

A field study on the growth and development of *Dumontia contorta**

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ABSTRACT: Young, crustose plants of *Dumontia contorta* grown in the laboratory from carpospores were transferred in September 1983 to their natural habitat in Lake Grevelingen (SW Netherlands). The number of upright fronds per crust, length of upright fronds, and diameter of crusts were determined monthly until October 1984 and the presence of tetrasporangia was noted. Although fronds were initiated from crusts throughout the period of short daylengths (< 13 h light per day, i.e. from September to March), the majority of the fronds was initiated in October and November when short daylengths coincided with optimum temperatures for frond initiation (ca 10–20 °C). By April, i.e. within 5–6 months, these plants had reached maximum sizes and had become fertile; subsequently, the plants decayed. The successively smaller numbers of fronds that were formed in December and January also reached maximum sizes after ca 5–6 months, i.e. by May and June, but these fronds remained much smaller than the fronds initiated in October–November, possibly because of lower temperatures and light levels at the start of their growth. It is suggested that the fronds have a fixed maturation period (ca 5–6 months) irrespective of their size and the moment of their initiation. Crusts were shown to "oversummer" and to produce new fronds at the onset of short-day conditions in September 1984.

INTRODUCTION

Dumontia contorta (S. G. Gmelin) Ruprecht has a life history in which male and female gametophytes alternate with morphologically similar tetrasporophytes. Both the gametophytic and tetrasporophytic plants consist of small crustose holdfasts from which one or several upright fronds arise (Rietema & Klein, 1981; Rietema, 1984; Wilce & Davis, 1984). The upright fronds form the reproductive structures. The formation of initials of the upright fronds from the crusts has been shown to be a short-day effect with a critical daylength of about 12–13 h and can take place in a broad temperature range of about 4–18 °C. Eight strains from various localities around the N Atlantic Ocean exhibited only minor differences in their temperature-daylength responses and these could not be related to differences in latitude (Rietema & Klein, 1981; Rietema, 1982, Rietema & Breeman, 1982; Rietema & van den Hoek, 1984). The temperature range is also similar for all eight strains: the upper lethal temperature is about 25 °C and a temperature as low as 0 °C can be survived. These temperature responses can explain the geographic distribu-

* Dedicated to Dr. Dr. h. c. Peter Kornmann on the occasion of his eightieth birthday.

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tion of *D. contorta* along the temperate shores of the N Atlantic Ocean (van den Hoek, 1982; Rietema & van den Hoek, 1984).

Throughout its geographic range, *D. contorta* behaves as a winter-spring annual; upright fronds appear in autumn or winter, achieving maximum development during the winter-spring period. In spring or early summer *D. contorta* becomes fertile and disappears, or only residual populations remain (Rosenvinge, 1909; Dunn, 1917; den Hartog, 1959; Kilar & Mathieson, 1978; Irvine, 1983; Klein, 1987). Although this maximum development of upright plants agrees with the supposition that they are initiated during the period with short days (September to March), the precise course, and the causes of their growth and development into fertile plants in nature are not yet well known.

The present study intends to trace, as precisely as possible, the initiation, the growth and development of upright *D. contorta* tetrasporophytic fronds in a natural locality of this species, and to retrace the role of photoperiod, temperature and possible other factors in the regulation of these phenomena.

MATERIAL AND METHODS

Experiments were conducted in the saline Lake Grevelingen (SW Netherlands), in which tidal fluctuations of the water level are lacking (for further details about this lake see Bannink et al., 1984). At various sites along the shores of Lake Grevelingen, *Dumontia contorta* is common at depths of 0.5–1.5 m.

