

Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence*

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ABSTRACT: Experimentally determined ranges of thermal tolerance and requirements for completion of the life history of some 60 seaweed species from the North Atlantic Ocean were compared with annual temperature regimes at their geographic boundaries. In all but a few species, thermal responses accounted for the location of boundaries. Distribution was restricted by: (a) lethal effects of high or low temperatures preventing survival of the hardiest life history stage (often microthalli), (b) temperature requirements for completion of the life history operating on any one process (i.e. [sexual] reproduction, formation of macrothalli or blades), (c) temperature requirements for the increase of population size (through growth or the formation of asexual propagules). Optimum growth/reproduction temperatures or lethal limits of the non-hardest stage (often macrothalli) were irrelevant in explaining distribution. In some species, ecotypic differentiation in thermal responses over the distribution range influenced the location of geographic boundaries, but in many other species no such ecotypic differences were evident. Specific daylength requirements affected the location of boundaries only when interacting with temperature. The following types of thermal responses could be recognised, resulting in characteristic distribution patterns: (A) Species endemic to the (warm) temperate eastern Atlantic had narrow survival ranges (between ca 5 and ca 25°C) preventing occurrence in NE America. In species with isomorphic life histories without very specific temperature requirements for reproduction, northern and southern boundaries in Eur/Africa are set by lethal limits. Species with heteromorphic life histories often required high and/or low temperatures to induce reproduction in one or both life history phases which further restricted distribution. (B) Species endemic to the tropical western Atlantic also had narrow survival ranges (between ca 10 and ca 35°C). Northern boundaries are set by low, lethal winter temperatures. Thermal properties would potentially allow occurrence in the (sub)tropical eastern Atlantic, but the ocean must have formed a barrier to dispersal. No experimental evidence is so far available for tropical species with an amphi-Atlantic distribution. (C) Tropical to temperate species endemic to the western Atlantic had broad survival ranges (< 0 to ca 35°C). Northern boundaries are set by low summer temperatures preventing (growth and) reproduction. Thermal properties would permit occurrence in the (sub)tropical eastern Atlantic, but along potential "stepping stones" for dispersal in the northern Atlantic (Greenland, Iceland, NW Europe) summer temperatures would be too low for growth. (D) In most amphi-Atlantic (tropical-) temperate species, northern boundaries are set by low summer temperatures preventing reproduction or the increase of population size. On European shores, species generally extended into regions with slightly lower summer temperatures than in America, probably because milder winters allow survival of a larger part of the population. (E) Amphi-Atlantic (Arctic-) temperate species survived at subzero temperatures. In species with

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isomorphic life histories not specifically requiring low temperatures for reproduction, southern boundaries are set by lethally high summer temperatures on both sides of the Atlantic. None of the species survived temperatures over 30°C which prevents tropical occurrence. Species with these thermal responses are characterized by distribution patterns in which southern boundaries in Eur/Africa lie further south than those in eastern N America because of cooler summers. In most species with heteromorphic life histories (or crustose and erect growth forms), low temperatures were required for formation of the macrothalli (either directly or through the induction of sexual reproduction). These species have composite southern boundaries in the north Atlantic Ocean. On American coasts, boundaries are set by lethally high summer temperatures, on European coasts by winter temperatures too high for the induction of macrothalli. Species with this type of thermal responses are characterized by distribution patterns in which the boundaries in Eur/Africa lie further north than those in eastern N America because of warmer winters.

INTRODUCTION

Why don't seaweeds spread beyond their present boundaries when there are no apparent obstructions to their dispersal? Continents and oceans apparently can be effective barriers to seaweed dispersal. The marked differences between the seaweed floras of the Atlantic and the Pacific and, to a lesser degree, the eastern and western sides of the oceans indicate that landmasses and large stretches of sea effectively limit seaweed distribution. These marked differences between disjunct floras have been attributed to historical factors such as the configuration of oceans and continents in the geological past and paleoclimatic events (van den Hoek, 1982a, b, 1984; Lüning, 1985; Joosten & van den Hoek, 1986; Hommersand, 1986). Another apparent limit to distribution is the absence of suitable substratum for macroalgal growth.

The question to be addressed in this paper is why a seaweed species does not extend beyond its present boundary along an uninterrupted rocky coastline. The reason for this could be that permanent populations either have not (yet) become established, or have not (yet) been found by collectors. Seaweed boundaries are not necessarily stable. Several recent examples (e.g. for *Bonnemaisonia hamifera*, *Asparagopsis armata*, *Codium fragile* ssp. *tomentosoides* and *Sargassum muticum*) have shown that seaweeds newly introduced into a region reach their potential limit of distribution only after a given amount of time (Irvine et al., 1975; Critchley et al., 1983; Carlton & Scanlon, 1985; Lüning, 1985). Moreover, a lack of records may simply reflect limited collecting efforts in the region or result from collections having been made during the wrong season.

Several physical and biological factors have been mentioned as potentially restrictive to seaweed distribution. Among these, temperature (sometimes in combination with some specific daylength requirements for reproduction) is probably the most important (van den Hoek, 1982a, b; Lüning, 1985). Other factors, such as lowered salinity caused by major intrusions of fresh water from the world's large river systems could potentially be obstacles to distribution in stenohaline marine species. In the only study in which the halotolerance of marine species has been related to their geographical distribution (i.e. in the genus *Gracilaria*; Bird & McLachlan, 1986) it was found that some of the most sensitive species, which did not tolerate salinities below 20‰, were not effectively curtailed in their distribution by the outflow of the Amazon, the world's largest river. So there is as yet little evidence that salinity is a major factor in restricting seaweed distribution on oceanic coasts.

The importance of biological factors such as herbivory and competition has also been stressed (Hay, 1981; Gaines & Lubchenco, 1982). It is difficult to assess the importance of

such factors without first establishing whether any limits are being set by the physiological tolerance of the species. Only a detailed analysis of the physical habitat at distribution boundaries combined with an experimental analysis of physiological tolerance and requirements will eventually allow an assessment of the importance of non-physical parameters in controlling geographic distribution.

A first approach in determining possible causes for the absence of a species beyond its limits of distribution may therefore comprise an experimental assessment of its critical temperature requirements for completion of the life history, combined with a description of the annual temperature regimes at distribution boundaries. Using such an approach, van den Hoek (1982a, b) has analysed distribution patterns of seaweeds belonging to various distribution groups. He was able to recognize two types of boundaries: firstly, boundaries set by a species' ability to grow and reproduce during the favourable season, and secondly, boundaries set by the species' potential to survive during the adverse season. For many species, boundaries in the North Atlantic Ocean appeared to be of a composite nature, being set by survival limits on American shores and by reproduction limits on European shores, this difference being caused by the far greater annual temperature fluctuations on the American side of the Atlantic.

The approach used by van den Hoek (1982a, b) of necessity contains a number of generalised assumptions. Firstly, for many species the experimental evidence was incomplete, particularly where upper and lower limits of thermal tolerance were concerned. Secondly, experiments had often been done with a single isolate, so that the occurrence of different thermal ecotypes in other parts of the species' distribution might invalidate conclusions. Finally, ocean isotherms were used to describe the annual temperature regimes at distribution boundaries, which are, at best, a rough estimate of the temperatures actually experienced by the plants *in situ*.

In recent years several new lines of evidence have become available. For several species, belonging to various distribution groups, complete ranges of thermal tolerance and requirements have been determined experimentally, sometimes in isolates from different climatic zones. For some of these species, detailed phenological observations have been made in populations close to a distribution boundary. Thus, evidence has been provided on the way in which some potentially limiting factor actually takes effect in the field.

This paper will concentrate on seaweeds from the North Atlantic Ocean, because most of the experimental evidence concerns species and isolates from this region. Where experimentally determined temperature responses have been compared with annual temperature regimes at distribution boundaries or in other parts of the distribution, temperature data were based on detailed local records whenever these were available. For other sites, estimates of mean monthly seawater temperatures were based on ocean isotherms (Gorshkov, 1978; U.S. Navy, 1981), whereas values for extreme years were estimated from the U.S. Navy Marine Climatic Atlas of the North Atlantic Ocean (1974). This atlas gives monthly graphs of the cumulative percent frequency of recorded seawater temperatures for selected oceanic sites and these were used to estimate temperature ranges around the mean as they regularly occur in various regions of the North Atlantic Ocean (see also Cambridge *et al.*, 1987).

This paper will first discuss the evidence for thermal ecotypes, and evaluate to what extent experiments based on one or only a few isolates can contribute to an understand-

ing of the nature of temperature-determined phytogeographic boundaries. Secondly, this paper will discuss how experimental evidence on the thermal responses of species may be applied to analyse the nature of their geographic boundaries. Thirdly, experimental and phenological evidence on the nature of biogeographic boundaries will be summarised for species belonging to various distribution groups in the North Atlantic Ocean. For each group the characteristic temperature responses which are responsible for that particular distribution pattern will be identified.

ECOTYPIC VARIATION IN THERMAL TOLERANCE AND REQUIREMENTS

Various types of evidence have been put forward in support of the existence of thermal ecotypes in seaweeds. These include: differences in optimum temperatures for growth and reproduction, differences in thermal ranges over which growth and reproduction proceed, and differences in tolerance to high and/or low temperatures. For the explanation of phytogeographic boundaries, optimum temperatures are largely irrelevant (see below), but differences in minimum and maximum temperatures permitting growth and reproduction and differences in tolerance to high and low temperatures among populations may be important in understanding the nature of a phytogeographic boundary.

Which kind of evidence can be accepted as proof for the existence of thermal ecotypes? Often, conclusions have been based on experiments performed in different laboratories or with material collected in different seasons. Caution is indicated in these cases because experimental conditions may have been slightly different or the plants in a different physiological state (see e.g. Lüning, 1984). Differences in performance were often found at just one single temperature and the interpretation of results may vary with the coincidental choice of experimental temperatures. The following example may serve to illustrate this point (Table 1). In the *Trailiella* phase of the red alga *Bonnemaisonia*

Table 1. Evaluation of experimental evidence on the possible existence of thermal ecotypes in Atlantic populations of the red alga *Bonnemaisonia hamifera*. Tetrasporangium formation in the *Trailiella*-phase at different temperatures is compared for isolates from Helgoland (North Sea) (Lüning, 1980a, 1981) and Galway Bay (W. Ireland), (Breeman et al., 1988; Breeman & Guiry, unpubl.). Plants were cultured in two different laboratories (Biologische Anstalt Helgoland, F.R.G. and Marine Biology Department, University of Groningen, Netherlands) in a slightly enriched seawater medium (Lüning, 1980a) under short day conditions (8:16) at $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. Responses were determined (as % reproduction) after 4 weeks incubation; n. d. = no data

Temperature (°C)	Reproduction (%)			
	Helgoland isolate *	Galway Bay isolate **		n
		mean	range	
10	0	0	-	3
11	n. d.	7	0-22	4
12	0	48	2-97	8
13	n. d.	88	48-100	4
15	97	91	87-98	3
17	73	67	23-94	3
20	0	0	-	3

* based on 150 individuals per treatment in a single experiment
 ** based on 3-8 (n) replicate experiments each with 32-52 individuals

hamifera tetrasporangia are formed in short-day conditions, but only over a comparatively narrow temperature interval. An isolate from Helgoland in the North Sea formed sporangia at 15 and 17 °C, but not at 10, 12 and 20 °C (Lüning, 1980a, 1981), whereas an isolate from Galway Bay (W Ireland) formed tetrasporangia at 12, 15 and 17 °C, but not at 10 and 20 °C (Table 1; Breeman et al., 1988; Breeman & Guiry, unpubl.). Thus, there appeared to be a difference of at least 3 °C between the two isolates in the minimum temperature permitting reproduction. Closer examination of the results (Table 1) shows that this apparent difference is, in fact, being caused by the very sharp transition of the response at the temperature of 12 °C, which made results at this temperature particularly variable and dependent upon small deviations in the experimental temperature. Had the original comparisons been made at, say, 10 and 13 °C probably no differences would have been found. In view of the above considerations the following discussion on thermal ecotypes will concentrate on species for which thermal tolerance and requirements of the isolates have been determined in parallel series of quantitative experiments which had been specifically designed to identify possible thermal ecotypes.

The enormous difference between species in the amount of genetic variability in thermal tolerance over the distribution range may be illustrated by comparing two brown algae: *Laminaria saccharina* (incl. ssp. *longicuris*) and *Ectocarpus siliculosus* (Fig. 1). These species occur on both sides of the Atlantic from the Arctic into the warm temperate (*L. saccharina*) or tropical (*E. siliculosus*) region (Bolton, 1983; Bolton & Lüning, 1982; Lüning, 1985). For both species isolates from different climatic zones along more or less uninterrupted coastlines in the eastern and western Atlantic have been compared.

In *Laminaria saccharina* there were no differences in thermal tolerance among the isolates and only minor differences in their growth responses (Fig. 1). Hybridization studies have shown virtually full compatibility among the different isolates (tested on the isolates from Helgoland, the Isle of Man, Halifax and Brittany as well as several Pacific isolates; Lüning, 1975; Lüning et al., 1978; Bolton et al., 1983). Thermal tolerance and requirements of each isolate would allow survival through the entire distribution range, but some isolates, for instance the one from Igloodik, is subjected in the field to suboptimal conditions yearlong (Fig. 1). The location of the geographic boundaries in the N Atlantic Ocean could be explained by the thermal responses shared by all isolates. On both sides of the Atlantic, southward extension of *L. saccharina* would be prevented by lethal, high summer temperatures (Bolton & Lüning, 1982; Lüning, 1984; van den Hoek, 1982a; Fig. 1).

For *Ectocarpus siliculosus* the story is quite different (Fig. 1). This cosmopolitan species showed gradually changing thermal tolerance and requirements over the distribution range. No differences were established in the lower survival limit of the isolates (they all tolerated 0 °C), but at low temperatures growth was better in the northern than in the southern isolates. Differences in upper survival limits amounted to ca 10 °C, northern isolates being unable to survive in the habitat of southern ones. In the isolates from the region in between, the responses changed gradually in an ecoclineal way. Sexual compatibility among the isolates did not show any direct relationship with the ecoclineal variation in thermal responses. Most isolates were compatible with respect to gamete fusion, but the Port Aransas isolate showed partial, the Woods Hole isolate complete incompatibility with the other isolates (Müller, 1979).

