

## Temperature responses of tropical to warm temperate *Cladophora* species in relation to their distribution in the North Atlantic Ocean

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**ABSTRACT:** The relationship between distribution boundaries and temperature responses of some North Atlantic *Cladophora* species (Chlorophyta) was experimentally examined under various regimes of temperature, light and daylength. Experimentally determined critical temperature intervals, in which survival, growth or reproduction was limited, were compared with annual temperature regimes (monthly means and extremes) at sites inside and outside distribution boundaries. The species tested belonged to two phytogeographic groups: (1) the tropical West Atlantic group (*C. submarina*: isolate from Curaçao) and (2) the amphiatlantic tropical to warm temperate group (*C. prolifera*: isolate from Corsica; *C. coelothrix*: isolates from Brittany and Curaçao; and *C. laetevirens*: isolates from deep and shallow water in Corsica and from Brittany). In accordance with distribution from tropical to warm temperate regions, each of the species grew well between 20–30 °C and reproduction and growth were limited at and below 15 °C. The upper survival limit in long days was < 35 °C in all species but high or maximum growth rates occurred at 30 °C. *C. prolifera*, restricted to the tropical margins, had the most limited survival at 35 °C. Experimental evidence suggests that *C. submarina* is restricted to the Caribbean and excluded from the more northerly American mainland and Gulf of Mexico coasts by sporadic low winter temperatures in the nearshore waters, when cold northerly weather penetrates far south every few years. Experimental evidence suggests that *C. prolifera*, *C. coelothrix* and *C. laetevirens* are restricted to their northern European boundaries by summer temperatures too low for sufficient growth and/or reproduction. Their progressively more northerly located boundaries were accounted for by differences in growth rates over the critical 10–15 °C interval. *C. prolifera* and *C. coelothrix* are excluded or restricted in distribution on North Sea coasts by lethal winter temperatures, again differences in cold tolerance accounting for differences in their distribution patterns. On the American coast, species were probably restricted by lethal winter temperatures in the nearshore and, in some cases, by the absence of suitable hard substrates in the more equable offshore waters. Isolates from two points along the European coast (Brittany, Corsica) of *C. laetevirens* showed no marked differences in their temperature tolerance but the Caribbean and European isolates of *C. coelothrix* differed markedly in their tolerance to low temperatures, the lethal limit of the Caribbean isolate lying more than 5 °C higher (at ca 5 °C).

### INTRODUCTION

The genus *Cladophora* consists at least of 42 species and is widely distributed over all oceans from the near polar regions to the tropics. Following taxonomic revisions (van den Hoek, 1963, 1982 b; van den Hoek & Womersley, 1984; Sakai, 1964), they form a group whose systematics and geographic distributions are relatively well known, although some problems with identifications, and thus misrepresentations of the geo-

graphic distribution remain because of the morphological plasticity of some species. In particular, consistent patterns of geographic distribution emerged on North Atlantic coasts where extensive north-south coastlines enable distribution to be compared with continuous thermal gradients. The coincidence of a distribution boundary with the same seawater isotherm on both the American and European coasts was notable and contrasted with the vastly different latitudinal ranges of the species on each coast. This led to the suggestion that the biogeographic distribution of the species was a direct result of limiting winter or summer temperatures (van den Hoek, 1979, 1982 b).

Direct evidence for the temperature control of distribution comes from laboratory studies on the effects of temperature on the life history and the tolerance of species to high or low temperatures. Studies on other seaweeds have shown that temperature responses (in combination with light and photoperiodic responses) determined in the laboratory can explain distribution patterns along latitudinal gradients (McLachlan & Bird, 1984; Yarish et al., 1984, 1986; and other studies reviewed in van den Hoek, 1982a, c).

Hutchins (1947) proposed that temperature could act as a limiting factor at the poleward and equatorward ends of the distribution range of a marine organism as follows:

(a) At the poleward boundary, temperatures may be too cool in summer for adequate growth and/or reproduction, or too cold in winter to survive even during the dormant phase, or a combination of both.

(b) At the equatorward boundary, temperatures may be too warm in winter in short days for adequate growth and/or reproduction, or too hot in summer to survive even in the dormant phase, or a combination of both.

In this paper, the existence of temperature limits at the distribution boundaries is examined for four species of *Cladophora* in the North Atlantic. One of these species, *C. submarina* Crouan frat. ex Schramm & Mazé, belongs to van den Hoek's (1982 a, b, c) "Tropical western Atlantic distribution group", whose species are restricted to the Caribbean. The other three species, *C. prolifera* (Roth.) Kütz., *C. coelothrix* Kütz. and *C. laetevirens* (Dillw.) Kütz. belong to van den Hoek's (1982a, b, c) "Amphiatlantic tropical-to-warm temperate group with a northeastern extension". Species in this group do not extend much beyond the tropics on American coasts but occur far into the temperate zone in Europe. Temperatures limiting growth, sporulation and long-term survival have been experimentally determined in unialgal cultures. These have been compared with the annual temperature regimes inside and outside the distribution boundaries on the European and American coasts, to determine whether adverse summer or winter temperatures prevent the species extending beyond their present boundaries.

## METHODS

Collections of the four *Cladophora* species (Table 1) were isolated into unialgal culture and maintained in tubes with 10 ml Provasoli's enriched seawater.

Table 1. Collection data for *Cladophora* isolates

Species	Collection	Habitat
<i>Cladophora submarina</i>	Curaçao	Boca Grandi; wavepounded littoral pools eroded from limestone (savahs)
<i>C. prolifera</i>	Calvi, Corsica	Sunlit sea wall, 1 m deep
<i>C. coelothrix</i>	Curaçao	Spaanse Water, on mud between mangrove roots entangled with other algae
	Roscoff, Brittany	Muddy harbour, low littoral
<i>C. laetevirens</i>	Calvi, Corsica	Sunlit sea wall, 1 m deep
	Calvi, Corsica	Under seagrass leaves, 10 m deep
	Roscoff, Brittany	Île Ledanet, deep, midlittoral pool on west shore

### Growth responses

Growth responses under constant temperature conditions ranging from 5–35 °C at 5 °C experimental intervals, were measured on 5 replicates at short (LD 8:16 h) and long (LD 16:8 h) day conditions, photon fluence rate 40  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , using tip cuttings from a single clone for each isolate. For general methods and equipment, see Yarish et al. (1984).

Growth at each condition was measured as relative growth rate (RGR). Fragments of approximately equal length, cut from actively growing tips, were placed singly in tubes, and after a settling period of 3 days, were drawn with a camera lucida and measured for length using a Hewlett Packard digitiser (Model 9835A). They were then remeasured 3, 7 and/or 10 days later. Relative growth rate was calculated as

$$\begin{aligned} \text{RGR} &= (\ln l_2 - \ln l_1) \cdot 100 \cdot T^{-1} \\ &= \% \text{ increment per day} \\ &\text{where } l_1 = \text{initial length, } l_2 = \text{length after } T \text{ days.} \end{aligned}$$

Upper and lower growth limits were arbitrarily defined as the 5 °C experimental interval in which the RGR fell below 20 % of the maximum.

### Long-term survival and sporulation

Survival potential at extreme temperatures was determined as follows: three or six well grown large plants or branches were placed in Erlenmeyer flasks with 200 ml of Provasoli enriched seawater and set at temperatures close to the lethal limit as determined from growth experiments (usually 0 or 5 °C and 30 or 35 °C). Plants were gradually brought to the experimental temperatures in steps of 5 °C each lasting a few days. Survival was tested at three photon fluence rates of 10, 20 and 40  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at short (8:16 h) and/or long (16:8 h) day conditions over 2, 6 and 12 weeks (see, for example, Fig. 2). Plants tested at 0 °C were placed in a water bath ( $\pm 0.5$  °C) in short days. At all other

temperatures plants were kept in controlled environment incubators ( $\pm 1^\circ\text{C}$ ) in long and short days. Plants at  $35^\circ\text{C}$  were tested in long days only. At the end of each test interval, the plants were removed and if they appeared to be in good condition, then this was recorded and they were given no further treatment. However, if they were extensively necrosed or appeared dead, then their ability to recover was tested by placing them in new medium and bringing them to the optimum growth temperature via  $5^\circ\text{C}$  steps each lasting a day or two at reduced photon fluence rate ( $20\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). If no new growth was evident after 6–8 weeks then the temperature was defined as lethal. Upper and lower lethal limits were defined as the  $5^\circ\text{C}$  experimental interval where survival was limited (less than 12 weeks) in long and short days, respectively.

Formation of zooids (zoospores or gametes) was determined in large plants which were kept at the experimental temperatures ranging from  $5\text{--}30^\circ\text{C}$  at  $5^\circ\text{C}$  intervals for 3 months.

#### Distribution and temperature records

Distribution data as summarized in Figs 5, 9, 13 and 17 have been derived from van den Hoek (1963, 1982b) with additional literature records for *C. coelothrix* and *C. prolifera*, which are easily recognized species. Only a few selected references to *C. laetevirens* have been added, as it has often been confused with other species, literature records being generally unreliable. For *C. submarina*, there are no reliable records at present in other literature sources.

Temperature regimes have been compiled from various sources. Winter (February) and summer (August) isotherms in the North Atlantic Ocean are shown in Figure 1, which is drawn to the same scale as the distribution maps so as to facilitate comparisons. Isotherms are from the U. S. Navy marine climatic atlas of the world (1981). Annual temperature regimes (monthly means and ranges) at stations within and outside distribution boundaries were based on detailed local records whenever these were available (see legend to Figs 4, 8, 12 and 16 for sources). For other sites, monthly means were based on sea surface isotherms given in Gorshkov (1978). For open coasts, ranges around the means 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 seawater temperatures for selected oceanic sites. The temperature interval encompassing 50–90 % of all records was used to estimate the range of regularly occurring temperatures above the mean; similarly the interval encompassing 10–50 % of all records was used to estimate the range below the mean.