Fertile carposporophytic plants kept in unialgal cultures, derived from material originally growing in Lake Grevelingen, produced carpospores which were seeded on 25 × 25 mm glass squares. On these glass squares the spores developed further into crusts. Culture methods are described in detail by Rietema & Klein (1981) and Rietema (1982). The glass squares with growing spores were kept for the first 5 weeks at 12 °C and later at 5 °C, long-day conditions (16 h light, 8 h dark; light intensity: 40 $\mu\text{Em}^{-2}\text{s}^{-1}$) in petri dishes containing Provasoli's enriched seawater. Under these conditions no upright fronds are formed. Before the glass squares were transferred to the field, the number of crusts on each square was reduced to 6–10 so that the distances between the crusts (initially about 1.5 mm diameter) were large enough to allow growth in diameter. Three sets of eight glass squares were mounted in PVC holders which were bolted to paving tiles placed in Lake Grevelingen at depths of 0.5, 1.5, and 2.5 m. Natural populations of *D. contorta* are found in these depth zones, especially at 0.5 m. This method is a modification of the one used by Roeleveld et al. (1974) and Dion & Delépine (1983).

Once a month the crusts on the glass squares were examined under a binocular dissection microscope in order to determine the diameter of the crusts, the number of fronds on the crusts, the length of these fronds and their reproductive status. For this purpose the PVC holders with the glass squares were loosened from the tiles and transported under water at ambient temperatures to the nearby Delta Institute for Hydrobiological Research (DIHO) at Yerseke. After examination the plants were brought back to their field sites. This procedure never took more than 30 h. At the laboratory the algae were kept in an oysterpond. We tried to follow individual crusts and upright fronds. However, sometimes crusts and upright fronds disappeared. These were replaced by other crusts or uprights growing on the glass squares in order to maintain a reasonable number for statistics.

At the start of the experiments (12 September 1983) the three PVC-holders with glass squares bearing a total of 195 crusts were transferred to the different depths mentioned above. In addition, 12 glass squares with crusts were kept in stock in nutrient-poor cultures (5 °C, long-day conditions, 40 $\mu\text{Em}^{-2}\text{s}^{-1}$). Of these, three were transferred to the field at a depth of 0.5 m on 19 January 1984, three on 16 February 1984, and six on 12 April 1984 to a depth of 0.5 m. Three of the last six squares had been kept in culture under short-day conditions (8 h light, 16 h dark), 40 $\mu\text{Em}^{-2}\text{s}^{-1}$ and at 5 °C for 4 weeks (i.e. conditions initiating upright fronds). These 12 additional glass squares with crusts were mounted in a fourth PVC-holder.

RESULTS

Initiation of upright fronds from crusts

One month after the start of the experiment (i.e. October 1983) most crusts were bearing frond initials and even a few small uprights, the longest of which were 10 mm, 13 mm and 8 mm at depths of 0.5 m, 1.5 m, and 2.5 m, respectively. Although the majority of fronds were initiated in the first two months, new fronds continued to be initiated in the following months and the last ones appeared in March 1984. The number of fronds per crust increased rapidly from September to November reaching roughly a constant level of about 10 fronds per crust at 0.5 m, about 4 fronds per crust at 1.5 m, and 1.5 to 2 fronds per crust at 2.5 m (Fig. 1). After April there was a sharp decline in the number of fronds per crust and all traces (even basal remnants) of fronds had disappeared by August 1984. Only some crusts transferred to the field in September 1983 at 1.5 and 2.5 m "oversummered" and started to give off new fronds again in October 1984 (Fig. 1). The crusts at 0.5 m had disappeared in August.

Sets of crusts transferred to the field in January, February and April 1984 (at 0.5 m only) were much less successful than crusts deposited in September 1983 (Fig. 1). Many crusts died, especially the April deposits. Surviving crusts of the January set and the February set started to produce a few upright fronds after a delay of two months. Of the April set only the crusts precultured under short-day conditions formed a few fronds.

Growth of upright fronds

Length of the upright fronds increased considerably and growth was almost exponential in the period October 1983–March 1984. This is shown in Figure 2 which depicts the average frond lengths with time, and even more clearly in Figure 3 which illustrates separately the growth of fronds initiated in October (Fig. 3a), November (Fig. 3b) and the following months on crusts placed into the field in September 1983.