Comparison of the tolerance ranges of *Ectocarpus siliculosus* isolates with tempera-

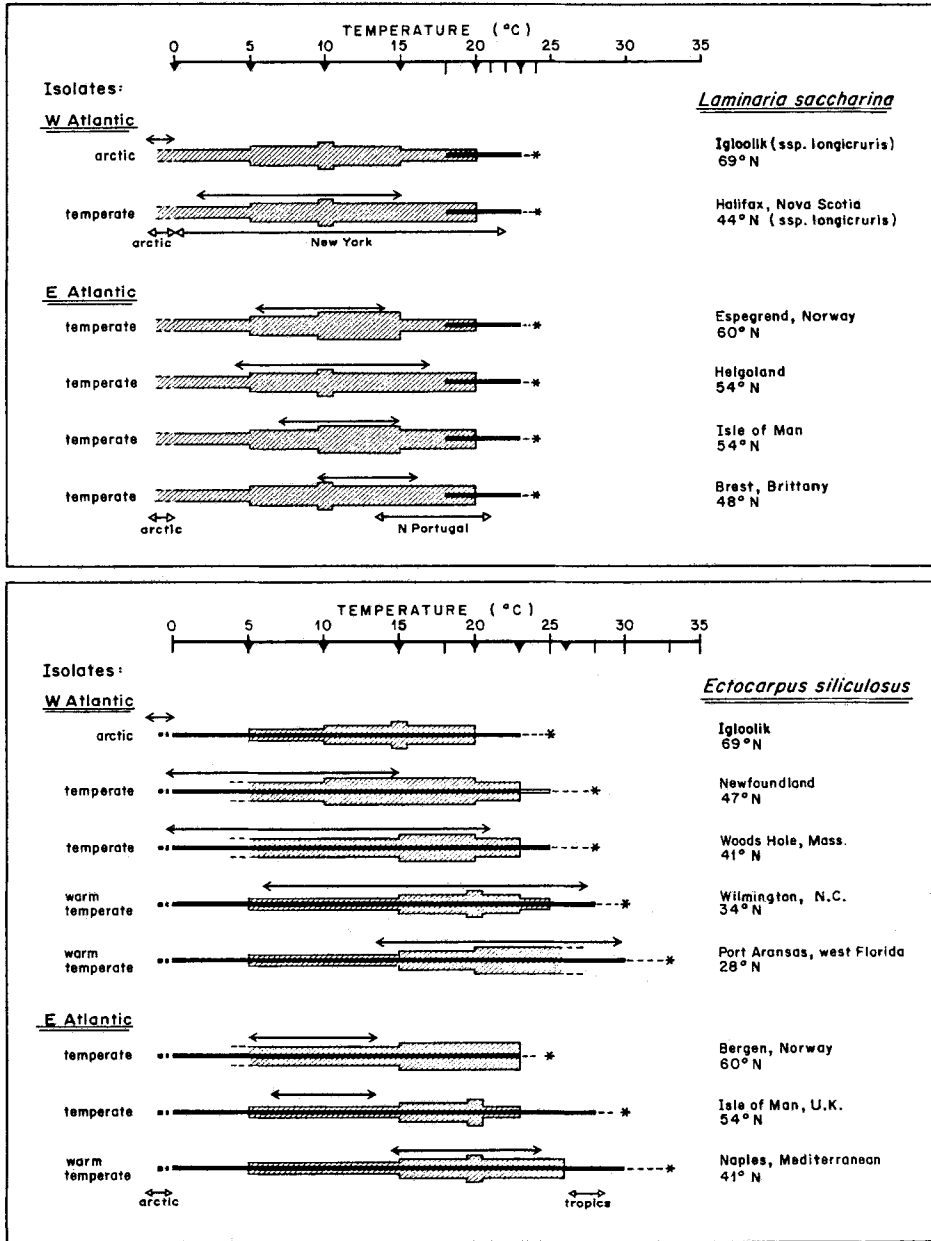


Fig. 1. Temperature ecotypes in seaweeds. Comparison of thermal ranges and growth in isolates from various points in the distribution range of two brown algae: *Laminaria saccharina* (incl. ssp. *longicruris*) (Bolton & Lüning, 1982) and *Ectocarpus siliculosus* (Bolton, 1983). Survival ranges defined as follows: plants capable of regrowth after 2 weeks incubation (solid bar), lethal temperature (*). Growth (hatched bars) represented in three categories (20–50%, 50–90% and >90% of maximum). Experimental temperatures (for growth [—▼—] and survival [—■—] experiments) indicated on temperature scale. Growth data for *L. saccharina* are based on young sporophytes, survival limits on gametophytes. Data for *E. siliculosus* are for male, female and/or heterozygous sporophytes. Annual temperature ranges are shown for the sites of collection of the isolates (black arrows, above) and for the extremes of the distribution range (open arrows, below)

ture conditions at their location of origin shows that, even in this species with a considerable potential for genetic adaptation, local populations are not always optimally adapted to local conditions. Again, some populations, for instance that at Igloolik and, to a lesser extent, those at Bergen and the Isle of Man, experience suboptimal conditions yearlong (Fig. 1). Another interesting point is the similarity of the ecocline variation along American and European coasts. Isolates from both sides of the Atlantic were relatively eurythermal, with broad survival and growth ranges, in spite of the fact that seasonal temperature fluctuations are much smaller on European than on American coasts. In consequence, there is a larger amount of "unused thermal potential" in European populations (Fig. 1). Evidently, the potential for genetic adaptation in *E. siliculosus* does not allow for the development of stenothermous ecotypes.

The genetic variability found in *Ectocarpus siliculosus* appears to be exceptional among seaweeds. Most other species investigated to date were remarkably uniform in their limits of thermal tolerance (Tables 2, 3), although growth responses were somewhat more variable (Table 3). No further evidence was found for ecocline variation in tolerance along continuous coastlines (e.g. *Dumontia contorta*, *Gigartina teedii*, *Chondrus crispus*, *Scytosiphon lomentaria*, *Cladophora laetevirens* and *Gracilaria tikvahiae*; Tables 2, 3). Nor is there much evidence for ecotypic differentiation between eastern and western Atlantic populations, particularly for species with an (arctic to) temperate distribution (e.g. *D. contorta*, *C. crispus*, *S. lomentaria* and *Laminaria digitata*; Tables 2, 3). Only in two tropical to temperate species of *Cladophora* differences in thermal limits of up to 5°C were found between tropical Caribbean and temperate European populations, but one species (*C. coelothrix*) was variable in its tolerance to low temperatures, the other (*C. vagabunda*) in its tolerance to high temperatures (Table 3).

Thermal ecotypes have also been found with regard to the temperature requirements for reproduction or the initiation of macrothalli, particularly in species, with photoperiodic responses. Examples include the brown alga *Scytosiphon lomentaria* (Lüning, 1980a, 1981; tom Dieck, 1987) and the red algae *Rhodochorton purpureum* (West, 1972; Dring & West, 1983) and *Dumontia contorta* (Rietema, 1982; Rietema & Breeman, 1982; Rietema & van den Hoek, 1984), all of which have been discussed in detail elsewhere (van den Hoek, 1982a, b; Dring & Lüning, 1983; Dring, 1984; Lüning, 1985). In *S. lomentaria* and *R. purpureum*, responses changed in a more or less ecocline way, although there were some irregularities. In both species there were also latitudinal daylength ecotypes which differed in their critical daylength, whereas in *S. lomentaria* daylength-neutral strains co-occurred with daylength-sensitive strains in at least part of the distribution range (Kristiansen, 1984; Correa et al., 1986; tom Dieck, 1987). In *D. contorta*, some of the differences among strains were related to local extremes in environment, but mostly, differences were of minor importance and could not be consistently related to differences in the temperature/daylength regimes at the location of origin of the isolates (Rietema & van den Hoek, 1984).

In conclusion, thermal ecotypes have evolved in some seaweeds but not in many others. In general, ranges of thermal tolerance varied less than temperature effects on growth and reproduction. Differences in tolerance were found between disjunct tropical and temperate isolates of species with a tropical extension, not in species with a temperate distribution. This may reflect the longer evolutionary history of the former distribution group, which is thought to be Tethyan in origin (van den Hoek, 1984; Lüning,

Table 2. Temperature ecotypes in seaweeds. Comparison of upper survival temperatures for isolates collected in various parts of the distribution range. Temperature was survived (+); temperature was lethal in 2-5 weeks (-). R = red alga. B = brown alga

Species (distribution-type)	Origin of isolate (n of strains)	Climatic zone (August-isotherm)	Upper survival temperature (°C)		References
			+	-	
R <i>Dumontia contorta</i> (arct.-temp.)	- E. Atlantic				
	Iceland	temperate (11)	24	26	Rietema & van den Hoek (1984)
	Isle of Man	temperate (15)	24	26	
	Netherlands	temperate (17)	24	26	
	Brittany	temperate (17)	24	26	
	- W. Atlantic				
Bay of Fundy	temperate (13)	24	26		
	Halifax (2)	temperate (16)	24	26	
R <i>Gigartina teedii</i> (trop.-temp.)	- E. Atlantic				
	W. Ireland	temperate (15)	31	32	Guiry et al. (1987)
	S. W. England	temperate (16)	31	32	
	Brittany	temperate (17)	31	32	
	- Mediterranean				
	Sicily	warm temp. (26)	31	32	
N. Greece	warm temp. (26)	31	32		
R <i>Chondrus crispus</i> (temperate)	- E. Atlantic				
	Iceland (3)	temperate (11)	28	29	Lüning et al. (1987)
	N. Norway	temperate (10)	28	29	
	Scotland	temperate (14)	28	29	
	W. Ireland (5)	temperate (15)	28/29	29/30*	
	Wales	temperate (15)	28	29	
	S. W. Engl. (2)	temperate (16)	28/29	29/30*	
	North Sea	temperate (17)	29	30	
	Brittany	temperate (17)	29	30	
	N. W. Spain	warm temp. (19)	28	29	
	- W. Atlantic				
	Halifax	temperate (16)	28	29	
B <i>Scytosiphon lomentaria</i> (arct.-temp.)	- E. Atlantic				
	Iceland	temperate (11)	28/29	29/30**	tom Dieck (1987)
	N. Norway	temperate (10)	28	29	
	W. Norway	temperate (13)	28/29	29/30**	
	S. Norway	temperate (15)	29	30	
	Denmark (2)	temperate (16)	29	30	
	Helgoland	temperate (17)	29	30	
	Canary Isles	warm temp. (22)	28/29	29/30**	
	- Mediterranean				
	Yugoslavia	warm temp. (25)	29	30	
	N. Greece	warm temp. (26)	27/28	28/29**	
	- W. Atlantic				
S. W. Greenland	arctic (5)	28	29		

* one strain survived 29 °C
 ** results varied between replicate experiments

Table 3. Temperature ecotypes in seaweeds. Comparison of temperature ranges for survival and growth and of optimum growth temperatures for isolates collected in different parts of the distribution range. G = green alga. R = red alga. B = brown alga

Species (distribution-type)	Origin of isolate	Climatic zone	Temperature range at collection-site (°C)	Survival range (°C)	Growth range (°C) (>20% of max.)	Optimum growth temperature (°C) (>90% of max.)	References
G <i>Cladophora coelothrix</i> (trop.-temp.)	- E. Atlantic Brittany - W. Atlantic Caribbean	temperate tropical	8-17 25-29	5-35 10-35	15-30 20-30	25-30 25-30	Cambridge et al. (1984, 1987)
G <i>Cladophora vagabunda</i> (trop.-temp.)	- E. Atlantic Brittany - W. Atlantic Caribbean	temperate tropical	8-17 25-33	0-30 0-35	15-30 15-35	25-30 30	Cambridge et al. (1984 and unpubl.)
G <i>Cladophora albida</i> (trop.-temp.)	- E. Atlantic Brittany - W. Atlantic Connecticut	temperate temperate	8-17 -1.8-24	<-5->35 <-5->35	15-35 15-35	25-30 25-30	Cambridge et al. (1984 and unpubl.)
G <i>Cladophora laetevirens</i> (trop.-temp.)	- E. Atlantic Brittany - Mediterr. Corsica	temperate warm temp.	8-17 11-25	0-30 0-30	15-30 15-30	25 30	Cambridge et al. (1987)
R <i>Gracilaria tikvahiae</i> (trop.-temp.)	- W. Atlantic Nova Scotia - W. Atlantic Florida	temperate warm temp.	-1.8-26 16-30	<0-34 <0-34	15-34 10-34	20 20	McLachlan & Bird (1984)
B <i>Laminaria digitata</i> (arct.-temp.)	- E. Atlantic Helgoland - W. Atlantic Halifax	temperate temperate	-1.8-18 -1.8-18	<0-22/23* <0-22/23*	0-20** 0-20**	10** 10**	Bolton & Lüning (1982)

* gametophytes: female/male
** young sporophytes

1985; Joosten & van den Hoek, 1986). There is no evidence for the existence of stenothermal ecotypes in the eastern, contrasted to eurythermal ecotypes in the western Atlantic, such as might have been expected in view of the far larger annual temperature fluctuations in the western Atlantic. Neither is there any evidence for the development of local ecotypes optimally adapted to local conditions, even in species with a considerable potential for genetic adaptation such as *Ectocarpus siliculosus*. Therefore, when addressing the question of temperature-determined biogeographic boundaries, experiments need not necessarily be done with boundary populations. In some species, thermal responses of a single isolate may represent the genetic potential of the species over the whole of the distribution range. Care should be taken not to extrapolate too far, particularly where biogeographic boundaries in other climatic zones or disjunct parts of the distribution range are being considered. The location of geographic boundaries set by the species' temperature requirements for reproduction (and growth) is more likely to be influenced by the existence of ecotypes than are boundaries set by lethal limits.

EXPERIMENTAL EVIDENCE ON THE NATURE OF DISTRIBUTION BOUNDARIES

Comparison of thermal responses with regional patterns of ocean isotherms:
lethal vs. growth limits at northern boundaries in Europe of three species of
Cladophora as an example

Comparison of distribution patterns of species with summer and winter isotherms in their boundary regions often provides indications as to the season when temperatures could potentially be limiting to distribution, particularly if summer and winter isotherms follow dissimilar patterns over the region. This is the case along the Atlantic coasts of the British Isles and western Norway and in the North Sea. The distribution of three species of *Cladophora* in this region (Fig. 2) suggests that in two species, i.e. *C. coelothrix* and *C. hutchinsiae*, low winter temperatures (< ca 5°C) are responsible for their absence in the North Sea, because summer temperatures in that area are higher than those experienced along Atlantic coasts of the British Isles and could therefore not be limiting. For *C. coelothrix* the restricted distribution on the south and west coasts of the British Isles suggests that adverse summer temperatures (< ca 15°C) prevent northward extension because, judged by its occurrence in the English Channel, winter temperatures would not be lethal all the way up the Irish and Scottish west coasts. Similarly, for *C. albida* low winter temperatures cannot be expected to restrict distribution in W Norway because up to the North Cape these are higher than those experienced at the entrance of the Baltic (<0°C). Again, adverse summer temperatures (< ca 13°C) preventing growth (or reproduction) may be expected to restrict distribution along this coast. Thus, when trying to explain the different distribution patterns of these three *Cladophora* species in the region differences in tolerance to temperatures below ca 5°C and differences in growth/reproduction responses at temperatures between, say, 10 to 15 (-20)°C should be considered (Fig. 2).