#### Length of growing season

The progressive decrease in length of the growing season at northern boundaries on the European coast was estimated from the period with seawater temperatures equal to or above  $10^\circ\text{C}$  (Fig. 18). Two estimates of the length of the growing season were made using firstly, mean monthly sea surface temperatures (from Gorshkov, 1978), and secondly, minimum temperatures [10 % of temperatures recorded were lower than this value (from the U. S. Navy marine climatic atlas of the North Atlantic Ocean 1974)] for sites on the Atlantic Irish, Scottish and Norwegian coasts. Estimates for Roscoff and Helgoland were based on local records (see legend to Fig. 18 for sources).

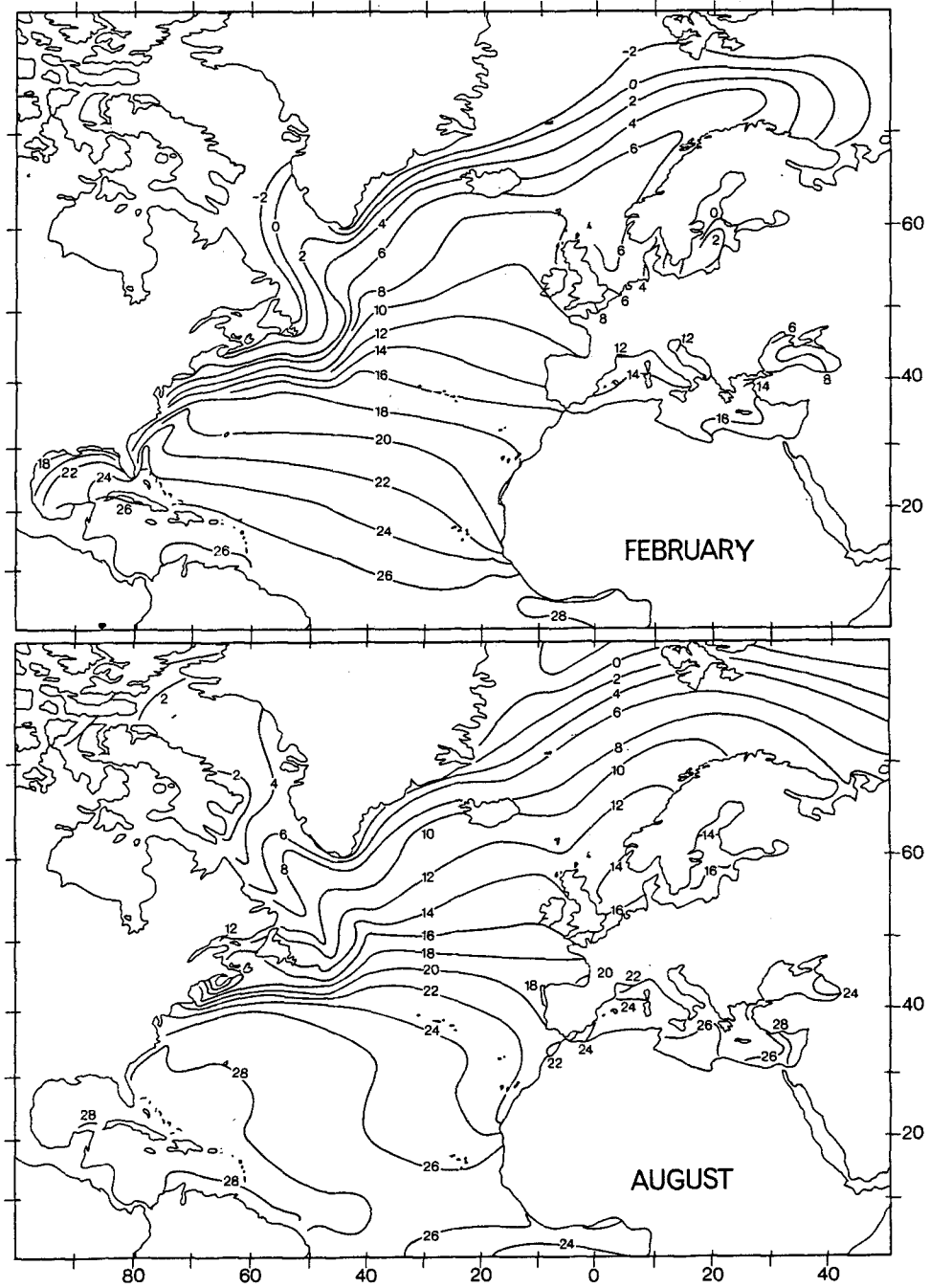


Fig. 1. Winter (February) and summer (August) isotherms in the North Atlantic Ocean in comparison with geographic distribution of four *Cladophora* species as shown in Figs 5, 9, 13 and 17

## RESULTS AND DISCUSSION

In the following section, we consider whether temperature responses can explain the distribution of the 4 species on N. Atlantic coasts. Their temperature responses and tolerances in culture are compared with the temperature regimes within and beyond the northern distribution boundaries. These species occur through the tropics, so there is no southern boundary in the N. Atlantic but tolerance to tropical temperature regimes is also considered in the question of distribution.

*Cladophora submarina*

This species' geographic range is restricted to islands of the Caribbean, and Bermuda is the northernmost record (Fig. 5). There are no records for the American mainland or African coasts. Its habitat also seems to be restricted as it has been found only in pools in the upper intertidal on limestone platforms of exposed tropical coasts (van den Hoek, 1982b). The constant wash of surf means that the water is rapidly replaced so despite the strong tropical sun, water temperatures probably do not rise above ambient.

*Northern boundary – America*

An isolate from Curaçao was tested for temperatures limiting survival (Fig. 2) and growth (Fig. 3). In short days, it could survive for 2 but not 6 weeks at 10 °C, whereas at 5 °C death occurred in less than 2 weeks. At 15 °C, plants could persist indefinitely and so in Figure 4, the lower lethal limit has been shown in the interval 10–15 °C. On the same figure, temperature curves are shown for Bermuda (the northernmost record), Key West, on the southern tip of Florida (N. B.: nearest record is from the Bahamas, Fig. 5), and Cedar Keys in the Gulf of Mexico, which lies well beyond the boundary.

Temperatures on Bermuda are never lethal but at Florida Keys, temperatures may fall below 15 °C during a cold winter (Earle, 1969; Walker et al., 1982), which is the temperature interval below which survival is limited. However, these cold spells last only 1–2 weeks, being caused by intrusions of polar air masses chilling the extensive shallow bays and bank waters of Florida. For example, Walker et al. (1982) recorded temperatures below 15 °C, lasting about 10 days in Florida Bay (mean 10.6 °C) with the

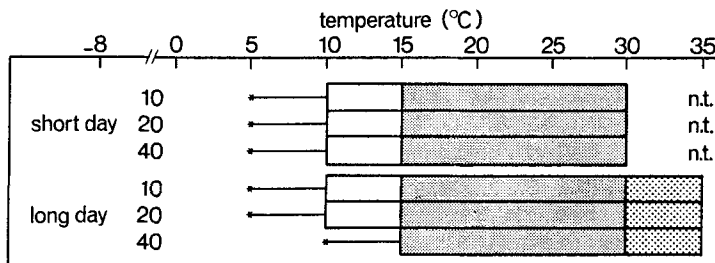


Fig. 2. Survival of *Cladophora submarina* isolates from Curaçao. Isolates were tested at 0 °C in short (LD 8:16 h) days, at 5 °C and 10 °C in short days and long (LD 16:8 h) days and at 35 °C in long days, at 3 photon fluence rates 10, 20 and 40 μmol·m<sup>-2</sup>·s<sup>-1</sup>. Survival intervals were defined as follows: \* = less than 2 weeks; blank bars = 2 weeks but not 6 weeks; stippled bars = 6 weeks but not 12 weeks; grey bars = more than 12 weeks; n. t. = not tested

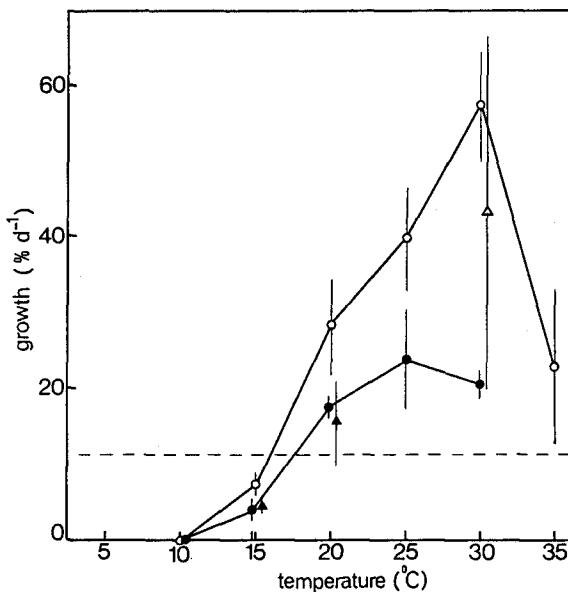


Fig. 3. Mean relative growth rates (RGR) and standard deviations ( $n = 5$ ) of *Cladophora submarina* from Curaçao measured from 5–35°C at 5°C intervals. Isolates were grown in long day (○) (LD 16:8 h) and short day (●) (LD 8:16 h) conditions with photon fluence rate of  $40 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . At some temperatures, growth was also measured at higher ( $\Delta = 72 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ) and lower ( $\blacktriangle = 20 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ) photon fluence rates. Broken line = 20% of maximum RGR, defining growth limits

minimum value recorded being as low as 8.7°C. At the highest light level tested *C. submarina* survived for more than 2 weeks at 10°C in short but not in long days (Fig. 2), so these winter cold spells in ca 11 h daylengths are probably very close to the lethal limit. Further north in the Gulf of Mexico, there would also be a clear lethal limit because temperatures drop well below 10°C during the cold spells, and this would be lethal to *C. submarina* (see, for example Cedar Keys, Fig. 4). *C. submarina*'s sensitivity to temperatures above 30°C (Figs 2, 4) means that in extreme years, maximum summer temperatures are also within the range of limited survival at Florida and Cedar Keys. Thus, in extreme years, the annual temperature fluctuations could potentially exceed both the upper and lower limit of temperature tolerance in the Gulf of Mexico.