Fronds on crusts placed in the field in September 1983, generally reached their maximum lengths in April 1984 (Fig. 2) together with the formation of tetraspores and their subsequent basipetal decay. However, as shown in Figure 3 this picture is caused by the predominance of fronds that were initiated in October 1983, reached their maximum lengths in March/April after which they started to decay (Fig. 3a). Fronds initiated in November reached their maximum lengths by April/May (Fig. 3b); fronds initiated in December reached their maximum lengths by June. The few fronds initiated in February and March, at 1.5 m depth, continued to grow until June after which they disappeared.

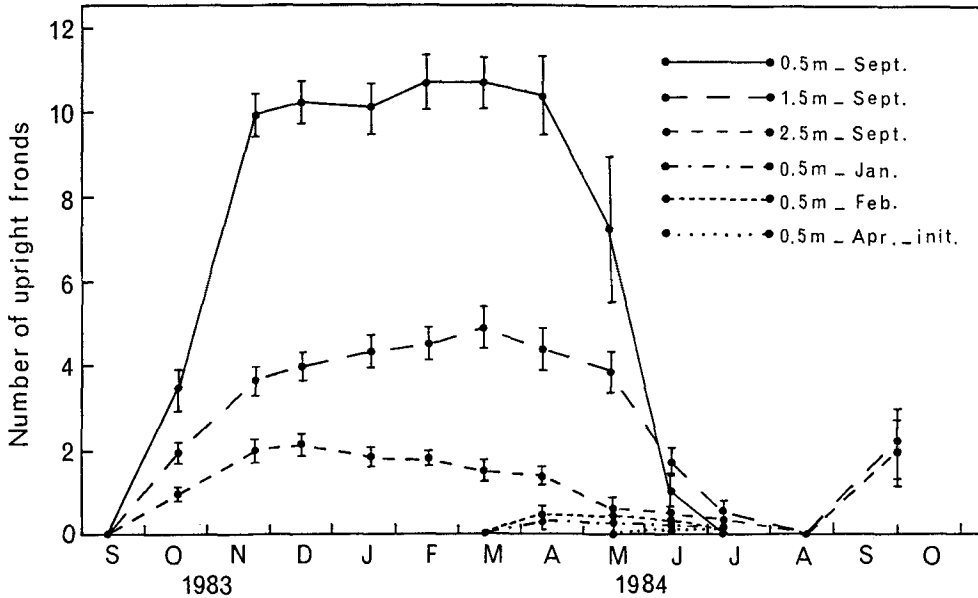


Fig. 1. *Dumontia contorta*. Mean number of upright fronds per crust in the course of the experiments. In September 1983 the crusts were transferred to three different depths: 0.5 m (in September '83 $n = 65$, from October '83 to April '84: $23 < n < 29$, from May '84 to July '84: $6 < n < 14$), 1.5 m (in September '83 $n = 65$, from October '83 to September '84: $21 < n < 31$, in October '84 $n = 8$) and 2.5 m (in September '83 $n = 65$, from October '83 to April '84: $20 < n < 32$, from May '84 to October '84: $10 < n < 25$). In January ($8 < n < 43$), February ($12 < n < 43$), and April ($3 < n < 25$) the crusts were only transferred to 0.5 m depth. April-init.: crusts ($3 < n < 31$) precultured under short-day conditions. Bars indicate standard errors

These plants were never observed fertile. However, the absolute lengths of fronds initiated in the coldest months remained far below those initiated in warmer autumn-months.

The fronds initiated on the crusts, transferred to the field in January, February and April, showed a much reduced growth (Fig. 2).

Growth and fate of crusts

Crusts transferred to the field in September immediately started to grow in diameter. Crusts at shallow depths (0.5 m) showed the fastest growth rate, and the deepest crusts (2.5 m) grew slowest (Fig. 4). Diameter increase was fastest during the first month in the field and slowed down thereafter.

Crusts transferred to the field in January, February and April 1984 suffered severely and it took the surviving ones about two months before they resumed growth which was then rapid, having an exponential phase in the crusts transferred into the field in January and February.

