

## Search for possible latitudinal ecotypes in *Dumontia contorta* (Rhodophyta)\*

H. Rietema & C. van den Hoek

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

**ABSTRACT:** Effects of daylength and temperature on the formation of erect fronds (macrothalli) from crusts (microthalli) of *Dumontia contorta* (S.G. Gmel.) Rupr. from three localities in Nova Scotia and one locality in Southern Iceland were investigated and compared to such effects shown by strains from three different East Atlantic localities (Isle of Man; Zeeland, S.W. Netherlands; and Roscoff, Brittany, France). Although these strains showed small differences in their temperature-daylength responses, these could not be interpreted as latitudinal adaptations, and consequently no latitudinal ecotypes could be found for *Dumontia contorta* in the N. Atlantic Ocean. Upright fronds are formed at a broad temperature range of about 4°–18°C and at daylengths  $\leq$  13 h. Only in the southernmost part of its distribution area can high autumnal temperatures be expected to block the reappearance of upright fronds after passage of the critical daylength in September. In the larger part of the distribution area even summer temperatures are not high enough to block formation of uprights and here apparently only short daylengths initiate the reappearance of young upright fronds in autumn. The consequences of these aspects of the life history regulation for the geographic distribution are discussed.

### INTRODUCTION

The life history of *Dumontia contorta* comprises isomorphic gametophytic and sporophytic stages producing carpospores and tetraspores, respectively. Both spore types develop into discs (microthalli) from which later erect thalli (macrothalli) arise (for details of the formation of these uprights, see Rietema, 1984). Culture experiments with strains from three northeastern Atlantic localities (Roscoff in Brittany, France, 48°44' N  $\times$  4° W; Port Erin, the Isle of Man, 54°05' N  $\times$  4°45' W; and Zeeland, SW Netherlands, 51°45'  $\times$  4° E) indicated that the development of macrothalli from microthalli is initiated by short photoperiods and promoted by limited temperature ranges (Rietema, 1982; Rietema & Breeman, 1982). The strains from Roscoff and the Isle of Man have an optimum daylength for macrothallus formation of about 8 h. At daylengths between 10 and 12 h the numbers of macrothalli initiated decrease drastically to reach a value of zero at about 12 to 14 h light per day. The optimum temperature for macrothallus formation is about 12–16°C in the Roscoff strain and about 8–12°C in the Man strain. At temperatures above 16°C and 12°C, respectively, the numbers of macrothalli formed

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decrease drastically to reach values of zero at about 20°C in the Roscoff strain and at about 16°C in the Man strain. The above small differences in the temperature-daylength responses of the Roscoff and Man strains suggested the possible existence of ecotypes, the Man strain showing an adaptation to the somewhat lower temperatures at the Isle of Man than at Roscoff. However, in the strain from Zeeland (situated at a latitude intermediate to those of the Roscoff and the Isle of Man locations) the number of uprights initiated decreases drastically to almost zero at about 14 h light per day and at a temperature of about 24°C. This different temperature-daylength response of the Zeeland strain cannot be explained as an adaptation to its latitude (Rietema & Breeman, 1982). Evidence for the existence of latitudinal ecotypes with different temperature-photoperiod responses has been brought forward by Lüning (1980) for *Scytosiphon lomentaria* (Phaeophyceae) and West (1972) for *Rhodochorton purpureum* (Rhodophyceae). The present study intends to investigate whether or not comparable latitudinal temperature-photoperiod ecotypes can be distinguished in *Dumontia contorta*. For this purpose the temperature-photoperiod responses during the formation of uprights was investigated for strains from the North Atlantic West shore and from the coast of Iceland.

#### MATERIAL AND METHODS

The following four strains of *Dumontia contorta* were used: (1) a strain from Halls Harbour, Bay of Fundy, Nova Scotia, 45°10' N × 64°36' W (July 15, 1982; high littoral rockpools); (2) a strain from Ketch Harbour, Nova Scotia, 44°29' N × 63°31' W (July 27, 1982, low littoral rockpools); (3) a strain from Halifax Harbour, Nova Scotia, 44°36' N × 63°29' W (July 29, 1982, on low littoral rocks; (4) a strain from the coast near Stokkseyri, Southern Iceland, 63°50' N × 21°W (August 17, 1983, on rocks, low littoral zone).