Experiments (Fig. 3) have shown that differences in performance over these critical temperature intervals did account for the observed differences in distribution (Cambridge et al., 1984, 1987). *Cladophora coelothrix* and *C. hutchinsiae* were unable to

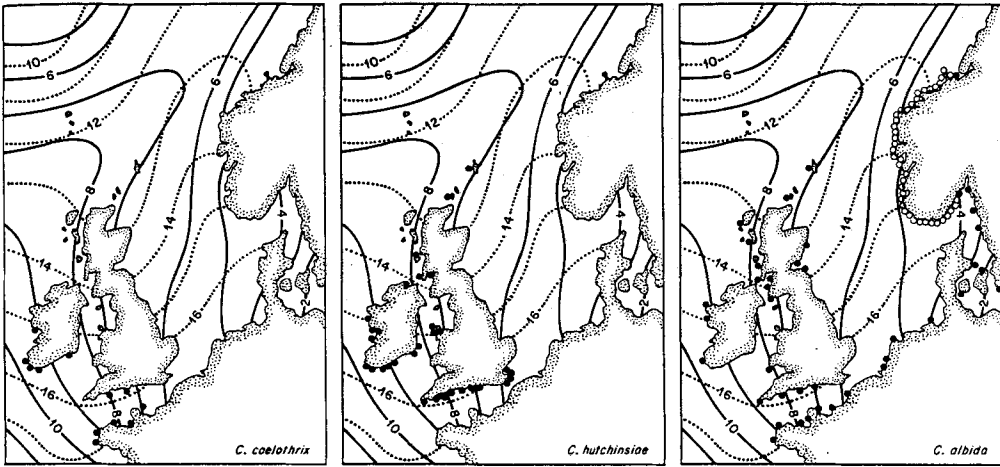


Fig. 2. Location of northern distribution boundaries of three species of *Cladophora* in relation to summer (dashed lines) and winter (solid lines) isotherms in the NE Atlantic and the North Sea. Distribution data based on van den Hoek (1963, 1982c); Cambridge et al. (1984, 1987). Summer (August) and winter (February) isotherms from Gorshkov (1978)

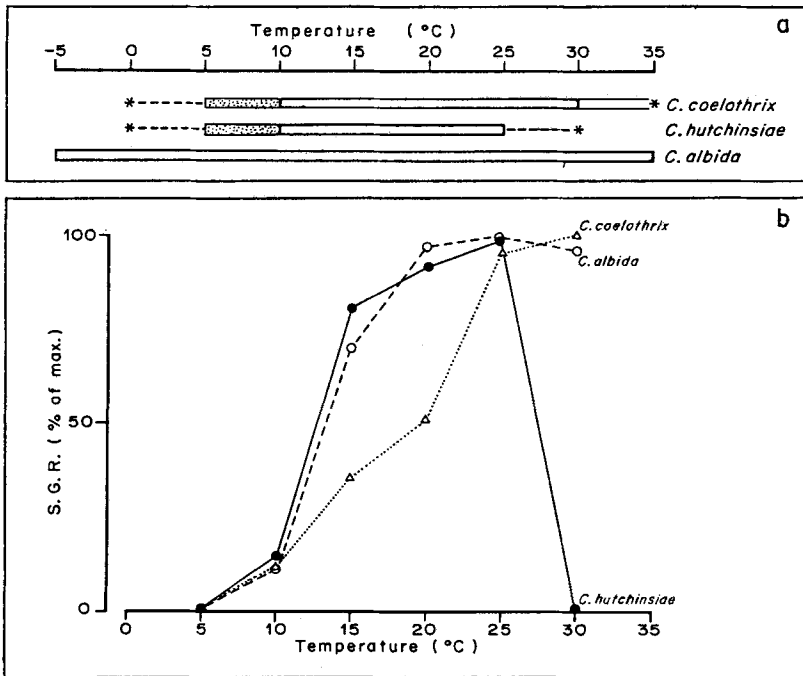


Fig. 3. Experimental evidence on the nature of distribution boundaries: lethal vs. growth limits in three species of *Cladophora* with different distribution patterns in NW Europe (Fig. 2). a: Thermal ranges of tolerance; survival ranges defined as follows: permanent survival (solid bar), survival in short but not in long days (stippled bar), temperature is lethal in less than 6 weeks (---*), less than 12 weeks (—*). b: Growth responses: growth was measured as the relative growth rate (% increase in length per day) and expressed relative to the maximum (ca 25% d⁻¹ in *C. coelothrix* and *C. hutchinsiae* and ca 40% d⁻¹ for *C. albida*, after Cambridge et al., 1984, 1987)

tolerate temperatures below ca 5°C and this prevents their occurrence in the North Sea. *C. albida* and *C. hutchinsiae* grew markedly better at 15 (–20)°C than *C. coelothrix* which explains their more northerly extension on Atlantic coasts. *C. hutchinsiae* would be excluded from the Norwegian coasts by lethal, low winter temperatures, whereas *C. albida*, with its capacity to survive these low winter temperatures, can go north to the Trondheimfjord, where summer temperatures rise to values of ca 13°C, which is just high enough for some growth.

The distribution pattern of *Cladophora coelothrix* shows that two comparatively nearby distribution boundaries in a region may be set by different limiting effects of temperature. Distribution of *C. coelothrix* in the English Channel is limited by lethal, low winter temperatures whereas extension on the Irish west coast is limited by summer temperatures remaining too low for growth. Evidently, distribution patterns in a region are sometimes caused by several different limiting effects of temperature, each operating in a different season.

The experimental results also indicate where there are "gaps" in the distribution which cannot be attributed to the limiting effects of temperature. For instance the absence of *Cladophora albida* from the English east coast represents such a "gap", and the lack of records in this area may be attributed to the presence of sediment coasts and the associated undersampling of hard substrate algae (cf. Dixon & Irvine, 1977; Norton, 1986).

The experimental data (Fig. 3) show that temperature responses outside the critical temperature intervals (10°C to 15/20°C for growth, –5°C to 5°C for survival) were irrelevant in explaining the location of distribution boundaries in the area. Thus, a higher optimum temperature for growth was in no way related to a more southerly located northern boundary. In fact, *Cladophora albida*, with the northernmost extension, had optimum growth temperatures as high as 25–30°C. These high optimum temperatures mean that temperatures are suboptimal for growth yearlong over a large part of the distribution range in W Europe. Several authors (e.g. Stewart, 1984; Mathieson & Dawes, 1986) have discussed distribution patterns of seaweeds in terms of optimum growth temperatures. However, it should be realised that distribution ranges of seaweeds are determined by the effect of limiting factors, restricting distribution at each boundary. Therefore, suboptimal or sublethal rather than optimum temperatures should be considered in the question of a species' geographic distribution.

Comparison of thermal responses among species which reach their limit of extension along the same stretch of coastline: lethal vs. reproduction limits at southern boundaries in Europe as an example

Comparisons of temperature responses among species which reach their distribution boundary on the same stretch of coastline may provide evidence on the factor(s) which are restrictive to distribution. Table 4 summarises temperature responses of various seaweeds, all of which reach their southern boundary along the eastern Atlantic coast in the Iberian Peninsula. All species are still to be found in NW Spain, whereas none extends to the south coast of Portugal. Along this coastline, mean winter temperatures increase from ca 12 to ca 15°C, whereas mean summer temperatures increase from ca 20 to ca 23°C. In *Chorda filum*, *Dumontia contorta*, *Desmarestia aculeata*, *Laminaria*

Table 4. Experimental evidence on the nature of distribution boundaries: lethal vs. reproduction limits. Comparison of temperature responses among seaweeds that all reach their southern boundaries in the eastern Atlantic on the west coast of the Iberian Peninsula. Species are listed in sequence of southward extension. Annual temperature ranges are shown for N. W. Spain (all spp. present) and S. Portugal (none of the spp. present) (based on Ardré, 1970, 1971). Occurrence in Bay of Biscay based on Meunier (1965) and van den Hoek & Donze (1966). Temperature responses which are restrictive to distribution in bold print. Sexual reproduction by gametophytes (g), initiation of macrothalli (m), new blades (b). B = brown alga. R = red alga

Location (annual temperature range, °C)	Species (references)	Lethal limit survival (°C)	Lethal limit hardest stage lethal (°C)	Reproduction optimum temp. (°C)	Reproduction limit inhibiting temp. (°C)	Presence in Bay of Biscay (11-25 °C)
N. W. Spain, Vigo, 42 °N (12-20 °C)	B <i>Chorda filum</i> (1, 2, 3)	26	28	12	14	+
	R <i>Dumontia contorta</i> (4)	24	26	12	15	-
	B <i>Desmarestia aculeata</i> (2, 3, 5)	23	25*	15	18	-
	B <i>Laminaria saccharina</i> (3, 6, 7)	22	23	15	18	-
	B <i>Laminaria hyperborea</i> (3, 6, 7)	20	21	8	15	-
	B <i>Punctaria latifolia</i> (9)	30	35	12	16	+
S. Portugal, Praia da Rocha, 37 ° N (15-23 °C)						

* lethal limit only determined for sporophyte

References: 1) Novaczek et al. (1986a); 2) Lüning (1980a); 3) Lüning (1984); 4) Rietema & van den Hoek (1984); 5) Müller & Luthe (1981); 6) Bolton & Lüning (1982); 7) Lüning (1980b); 8) Lüning. (1986); 9) Rietema & van den Hoek, (1981)

hyperborea and *Punctaria latifolia*, temperatures over 14–16°C were partially or completely inhibitory for sexual reproduction or the initiation of blades or macrothalli. In these species, southward extension will be limited by winter temperatures that are too high for completion of the life history. For two species, *L. saccharina* and *L. hyperborea*, southward extension was (also) limited by high lethal summer temperatures above ca 20°C (Table 4).

The example of *L. hyperborea* shows that more than one critical effect of temperature may restrict a species along a certain coastline. In this species, southward extension is prevented both by winter temperatures too high for the initiation of the new blades and by lethal, high summer temperatures. Temperature requirements for sexual reproduction do not seem to be limiting, as gametangia were still being formed at 15°C, a temperature inhibitive to blade initiation. Evidently, critical effects of temperature may operate on any given process in the life history to restrict distribution.

Further details of the distribution pattern of the species in this area were accounted for by restrictive effects of temperature other than those setting the limit on the Iberian coast (Table 4). For example, the absence of most of the species from the Bay of Biscay, where, locally, summer temperatures may rise to values of ca 25°C, must be attributed to the lethal effect of these high temperatures. The only two species which have been reported from the Bay of Biscay, *Chorda filum* and *Punctaria latifolia*, have a higher upper lethal limit than any of the other species.

In conclusion, comparison of thermal responses among species reaching their limit of distribution along the same stretch of coastline, may show which thermal responses are effective in limiting distribution. It will also indicate whether a species does not extend towards its potential thermal limits so that some other factor should be considered as restrictive to distribution on that coast.

TEMPERATURE RESPONSES AND DISTRIBUTION BOUNDARIES IN SEAWEEDS BELONGING TO VARIOUS DISTRIBUTION GROUPS

Temperature ranges for survival, growth and reproduction have now been determined experimentally for some 60 seaweed species from the North Atlantic Ocean, belonging to various distribution groups (cf. van den Hoek, 1982a, b, for designation of groups). Although, in many species, the experimental evidence is still far from complete, some general patterns as to the thermal responses characteristic for the different distribution groups are beginning to emerge (Fig. 9). In the following discussion, only results from long-term experiments (one to several weeks) have been included as short-term exposures (hours or days) may have an opposite effect to those observed in the long run (cf., for instance, Strömberg, 1977, 1983), the latter being more relevant for geographic distribution. In determining thermal ranges of tolerance and requirements various authors have applied widely different experimental temperature intervals so that critical temperatures are known with a varying amount of precision. Therefore, through the following discussion, both the temperature-values that did, and those that did not, allow survival or growth and reproduction will be presented (cf., for instance, Tables 4–14).

Firstly, a comparison will be made of thermal responses in three distribution groups, endemic either to the eastern or western Atlantic, each being characteristic of a different climatic zone. Subsequently, different types of temperature limits setting northern and

Table 5. Survival ranges of seaweeds belonging to the warm-temperate Mediterranean-Atlantic distribution group. Temperatures between brackets were survived only when in dim light and/or in short days. G = green alga. R = red alga. B = brown alga

Species	Temperature (°C)		References
	lethal	survival	
G <i>Cladophora hutchinsiae</i>	0 (5)	10–25	30 (1)
R <i>Bonnemaisonia asparagoides</i>		<3–22	24 (2)
R <i>Halurus equisetifolius</i>	5	10–26	27 (3, 4)
R <i>Callophyllis laciniata</i>	0 (5)	10–24 (25)	26 (3, 4)
R <i>Polyneura hilliae</i>	0 (5)	10–24	25 (4, 5)
R <i>Calliblepharis ciliata</i>	0 (5)	10–27	28 (4, 5)
R <i>Cryptopleura ramosa</i>	0	5–27	28 (4, 5)
R <i>Lomentaria articulata</i>		<0–27	28 (4, 5)
B <i>Laminaria hyperborea</i>		<–1.5–20	21 (6, 7)
B <i>Saccorhiza polyschides</i>	3	5–23	25 (8)
B <i>Phyllariopsis brevipes</i>	5	10–20	25 (9)

References: 1) Cambridge et al. (1984); 2) Rueness & Asen (1982); 3) Yarish et al. (1984); 4) Yarish et al. (1987); 5) Yarish et al. (1986); 6) Bolton & Lüning (1982); 7) Lüning (1986); 8) Norton (1977); 9) Henry (1987a)

southern boundaries in amphi-Atlantic species will be discussed. In each case an attempt will be made to analyse which particular kind of thermal response causes the observed distribution patterns (summarised in Fig. 9).

Species endemic to the eastern or western Atlantic

The warm temperate, Mediterranean-Atlantic group: northern and southern boundaries set by lethal or by reproduction limits

In general, representatives of this distribution group had relatively narrow ranges of tolerance, temperatures below ca 5 °C and above ca 25 °C being lethal (Table 5). This will prevent occurrence on the American side of the Atlantic, where annual temperature fluctuations are over 20 °C everywhere in the (warm)temperate zone and temperatures over 25 °C prevent occurrence in the tropics (Fig. 9a).

In several red algal representatives of this distribution group having isomorphic life histories, lethal limits set both northern and southern boundaries in W Europe/NW Africa (Figs 4, 9a). Adverse temperatures for growth and reproduction in the favourable season do not seem to restrict distribution as temperatures are within the favourable range of 10–20 °C for at least part of the year, even in regions beyond the boundaries (Figs 4, 9a). Their absence from the eastern North Sea must also be attributed to lethal, low winter temperatures (<5 °C), and their absence from the eastern Mediterranean to lethal, high summer temperatures (>25 °C) (Fig. 4). In the central part of the Mediterranean several species can survive because they are restricted to deep, colder water. However, on open Atlantic coasts in NW Europe and NW Africa several species appear not quite to reach their potential thermal limits (Fig. 4).