Temperature extremes may also be an important component of the apparently specific habitat requirements of this species for wave washed intertidal pools where temperatures are maintained very close to ambient seawater. This contrasts with the calm sediment coasts with lagoons and estuaries common along much of the Florida coast and the Gulf of Mexico, where temperatures may reach extreme values.

Low summer temperatures do not restrict the species' northward spread along the American coast. At Bermuda and Florida Keys, summer temperatures range from 25 to more than 30°C, corresponding to the temperatures with the maximum growth rates in long days (Figs 3, 4). This is also the case much further north along the American coast up to about N. Carolina (compare to Fig. 8). Sporulation occurred between 15–30°C and so would not be limiting to northward extension either.

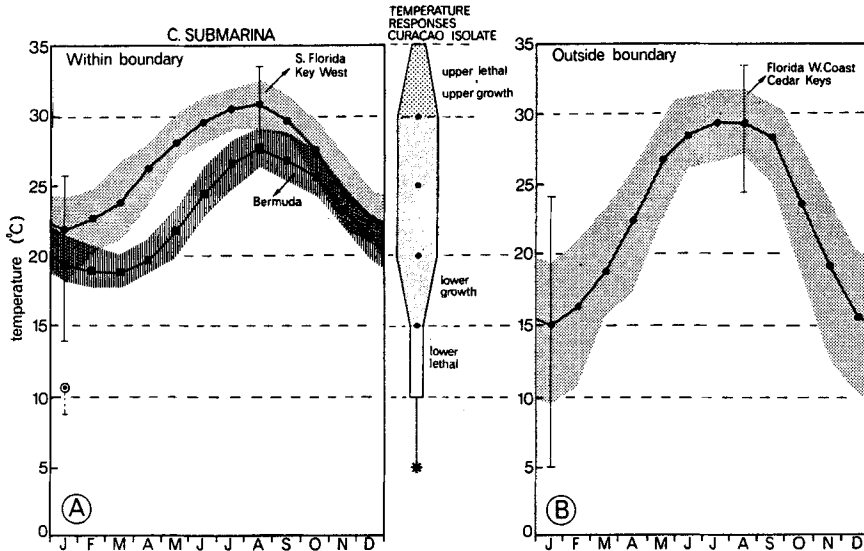


Fig. 4. *Cladophora submarina*. Annual temperature regimes as monthly means and ranges (shaded) at sites within and outside the northern boundaries compared to experimentally determined temperature tolerances. (A) Within boundaries, ■—■ Bermuda, means after Gorshkov, 1978, ranges based on U. S. Navy Marine climatic atlas, 1974; ●—● S. Florida, Key West, means and ranges based on Earle, 1969; shaded range shows 28-year mean values of monthly maxima and minima; extreme records shown for January and August (vertical lines); 10-day mean (C) and lowest record (dashed line) during extreme cold spell in January 1981 based on Walker et al., 1982. (B) Outside boundaries, ●—● Cedar Keys, means and ranges based on Earle (1969); shaded range shows 18-year mean values of monthly maxima and minima; extreme records shown for January and August (vertical lines). Bar diagram shows experimentally determined upper and lower lethal limits and growth limiting temperatures at  $40 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  for an isolate from Curaçao (from Figs 2 and 3). Upper lethal limit taken from response in long days (LD 16:8 h), lower lethal limit taken from response in short days (LD 8:16 h); \* = lethal in less than 2 weeks; blank column = survived 2 weeks but not 6 weeks; stippled column = survived 6 weeks but not 12 weeks; grey column = survived more than 12 weeks; tapering column: growth limit lies in this interval, in which RGR exceeds 20% of the maximum; ● = sporulation within 12 weeks

#### Potential vs actual distribution

*C. submarina* is only known from the Caribbean and Bermuda and has not been found on the American mainland or the eastern Atlantic coasts (Fig. 5). The species' absence from the W. Caribbean is a noticeable gap in its distribution, which is not attributable to limiting temperatures (Figs 1, 5) but to limited sampling (van den Hoek, 1982b, mentions 4 *Cladophora* records in total from W. Caribbean shores). Beyond the Caribbean, its potential distribution would include the tropical coasts of W. Africa, Canary Islands and the E. Mediterranean where temperatures lie within the tropical range (Fig. 1).



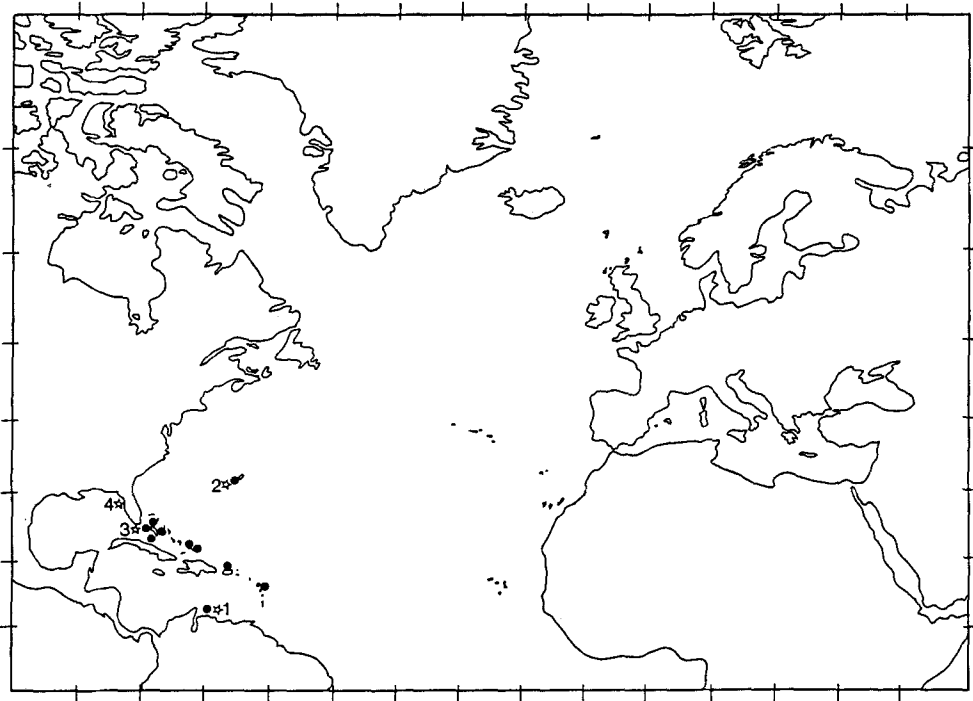


Fig. 5. Distribution of *Cladophora submarina* in the N. Atlantic (from van den Hoek, 1982b). Sampling site of cultured isolate (\*1 Curaçao) and stations for which temperature regimes are shown in Fig. 4 indicated (within boundaries: \*2 Bermuda, \*3 Florida Keys; outside boundaries: \*4 Cedar Keys)

### *Cladophora prolifera*

This species occurs on both sides of the Atlantic in tropical and warm temperate zones (Fig. 9). It has been recorded from habitats ranging from shallow waters, either sunlit or deeply shaded by overhangs, to deep reefs off the N. Carolina coast and at depths from 0–70 m. On European Atlantic coasts, it also grows in the lower littoral, on steep north facing rocks (van den Hoek, 1963, 1982b).

#### *Northern boundary – Europe*

The northernmost records of *C. prolifera* are from Clare Island on the west coast of Ireland and the English Channel (Fig. 9). The Clare Island record is an old collection and the sole record from Ireland, the next most northerly records being from the English Channel. Here populations have been consistently collected and thus this site might be regarded as a better indication of the northern boundary.

An isolate from Calvi, Corsica, was tested for temperatures limiting survival (Fig. 6) and growth (Fig. 7). In short days, the Corsican isolate could survive for 6 but not 12 weeks at 5°C whereas at 0°C death occurred in less than 2 weeks, or between 2–6 weeks at lower light intensity. At 10°C, plants could persist indefinitely. The lower lethal limit is thus shown in the interval 5–10°C in Figure 8. In the same figure, it can be seen that

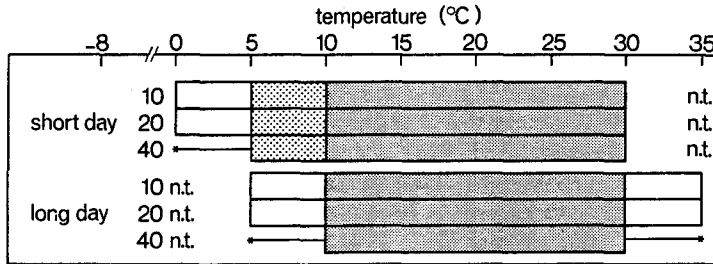


Fig. 6. Survival of *Cladophora prolifera* isolate from Corsica. Survival intervals defined in Fig. 2

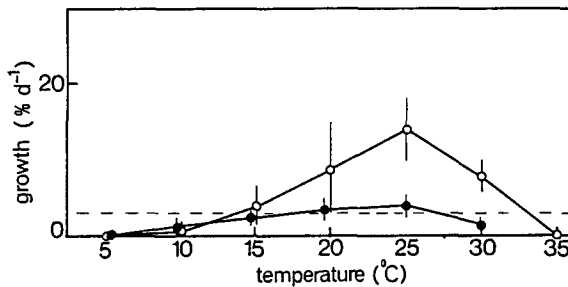


Fig. 7. Mean relative growth rates and standard deviations ( $n = 5$ ) of *Cladophora prolifera* from Corsica. Growth conditions described in Fig. 3

minimum winter temperatures at Roscoff, near the northern boundary, can fall within this interval of limited survival for 4 months in cold years and this may account for the species' rarity at Roscoff. Mean winter temperatures are near 10°C and these could be easily survived, and even during a cold winter, temperatures do not reach 5°C, which temperature could be survived for more than 6 weeks. However, it is easy to see why *C. prolifera* does not penetrate into the North Sea from the temperature curve of Helgoland, shown in Figure 8b. Here, mean winter temperatures drop below 5°C for more than 3 months and this was lethal to plants in culture.