Unialgal cultures were established and experiments conducted as described previously (Rietema & Klein, 1981; Rietema, 1982). Spores were precultured for 5 weeks at 12°C, long-day (16:8) conditions, 2,000 lux (ca 40  $\mu\text{Em}^{-2} \text{s}^{-1}$ ).

#### RESULTS

##### Effects of photoperiod and temperature on the sporophytic microthalli from Nova Scotia (Eastern Canada)

Results of experiments with sporophytic microthalli (Bay of Fundy material) precultured for 5 weeks at 12°C, long-day (16:8) conditions and kept thereafter at 7 different photoperiods and at a constant temperature of 12°C, are given in Figure 1a. Numerous macrothalli developed under the following conditions: 4:20, 8:16, 10:14 and only small numbers at a daylength of 13:11. No macrothallus development occurred at all at a daylength 14:10 or longer.

The results of experiments with sporophytic microthalli (Bay of Fundy material) kept at 7 different temperatures and on short-day regime (8:16) are given in Figure 1b. Macrothallus development mainly occurred at 8 and 12°C and in small numbers after a relatively long incubation period (59 days) also at 16, 18 and 20°C. No macrothallus development occurred at all at 24°C. At 24°C the margins of microthalli curled upward and at 26°C the microthalli died gradually within 5 weeks. Macrothalli obtained under

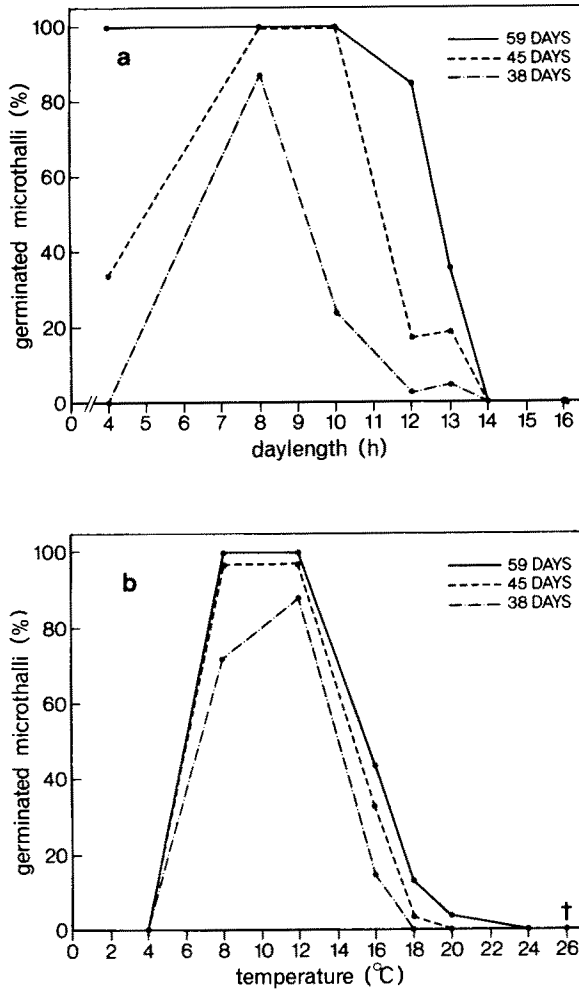


Fig. 1. Development of 5-week old discoid sporophytic microthalli of *Dumontia contorta* (Bay of Fundy material, Nova Scotia) at different daylengths (2,000 lux and 12°C) (Fig. 1a) and at different temperatures (short-day and 2,000 lux) (Fig. 1b). Percentages microthalli (n > 100) with macrothalli 38, 45 and 59 days after the start of the experiment are given

12°C short-day conditions and exposed thereafter to 12 and 16°C long-day conditions produced carpospores after 4 and 6 months, respectively. Both microthalli and macrothalli survived 0°C very well. At this temperature, no macrothallus initiation occurred under short-day conditions within the 3.5 months of observation. The upper lethal temperature was 26°C.

Experiments with sporophytic microthalli from the two other east Canadian localities (Ketch Harbour and Halifax Harbour) which were also precultured for 5 weeks at 12°C long-day (16:8) produced results similar to those obtained with the Bay of Fundy strain. These results are presented in Figure 2 (a and b). The upper lethal temperature was 26°C.