In contrast, some species with heteromorphic life histories were restricted in distribu-

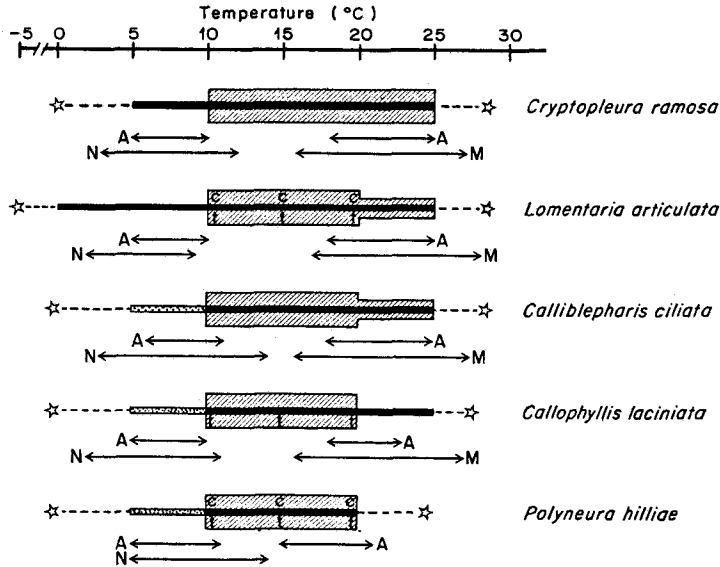


Fig. 4. Northern and southern lethal boundaries in five red algal representatives of the warm temperate Mediterranean-Atlantic distribution group with isomorphic life histories. Comparison of thermal ranges of tolerance and growth/reproduction (bar diagrams) with annual temperature ranges at distribution boundaries (arrows, below). Northern boundaries at the entrance of the North Sea or in SW Norway (N) and on the Atlantic coasts of the British Isles (A); southern boundaries in the Mediterranean (M) and on the Atlantic coast of NW Africa (A). Distribution data based on Yarish et al. (1984, 1986); South & Tittley (1986); Maggs (1986); Furnari (1984). Temperature data are estimates for an "unfavourable year" based on Gorshkov (1978); U.S. Navy (1974, 1981). Survival ranges as defined in Figure 3 (Yarish et al., 1984, 1986, 1987); growth (hatched bars) presented in two categories based on visual estimation (Yarish et al., 1984, 1986 and unpubl.). Reproduction for gametophytes (c) and tetrasporophytes (t) indicated within bars

tion not by lethal limits but by their temperature requirements for completion of the life history. For instance, in *Laminaria hyperborea* and *Saccorhiza polyschides*, low temperatures were required for blade initiation and sexual reproduction, respectively (see Table 12), and this would limit southward extension. In two red algal representatives of this group with heteromorphic life histories, i.e. *Acrosymphyton purpuriferum* and *Atractophora hypnoides* (Table 6), a requirement for alternating high and low temperatures for completion of the life history restricts distribution. In *A. purpuriferum* summer temperatures above 16°C and winter temperatures below 18°C are required for reproduction of the gametophyte and the tetrasporophyte, respectively, and this restricts the distribution range to the Mediterranean and NW Africa. Similarly, in *A. hypnoides*, summer temperatures above ca 10°C and winter temperatures below ca 15°C are required for completion of the life history, which accounts for the narrow distribution range from N Ireland to the Bay of Biscay (Table 6).

For some species in this distribution group, the location of some of their geographic boundaries was not adequately explained by their temperature responses in culture. For instance, the ability of *Lomentaria articulata* to survive and even grow slowly at 0°C would allow this species to occur in the North Sea and possibly even in northeast America

Table 6. Reproduction limits at northern and southern boundaries in two red algal representatives of the warm-temperate Mediterranean-Atlantic distribution group with heteromorphic life histories. Comparison of temperature requirements for completion of the life history with annual temperature ranges at distribution boundaries. Temperatures inducing reproduction (+), temperatures substantially or completely inhibiting reproduction (-). Annual temperature ranges (in brackets, °C) are mean values for February and August at 25 m depth (after Goshkov, 1978). Based on Breeman & ten Hoopen (1981) and Maggs & Guiry (1987)

Species	N. boundary	S. boundary	Reproduction (°C)			
			gametophytes		tetrasporophytes	
			+	-	+	-
<i>Acrosymphyton purpuriferum</i>			≥ 18	16	≤ 16	18
	S. Portugal (14-17)	Canaries (18-22)				
	N. W. Mediter. (12-17)	E. Mediter. (17-26)				
<i>Atractophora hypnoides</i>			≥ 15	10	≤ 10	15
	N. Ireland (8-14)	Bay of Biscay (11-18)				

(Yarish et al., 1986; Fig.4). Similarly, there is, so far, no evidence to explain why *Laminaria hyperborea* does not go up into the high arctic, as blade initiation and normal sporophyte growth were possible in this species even at -1.5°C (Lüning, 1986; Table 5).

The tropical western Atlantic group: northern boundaries set by lethal limits

Thermal ranges of tolerance and temperature requirements for growth and reproduction have now been determined for three representatives of this distribution group (Table 7). As in the previous group, species had a relatively narrow survival range with temperatures below 15°C and above ca 34/35°C being lethal. Growth (and reproduction) proceeded from ca 20-30°C. Surprisingly, these strictly tropical algae had a comparatively low upper lethal limit (<35°C). The limited survival potential at temperatures below 15°C will restrict them to the (sub)tropics. Northward extension would be prevented by lethal, low winter temperatures (Fig. 9b), and not by summer temperatures too low for growth and reproduction, because sufficiently high summer temperatures occur

Table 7. Survival ranges of seaweeds belonging to the tropical western Atlantic distribution group. Growth/reproduction ranges: ca 20-30 °C. G = green alga. R = red alga

Species	Temperature (°C)			References
	lethal	survival	lethal	
G <i>Cladophora submarina</i>	10	15-30	35	(1)
R <i>Gracilaria wrightii</i> *	10	15-32	34	(2)
R <i>Gracilaria mammillaris</i>	10	15-32	34	(2)

* as *G. debilis* (cf. Wynne, 1986)
References: 1) Cambridge et al. (1987); 2) McLachlan & Bird (1984)

as far north as Cape Cod on open coasts (Fig. 9b) and even further north in enclosed embayments.

Species belonging to this distribution group are (by definition!) absent from the tropical eastern Atlantic although, on that side of the ocean, their thermal responses would enable occurrence over an even broader latitudinal range than in the western Atlantic (Fig. 9b). Intermittent catastrophic cold spells during glaciations, either in Pleistocene (van den Hoek, 1982a, b) or, more probably, in early Coenozoic to late Miocene (Joosten & van den Hoek, 1986; Cambridge et al., 1987), when temperatures were generally lower on African than on Caribbean coasts, have been invoked as the cause for their possible extinction in the eastern Atlantic. Since then, the central Atlantic Ocean must have constituted a barrier to dispersal. There is, so far, no experimental evidence on the thermal responses of tropical species with an amphi-Atlantic distribution.

The north-east American tropical to temperate group: northern boundaries set by growth/reproduction limits

Survival and growth/reproduction ranges have been determined for several red algal representatives of this group (Table 8). These species penetrate, at least marginally, into the tropics; northward they extend up into New England or enclosed embayments in the southern Gulf of St. Lawrence.

Table 8. Survival ranges of seaweeds belonging to the tropical to temperate western Atlantic distribution group. Growth/reproduction ranges: ca 15/20–30 °C. R = red alga

Species	Temperature (°C)		References
	survival	lethal	
R <i>Gracilaria tikvahiae</i>	<0–34	36	(1)
R <i>Grinnellia americana</i>	<0–31	32	(2, 3)
R <i>Agardhiella subulata</i>	<0–33	34	(2, 3)
R <i>Solieria filiformis</i> ***	<0–33	34	(2, 3)
R <i>Lomentaria baileyana</i> *	<0–33	34	(2, 3, 4)
R <i>Griffithsia globulifera</i>	<0–28	31	(4)
R <i>Chondria baileyana</i>	<0–28	31	(4)

* Isolated records known from eastern Atlantic.
 ** as *S. tenera* (cf. Wynne, 1986)
 References: 1) McLachlan & Bird (1984); 2) Yarish et al. (1984); 3) Yarish et al. (1987); 4) Novaczek et al. (1987)

In contrast to the previous two distribution groups, these species are characterised by wide tolerance ranges, with temperatures from 0 °C to over 30 °C being survived. Growth proceeded from 15–30 °C. Lack of growth or reproduction at temperatures below 15–20 °C will set their northern boundary (Fig. 9c and see below). Near the northern limit, winter temperatures below 0 °C will have to be survived, for which purpose special cold-resistant structures are formed (Yarish et al., 1984; Novaczek et al., 1987).

Potentially, temperature tolerance and requirements would enable these species to survive, grow and reproduce in the (sub)tropical eastern Atlantic (Fig. 9c), but only for a few species are there some scattered records from that side of the ocean. In the northern

part of Europe and along the potential "stepping stones" for dispersal in the North Atlantic Ocean (Greenland, Iceland) summer temperatures remain too low for growth and reproduction. These species, therefore, may have evolved in NE America whereafter the central Atlantic Ocean must have formed a barrier to eastward dispersal.

Phenological evidence for one example: the red alga *Lomentaria baileyana*

In several of the species discussed above (Table 8), phenological observations combined with in situ temperature measurements in populations near the northern distribution limit have confirmed the restrictive effect of low summer temperatures to northward extension (Novaczek et al., 1987). An example is the red alga *Lomentaria baileyana*, which is found from the Gulf of Mexico up into the southern Gulf of Saint Lawrence (Fig. 5). Experiments have shown that this species needs temperatures over 15°C for growth and over 20°C for reproduction. Temperatures up to 33°C and below 0°C were survived, the lower temperatures only by starch-filled basal holdfast pads which developed at temperatures of 15°C or below (Yarish et al., 1984, 1987; Novaczek et al., 1987; Fig. 5).

These temperature requirements appeared to regulate the phenology of the species over the whole of the distribution range. Particularly the onset of reproduction and the formation of cold-resistant holdfast-pads were strictly regulated by temperature (Fig. 5). In W Florida, the species is an autumn to spring annual which reproduces in autumn and late spring. At more northerly locations *Lomentaria baileyana* behaves as a summer annual. Going north along the coast of northeast America the reproductive season gradually shortens to a period of 2 summer months (Fig. 5). The temperature curve of Cape Cod shows why this species is restricted to warm embayments north of this point. On open oceanic coasts seawater temperatures remain too low for (growth and) reproduction all through the summer (Fig. 5).

Near its northern limit of distribution in the southern Gulf of Saint Lawrence, *Lomentaria baileyana* may become locally extinct during a period with repeated cool or brief summers because temperatures remain below those minimally required for reproduction (Fig. 5). It is possible that several other species in this distribution group (e.g. *Grinnellia americana* and *Agardhiella subulata*; Table 8), which are now restricted to the Cape Cod area, once extended north to the Gulf of St. Lawrence during a warmer climatic period and have since become extinct (Novaczek et al., 1987).

Species with an amphi-Atlantic distribution

Northern boundaries set by growth/reproduction limits or by lethal limits

Experimental and phenological evidence similar to that discussed above has confirmed the existence of northern growth and reproduction boundaries in the north Atlantic Ocean for several species with an amphi-Atlantic distribution (Tables 9, 10; Figs 9d, e). Species with this type of northern boundary are characterised by distribution patterns in which the boundary is shifted northward in NW Europe because the Gulf Stream causes summers to be warmer (Figs 9d, e). In general, species going north to the southern Gulf of St. Lawrence and N Britain or S Norway needed temperatures over

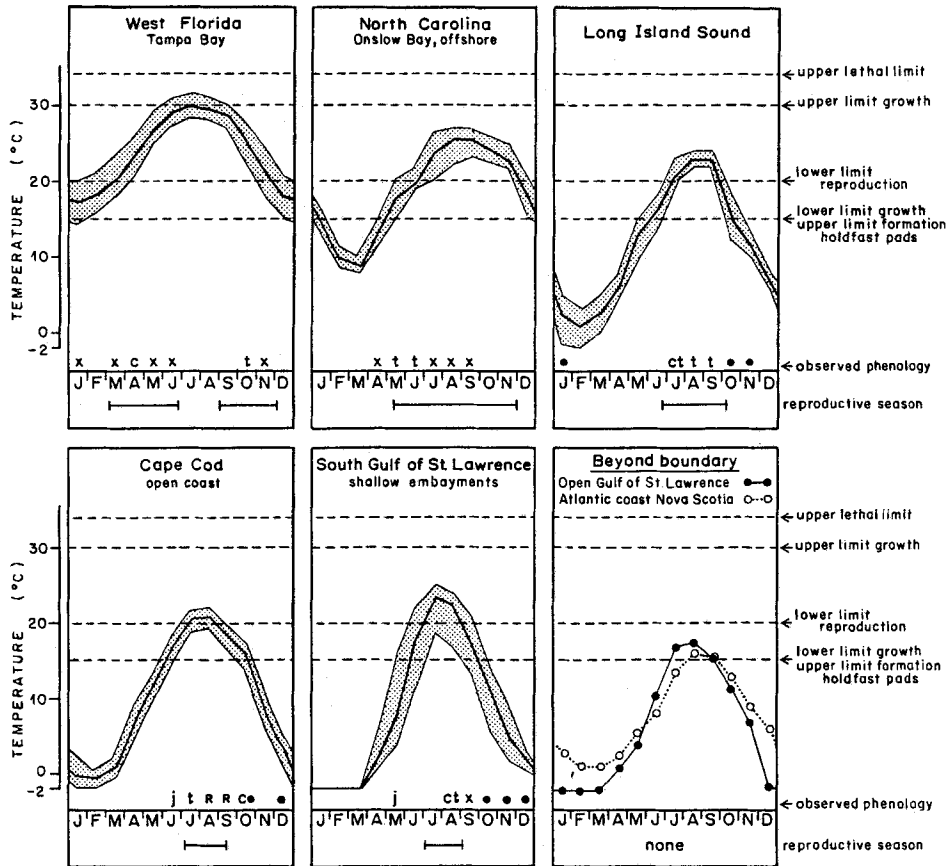


Fig. 5. Temperature responses and phenology of the red alga *Lomentaria baileyana* in relation to seasonal variation in seawater temperatures at locations within and just beyond the northern boundary in NE America. Example of a northern reproduction limit. Experimentally determined limits of thermal tolerance and temperature requirements for growth, reproduction and the formation of cold-resistant holdfast pads are indicated (Yarish et al., 1984, 1987; Novaczek et al., 1987). Expected duration of reproductive season shown below (—). Phenological observations: juvenile plants (j), upright thalli (x), holdfast pads (or detached plants) (●); reproduction: tetrasporangia (t), cystocarps (c), nature of reproduction not stated (R). Temperature curves represent means (solid line) and ranges (shaded). Phenological and temperature data based on Mathieson & Dawes (1975), Earle (1969) (Florida); Peckol (1982), Peckol & Searles (1984) (N Carolina); Yarish et al. (1984) (Long Island Sound); Sears & Wilce (1975) (Cape Cod); Novaczek et al. (1987) (S Gulf of St. Lawrence); Bird et al. (1983) (Open Gulf of St. Lawrence and Atlantic coast of Nova Scotia)

15–20°C for growth and reproduction. None of these species has been reported from Iceland where summer temperatures remain below 12°C (Table 9). Species with northern boundaries in Newfoundland and (N)W Norway required temperatures over 10°C and some of these have been found on Iceland where these requirements will just be met. Species occurring further north up to SW Greenland and W Nova Zemlya required temperatures over 5°C (Table 10), and those occurring as far north as the high Arctic

grew and reproduced adequately at 0°C. These species have consistently been found on Iceland (Table 9).