Winter temperatures on the western coasts of Ireland and Scotland are warmer than North Sea temperatures (Fig. 1) and so do not constitute a lethal boundary. However, summer temperatures are close to the lower growth limit. No growth occurred in cultures at 10°C and growth was still very slow at 15°C: 3% per day (Fig. 7). At this growth rate a plant would take more than one month to double in size, so that summer temperatures limiting growth are suggested as limiting northward extension along Irish and Scottish coasts. Sporulation only occurred at 20 and 25°C in the Mediterranean isolate used (Fig. 8) and these temperature requirements for sporulation would not be met in areas closer to the northern boundary.

#### Northern boundary – America

No isolate was tested from the American side of the Atlantic and therefore only tentative suggestions are given on the nature of the northern boundary on the American coast. The northernmost record for *C. prolifera* is New River, North Carolina, and it is also commonly found on the adjacent Outer Shelf reefs (Schneider, 1976). In Figure 8,

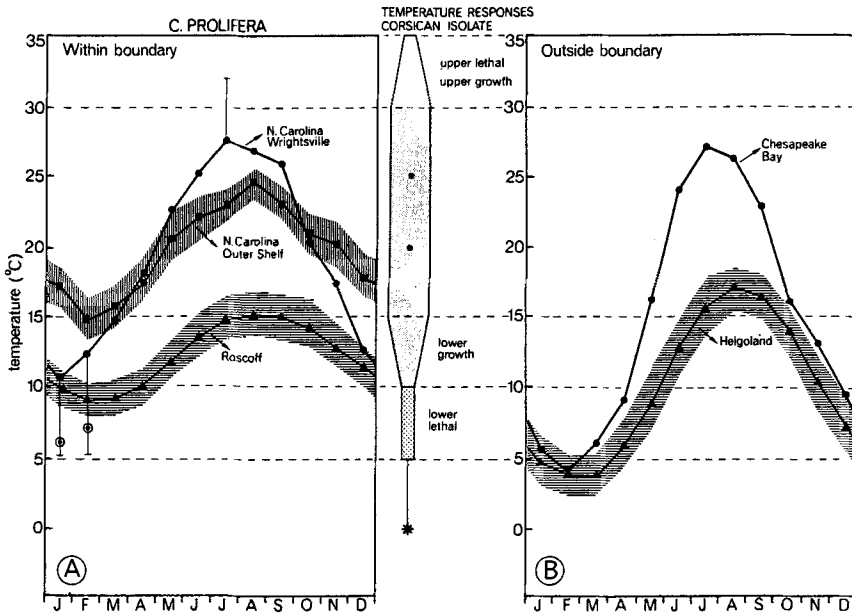


Fig. 8. *Cladophora prolifera*. Annual temperature regimes as monthly means and ranges (shaded) at sites within and outside the northern boundaries compared to experimentally determined temperature tolerances. (A) Within boundaries:  $\blacktriangle$ — $\blacktriangle$  Roscoff, Brittany, means after I.I.S.T.P.M., Roscoff (1976), ranges based on U. S. Navy Marine climatic atlas, 1974;  $\bullet$ — $\bullet$  N. Carolina inshore, Wrightsville Beach, means after Kapraun (1978), January and February means for a cold year ( $\circ$ ) and extreme records for January, February and August (vertical lines) based on data from 1976 (Kapraun & Zechman, 1982);  $\blacksquare$ — $\blacksquare$  N. Carolina offshore, Outer Shelf reefs, means after Gorshkov (1978), ranges based on U. S. Navy Marine climatic atlas (1974). (B) Outside boundaries:  $\blacktriangle$ — $\blacktriangle$  Helgoland, means after Weigel (1978), ranges based on U. S. Navy Marine climatic atlas (1974);  $\bullet$ — $\bullet$  inshore Chesapeake Bay at Gloucester Point, Virginia, means only (after Humm, 1979). Bar diagram shows experimentally determined upper and lower lethal limits and growth limiting temperatures (details as in Fig. 4) for an isolate from Corsica (from Figs 6 and 7)

temperature curves are shown for Wrightsville Beach, near New River Inlet and for the N. Carolina Outer Shelf reefs. Winter temperatures are much lower at the inshore Wrightsville Beach site, averaging 6–7°C for 2 months during cold winters (Kapraun & Zechman, 1982) and this would be close to the lethal limit for the Corsican isolate (Figs 6, 8). On the Outer Shelf reefs, temperatures are favourable for growth most of the year (Figs 7, 8) although winter minima of 8–10°C have been recorded (Peckol & Searles, 1984). These reefs, providing the only hard substrate for algae in the warmer offshore waters do not extend further north. Beyond the northern boundaries, for example in Chesapeake Bay (Fig. 8), even average winter temperatures are below 5°C for about 3 months and this would be lethal for the Corsican isolate (Fig. 8).

In the absence of temperature responses for an American isolate, we tentatively conclude that this northern boundary is a winter lethal one, particularly since there is a rapid decline in winter temperatures within a relatively short length of coast north of this boundary in the Cape Hatteras area (Fig. 1). Inshore summer temperatures would be optimal for growth of the Corsican isolate much further north (Figs 1, 8) and this is in

contrast to the situation on the European northern boundary, which is set by a summer growth limit.

*Potential vs actual distribution*

*C. prolifera*'s distribution range, from tropical to warm temperate zones, has gaps for the central and western Caribbean and the Gulf of Mexico, where the species might be expected to occur in view of their tropical temperatures (Figs 1, 9). However, the limited survival potential of the Corsican isolate above 30 °C (Fig. 6) suggests that high temperatures might be responsible.

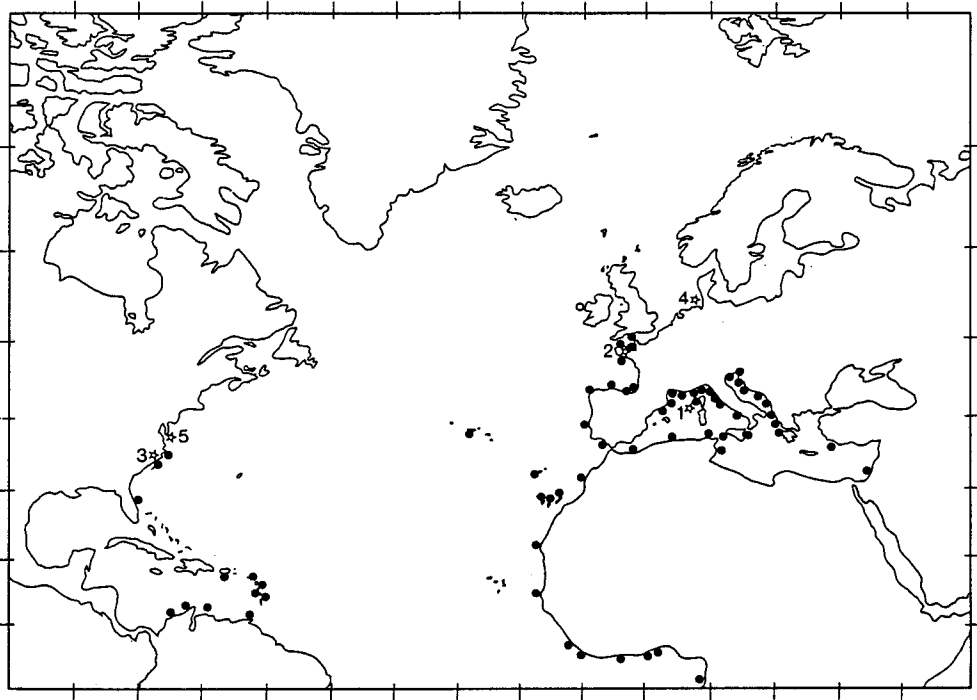


Fig. 9. Distribution of *Cladophora prolifera* in the North Atlantic (from van den Hoek, 1963, 1982b) (○ = isolated record from 1912). Additional records: tropical West Africa (Lawson & John, 1982); Cap Blanc (Lawson & John, 1977); Morocco (Gayral, 1958); Canary Islands (Börgesen, 1925; Gil-Rodríguez & Alfonso-Carillo, 1980); Azores (Feldmann, 1946); Madeira (Levring, 1974); Portugal (Ardre, 1970); NW Spain (Perez-Cirera, 1975; Neill, 1978); Pelagie Islands, south of Sicily (Cinelli et al., 1976); Alboran Sea (Conde, 1984); eastern Sicily (Cormaci & Furnari, 1979); Rhodos (Diannelidis et al., 1977); Israel (Lipkin & Safriel, 1971); Tunisia (Meñez & Mathieson, 1981). Sampling site of cultured isolate (\*1 Corsica) and stations for which temperature regimes are shown in Fig. 8 indicated (within boundaries: \*2 Roscoff, \*3 N. Carolina; outside boundaries: \*4 Helgoland, \*5 Chesapeake Bay)

*Cladophora coelothrix*

This species occurs on both sides of the Atlantic, in tropical and warm temperate zones (Fig. 13). It has often been recorded from muddy habitats; in the tropics, from mangrove roots and forming cushions on the muddy tidal flats between mangrove trees

(van den Hoek, 1982b) and in temperate regions, from muddy estuaries and harbours (van den Hoek, 1963), such as La Rance, Brittany as well as bays, such as Galway Bay, Ireland.