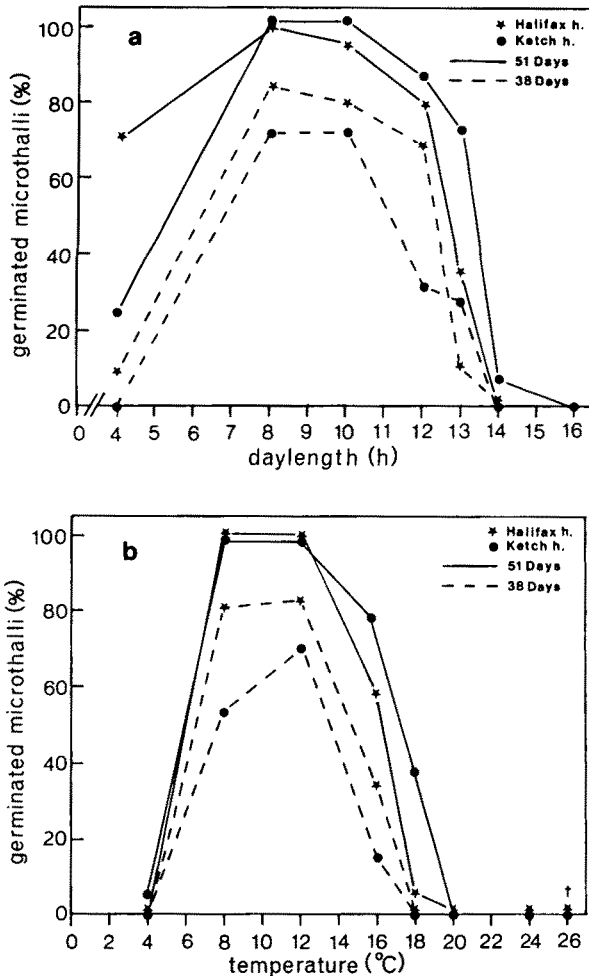


Fig. 2. Development of 5-week old discoid sporophytic microthalli of *Dumontia contorta* (Halifax harbour and Ketch harbour material, Nova Scotia) at different daylengths (2,000 lux and 12°C) (Fig. 2a) and at different temperatures (short-day and 2,000 lux) (Fig. 2b). Percentages of microthalli ( $n > 100$ ) with macrothalli 38 and 51 days after the start of the experiment are given

### Effect of photoperiod and temperature on the gametophytic and sporophytic microthalli from Iceland

Results of experiments with sporophytic and gametophytic microthalli (S. Iceland strain) precultured for 5 weeks at 12°C, long-day (16:8) conditions and transferred thereafter to different regimes of daylength and temperature are presented in Figure 3 a and b. These results do not essentially differ from those obtained with the three strains from Nova Scotia. Both microthalli and macrothalli survived 0°C very well. At this temperature no macrothallus initiation occurred under short-day conditions within 3.5 months of observation. The lethal temperature was 26°C for both gametophytic and sporophytic microthalli.