In general, these temperature requirements corresponded quite closely with summer temperatures at the respective limits of distribution (Tables 9, 10). In Europe, northern

Table 9. Northern growth and/or reproduction boundaries in ampho-Atlantic red and brown algae. Comparison of minimum temperatures permitting growth and reproduction among species reaching their northern boundaries at various points along the coast of N. E. America and N. Europe. Nature of temperature-inhibited process: growth (gr); formation of gametangia (g), tetrasporangia (t), parasporangia (pa), sporangia (s), plurilocular zoidangia (p), unilocular zoidangia (u), propagules (pr); development of microthalli (mi). Minimum temperature inducing adequate growth and reproduction (+); growth or reproduction substantially or completely inhibited (-). Experimental data based on N. E. American isolates. Phenological observations in N. E. American populations supported experimental evidence (*); phenological evidence only (**). R = red alga. B = brown alga. Annual temperature ranges at distribution boundaries and in the Arctic based on: Novaczek et al., 1987 (embayments S. Gulf of St. Lawrence); Wilce, 1959 (fjords N. Labrador); Gorshkov, 1978; U. S. Navy, 1981 (open coast other locations). Distribution data based on South & Tittley (1986) and references cited below.

Location of N. boundaries in W. and E. Atlantic (ann. temp. range °C)	Lower limit growth/ reproduction		Occurrence on Iceland (3/6-9/11)	References
	-	+		
Protected embayments in S. Gulf of St Lawrence (-1.8->20)				
N. British Isles or S. W. Norway (5/7-13/16)				
R * <i>Dasya baillouviana</i> (gr, t, g)	10	15	-	(1) †
R <i>Polysiphonia denudata</i> (t, g)	10	15	-	(2) †
B <i>Stilophora rhizodes</i> (u)	<20	>20**	-	(3)
B * <i>Giffordia mitchelliae</i> (u)	15	20	-	(4) †
Ins. Newfoundland (-1.8-10/13)				
W. & N. W. Norway (3/5-9/12)				
R * <i>Callithamnion hookeri</i> (g, t?)	5	10	+	(5, 6)
R <i>Callithamnion corymbosum</i> (gr, t)	5	10	-	(7)
R * <i>Plumaria elegans</i> (pa)	5	10	+	(8)
B * <i>Acrothrix gracilis</i> (gr, u, p)	5	10	-	(9)
B * <i>Leathesia difformis</i> (mi)	5	10	+	(10)
B <i>Sphacelaria rigidula</i> (pr)	4	12	-	(6) ††
Fjords in N. Labrador (-1.8-10)				
N. W. Norway (5-11)				
B * <i>Sphaerotrichia divaricata</i> (u)	5	10	-	(11, 12)
Arctic distribution (-1.8-2)				
B <i>Haplospora globosa</i> (gr, sp, g)		1	+	(13)
B * <i>Eudesme virescens</i> ††† (gr, u)		0	+	(10)
B * <i>Punctaria latifolia</i> †††† (gr, p)		0	+	(10) †
† northern isolate; †† isolate from W. Europe; ††† as <i>Eudesme</i> sp. (Novaczek, pers. comm.); †††† as <i>Desmotrichum undulatum</i> (Rietema & van den Hoek, 1981)				
References: 1) Novaczek et al. (1987); 2) van den Hoek (1982b); 3) Novaczek et al. (1986b); 4) Amsler (1985); 5) Whittick (1981); 6) van den Hoek (1982a); 7) Whittick (1978); 8) Whittick (1977); 9) Forward & South (1985); 10) Novaczek (1987 and pers. comm.); 11) Novaczek & McLachlan (1987); 12) Ajisaka & Umezaki (1978); 13) Kuhlenkamp & Müller (1985).				

boundaries were often located at latitudes where summer temperatures remained slightly lower than in the western Atlantic (Tables 9, 10). As most of the tested isolates came from the western Atlantic, it is possible that European populations generally have a somewhat lower temperature requirement. It is, however, more likely that the much higher winter temperatures in Europe allow a larger amount of biomass to persist through winter, allowing northward extension into regions with slightly less favourable temperatures in summer. In NE America, habitats are covered in ice for several months (Stephenson & Stephenson, 1972; Gorshkov, 1980), which causes a severe reduction in the established populations every year (Novaczek et al., 1986a, 1987; Novaczek & McLachlan, 1987; Novaczek, 1987).

In several species, northern boundaries appear to be set by specific temperature requirements for reproduction (Table 9) and often the effect of temperature on a single process seems to be limiting. For two brown algae, i.e. *Stilophora rhizodes* and *Sphaerotrachia divaricata*, this appears to be the possibility to form unilocular sporangia, which are required for the initiation of a new generation of gametophytes and thus, eventually, for sexual reproduction. In other species, e.g. *Leathesia difformis*, the development of a large population of microthalli, which only occurs at higher temperatures, seems to be essential for persistence of the species. Similarly, in *Sphacelaria rigidula* the possibility of increasing population size by the formation of propagules seems to limit northward extension.

In some red algae a predominance of tetrasporophytes or asexual plants has been noted in the northern part of their distribution range (Dixon, 1965). In species where completion of the sexual cycle is no prerequisite for persistence, temperature requirements for growth (e.g. in *Callithamnion corymbosum*) or for the formation of asexual spores (e.g. in *Plumaria elegans*) will eventually delimit geographic distribution (Table 9).

For several species of *Cladophora*, experimental evidence has indicated that northern boundaries on both sides of the Atlantic are set by summer growth limits (Table 10; Figs 9d, e). A special case is *C. coelothrix*, whose northern boundary in the western Atlantic is shifted far to the south (to W Florida) compared to that in Europe (Table 10). In this species, an isolate from the tropical Caribbean was less cold-tolerant than its temperate European counterpart (Table 3), which accounts for the different location of boundaries (Cambridge et al., 1987). Thus, *C. coelothrix* has a composite northern boundary in the North Atlantic Ocean. On American coasts, northward extension is prevented by lethal, low winter temperatures, and in this respect it resembles species belonging to the tropical western Atlantic distribution group (see above). In Europe, northward extension on open Atlantic coasts is prevented by low summer temperatures preventing growth, whereas, in addition, occurrence in the North Sea is prevented by low winter temperatures (see above). Van den Hoek (1982a, b) has discussed several other species with similar composite northern boundaries. He attributed this distribution pattern solely to the occurrence of low winter temperatures far to the south on American coasts. The existence of tropical ecotypes on the American coast may also account for this type of distribution.

Table 10. Northern growth and northern lethal boundaries in 6 species of *Cladophora*. Comparison of the location of northern boundaries in the eastern and western Atlantic with minimum temperatures required for growth and with lower lethal limits. Temperature lethal in less than 6 weeks (l), survival (s), survival in short days only (s*), relative growth rate > 20% of maximum (g). Based on Cambridge et al. (1984, 1987 and unpubl.). Temperature data based on: Gorshkov (1978) (Massachusetts, British Isles: means for open coasts); U.S. Navy (1981) (S.E. Labrador, White Sea, W. Nova Zemlya, S.W. Greenland: means for open coasts); Hooper et al. (1980) (W. Ins. Newfoundland: inshore means); Printz (1926) (Trondheimfjord W. Norway: inshore means); Earle (1969) (W. Florida: inshore means and 18 year mean of minima)

Species	Location of N. boundaries (summer temperature in warmest month, °C)		Temperature responses (°C)				
I. Northern growth boundaries							
	N.E. America	N.W. Europe	0	5	10	15	20
<i>Cladophora dalmatica</i>	Mass. (16)	W. Norw. (15)	s	s	s	g	g
<i>Cladophora albida</i>	Nwfncl. (16)	W. Norw. (15)	s	s	s	g	g
<i>Cladophora vagabunda</i>	Nwfncl. (16)	W. Norw. (15)	s	s	g	g	g
<i>Cladophora sericea</i>	S.E. Labrador (9)	White Sea (9)	s	s	g	g	g
<i>Cladophora rupestris</i>	S.W. Greenl. (5)	W. Nova Zem. (4)	s	g	g	g	g
Species	Location of N. boundaries (temperature in warmest and coldest month, °C)		Temperature responses (°C)				
II. Composite northern boundary: lethal limit in W. Atlantic; growth limit in E. Atlantic							
	N.E. America	N.W. Europe	0	5	10	15	20
<i>C. coelothrix</i> (Carib. isol.)	W. Florida [(10) 15–29]		l	l	s	s	g
<i>C. coelothrix</i> (W. Eur. isol.)		Br. Isles (5–15)	l	s*	s	g	g

Composite southern boundaries

Phenological evidence for two examples: the brown algae *Chorda tomentosa* and *C. filum*

In several (arctic to) temperate species, southern distribution boundaries in the North Atlantic Ocean are of a composite nature. On American coasts, boundaries are set by lethal, high summer temperatures, whereas in Europe they are set by high winter temperatures inhibiting reproduction (van den Hoek, 1982a, b; Lüning, 1985). Recent experimental evidence (Lüning, 1980a, 1984; Maier, 1984; Novaczek et al., 1986a) on two closely related brown algae, *Chorda tomentosa* and *C. filum*, illustrates how comparatively minor differences in thermal tolerance and requirements between species affect their phenology in various parts of the distribution range and determine the location of their geographic boundaries (Figs 6, 7).

Both in *Chorda tomentosa* and in *C. filum*, gametophytes tolerated a wider range of temperatures than sporophytes. In addition, they required low temperatures for sexual reproduction (Figs 6, 7). Gametophytes of *Chorda tomentosa* survived up to 24 °C, sporophytes up to 15–18 °C (Sundene, 1963; Lüning, 1984; Novaczek et al., 1986a), and temperatures below ca 8 °C were required for the formation of gametangia (Maier, 1984; Novaczek et al., 1986a) (Fig. 6). Gametophytes of *C. filum* survived up to 26 °C, sporophy-

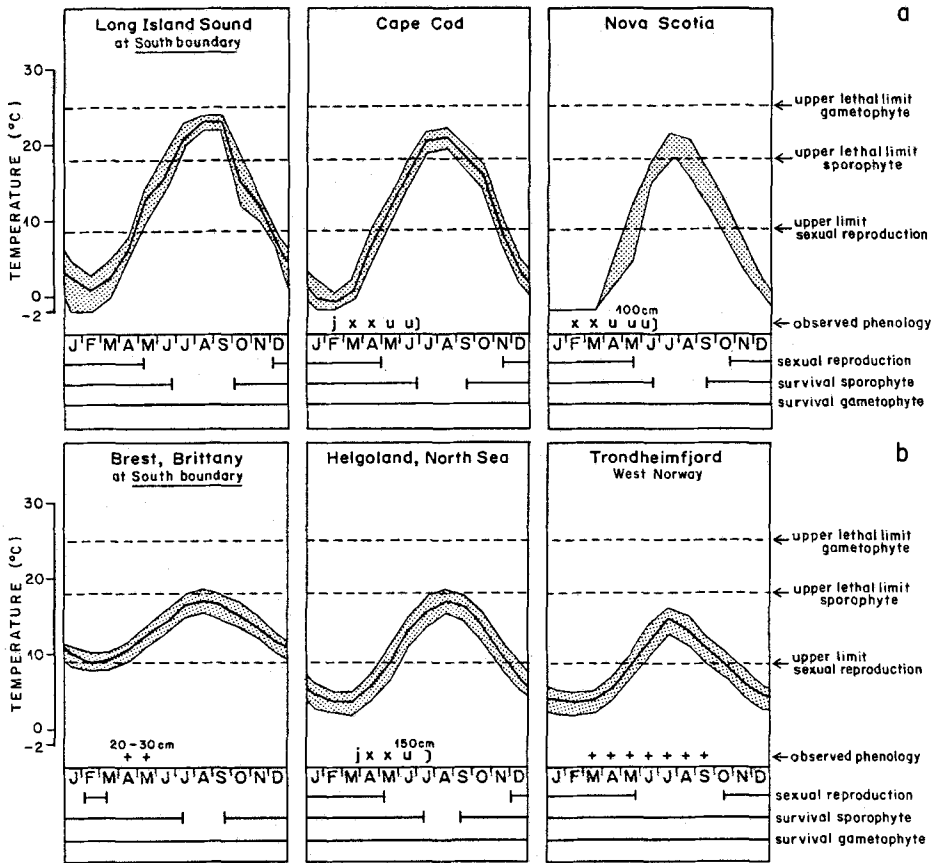


Fig. 6. Temperature responses and phenology of the brown alga *Chorda tomentosa* in relation to seasonal variation in seawater temperatures in different parts of the distribution range and at southern boundaries in the western (a) and eastern (b) Atlantic. Example of a composite southern boundary: lethal limits in NE America and reproduction limits in W Europe. Experimentally determined limits of thermal tolerance of gametophytes and sporophytes and highest temperature permitting sexual reproduction are indicated (Novaczek et al., 1986a; Maier, 1984; Lüning, 1984). Expected duration of reproductive season for gametophytes and potential survival periods for gametophytes and sporophytes shown below (—). Phenological observations: present, no details (+), juvenile plants (j), adult thalli (x) (size given), unilocular sporangia (u), decay of sporophytes (j). Temperature curves represent means (solid line) and ranges (shaded). Phenological and temperature data based on Novaczek et al. (1986a) (Nova Scotia); Sears & Wilce (1975) (Cape Cod); Yarish et al. (1984) (Long Island Sound); Rueness (1977), Printz (1926), U.S. Navy (1974) (Trondheimfjord); Kornmann & Sahling (1977), Weigel (1978), U.S. Navy (1974) (Helgoland); Hamel (1931–1939), Gorshkov (1978), U.S. Navy (1974) (Brittany)

tes between 0°C and (20)–24°C (Lüning, 1984; Novaczek et al., 1986a), and temperatures below ca 13°C were required for the formation of gametangia (Novaczek et al., 1986a) (Fig. 7).

In both species southern boundaries on the American coast were set by lethal, high summer temperatures, preventing survival of the hardest stage in the life history, the

gametophyte (Figs 6, 7). In *C. filum* sporophytes were only slightly less tolerant than gametophytes, and, accordingly, sporophytes generally persisted through summer over the whole of the distribution range (Fig. 7). In contrast, sporophytes of *C. tomentosa* were distinctly less tolerant than gametophytes, and this is the reason why this species is a winter to spring annual in the southern part of its range (Fig. 6).