*Northern boundary – Europe*

Northernmost records in Europe are from W. Ireland on the Atlantic coast and Northumberland on the North Sea coast (Fig. 13). The Northumberland record is an old collection and the sole record for the North Sea, the next most northerly record being from the Irish S. W. coast (Guiry, 1978). Here populations have been consistently collected and thus this site might be regarded as a better indication of boundary populations.

An isolate from Roscoff, Brittany, was tested for temperatures limiting survival (Fig. 10a) and growth (Fig. 11). In short days corresponding to winter conditions, the Roscoff isolate survived permanently at 5°C whereas at 0°C it survived for 6 weeks but not 12 weeks. The light intensity did not affect survival much but daylength did. Accordingly, the lower lethal limit for the Roscoff isolate is shown in the interval 0–5°C in Figure 12. In the same figure, it can be seen that winter temperatures for the west of Ireland remain above 5°C even in a cold winter and above 10°C in a warm winter. Thus, even cold winters could be easily survived by sublittoral populations of *C. coelothrix* and we suggest that winter temperatures do not prevent the species extending further north.

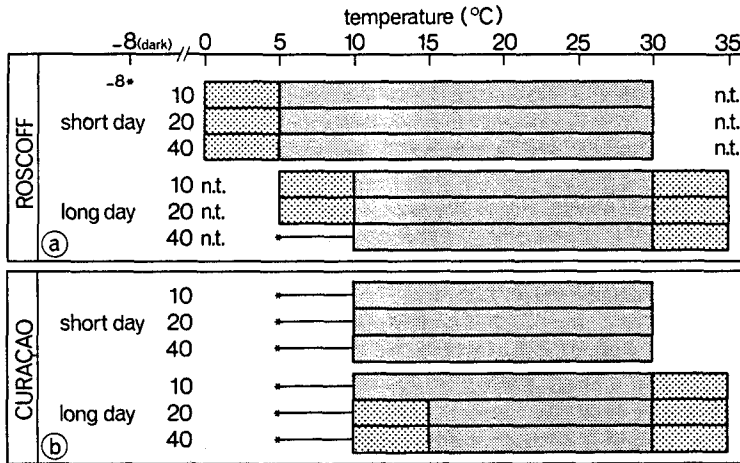


Fig. 10. Survival of *Cladophora coelothrix* isolates from (a) Roscoff, Brittany, near the northern boundary in Europe and (b) Curaçao, Netherlands Antilles, in tropical waters. Survival intervals as defined in Fig. 2

However, summer temperatures in the west of Ireland are between 10 and 15°C in cool summers (Fig. 12) and so approach the lower growth limit (Figs 11, 12). This indicates that beyond this region, summer temperatures will sometimes be too cool to allow sufficient growth, setting the limit for northward extension. Thus on N. Scottish and Norwegian coasts, which lie beyond the northern boundary (Fig. 13), winter temperatures are not lethal due to the moderating influence of the Gulf Stream (Fig. 1) but

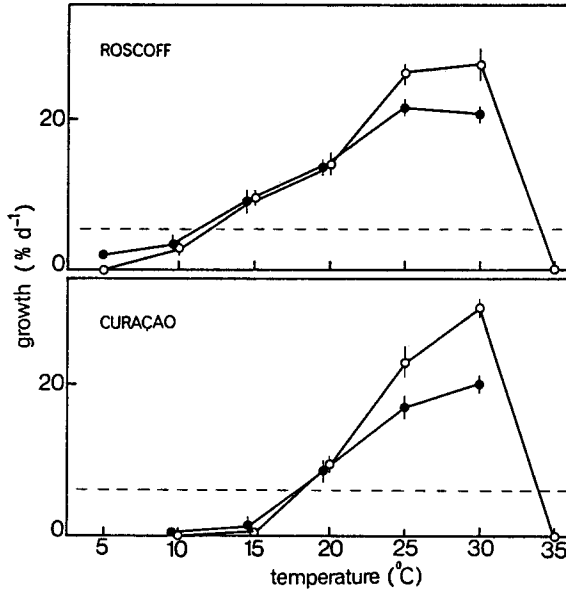


Fig. 11. Mean relative growth rates and standard deviation ( $n = 5$ ) of *Cladophora coelothrix* isolates from (a) Roscoff, Brittany, near the northern boundary in Europe and (b) Curaçao, Netherlands Antilles, in tropical waters. Growth conditions as described in Fig. 3

the summers are short and in cool summers temperatures will not even reach the lower growth limit.

*C. coelothrix* is not found on the mainland European coasts in the North Sea and reference to Figure 12b, where the temperature curve for Helgoland is shown, provides an explanation for its absence from the North Sea. Summer temperatures are several degrees warmer than those for the west of Ireland and so are well above the lower growth limit although the growing season is shorter. However, in cold winters the temperature falls below  $0^{\circ}\text{C}$  (Lüning, 1985), which is beyond the lethal limit. Plants in culture survived only 6 weeks at  $0^{\circ}\text{C}$  (Fig. 10a) but were extensively damaged and so had to regrow from a few surviving basal cells requiring rather a long recovery time.

In addition to generally low water temperatures, intertidal populations will also have to contend with freezing of the shallows in estuarine habitats, with air temperatures below  $0^{\circ}\text{C}$  on North Sea coasts. The Roscoff isolate did not survive freezing for 2 weeks at  $-8^{\circ}\text{C}$  in total darkness and in view of the enhancing effects of light on frost damage (e.g. Larcher, 1981), plants exposed to frost and bright sunshine during frosty days in the intertidal would not be expected to survive.

#### *Northern boundary – America*

The northernmost record on the Amercian coast at Carrabelle, on the west coast of Florida, lies far to the south of the northern boundary in Europe (Fig. 13). An isolate from the tropical waters of Curaçao, Netherlands Antilles was tested for temperatures limiting survival (Fig. 10b) and growth (Fig. 11). This tropical isolate was more sensitive to cold than the temperate Roscoff isolate, not even surviving for 2 weeks at  $5^{\circ}\text{C}$  in short days. At

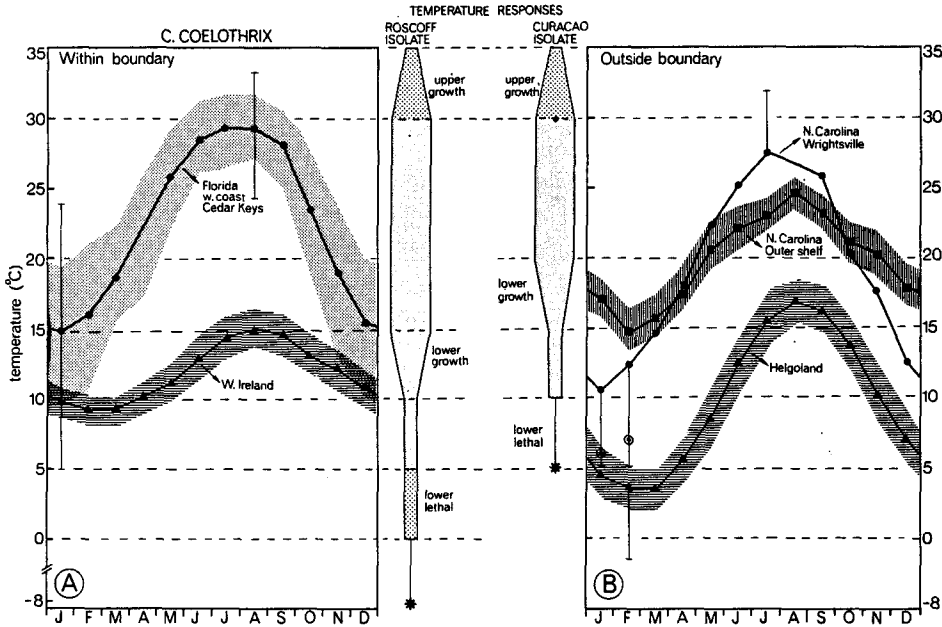


Fig. 12. *Cladophora coelothrix*. Annual temperature regimes as monthly means and ranges (shaded) at sites within and outside the northern boundaries compared to experimentally determined temperature tolerances. (A) Within boundaries,  $\blacktriangle$ — $\blacktriangle$  W. Ireland, means after Gorshkov (1978); ranges based on U. S. Navy Marine climatic atlas (1974);  $\bullet$ — $\bullet$  Cedar Keys, W. Florida (see Fig. 4). (B) Outside boundaries,  $\blacktriangle$ — $\blacktriangle$  Helgoland (see Fig. 8); extreme for February is 10-day mean value in cold year (vertical bar) (Lüning, 1985);  $\bullet$ — $\bullet$  N. Carolina inshore, Wrightsville Beach and  $\blacksquare$ — $\blacksquare$  offshore (see Fig. 8). Bar diagram shows experimentally determined upper and lower lethal limits and growth limiting temperatures (details as in Fig. 4) for isolates from Roscoff, Brittany, and from Curaçao, Netherlands Antilles (from Figs 10 and 11)

10 °C, it survived for more than 12 weeks and so, in Figure 12 the lower lethal limit of the Curaçao isolate has been shown in the interval 5–10 °C. On the same figure, it can be seen that, in cold years, winter temperatures at Cedar Keys near the northern boundary on the Florida west coast can fall below 10 °C with minimum values recorded being as low as 5 °C. These periods of low temperature last for 1–2 weeks and arise from the same weather systems as described for *C. submarina*. Temperatures of 5 °C were lethal to *C. coelothrix* from Curaçao in less than 2 weeks (Fig. 10). Besides, the species has been recorded in shallow waters on this coast, often on mangrove roots; and so, in this habitat, it is also vulnerable to low air temperatures.

Summer temperatures are high along this coast and would not in general limit growth (Figs 11, 12). However, the highest summer temperatures shown for Cedar Keys approach the upper lethal limit, so the tolerance range of the Curaçao isolate would probably be only just broad enough for year long survival at the species' northern boundary in extreme years.

