	3	5	7	14
PCAN1	+	+	+	+	+
PCAN2	+	+	+	+	+
PEUR1	+	+	–	–	–
PEUR2	+	+	+	–	–
PEUR3	+	+–	–	–	–

Canadian isolates remained healthy for at least two weeks, while European material died after 3–5 days (Table 8).

DISCUSSION

In trying to determine the best experimental procedure to reflect potential survival at geographic limits, we tested plants for both 2-wk and 3-mo time periods. In contrast to earlier reports (Yarish et al., 1987), results from three-month trials at high temperatures provided upper limits that were several degrees below those indicated in two-week trials. The longer trials may therefore better represent the effect of a summer season in the field. It is also important to note the evidence that a rapid decline in growth rate over the first 2–3 weeks is characteristic of plants experiencing sub-lethal high temperatures. This loss of growth potential may in fact mark the true upper limit for long-term survival in the field, as plants would lose the ability to replace lost biomass. In species lacking perennating structures or an alternate morphological phase this could result in local extinction. For algae of this sort, it may be best to monitor growth for 2–4 weeks at high temperatures rather than attempt to measure survival. Loss of growth potential is more easily quantified than plant death, and does not involve the long incubations needed to establish regenerative ability. For those plants having alternate or perennating structures, however, there is no alternative to long-term incubation of the relevant structures.

In the three pan-Arctic algae we have studied, three different patterns of variation in thermal tolerance have been observed.

Among isolates of *Chaetomorpha melagonium*, there were no differences in lower

lethal limits or in growth rates and only a minor difference in upper lethal limits. This alga combined a relatively high upper thermal limit with consistently low growth rates at very low temperatures. All isolates were intolerant of desiccation but were able to survive freezing at −20 °C for 1 day and tolerated freezing at −5 °C for at least 1 week.

Both *Devaleraea ramentacea* and *Phycodrys rubens* had upper thermal limits of 18–20 or 20–23 °C, which is characteristic of seaweeds with an Arctic to cold temperate distribution (Lüning, 1985). The upper thermal limits determined for European isolates of *D. ramentacea* corroborate findings by Rueness & Tananger (1984). In this species, growth rates at low temperatures were exceptionally high, especially in one Canadian isolate which had the lowest temperature optimum (0 °C) yet recorded in an Arctic macroalga. Also, growth at low temperatures was enhanced when plants were kept at high photon fluence rates and long days, in contrast to southerly species which are often damaged when experiencing high light levels at low temperatures (e.g. Cambridge et al., 1987; Yarish et al., 1984; 1986). *D. ramentacea* tolerated both desiccation and freezing to −20 °C better than did *C. melagonium*. Interestingly, the Canadian isolates of *D. ramentacea* that grew well at low temperatures also had upper lethal limits that were several degrees higher than those of European isolates. In *P. rubens*, the situation was reversed. European plants were the most sensitive to freezing but also were more heat tolerant over the short term. In this species, as in *C. melagonium*, growth was limited at very low temperatures.

Pan-Arctic algae on opposite sides of the Atlantic Ocean may, therefore, be uniform in their thermal tolerance; they may also exhibit ecotypic variation in terms of growth or survival.

Although thermal ecotypes certainly exist, it is of interest to note that the variations in absolute tolerance that have been found to date within good morphological species do not, in general, exceed 2–3 °C. Also, in some species thermal tolerance does not vary over wide geographic distances (Breeman, 1988), even when the populations have been disjunct and under different thermal regimes for millions of years. Major differences in absolute tolerance have, so far, only been found between eastern and western Atlantic populations of species with a tropical to (warm)-temperate distribution. For instance, in *Cladophora coelothrix* Kuetz. the lower limit for survival differed by more than 5 °C between a Caribbean and a European isolate (Cambridge et al., 1987), and the same pattern has been found in several red algae of this distribution-type (Breeman, unpubl.). This must reflect the longer divergence time between eastern and western Atlantic populations in these presumably Tethyan species compared with species of more northerly distribution.

Thermal tolerance, then, appears to be a relatively stable genetic feature. In contrast, sublethal growth rates (Innes, 1988), copper tolerance (Russell & Morris, 1970), salinity tolerance (Russell & Bolton, 1975), daylength response (Lüning, 1980), photophysiology (Gerard, 1988) and nutrient physiology (Espinosa & Chapman, 1983) all may vary widely within narrow latitudinal ranges.

Because of its stable nature, thermal tolerance may be a valuable clue in sorting out evolutionary relationships, patterns of origin and past geographical distributions of groups of isolates and species (Lüning et al., 1987). For instance, the slightly but distinctly different thermal responses of eastern and western isolates of *D. ramentacea* and *P. rubens* indicate that populations have once been effectively isolated even though the

distribution is now continuous through the Arctic. The similarity of the Icelandic isolate of *D. ramentacea* to other European isolates indicates that recolonization of the Icelandic coast after the glaciation has occurred from the European side of the ocean.

However, the reasons why species should have developed somewhat different patterns of variation in their thermal responses are not immediately clear. For instance, the broadening of the thermal range found in Canadian isolates of *D. ramentacea*, which makes them better adapted to the strong seasonality on that side of the ocean, has not occurred in *P. rubens* where, instead, there was a downward shift in the thermal range. Before we can further speculate on possible evolutionary origins of isolates and species, we need to know more about the temperature requirements for reproduction and about the morphology and thermal tolerances of putative con-specific populations occurring in the North Pacific.

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