Differences between the two species in the upper survival limit of their gametophytes accounted for the different location of their southern boundaries on the American coast. *C. filum* goes slightly further south than *C. tomentosa* (New Jersey vs. Long Island, respectively) which is in accordance with its higher tolerance limit (Figs 6, 7). At these boundaries, winter temperatures are low enough for the formation of gametangia for more than 5 months, and would therefore not be limiting (Figs 6, 7).

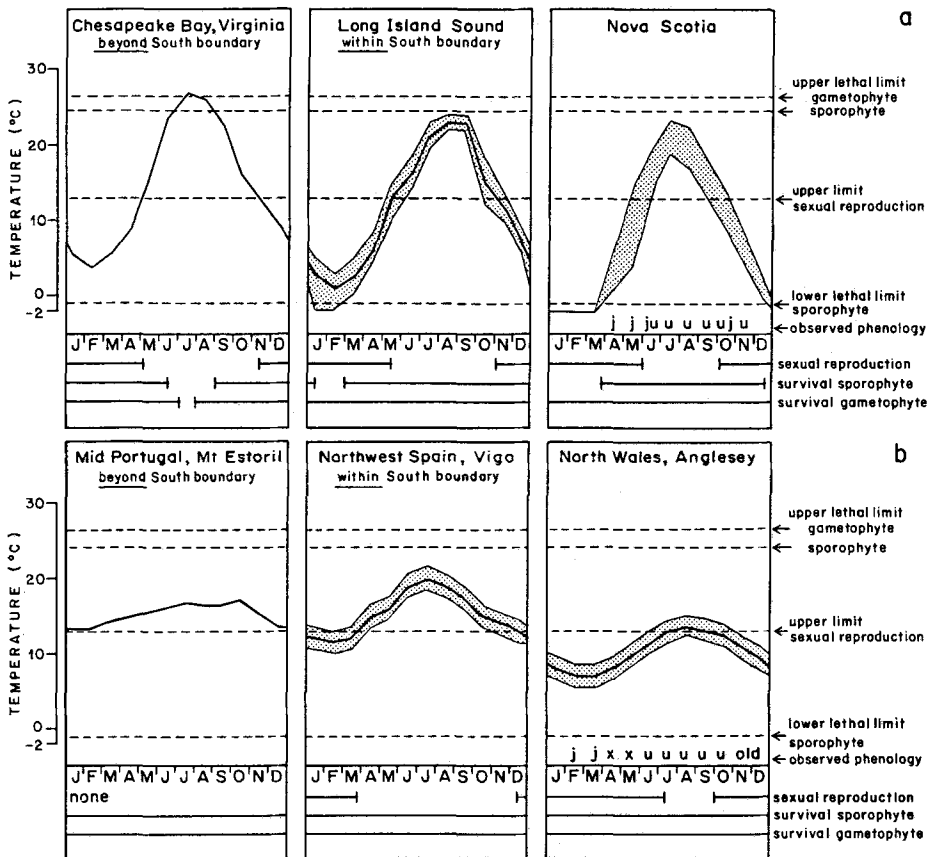


Fig. 7. Temperature responses and phenology of the brown alga *Chorda filum* in relation to seasonal variation in seawater temperatures at locations within and just beyond the southern boundaries in the western (a) and eastern (b) Atlantic. Example of a composite boundary with lethal limits in NE America and reproduction limits in W Europe. See Figure 6 for further explanation. Experimental evidence based on Lüning (1980a, 1984); Novaczek et al. (1986a). Phenological and temperature data based on Novaczek et al. (1986a) (Nova Scotia); Yarish et al. (1984) (Long Island Sound); Humm (1979) (Virginia); South & Burrows (1967), Gorshkov (1978), U.S. Navy (1974) (N Wales); Ardré (1970, 1971) (NW Spain, Portugal)

In contrast, southern boundaries in Europe were set by high winter temperatures preventing sexual reproduction. *Chorda tomentosa* reaches its southern boundary in Brittany, where water temperatures fall just below 10°C in winter, whereas *C. filum* goes south to N Portugal, where temperatures fall to about 13°C (Figs 6, 7). At these boundaries, summer temperatures remain well below the upper lethal limit for gametophytes, and, in *C. filum*, even below the upper lethal limit for sporophytes.

When comparing the phenology of *Chorda tomentosa* in various parts of its distribution range (Fig. 6) it becomes evident that its seasonal behaviour is regulated by its temperature requirements for sexual reproduction, which determines when a new generation of sporophytes is initiated, and by the tolerance of sporophytes to high temperatures, which determines their longevity. Thus, *C. tomentosa* is a winter to spring annual in the southern part of its range, but persists through summer at more northerly locations. Sporophytes disappeared in early summer as soon as seawater temperatures had risen above 16–18°C (e.g. Cape Cod, Nova Scotia, Helgoland; Fig. 7; and in the Oslofjord, Sundene, 1963). Going north, the first station for which *C. tomentosa* has been reported to persist through summer is the Trondheimfjord in W Norway (Printz, 1926), where summer temperatures remain below 16°C (Fig. 6; Printz, 1926).

The occurrence of young sporophytes in winter is accounted for by the requirement for temperatures below 8–10°C to permit sexual reproduction. Generally, temperatures will drop below this value in autumn (e.g. Cape Cod, Nova Scotia, Helgoland, Trondheimfjord; Fig. 6), but near the southern distribution boundary in Europe (Brittany; Fig. 6) temperatures would not be low enough for the induction of gametangia before February. As sporophyte survival is limited by high temperatures from July, the growing season will be several months shorter than at more northerly locations. This may account for the difference in size of the plants, which reach only 20–30 cm in Brittany (Hamel, 1931–1939), but attain a size of 1–2 m elsewhere (Sundene, 1963; Kornmann & Sahling, 1977; Novaczek et al., 1986a).

Composite southern boundaries in various other species

Experimental and phenological evidence similar to that discussed above is now available for several red and brown algae (Tables 11, 12). All species with composite southern boundaries had heteromorphic life histories (or distinctive crustose and erect thalli in the two phases of an isomorphic life history) and they all required low temperatures for the initiation of macrothalli, either directly or through the induction of sexual reproduction (Tables 11, 12). These thermal responses result in distribution patterns which are characterised by the fact that southern boundaries are shifted northward on Eur/African relative to American coasts because of the warmer winters (Fig. 9f).

Along American coasts, high summer temperatures prevented southward extension. Thermal limits of the hardiest stage, which is often the microthallus phase, determined the location of boundaries along this coast. This does not only apply to species with annual macrothalli, but also to perennials as these may become seasonal annuals close to their southern limit of distribution (e.g. *Laminaria saccharina* in Long Island Sound; Lee & Brinkhuis, 1986).

Increased tolerance to high temperatures was found in species with a more southerly

Table 11. Composite southern boundaries in amphi-Atlantic red and brown algae. Lethal limits in the western Atlantic (this Table) and reproduction limits in the eastern Atlantic (Table 12). Comparison of upper lethal limits (and maximum temperatures permitting reproduction) among species reaching their southern boundaries at various points along the coast of N.E. America. Temperature was survived or induced reproduction (+); temperature was lethal in 2–6 wks or inhibited reproduction substantially or completely (–). Reproduction of gametophytes (g), sporophytes (s), tetrasporophytes (t); initiation of macrothalli (m), new blades (b). R = red alga. B = brown alga. R! = reproduction limit also restrictive in W. Atlantic. Annual temperature ranges at distribution boundaries based on: U.S. Navy (1974, 1981) (all sites); Earle (1969) (Gulf of Mexico); Searles (1984) (N. Carolina); Stephenson & Stephenson (1972) (E. Florida, N. Carolina); Orris & Taylor (1973) (Delaware); Yarish et al. (1984) (Connecticut). Distribution data based on: Taylor (1960); Earle (1969); Searles & Schneider (1978); South & Tittley (1986); Wynne (1986); and references cited below

Location of S. boundaries (annual temperature range, °C)	Upper lethal hardest stage (°C)		Upper limit reproduction (°C)		References
	+	–	+	–	
Connecticut and Long Island (1–23)					
B <i>Laminaria digitata</i>	21	24	10	15 (g)	(1, 2, 3)
B <i>Chorda tomentosa</i>	24	26	5	10 (g)	(2, 4, 5)
R <i>Rhodochorton purpureum</i>	24	26	16	18 (t)	(6, 7, 8)
R <i>Dumontia contorta</i>	24	26	12	16 (m)	(9)
R <i>Nemalion helminthoides</i>	25	27	12	16 (t)	(6, 10)
New Jersey (3–25)					
B <i>Desmarestia aculeata</i>	23	25*	12	15 (g)	(2, 11, 12)
B <i>Desmarestia viridis</i>	23	25*	5	10 (g)	(2, 11)
B <i>Chorda filum</i>	26	28	12	14 (g)	(2, 4, 11)
Delaware (3–26)					
R <i>Chondrus crispus</i>	28	30	15	20 (m)	(2, 6, 13)
N. Carolina (3 (10)–30)					
B <i>Punctaria latifolia</i>	30	35	12	16 (m)	(6)
E. Florida (14 (20)–28)					
B <i>Scytosiphon lomentaria</i> R?	28	30	20	23 (m)	(14, 15)
N. Gulf of Mexico (11 (17)–30)					
B <i>Stilophora rhizodes</i> R!	28	31	10	12 (g)	(16, 17)
* tested for sporophytes only.					
References: 1) Bolton & Lüning (1982); 2) Lüning (1984); 3) Lüning (1980b); 4) Novaczek et al. (1986a); 5) Maier (1984); 6) van den Hoek (1982b); 7) Breeman et al. (1984); 8) Breeman & Hoeksema (1987); 9) Rietema & van den Hoek (1984); 10) Fries (1966); 11) Lüning (1980a); 12) Müller & Luthe (1981); 13) Lüning et al. (1987); 14) van den Hoek (1982a); 15) tom Dieck (1987); 16) Novaczek et al. (1986b); 17) Peters & Müller (1986)					

extension. Thus, species going south to the Connecticut/Long Island Sound area did not tolerate temperatures over 20–25 °C, those with southern boundaries in New Jersey did not tolerate temperatures over 23–26 °C, whereas those going south to N Carolina, E Florida or the northern Gulf of Mexico tolerated temperatures up to 28–30 °C (Table 11). These limiting temperatures corresponded closely with actual maximum summer temperatures at the respective boundaries. Table 11 shows that there was no

Table 12. Composite southern boundaries in amphi-Atlantic red and brown algae. Reproduction limits in the eastern Atlantic (this Table) and lethal limits in the western Atlantic (Table 11). Comparison of maximum temperatures permitting completion of the life history (and of upper lethal limits) among species reaching their southern boundaries at various points along the Eur/African coast. For comparison some species endemic to the eastern Atlantic also having southern reproduction limits are included (E). Occurrence in Mediterranean (M). Further explanation and references in Table 11. Annual temperature ranges at distribution boundaries based on Gorshkov (1978) and U.S. Navy (1974, 1981) (all sites); Lawson & John (1977) (N. W. Africa); Ardré (1971) (Portugal). Distribution data based on South & Tittley (1986); Lawson & John (1977, 1982); Furnari (1984) and references cited below

Location of S. boundary (annual temperature range, °C)	Upper limit reproduction (°C)		Upper lethal hadiest stage (°C)		References
	+	-	+	-	
Brittany (10-18)					
B <i>Chorda tomentosa</i>	5	10 (g)	24	26	
B <i>Desmarestia viridis</i>	5	10 (g)	23	25*	
B <i>Stilophora rhizodes</i> M	10	12 (g)	28	31	
B <i>Laminaria digitata</i>	10	15 (g)	21	24	
N.W. Spain, N. Portugal (13-21)					
R <i>Delesseria sanguinea</i> E	12	14 (b)	23	25	(1, 2)
B <i>Chorda filum</i>	12	14 (g)	26	28	
B <i>Desmarestia aculeata</i>	12	15 (g)	23	25*	
R <i>Dumontia contorta</i>	12	16 (m)**	24	26	
Mid-Portugal (14-22)					
B <i>Laminaria hyperborea</i> E	8	15 (b)	21	22	(2, 3, 4)
B <i>Punctaria latifolia</i> M	12	16 (m)	30	35	
N. Morocco (16-24)					
R <i>Rhodochorton purpureum</i> M	16	18 (t)	24	26	
W. Sahara, Mauretania (17-25)					
R <i>Chondrus crispus</i>	15	20 (m)	28	20	
B <i>Saccorhiza polyschides</i> E M	17	20 (g)	23	25*	(5, 6)
R <i>Nemalion helminthoides</i> M	18	22 (t)	25	27	
Canaries (19-25)					
B <i>Scytosiphon lomentaria</i> M	20	23 (m)**	28	30	
* tested for sporophytes only					
** southern isolate					
References: 1) Kain (1987); 2) Lüning (1984); 3) Bolton & Lüning (1982); 4) Lüning (1986); 5) van den Hoek (1982a); 6) Norton (1977); other references see Table 11					

apparent correlation between temperature requirements for reproduction and the location of southern boundaries along the American coast. In general, winter temperatures were low enough for reproduction all along the coast of NE America. Only in *Stilophora rhizodes* and possibly in *Scytosiphon lomentaria* was southward extension (also) prevented by high winter temperatures. These species combine a requirement for relatively low temperatures for sexual reproduction with a high upper lethal limit (Table 11).

On Eur/African coasts summer temperatures at the southern boundaries were much

lower, but reproduction limits prevented southward extension (Table 12). Thus, species with southern boundaries in Brittany required temperatures below 5–10 °C, those with southern boundaries in the Iberian Peninsula required temperatures below ca 12 °C, and those with southern boundaries in NW Africa required temperatures below 15–20 °C for completion of the life history. Again, these limiting temperatures closely corresponded with the lowest winter temperatures at the respective boundaries (Table 12). They also accounted for details in the distribution pattern near southern limits of extension. Thus, the absence from the Canaries and Madeira of several species occurring on the African mainland (i.e. *Rhodochorton purpureum*, *Nemalion helminthoides*, *Chondrus crispus*) must be attributed to the higher winter temperatures on these islands. Indeed, the only species in Table 12 occurring on the islands (i.e. *Scytosiphon lomentaria*) had the highest critical temperature for completion of the life history.

In general, species extending south to mid-Portugal and NW Africa were also found in the Mediterranean (Table 12), with the notable exception of *Laminaria hyperborea* and *Chondrus crispus*. The former species will be excluded from the Mediterranean by lethal, high summer temperatures but there is as yet no evidence to explain the absence of the latter species. As might be expected, species that combined a high upper lethal limit with a high upper limiting temperature for completion of the life history (e.g. *Scytosiphon lomentaria* and *Nemalion helminthoides*; Table 12) occurred throughout the Mediterranean. Other species were confined to the western parts, because either lethal high summer temperatures (≥ 25 – 28 °C; e.g. *Saccorhiza polyschides* and *Rhodochorton purpureum*) or inhibitive high winter temperatures (≥ 15 °C; e.g. *Punctaria latifolia*) would prevent occurrence in the eastern parts of the Mediterranean. *Stilophora rhizodes* has a distinctly disjunct distribution pattern in the eastern Atlantic/Mediterranean region. On open Atlantic coasts the species goes no further south than Brittany (Table 12), which is in accordance with the temperature requirements for sexual reproduction found in an isolate from Sweden (≤ 9 °C; Peters & Müller, 1986). Evidently, the Mediterranean populations have either a higher critical temperature for sexual reproduction or reproduce only by asexual means. The upper lethal limit of a western Atlantic isolate (≥ 28 °C; Novaczek et al., 1986b) would be sufficient for survival of the Mediterranean populations.