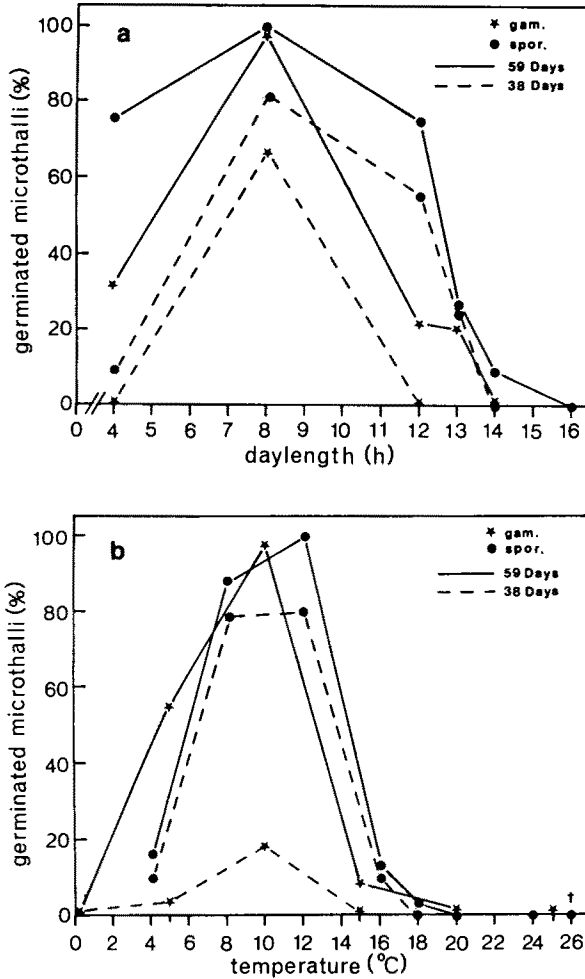


Fig. 3. Development of 5-week old gametophytic and sporophytic microthalli of *Dumontia contorta* (Icelandic material) at different daylengths (2,000 lux and 12°C) (Fig. 3a) and at different temperatures (short-day and 2,000 lux) (Fig. 3b). Percentages microthalli (n > 100) with macrothalli 38 and 51 days after the start of the experiment are given

DISCUSSION

There are no distinct differences in the daylength responses between the strains from S. Iceland (~ 64°N latitude) and those from Nova Scotia (~ 44–45°N latitude) (compare Figure 3a with Figures 1a and 2a). In all cases the daylength at which no (or only very few) uprights were formed after about 7–8 weeks was 14 h (or more). Figures 1a, 2a and 3a, however, show that the duration of the experiments influenced the results obtained especially at suboptimal daylengths. For instance, after 38 days at 12:12 (L:D), the Bay of Fundy strain (Figure 1a) and the Iceland gametophytic strain (Figure 3a) had not yet, or had hardly, formed uprights, whereas the Halifax and Ketch Harbour strains

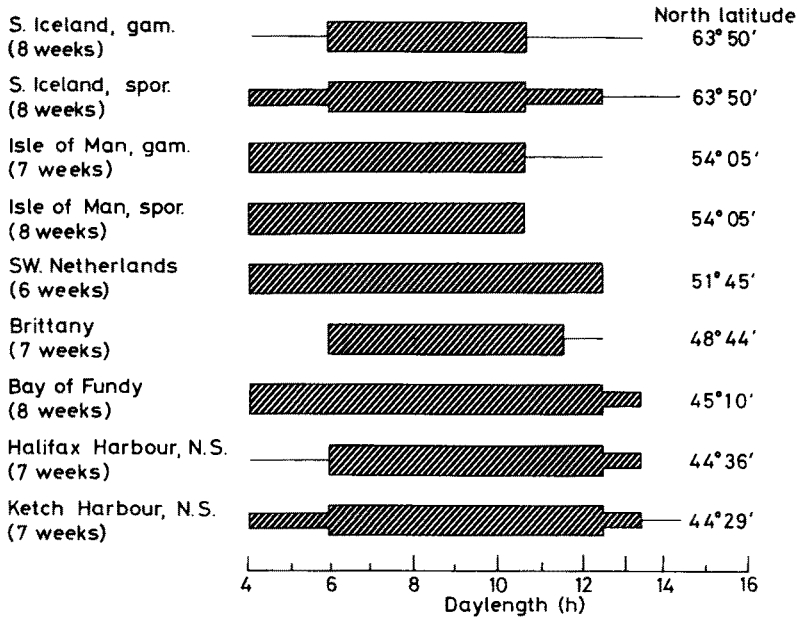


Fig. 4. Daylength ranges permitting development of upright fronds from crusts in 9 strains of *Dumontia contorta*. The strains are arranged according to the latitudes of their original localities. The broad bar indicates 80–100 % germination of crusts (microthalli); the narrow bar 40–80 % germination of microthalli; the single line 5–40 % germination of microthalli. The experimental points are indicated on the daylength scale

(Figure 2a) as well as the Iceland sporophyte strain (Figure 3a) had formed considerable numbers of upright fronds. In general, prolongation of the experiments tends to increase considerably the numbers of crusts bearing uprights at suboptimal daylengths (see also Rietema, 1982; and Rietema & Breeman, 1982). Figure 3a shows moreover, a considerable difference in the numbers of crusts bearing uprights between a sporophytic and a gametophytic strain from the same locality, and this again at a suboptimal daylength (12:12). Comparable differences at suboptimal daylengths have been found between sporophytic and gametophytic strains from the Isle of Man (Rietema, 1982). We think that these differences reflect rather the variance of the method (determining percentage germination of crusts) near the critical daylength, than real differences between sporophytes and gametophytes and, consequently, also between strains from different localities.