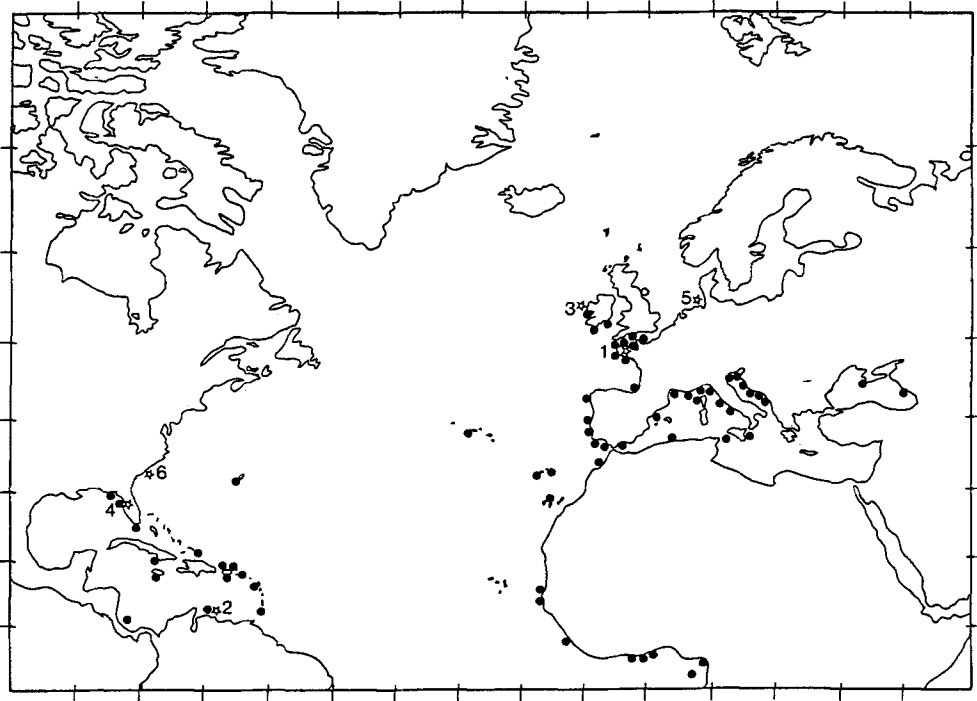


Fig. 13. Distribution of *Cladophora coelothrix* in the North Atlantic (van den Hoek, 1963, 1982b) (○ = isolated record from 1902). Additional records: tropical W. Africa (Lawson & John, 1982). Senegal, as *C. repens* (Sourie, 1954), Selvagem Pequena, Selvagem Grande (Weisscher, 1983), Morocco (Weisscher 1983), Canary Islands (Gil-Rodriguez & Alfonso-Carillo, 1980), as *C. trichotoma* (Börge- sen, 1925), Azores (Feldmann, 1946), Madeira (Levring, 1974), Portugal (Ardré, 1970), NW Spain (Donze, 1968), Pelagic Islands, south of Sicily (Cinelli et al., 1976), E. Sicily (Cormaci & Furnari, 1979), Ireland (Guiry, 1978; and pers. comm.). Sampling sites of cultured isolates (\*1 Roscoff, \*2 Curaçao) and stations for which temperature regimes are shown in fig. 8 indicated (within bound- aries: \*3 W. Ireland, \*4 W. Florida; outside boundaries: \*5 Helgoland, \*6 N. Carolina

#### *Potential vs actual distribution*

There are two noticeable gaps in the latitudinal range; firstly, the reefs on the Carolina shelf, where the temperature range from 15–25 °C would not limit either survival in winter or growth in summer (see above, Fig. 12). This contrasts to the inshore situation, where low temperatures do seem to account for the species' absence. Although the inshore areas of N. Carolina experience winter minimum temperatures similar to those at the northern boundary in W. Florida, these low temperatures occur regularly for several months each year rather than occurring sporadically for a week or two (Fig. 12). The second gap in distribution lies in the Western Gulf of Mexico (Fig. 1, 13), which includes extensive estuarine areas with violent fluctuations in salinity and long stretches of sediment coasts. Extremes in temperature probably do limit the persistence of *C. coelothrix* here, as winter temperatures have been recorded for example, in January, of 0–5 °C (Earle, 1969) (compare Fig. 12).

The temperature responses for the Roscoff and the Curaçao isolates (Figs 10a, b, 11)



were the same at the upper end of the range, with upper growth limits and lethal limits in the same 5°C interval, 30–35°C, but at the lower end of the range, the Curaçao isolate could only survive at 10°C for more than 12 weeks in short days, whereas the Roscoff isolate could persist indefinitely in either long or short days. At 5°C, the difference was even more marked with the Curaçao strain not even tolerating 2 weeks, whereas in short days the Roscoff isolate could persist indefinitely. This means that the Roscoff isolate is capable of living under tropical conditions but that the tropical isolate could not extend to the temperate end of the geographical range.

*Cladophora laetevirens*

This species occurs on both sides of the Atlantic, in tropical and temperate zones (Fig. 17). *C. laetevirens* has been recorded from a variety of habitats, from the intertidal and brightly lit shallows where it tends to form compact cushions or a component of algal turfs, as an epiphyte on seagrasses in subtidal environments and even as deep as 65 m from coral reefs in Curaçao (van den Hoek, 1963, 1982b).

Northern boundary – Europe

Northernmost records in Europe are from southern Sweden on the Baltic coast and W. Scotland on the Atlantic coast. *C. laetevirens* also occurs in the North Sea (Fig. 17). Three isolates were tested for temperatures limiting survival (Fig. 14) and growth (Fig.

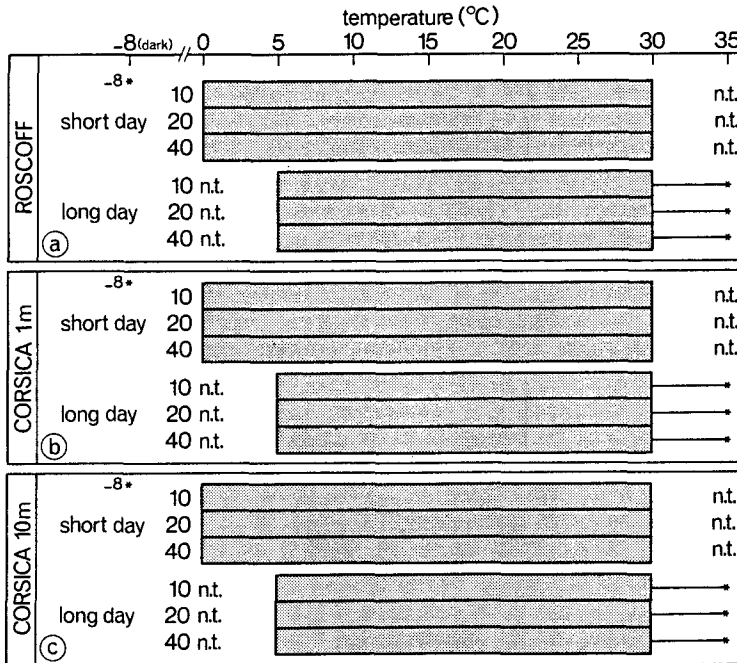


Fig. 14. Survival of *Cladophora laetevirens* isolates from Roscoff, Brittany (a) in temperate waters, and Calvi, Corsica in warm temperate waters at 1 m depth (b) and at 10 m depth (c). Survival intervals as defined in Figure 2

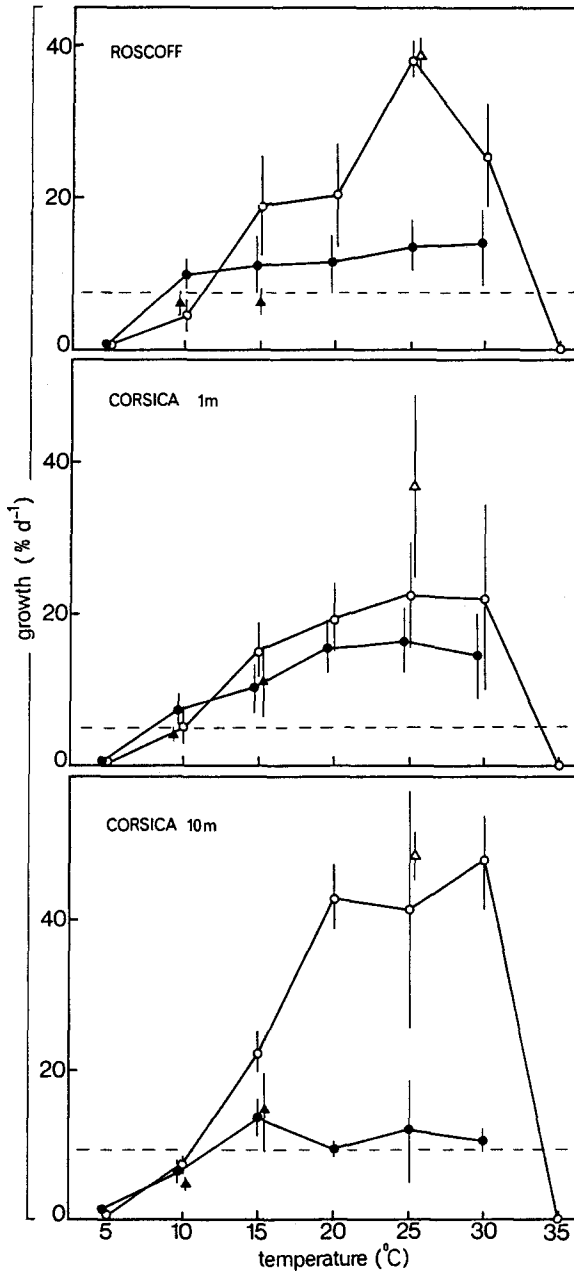


Fig. 15. Mean relative growth rates and standard deviations ( $n = 5$ ) of *Cladophora laetevirens* isolates from Roscoff, Brittany (a), and Calvi, Corsica at 1 m depth (b) and at 10 m depth (c). Growth conditions as described in Fig. 3

15), one from Roscoff, Brittany and two from Calvi, Corsica. The Corsican isolates were collected from nearby sites, one a shallow sunlit site at 1 m depth and the other a deeper shaded site at 10 m depth.