Southern boundaries set by lethal limits on both sides of the Atlantic

Not all ampho-Atlantic species had a composite southern boundary in the North Atlantic Ocean. In several species with isomorphic life histories having no specific temperature requirements for reproduction (i.e. *Haplospora globosa*, *Cladophora rupestris*, *C. sericea*; Table 13) boundaries appear to be set by lethal limits on both sides of the Atlantic. Species with this type of thermal response are characterised by distribution patterns in which southern boundaries on Eur/African coasts are located further south than those on American coasts (Fig. 9e) because of the cooler summers. However, in *Laminaria saccharina*, a species with a heteromorphic life history requiring low temperatures for sexual reproduction, southern boundaries on both sides of the Atlantic also appear to be set by lethal limits. This species combines a relatively low upper lethal limit (< 24 °C) with a relatively high upper temperature limit for reproduction (15–18 °C) (Table 13).

So far, no examples have been found of southern boundaries set by a species' temperature requirements for growth alone, and it is unlikely that such boundaries will be found in seaweeds. There are two reasons for this conclusion. First, temperature

Table 13. Southern lethal boundaries in amphi-Atlantic green and brown algae. Comparison of upper lethal limits (and maximum temperatures permitting growth/reproduction) among species reaching their southern boundaries at various points along eastern and western Atlantic coasts. G = green alga. B = brown alga. For further explanation see Table 11. Annual temperature ranges at distribution boundaries based on: Gorshkov (1978) and U.S. Navy (1974, 1981) (all sites). Distribution data based on South & Tittley (1986); Taylor (1960); Wynne (1986), Furnari (1984) and references cited below

Species	Location of S. boundaries (annual temperature range, °C)		Upper lethal hadiest stage (°C)		Upper limit growth/reproduc- tion (°C)		Refer- ences
	W. Atlantic	E. Atlantic	+	-	+	-	
B <i>Haplospora globosa</i> Mass. (1-19)		Brittany (10-18)	18	> 18	18	> 18 (g, s)	(1)
B <i>Acrothrix gracilis</i> Conn. (1-23)		S.W. Eng. (10-18)	15	20	15	20 (s)	(2)
B <i>Laminaria saccharina</i> Conn. (1-23)		N. Portug. (13-21)	22	24	15	18 (g)	(3, 4, 5)
G <i>Cladophora rupestris</i> Conn. (1-23) ?Virgin. (3-26)		Morocco (16-24) Mediterr. (17-27)	25	30	25	30 (gr)	(6, 7)
G <i>Cladophora sericea</i> * Nw. Jersey (3-25) ?Virgin. (3-26)		Mediterr. (17-27)	25	30	25	30 (gr)	(7, 8)

* excluding "gracilis"-type (Cambridge et al., unpubl.; van den Hoek, 1982c and pers. comm.)
References: 1) Kuhlenkamp & Müller (1985); 2) Forward & South (1985); 3) Bolton & Lüning (1982); 4) Lüning (1980b); 5) Lüning (1984); 6) Cambridge et al. (1984); 7) Cambridge et al. (unpubl.); 8) van den Hoek (1982c and pers. comm.)

ranges for reproduction are generally narrower than for growth, so that reproduction limits will restrict distribution before growth limits may take effect. Second, growth generally still proceeds at temperatures close to the upper lethal limit, so when high winter temperatures would become limiting for growth, summer temperatures would already be in the lethal range.

DISTRIBUTION BOUNDARIES SET BY TEMPERATURE/DAYLENGTH INTERACTIONS

Theoretically, photoperiodic responses could restrict geographic distribution of marine algae in the following ways: in short day plants (SDP) with a critical daylength of less than 12 h, and in long day plants (LDP) with a critical daylength of more than 12 h, distribution across the equator and in the tropics could be prevented by their photoperiodic requirements, because daylengths never deviate far from 12 h. In some SDP, for instance *Scytosiphon lomentaria* and *Rhodochorton purpureum*, critical daylengths of less than 12 h have been found in some isolates from subtropical regions (Lüning, 1980a, 1981; Dring & West, 1983), but in both species, temperature rather than daylength

requirements seem to set the southern boundary in the North Atlantic Ocean (Tables 11, 12). For instance, in *S. lomentaria*, the critical daylength in an isolate from the Mediterranean was 11.3 h (50% response at 15°C), which would prevent occurrence south of 15° N latitude. However, temperatures over 20°C also prevented the initiation of macrothalli, and these would set the actual southern boundary as far north as the Canaries (28° N).

In two long day plants, the brown algae *Sphacelaria rigidula* and *Sphaerotrichia divaricata*, critical daylengths of between 12 and 14 h have been found in isolates from the temperate region (ten Hoopen et al., 1983; Novaczek & McLachlan, 1987), and these daylength requirements would prevent extension through the tropics. In *S. divaricata* additional temperature requirements shift the southern boundary far to the north (see below), whereas in *S. rigidula* neither these daylength requirements nor an additional requirement for low temperatures seem to have prevented a tropical distribution. In the latter species either different temperature/photoperiodic ecotypes must have evolved in the tropics, or populations must persist solely through vegetative propagation (van den Hoek, 1982b).

Photoperiodic responses could also restrict poleward distribution of SDP at high latitudes when a relatively short critical daylength would restrict the inductive season to a period when there is very little light, or when habitats are covered in ice. Some SDP (e.g. *Scytosiphon lomentaria*) have evolved photoperiodic ecotypes with longer critical daylengths in the northern parts of their distribution range (Lüning, 1980a, 1981) thus shifting the inductive season towards summer and enabling extension in the Arctic.

Thus, there are at present no examples of seaweeds which are restricted in their distribution by their photoperiodic requirements alone. Nevertheless, in several species, photoperiodic responses restrict distribution because they confine the reproductive season to a time of year when temperatures are suboptimal. Distribution can be affected in two different ways: northern boundaries may be shifted southward for SDP because their short-day requirements prevent their taking full advantage of the period with the highest summer temperatures. In these species, the reproductive season in regions close to the boundary is confined to autumn, when short days coincide with relatively high temperatures. In contrast, southern boundaries may be shifted northward in LDP because their long-day requirements prevent their taking full advantage of the period with the lowest winter temperatures. In these species, the reproductive season in regions close to the boundary is confined to late spring, when long days coincide with relatively low water temperatures. Presently, there is only one example of a species with the latter type of southern boundary. In the brown alga *Sphaerotrichia divaricata* (Novaczek & McLachlan, 1987), sexual reproduction was prevented by short days and by temperatures over 15°C. In the southern Gulf of St. Lawrence, where the phenology of this species has been studied in relation to water temperatures and daylength (Fig. 8), there were two "reproductive windows", one in spring, and another, very brief one in autumn. Young macrothalli were observed from April to June, and again in October (Fig. 8). Autumn recruitment only occurred in some years, probably induced by occasional low minima. Further south along the American coast, there will be only one, brief reproductive season in late spring. For instance, in Long Island Sound temperature/daylength requirements for reproduction would be met only in late April and May. *S. divaricata* reaches its southern boundary at 40° N, and it is clear that in regions beyond the boundary (for instance in North Carolina; Fig. 8) conditions would be unfavourable for sexual reproduc-

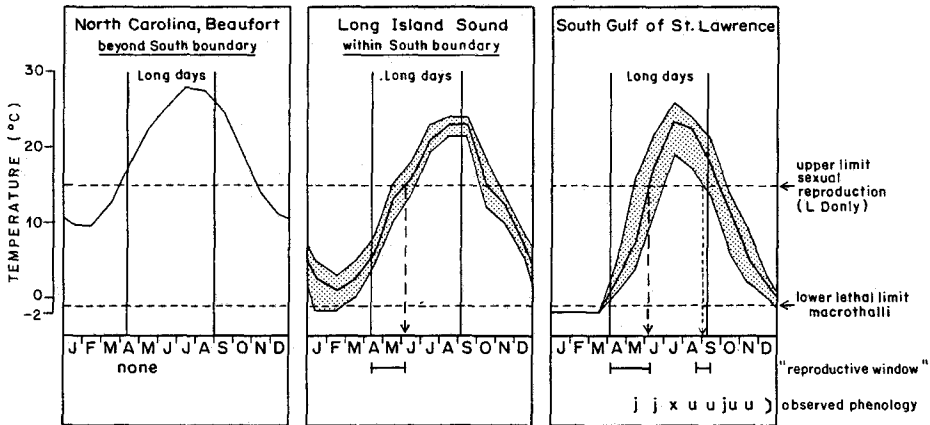


Fig. 8. Temperature/daylength responses and phenology of the brown alga *Sphaerotrichia divaricata* in relation to seasonal variations in daylength and seawater temperature at locations within and beyond the southern boundary in NE America. Example of a southern boundary set by a requirement for low temperatures in long days to induce sexual reproduction. See Figure 6 for further explanation. Experimental evidence based on Novaczek & McLachlan (1987). Phenological and temperature data based on Novaczek & McLachlan (1987) (S Gulf of St. Lawrence); Yarish et al. (1984) (Long Island Sound); Earle (1969) (N. Carolina)

tion all year long. By contrast, the related species *Stilophora rhizodes* (Novaczek et al., 1986b), which has similar temperature requirements but reproduces in both long and short days, goes as far south as the northern Gulf of Mexico (Table 11).

There are several examples of species which have their northern boundaries set by a requirement for short days combined with relatively high temperatures (reviewed by Dring, 1984). In areas close to the boundary the inductive period will be restricted to early autumn. In two of these species, the red algae *Gigartina acicularis* (Guiry & Cunningham, 1984; Guiry, 1984) and *Bonnemaisonia hamifera* (Breeman et al., 1988; Breeman & Guiry, unpubl.) the critical temperature for induction appeared to be very sharply defined. *G. acicularis* formed cystocarps at 14 but not at 13 °C, whereas in *B. hamifera* the percentage of plants forming tetrasporangia fell sharply from 91 to 7% between 13 and 11 °C (Table 1). The comparatively minor difference between the two species in their critical temperature seems to account for the different location of their northern boundary. *G. acicularis* has not been reported north of County Galway on the Irish West Coast (Guiry, 1984), where mean October temperatures are about 13 °C, whereas *B. hamifera* has been reported from the Norwegian west coast (Haugen, 1970), where mean October temperatures are about 10 °C (Table 14).

When we compare the temperature requirements of *B. hamifera* with those of several non-photoperiodic species also reaching their northern boundary in W Norway (Table 9) it seems incongruous that *B. hamifera* has been reported so far to the north. These non-photoperiodic species, which can take full advantage of the period with highest summer temperatures because they have no photoperiodic requirements, grew and reproduced at 10 °C, whereas *B. hamifera* needed temperatures over 12 °C in short days, which would prevail only in autumn. The explanation is probably that the response in *B. hamifera* is triggered by a comparatively brief exposure to the inductive temperature, whereas non-

Table 14. Northern boundaries set by temperature/daylength interactions. Comparison of the location of northern boundaries with minimum temperatures required for induction in two red algae with a short-day response. Temperature induced reproduction (+); temperature inhibited reproduction (-). Nature of temperature/daylength-inhibited process: formation of cystocarps (c), tetrasporangia (t). Mean October temperatures at distribution boundaries (in brackets, °C) based on Gorshkov (1978)

Species	Location of boundary	Critical temperature for induction (°C)		References
		+	-	
<i>Gigartina acicularis</i>	W. Ireland (13)	14	13 (c)	(1, 2)
<i>Bonnemaisonia hamifera</i>	W. Norway (10)	12	10 (t)	(3, 4, 5, 6)

References: 1) Guiry & Cunningham (1984); 2) Guiry (1984); 3) Lüning (1980a); 4) Lüning (1981); 5) Breeman et al. (1988) and Breeman & Guiry (unpubl.); 6) Haugen (1970)

photoperiodic species require exposure to the adequate temperatures over a considerable amount of time.

The importance of short-term "trigger" responses was recently demonstrated by detailed in situ observations on two populations of *B. hamifera* in W Ireland (Breeman et al., 1988; Breeman & Guiry, unpubl.). Tetrasporangia were found from early September until the end of January. This was much longer than the brief "reproductive window" that had been expected. In situ temperature measurements revealed that brief spells with temperatures over 12 °C occurred during sunny days at low tide as late in the year as December. Evidently, such brief exposures were effective in inducing the formation of tetrasporangia. Some tetrasporangia were also present early in autumn before daylengths reached the critical value of about 12 h. This was attributed to light reduction at dawn and at dusk during high water of spring tides on heavily clouded days. It reduced the "effective daylength" for the plants and briefly exposed them to short-day conditions even in late August. In two other intertidal red algae (i.e. *Rhodochorton purpureum* and *Dumontia contorta*) phenological observations have also provided evidence for a tide-induced reduction of the "effective daylength" for the plants (Breeman et al., 1984; Klein, 1987). In *R. purpureum* a heavily shaded estuarine population even produced tetrasporangia for several months after the end of the short-day season (Breeman et al., 1984).