Figure 4 summarizes semidiagrammatically the daylength responses of 9 different strains based on experiments of 6–8 weeks duration. The strains are arranged according to the latitudes of their original localities, which vary from ca 64°N (S. Iceland) to ca 44°N (Ketch Harbour, N.S.). The northernmost and southernmost localities of *Dumontia contorta* are situated at 71°N (N. Norway) and 40°N (Long Island Sound and N. Portugal), respectively. Again, Figure 4 does not indicate the existence of daylength ecotypes in *Dumontia contorta*. If such ecotypes exist, one would expect the Iceland strain to have the highest critical daylength, and the three Nova Scotia strains to have the lowest critical daylengths, which is apparently not the case. For *Scytosiphon*

*lomentaria* (Phaeophyceae) the existence of such daylength-ecotypes has been demonstrated by Lüning (1980). A strain from Iceland (66°N) had a critical daylength of 17 h, one from Helgoland (54°N) of 13 h, and one from the Adriatic Sea (45°N) of 12 h.

With regard to the temperature responses, there are also no clear cut differences between the strains from S. Iceland and those from Nova Scotia (compare Figure 3b with Figures 1b and 2b). In all strains the temperature at which no (or only very few) uprights were formed after about 7–8 weeks was 20°C or more. At 4°C no, or very few uprights were formed. 26°C was lethal to all strains. However, if we compare the responses at suboptimal temperatures (e.g. 16°C), then the responses of the two Icelandic strains seem to be distinctly smaller (~ 10 % germination after 51 or 59 days) than those of the three Nova Scotian strains (~ 60–80 % germination after 51 or 59 days) and this might indicate a disposition for somewhat higher temperatures in the Nova Scotian strains (compare Figure 3b with Figures 1b and 2b). However, as in the daylength responses, a longer duration of the experiments tends to increase the numbers of crusts with uprights, and there may be considerable differences between the responses of sporophytic and gametophytic crusts, especially at suboptimal temperatures (cf. Figure 3b and Rietema, 1982). Here, again, we think that the variance of the response at suboptimal temperatures is rather due to the method than to real differences in temperature response. This interpretation is largely supported by Figure 5, which summarizes the temperature

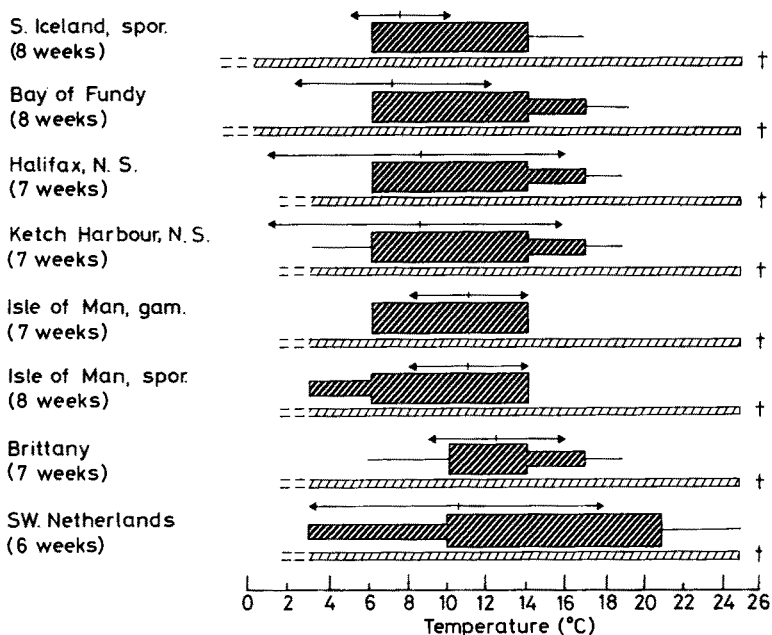


Fig. 5. Thermal ranges of tolerance (lightly shaded bars) and development of uprights from crusts (heavily shaded bars) in 8 strains of *Dumontia contorta*. The strains are arranged according to the mean annual sea surface temperatures of their original localities (indicated in the middle of the seasonal temperature ranges:  $\leftrightarrow$ ). † = lethal temperature. The broad bar indicates 80–100 % germination of microthalli (crusts); the narrow bar 40–80 % germination of microthalli; the single line 5–40 % germination of microthalli. The experimental points are indicated on the temperature scale