In short days, both the Roscoff and Corsican isolates could survive for more than 12 weeks at 0°C (shown in Fig. 14a, b, c) but not freezing to -8°C for 2 weeks.

In Figure 16, the lower lethal limit is shown in the interval -8 to 0°C. Comparison with the annual temperature regime from Helgoland on the North Sea coast inside the northern boundary, and with W. Norway beyond the boundary, shows that minimum winter temperatures recorded at Helgoland can fall below 0°C during cold winters and so are in fact lower than those off the Norwegian west coast much further north (compare Fig. 1). In Helgoland, temperatures below 0°C in cold winters may approach the lower lethal limit, but survival at 0°C was more than 3 months and plants were not even damaged by this length of exposure to cold. During average winters at Helgoland and further north, mean winter temperatures of about 3°C could easily be survived.

Growth rates (Fig. 15) for all isolates were highest at 25–30°C, and dropped below 20% of the maximum between 10 and 15°C for all three isolates. Sporulation occurred at

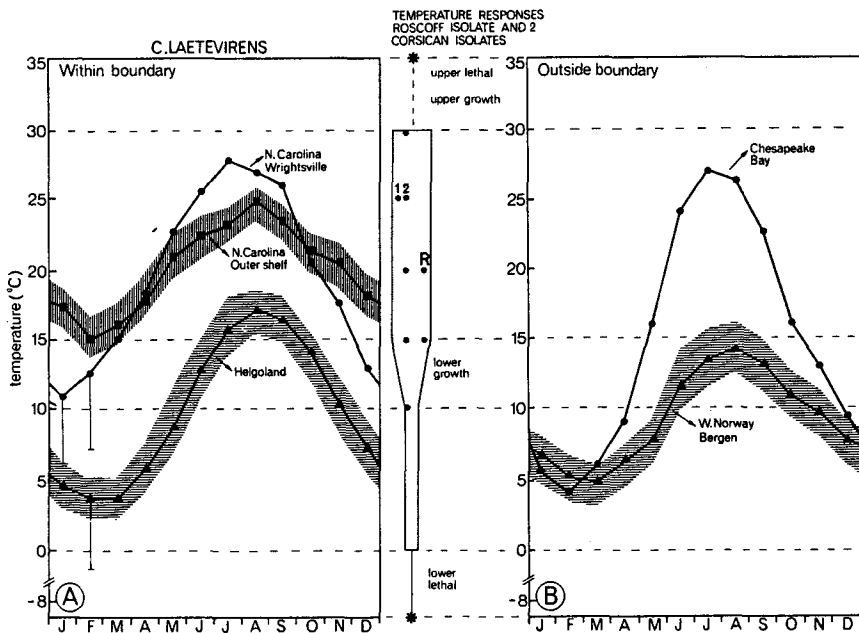


Fig. 16. *Cladophora laetevirens*. Annual temperature regimes as monthly means and ranges (shaded) at sites within and outside the northern boundaries compared to experimentally determined temperature tolerances. (A) Within boundaries, ▲—▲ Helgoland (see Figs 8 and 12); ●—● N. Carolina inshore, Wrightsville Beach and ■—■ offshore (see Fig. 8). (B) Outside boundaries, ▲—▲ W. Norway, offshore Bergen, means after Gorshkov (1978), ranges based on U. S. Navy Marine climatic atlas (1974); ●—● Chesapeake Bay inshore, Gloucester Pt, Virginia (see Fig. 8). Bar diagram shows experimentally determined upper and lower lethal limits and growth limiting temperatures (details as in Fig. 4) for one isolate from Roscoff, Brittany, and two isolates from Corsica (10 m and 1 m deep), from Figs 14 and 15. ●R = sporulation in Roscoff isolate; ●1, ●2 = sporulation in isolates 1 (10 m) and 2 (1 m) from Corsica

15 and 20 °C for the Roscoff isolate, at 10–30 °C for the shallow water Corsican isolate, and only at 25 °C for the deep water Corsican isolate (Fig. 16). Summer temperatures for Helgoland (Fig. 16) are above 10–15 °C, the interval defined as the lower growth limit, and so are not expected to limit growth in summer. Similarly, in the entrance of the Baltic near Copenhagen, summer temperatures near 18 °C from July to September (Kristiansen, 1972, 1981) would not limit growth. Beyond the northern boundary off the W. Norway coast, offshore summer temperatures approach the lower growth limit during cool years (14 °C mean for August) (Fig. 16). Sporulation occurred between 15–30 °C for the Roscoff isolate and so summer temperatures below 15 °C may also pose a reproductive limit. The nature of the boundary appears to be a summer growth limit on open coasts.

The growth rates of the deep and shallow water Corsican isolates were very different (Fig. 15) and this is attributed to the abundant sporulation of the shallow water isolate, where zoids rather than new cells were produced. The sporulation of the deep water isolate at 25 °C only (Fig. 16) would restrict reproduction to mid summer.

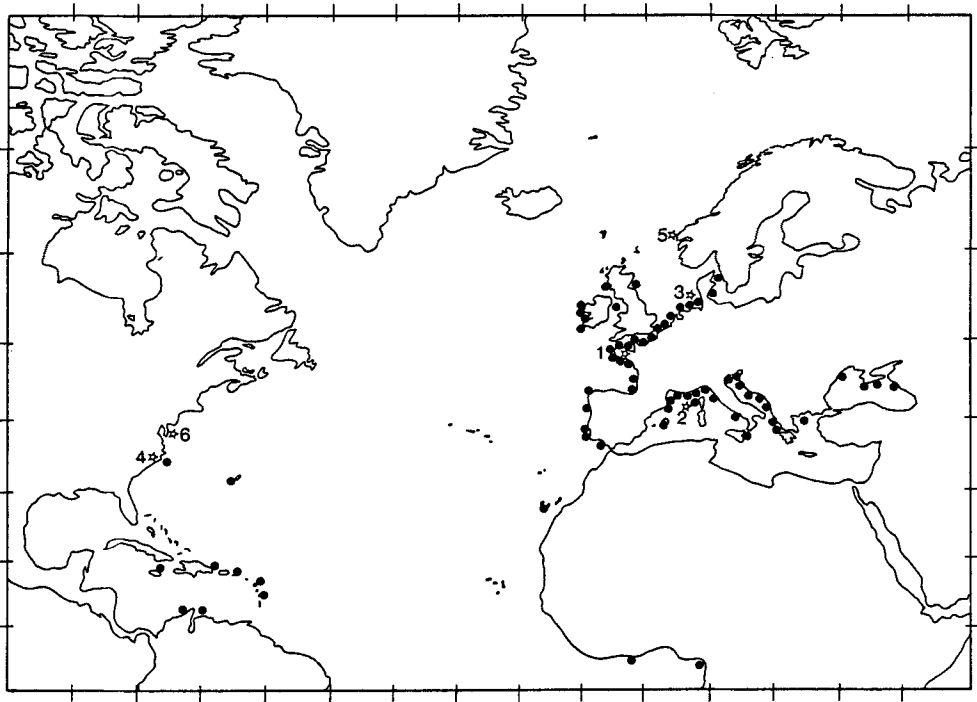


Fig. 17. Distribution of *Cladophora laetevirens* in the North Atlantic (from van den Hoek, 1963, 1982b). Additional records: tropical W. Africa (Lawson & John, 1982); Elie, Scotland (Wilkinson & Tittley, 1979); N. Carolina Outer Shelf reefs (Searles, pers. comm.). Sampling sites of cultured isolates (\* 1 Roscoff, \* 2 Corsica) and stations for which temperature regimes are shown in Fig. 16 indicated (within boundaries: \* 3 Helgoland, \* 4 N. Carolina; outside boundaries: \* 5 Bergen, \* 6 Chesapeake Bay)

*Northern boundary – America*

No isolate from the American side of the Atlantic was tested and so only tentative suggestions are given as to the nature of the boundary on the American coast. The northernmost and only record of *C. laetevirens* from the American mainland is from the N. Carolina reefs on the Outer Shelf (specimen collected by Searles in 1986, identified by van den Hoek). All previous records are from Bermuda and the islands in the Caribbean (van den Hoek, 1982b) (Fig. 17). In Figure 16, temperature curves are shown for inshore and offshore N. Carolina, and just beyond the boundary at Chesapeake Bay. They show that, on the basis of the temperature responses of the European isolates, *C. laetevirens* could be expected further north than its present boundary as well as at inshore sites in N. Carolina. Perhaps a warm water strain has developed similar to that for *C. coelothrix* from the Caribbean, and the low winter temperatures which occur in shallow nearshore areas exclude the species from the mainland coast.

## DISCUSSION AND CONCLUSION

The geographic distribution of *Cladophora submarina*, *C. prolifera*, *C. coelothrix* and *C. laetevirens* in the N. Atlantic can be understood, in most cases, on the basis of their temperature/light responses in culture. They all occur in the tropics, *C. submarina* being restricted to the Caribbean tropics. *C. prolifera*, *C. coelothrix* and *C. laetevirens* extend into the warm temperate zones on both sides of the N. Atlantic but their northern boundaries in Europe are 20–25° latitude further northward than those in America. In accordance with their occurrence in the tropics, temperatures up to 30°C were optimal for growth. However, the upper temperature limits for survival lay close to the optimum growth temperatures for all four species in the interval 30–35°C (Figs 2, 6, 10, 14). *C. submarina* and *C. coelothrix* tolerated these high temperatures for longer than *C. prolifera* and *C. laetevirens*, *C. laetevirens* being the most sensitive of the four.