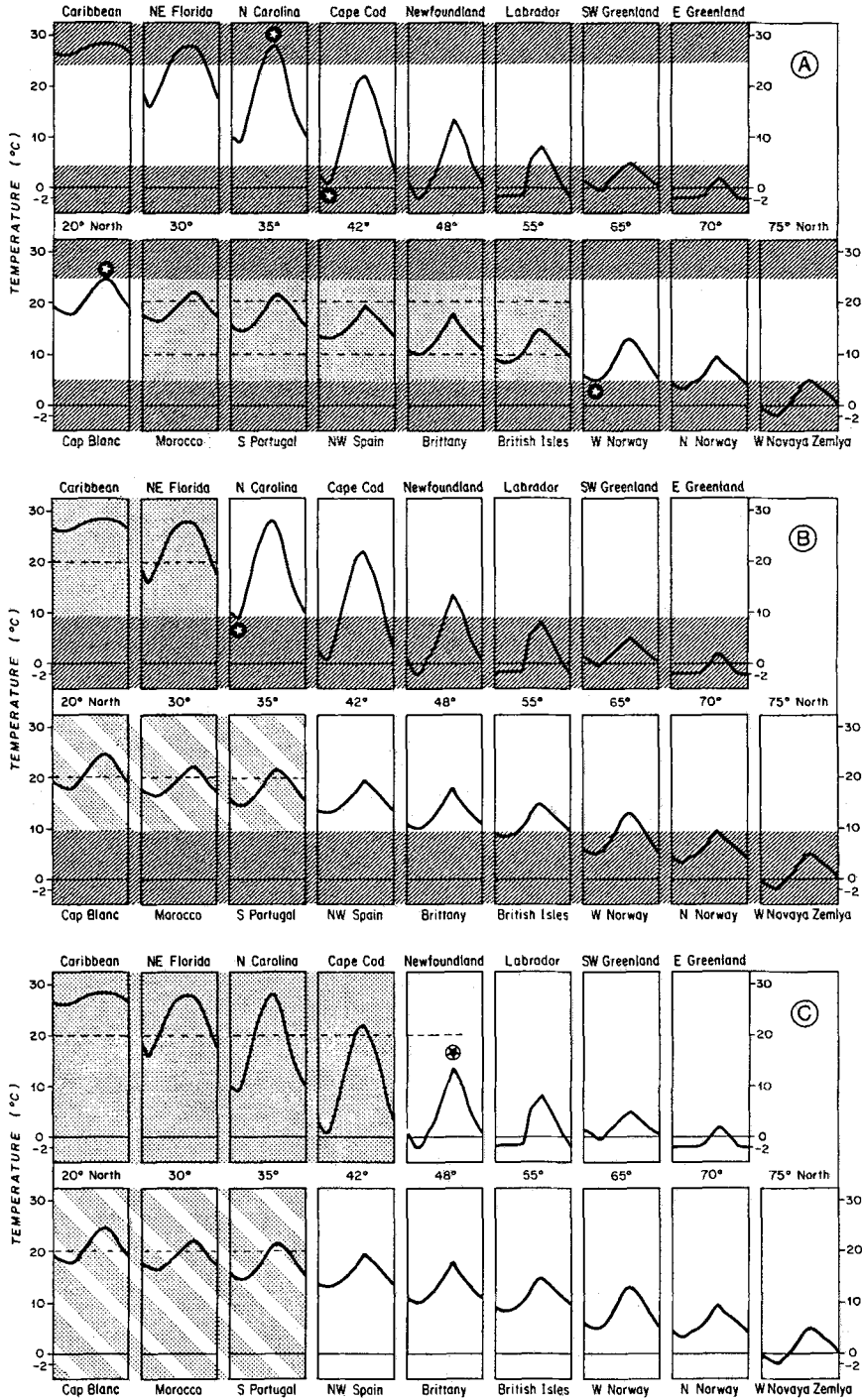
In conclusion, microclimatic factors may have a pronounced influence on these inductive responses. In species where microthallus phases have wider geographical distributions than macrothallus phases, or where there are persistent cryptic phases in the life history, inductive conditions may prevail only in occasional years and this may account for the very sporadic occurrence of some of these species in areas close to their known limits of distribution (for instance *Bonnemaisonia hamifera* [see above] and *Nemalion helminthoides* in NW Europe; van den Hoek, 1982b; Maggs, 1986; Kornmann & Sahling, 1977).

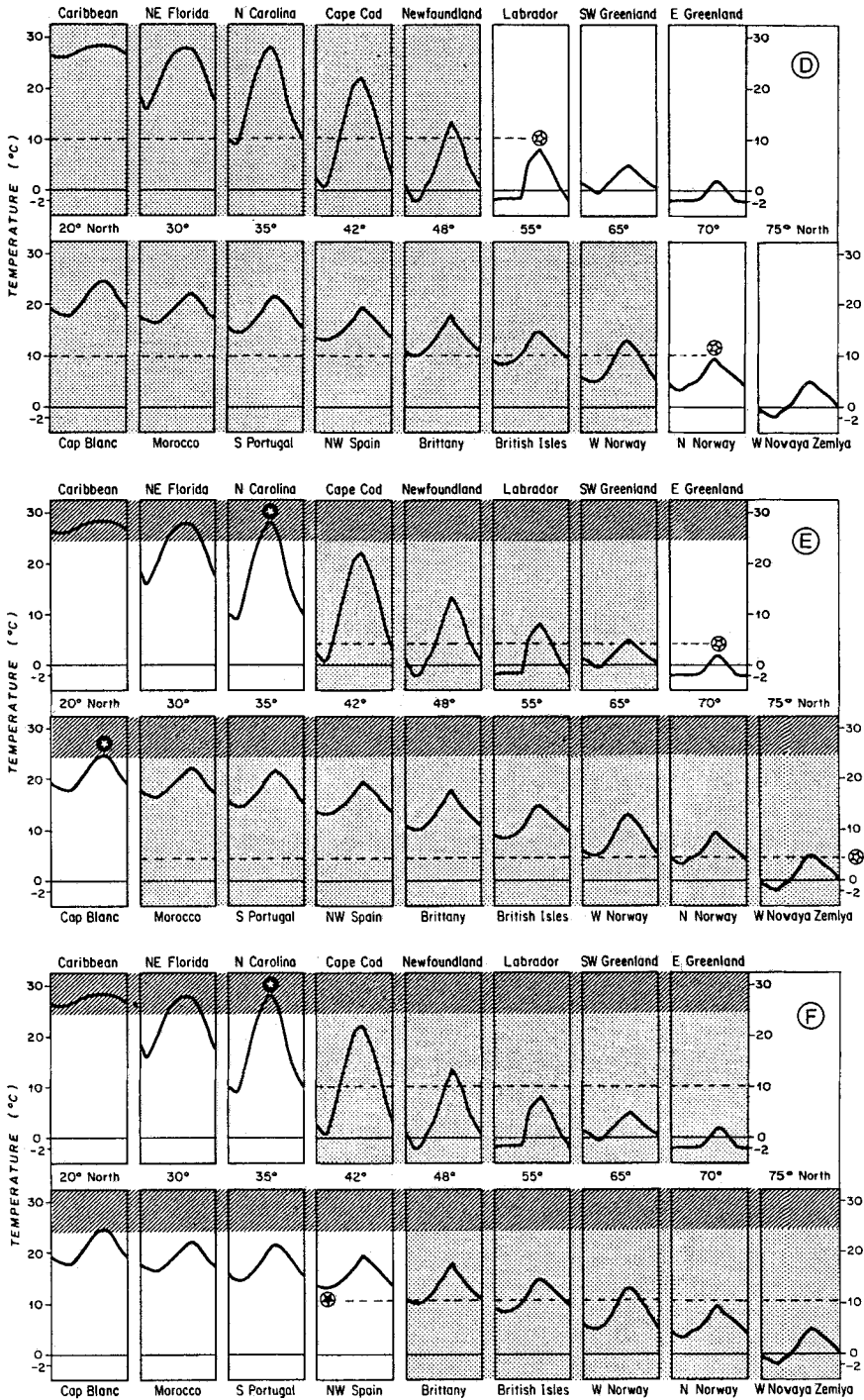
FUTURE PROBLEMS

For the majority of seaweed species investigated to date, thermal responses accounted quite well for the location of geographic boundaries. Typical thermal response patterns, often associated with life history-type, caused characteristic distribution patterns in the North Atlantic Ocean, some of which have been summarised in Figure 9. However, several problems remain. These are of two types: in the first place there are species which extend into regions where their thermal tolerance would not permit survival in the adverse season or where their thermal requirements for completion of the life history would not be met in the favourable season. Some of these discrepancies probably result from the fact that the experimental evidence is still incomplete. For instance, for many species the limits of thermal tolerance have as yet only been determined for the macrothallus phase and microthalli may be more tolerant. Other discrepancies may result from taxonomic problems (see for instance Yarish et al., 1986: *Callithamnion tetragonum*). Nevertheless, different thermal ecotypes are still likely to be found in some species where the experimental evidence seemed to be at variance with observed distribution ranges. An example is the red alga *Hypoglossum hypoglossoides* (Yarish et al., 1984, 1987; as *H. woodwardii*). The upper limit of thermal tolerance of a temperate W European isolate of this species (ca 25°C) is too low for survival of the disjunct (sub)tropical populations that have now been reported from the western Atlantic (Wynne & Ballantine, 1986), so these must have a higher upper thermal limit. In such cases the question of conspecificity of these widely separated entities arises.

Another type of problem concerns species which did not reach the potential limit set by their thermal responses, or had notable "gaps" in their distribution range. Several examples have briefly been mentioned above. Undersampling (e.g. W Africa, E England), lack of suitable substratum, or locally reduced salinity are obvious reasons for some distributional "gaps" shared by many species. Some species with seemingly "haphazard" distribution patterns (e.g. *Dasya baillouviana* in NW Europe; South & Tittley, 1986; Furnari, 1984) may be relatively recent introductions to the region, and still in the process of extending their ranges, possibly locally hindered by the fact that suitable niches have already been occupied by other species. Finally, in many cases the apparent discrepancies probably result from a lack of data on the thermal requirements for a

Fig. 9. Summary of thermal response types responsible for some characteristic distribution patterns of seaweeds in the North Atlantic Ocean. Comparison of ranges of thermal tolerance and of temperature requirements for growth or completion of the life history with annual temperature curves at different latitudes in the western (above) and eastern (below) Atlantic Ocean. Observed distribution ranges are shaded, potential ranges are indicated with an interrupted shading. Temperatures beyond survival limits are hatched, critical temperatures for growth or for completion of the life history are indicated by dotted lines. Temperature responses restrictive to distribution are indicated as follows: lethal limit (blank asterisk in closed circle), growth limit (blank asterisk in open circle), limit set by life history requirements (black asterisk in open circle). (A) *Callophyllis laciniata* (eastern Atlantic temperate) with northern and southern lethal limits; (B) *Gracilaria wrightii* (western Atlantic tropical) with northern lethal limit; (C) *Lomentaria baileyana* (western Atlantic tropical-temperate) with northern reproduction limit; (D) *Cladophora vagabunda* (amphi-Atlantic tropical to temperate) with northern growth limits; (E) *Cladophora rupestris* (amphi-Atlantic temperate) with northern growth limits and southern lethal limits; (F) *Chorda tomentosa* (amphi-Atlantic arctic to temperate) with composite southern boundary (lethal limit in western, reproduction limit in eastern Atlantic)





crucial step in the life history. For instance in many larger red and brown algae the temperature (daylength) requirements for reproduction of macrothalli are as yet unknown due to the difficulty of culturing large plants under a variety of experimental conditions. Additional evidence of this type may be particularly important in understanding the nature of many northern boundaries in the North Atlantic Ocean (e.g. in *Laminaria hyperborea*; see above).

More problematic is the question why some species do not go further south. For instance, the distribution pattern of *Saccorhiza dermatodea* suggests that this species has a composite southern boundary in the North Atlantic Ocean (lethal limit in NE America, boundary shifted northward by reproduction limit in W Europe) and, at first, experimental evidence seemed to confirm this conclusion (Norton, 1977; van den Hoek, 1982a). However, recently the identity of the cultured plants has been questioned (Henry, 1987b) since *S. dermatodea* has proved to be monoecious (Henry, 1987b) instead of dioecious (Norton, 1972). The experimental evidence now available (Henry, 1987b) suggests that, on European coasts, this species could go as far south as Brittany because temperatures of up to 10°C still permitted sexual reproduction (cf. Table 12). However, *S. dermatodea* has not been reported south of Nordland in NW Norway, and there is, as yet, no indication that other critical temperature requirements affecting other life history stages might restrict distribution (Keats & South, 1985). Possibly, competitive interaction with Laminariales such as *L. hyperborea* or with the closely related species *Saccorhiza polyschides*, has prevented southward extension. In fact, as *S. dermatodea* does not go further south on the very point where *S. polyschides* reaches its northern boundary (Rueness, 1977; Norton, 1977). In general, however, geographic ranges of closely related species seem to be unaffected by interspecific competition (Pielou, 1977).

Another problem is why some species are relatively rare in the tropics. The experimental evidence now available indicates that species absent from the tropics generally are excluded from this region because of their thermal responses as they either did not tolerate temperatures over (28–)30°C (Tables 11, 13) or required low temperatures (<23°C) for completion of the life history (Table 12). Several species without these thermal restrictions are, however, confined to the tropical margins (e.g. *Grinnellia americana*, *Lomentaria baileyana*; Yarish et al., 1984; Table 8) or are extremely rare in tropical waters (e.g. *Cladophora albida*; Cambridge et al., 1984 and unpubl.; Table 3). These species generally had high growth rates at temperatures of up to 30°C. Probably they require high nutrient levels to support these high growth rates, failing which, they may not be able to sustain the high grazing pressure characteristic of tropical regions.

Apart from these unexplained points in the distribution of individual species, conspicuous short-comings in the data-base may now be indicated on which future work might concentrate. Experimental evidence on temperature tolerance and requirements is almost completely lacking for some distribution groups, in particular the Arctic and the amphi-Atlantic (sub)tropical groups. More data, including an evaluation of the occurrence of thermal ecotypes will be valuable, particularly because the former group is considered to be a relatively young, the latter a relatively old distribution type (Lüning, 1985).

The question of thermal ecotypes still calls for attention, also in other distribution groups. There is virtually no information on variability on a local scale or within a population. Results obtained with *Chondrus crispus* indicate that locally (i.e. among

populations from the Irish west coast; Table 2), thermal tolerance may vary to the same extent as for widely separate parts of the distribution (Table 2).

Most of the experiments on ecotypic differentiation in upper thermal limits have been done with isolates from the temperate European coast (Table 2). This is unfortunate, since in many temperate species upper tolerance limits restricted the distribution on American, but not on European coasts (Table 11). Comparisons among American populations would have been more useful, because on that coast selection pressure would act on upper tolerance limits. In contrast, European populations should be compared for their thermal requirements for reproduction (Table 12).

It is important that future experimental work on thermal responses should take into account a number of methodological points. Since geographic boundaries are set by suboptimal or sublethal conditions, possible interactions of temperature with other factors are of importance. This calls for a multifactorial design of experiments. For instance, low light levels and short days enhanced survival at low, sublethal temperatures in many seaweeds (Figs 3, 4; Table 5). This would mean, that in the field, near a northern boundary, lethal conditions would operate in early spring, rather than in midwinter.

Incubation periods should also be chosen so as to give a realistic simulation of the duration of the season with potentially limiting conditions. This may be in the order of weeks or months, but there is no standard procedure to be recommended, because in the field the duration of periods with stressful temperatures will vary both locally and for eastern and western Atlantic coasts, depending on the shape of the annual temperature curve (see for instance Fig. 9). Realistic acclimation periods of at least several weeks should also be applied as these may induce the formation of more stress-resistant tissue (e.g. Novaczek et al., 1987).

The application of experimental results to the field situation near a geographic boundary remains problematic. It should be realised that conditions which are limiting for one species need not necessarily be so for another, even when experiments gave comparable results. For instance, when comparing the amount of growth minimally required at a "northern growth boundary" herbivore-resistant species will need to grow less than non-resistant species in order to build up a sufficient amount of biomass during the summer. Therefore, the final interpretation of factors that set biogeographic boundaries will depend on phenological and demographic work in boundary populations, including in situ monitoring of environmental conditions over a period of several years.

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