responses of 8 strains based on experiments of 6–8 weeks. The strains are arranged here according to the average temperatures of the sea surface at their original localities (except for the lowermost strain with its aberrant response). The temperature responses of the uppermost seven strains are quite similar, and the small differences cannot be related to the differences in the sea surface temperatures at their original localities. Only the lowermost strain, from SW. Netherlands, has a much broader temperature range permitting initiation of uprights from crusts than any other strain (Rietema & Breeman, 1982). This could perhaps be interpreted as an adaptation to the much greater seasonal temperature range at its original locality. However, one wonders why then comparably broad thermal ranges did not develop in the strains from Halifax and Ketch Harbour, with comparably wide seasonal ranges of sea surface temperatures (Figure 5). The similarity of the temperature responses of the seven uppermost strains in Figure 5 can be appreciated by comparing this figure with Figure 1 in McLachlan & Bird (1984) and Figure 1 in Cambridge et al. (1984) showing the distinctly different thermal ranges of tolerance and growth for different species of one genus (*Gracilaria* and *Cladophora*, respectively).

In conclusion, Figure 5 shows that eight strains of *Dumontia contorta* from differing points along the N. Atlantic coasts have identical ranges of thermal tolerance; of these, seven also have quite similar thermal ranges for the development of uprights from crusts. Apparently, the present study does not present evidence for the existence of latitudinal temperature-daylength ecotypes in *Dumontia contorta*, although it does not exclude the possibility of subtle differences between local populations. Such ecotypes could be distinguished in *Scytosiphon lomentaria* (Lüning, 1980) and *Rhodochorton purpureum* (West, 1972). Temperature ecotypes were demonstrated also for the widely occurring (arctic to tropical) phaeophyte *Ectocarpus siliculosus* (Bolton, 1983), but not in the *Laminaria* species (Bolton & Lüning, 1982) and in the *Gracilaria* species (McLachlan & Bird, 1984).

The lowest temperature so far investigated is 0 °C (for the strain from Iceland and one strain from Nova Scotia) and this inhibits initiation of macrothalli, whereas macrothalli are initiated at 4 °C, although with much retardation. The present observations on temperature responses in culture suggest that crusts are able to form upright fronds within a broad temperature range of 4–18 °C (16 °C in the Isle of Man strain). This temperature range surpasses the average seasonal temperature ranges of some sites (S. Iceland; Isle of Man; Roscoff, Brittany, cf. Figure 5) where investigated strains have been collected and here daylength is probably the main physical parameter involved in the regulation of the seasonal reappearance of *Dumontia* in nature (Figure 6). At the boundaries, however, the situation can be expected to be different. This is illustrated by Figure 6 which compares the temperature-daylength regulation of *Dumontia contorta*'s life history in the course of the year for three localities of investigated strains (Roscoff, Isle of Man, S. Iceland) with the presumptive temperature-daylength regulation of this species near its northern limits (N. Newfoundland, N. Iceland) and its southern limits (N. Portugal (Ardré, 1970) and Long Island Sound (Schneider et al., 1979)). The values given in Figure 6 are estimates based on the distribution of isotherms (cf. van den Hoek, 1982 pp. 86–88) and need verification by precise in situ studies. The maximum summer temperature (24 °C) on the coast of Long Island Sound is close to the lethal temperature of *Dumontia contorta* (26 °C) and therefore the southern limit in NE. America is likely to be