The northern boundaries on the European coasts can be explained as a combination of summer growth limits on the open Atlantic coasts and winter lethals on the North Sea or Baltic coasts. On the European Atlantic coasts, *C. prolifera*, *C. coelothrix* and *C. laetevirens* have in this order, stepwise more northerly distributions and at first sight, this would appear to accord with their increasingly lower lethal limiting temperatures. However, winter temperatures at the respective boundaries are above the lower lethal limits and so are irrelevant in explaining distribution.

Closer examination of summer temperatures at and beyond the boundaries shows a link between the position of the northern boundary, the length of the growing season when temperatures are above 10°C (Fig. 18) and growth rates at the lower end of the temperature range.

For *C. prolifera*, growth (RGR) increased from 0 to 3 % d<sup>-1</sup> over the interval 10–15°C (Fig. 7). At Roscoff, Brittany, mean seawater temperatures rise above 10°C from about April to December (Figs 8, 18), so the growing season is estimated to be about 8 months long in an average year. In cool years the growing season would last from May to December, about 7 months. In addition, even in cool years midsummer temperatures rose 4°C above the lower limit of 10°C, so appreciable growth could be expected. Further north, in W. Ireland, where *C. prolifera* has been found only once, temperatures in warm

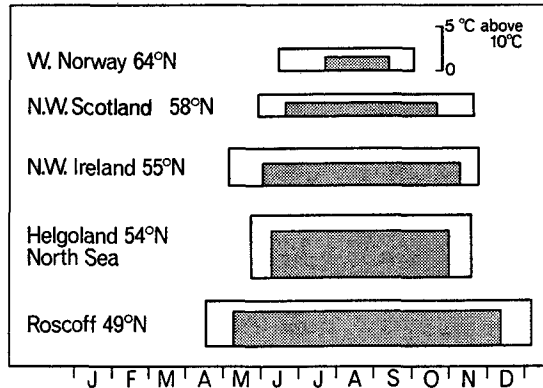


Fig. 18. Periods over which temperatures rise above 10°C as an indication of decreasing length of growing season in relation to progressively more northerly European boundaries. The periods above 10°C were estimated from means (blank bars) and minima (stippled bars). They are contrasted in order to indicate the difference in the length of the growing season in normal summers versus abnormally cool summers. Height of bars shows number of °C by which mid-summer temperatures exceed 10°C. Sources; N. W. Ireland, N. W. Scotland and W. Norway; means for open coasts from Gorshkov (1978); minima based on U. S. Navy Marine climatic atlas (1974); Roscoff, Brittany, and Helgoland from inshore monthly means and minima as in Fig. 8

or normal summers would be adequate for a growing season of 6–7 months but in cold summers, the growing season is only about 4–5 months (Fig. 18), and more importantly for a species with an inherently slow growth rate, mid summer temperatures are close to 10°C at which there was no measurable growth in culture. Thus *C. prolifera* is clearly excluded from the more northerly coasts of Scotland and Scandinavia even though the winters are mild enough.

For *C. coelothrix*, with the northern boundary on the Irish northwest coast, a growth rate of 3% at 10°C increasing to 10% at 15°C (Fig. 11) means that some growth can take place even with a cold summer. The growing season with temperatures above 10°C would be about 4–5 months long in a cold summer, contrasting to 3 months for the north of Scotland or 1 month on the west coast of Norway, respectively (Fig. 18). Thus, a higher growth rate at the lower growth temperatures, as well as a more rapid increase in growth rate over the critical 10–15°C interval enables *C. coelothrix* to extend further north than *C. prolifera*. *C. laetevirens* has an even greater increase in growth rate over the 10–15°C interval, from 3–20% d<sup>-1</sup> (Fig. 15), and extends furthest north up the coast of Scotland to its northern boundary in southern Scandinavia but is presumably excluded from the west coast of Norway by the brief period (3 months in normal summers, 1 month in cool summers) in which temperatures rise a few degrees above 10°C on open coasts (Fig. 18).

The northern boundaries of *C. submarina* and *C. coelothrix* on the American coasts can be explained as winter lethal boundaries and the slightly better cold tolerance of the Curaçao isolate of *C. coelothrix* at 10°C means that it can extend further north along the Florida mainland coast than *C. submarina*. The restriction of the tropical species *C. submarina* to the E. Atlantic Caribbean region cannot be explained by temperature responses in culture which would predict its occurrence in W. Africa and the E. Mediterranean. However, its temperature responses were similar to those reported for

three Caribbean *Gracilaria* species (*G. mammilaris*, *G. debilis* and *G. sp. indef.*), which also have lower lethal temperatures around 15 °C, upper lethals at 31–32 °C, and the lower growth limit between 15–20 °C (McLachlan & Bird, 1984). In these truly tropical species the upper lethal temperature was also less than 35 °C, a temperature often reached in inshore tropical waters. For species with such distribution patterns, van den Hoek (1982a, c) has hypothesized extinctions during the Pleistocene glaciations along the eastern side of the Atlantic, without subsequent dispersal back. However, Pleistocene glacial temperatures, which were about 3–5 °C lower than present temperatures (McIntyre & Kipp, 1976) were probably not as low as the lower lethal limit of, for example, the present day Caribbean *C. submarina* strain (< 15 °C). The tropical W. African seaweed flora is in any case impoverished, probably due to adverse present-day conditions in combination with extinctions associated with climatic changes and habitat reductions during the Neogene (Shackleton, 1984).

Whilst the minimum temperature allowing "sufficient growth" (defined as 20 % of the maximum growth rate) could be meaningfully related to all the northern boundaries in Europe, this was not the case for minimum temperature for sporulation. These sometimes coincided with minimum temperature for growth (*C. submarina*, Fig. 4 and the shallow water isolate of *C. laetevirens* from the Mediterranean, Fig. 16) and sometimes were higher (the Roscoff strain of *C. laetevirens*, Fig. 16 and *C. prolifera*, Fig. 8). For *C. coelothrix*, sporulation only occurred once in the Curaçao strain. The wide differences in sporulation between two Mediterranean isolates of *C. laetevirens* (Fig. 16), which were collected from nearby sites, suggest that this is a trait with possible local intraspecific variation.

The temperature responses of the four *Cladophora* species are based on experiments with one Caribbean strain of *C. submarina*, one Mediterranean strain of *C. prolifera*, one Caribbean and one W. European strain of *C. coelothrix*, and one W. European and two Mediterranean strains of *C. laetevirens*. In the case of *C. coelothrix*, the difference in the lower lethal temperatures of the Caribbean and W. European strains was relevant in explaining their distributions on opposite sides of the Atlantic. In Europe, *C. coelothrix* extended further north into regions with both lower summer and lower winter temperatures than at the N. boundary in America, and accordingly, the European isolate proved to be more cold tolerant. For *C. laetevirens*, the development of similar "transatlantic ecotypes" might also have occurred, as on the American coast the N. boundary stays further south than expected from the temperature tolerance of the tested European isolates. However, there was no such marked difference in the response of strains from the European side of the Atlantic in *C. laetevirens* (the Mediterranean, and Brittany) and each could explain the distribution on the whole of the European coast quite well.

When testing for lower lethal temperatures, both long and short day conditions should be included. Survival was enhanced for all species in short day conditions. Those species which have a northern boundary on the subtropical American coast will experience the irregular cold water periods in daylengths somewhat longer than the short day 8:16 h regime tested. Light damage at low temperatures is a well documented phenomenon in higher plants (e.g. see review in Larcher, 1981) and has also been documented for several green and red algae (Cambridge et al., 1984; Yarish et al., 1984, 1986). In these locations, lethal conditions may occur in early spring rather than in mid winter.

Several gaps in distribution appear rather consistently in the species' distributions.

Some of these areas have been so poorly surveyed that lack of species records is as likely to be due to the "biogeography of the collector" as any valid biological reason. The lack of records from the western Caribbean, the eastern American coast from Florida to the Carolinas, most of tropical West Africa excepting those areas visited by Lawson & John (1977, 1982) and the eastern Mediterranean fall into this category. Other gaps occur in areas more frequently visited by collectors but having rather extreme environments, in particular, the coasts of the Gulf of Mexico. Here, the lagoons and long sandy stretches incorporate two major difficulties for marine species: lack of firm substratum and increasingly violent fluctuations in temperature and salinity towards the west. *C. coelothrix* is the only species to penetrate the Gulf of Mexico and even this species, which favours muddy, mangrove environments, drops out from the western regions of the Gulf of Mexico. Another area of long sandy stretches and lagoons, the eastern coast of the American mainland from Florida and Georgia to the Carolinas is also patchily collected, in addition to the extremes of temperature (less than 5 °C to more than 32.5 °C), so that either reason might account, for example, for the long gap in *C. prolifera*'s distribution from the Caribbean to N. Carolina. This leaves several areas where paucity of collecting or extremes in environments do not provide an obvious reason for lack of records. *C. submarina* is not recorded from Jamaica or from the East Atlantic islands (Canaries). *C. prolifera* is not recorded from the central Caribbean. The absence of *C. prolifera* from the central islands in the Caribbean is hard to explain but it is a similar pattern to the tropical-temperate N. E. America red alga, *Grinellia americana* (Yarish et al., 1984). It is perhaps due to the high summer temperatures, as the 29 °C summer isotherms surround the islands and correspond to locally higher temperatures which would be lethal. This sensitivity to temperatures only slightly above normal optimal tropical temperatures has been observed in other tropical organisms; for example, Glynn (1985) reports widespread coral mortality on W. Panamanian reefs due to abnormally high water temperatures (mean values 30–31 °C, lasting 6 months) associated with an El Niño disturbance.

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