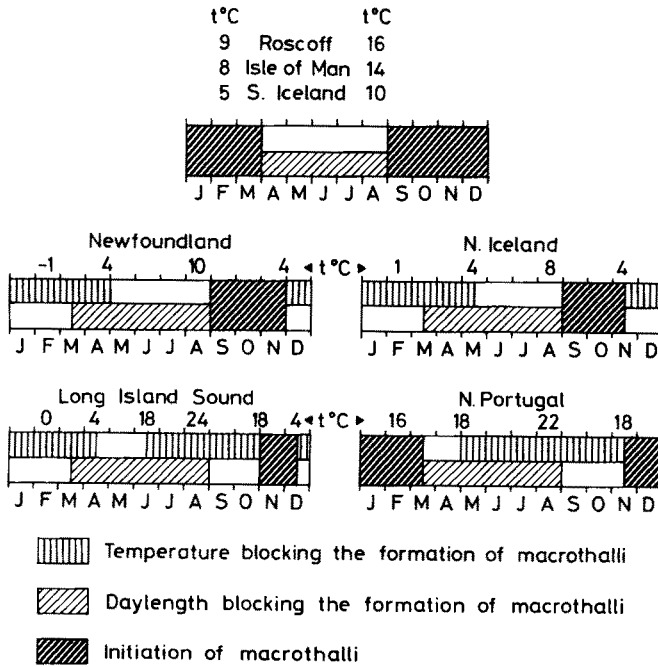


Fig. 6. Temperature-daylength conditions influencing the initiation of upright fronds of *Dumontia contorta* from crusts at seven points of its distribution area. The temperature ranges at Roscoff (Brittany, France), the Isle of Man and S. Iceland (top bar) are entirely within the temperature range (4–18°C) permitting initiation of uprights, and here only daylength regulates the reappearance of fronds in autumn. At the northern boundary, initiation of uprights is blocked by low winter temperatures ( $\leq 4^\circ\text{C}$ ) and is restricted to autumn; at the southeastern boundary (N. Portugal), the initiation is blocked by high autumnal temperatures and virtually restricted to winter; at the southwestern boundary (Long Island Sound), the initiation is blocked by both high autumnal ( $> 18^\circ\text{C}$ ) and low winter ( $\leq 4^\circ\text{C}$ ) temperatures and is hence restricted to a very short period in late autumn

a southern lethal boundary, and not a growth boundary. Temperatures allowing initiation and growth of uprights (4–18°C) occur in late autumn even far south of Long Island Sound. In winter, temperatures here are even too low to permit initiation of uprights. The high autumnal temperatures at Long Island Sound block formation of uprights far into autumn, and low winter temperatures ( $< 4^\circ\text{C}$ ) block formation during winter.

In N. Portugal high autumnal temperatures also block formation of uprights far into autumn; however, the highest temperature experienced in summer is several degrees C below the lethal temperature which can be expected intermittently further to the South, along the coast of Mauretania (at about the 22°C summer isotherm) (van den Hoek, 1982). The southern limit in Portugal can therefore be better explained as a southern growth limit where winter temperatures between 16 and 18°C just allow initiation and growth of uprights fronds throughout winter (cf. Figure 6). These winter temperatures between 16 and 18°C correspond with a southern boundary near the 14°C winter isotherm (rather than the 12°C winter isotherm as earlier suggested by van den Hoek, 1982). However, along the southernmost coasts of Portugal the predominantly sunny,

summer weather (Ardré, 1971) may warm up low littoral rockpools (where *Dumontia* usually abound) to temperatures higher than the lethal temperature. Only in situ studies can substantiate this suggestion.

Near its northern boundary (Newfoundland, Iceland, northern Norway) *Dumontia contorta* is exposed to summer temperatures between 8 and 10°C and winter temperatures between -1° and 1°C. Initiation of uprights is only possible in early autumn, and not in winter when temperatures are too low (< 4°C). A summer temperature of somewhat > 4°C is just high enough for a minimal initiation of macrothalli and this would be in accord with *Dumontia contorta*'s northernmost boundary just south of the 5°C August isotherm as suggested by van den Hoek (1982). *Dumontia contorta*'s northern boundary can therefore be conceived as a northern growth and reproduction boundary. This species is apparently capable of surviving winter temperatures as low as 0 to -2°C, probably even lower. In August 1983, mainly sterile *Dumontia* fronds could be found along the south coast of Iceland and this suggests that the populations there could hardly reach maturity, and perhaps need more than one season to reach fertility.

The absence of distinct latitudinal ecotypes in *Dumontia contorta* permits one practical conclusion: it is possible to use the temperature daylength responses of one strain to infer the approximate geographic boundaries for this species.

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