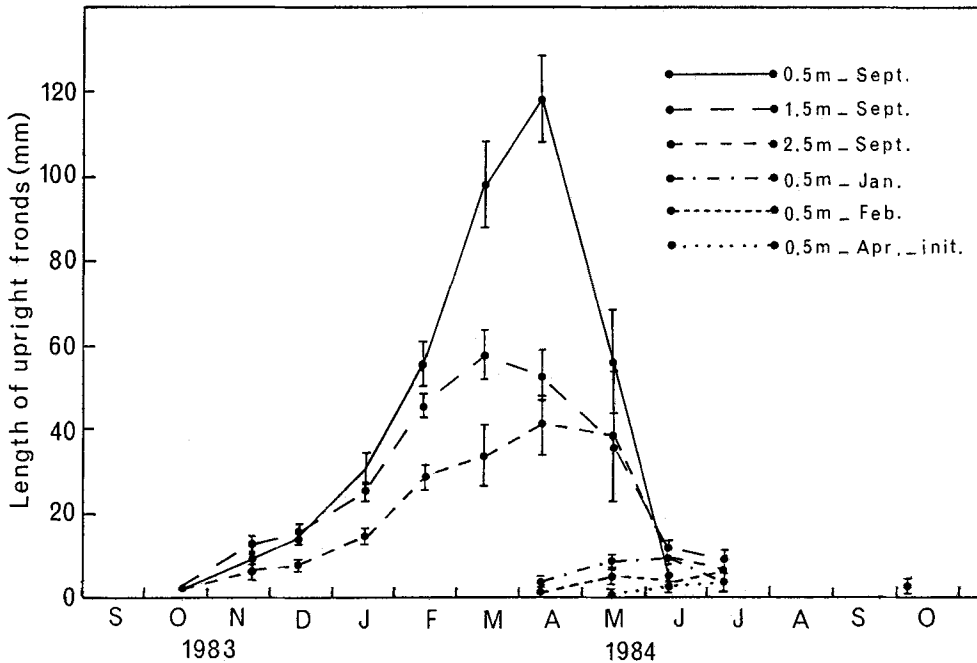


Fig. 2. *Dumontia contorta*. Mean length of upright fronds in the course of the experiments on crusts transferred in September to three different depths: 0.5 m ($11 < n < 83$), 1.5 m ($8 < n < 101$) and 2.5 m ($5 < n < 66$). In January ($2 < n < 6$), February ($3 < n < 15$) the crusts were only transferred to 0.5 m depth together with the crusts from April ($1 < n < 5$) which were precultured under short-day conditions. Bars indicate standard errors

Some observations on environmental stress and disturbance

In the course of the experiments, some crusts bearing uprights were lost from the glass squares. Nematodes were observed on and under every crust and these animals were possibly responsible for the loosening of the crusts. In addition, wave action may have caused loosening and/or removal of the crusts. This may also have resulted in the removal of fronds (with or without attached crusts) in winter and spring. Various invertebrates (e.g. *Microdeutopus gryllotalpa* A. Costa, *Corophium insidiosum* Crawford, *Platynereis dumerili* Audouin and Milne Edwards and *Harmothoe imbricata* L.) were observed to use the fronds as building material for their dwellings.

In the course of spring and in summer the recently introduced brown alga *Sargassum muticum* (Yendo) Fensholt developed dense stands along the shores of Lake Grevelingen. These stands had disappeared at the beginning of September 1984. Especially *Dumontia contorta* transplants at 0.5 m suffered from *Sargassum*, in consequence of a very low light penetration below the canopy. The almost complete disappearance of *D. contorta* crusts and fronds, during April-May at the 0.5 m site, was probably a result of the severe shading by *S. muticum*. At 1.5 and 2.5 m depth, where *Sargassum* was much more scattered, 8 and 11 (out of 65) crusts, respectively, survived the summer and were still present in October 1984 when they gave rise again to new upright fronds (Fig. 1).

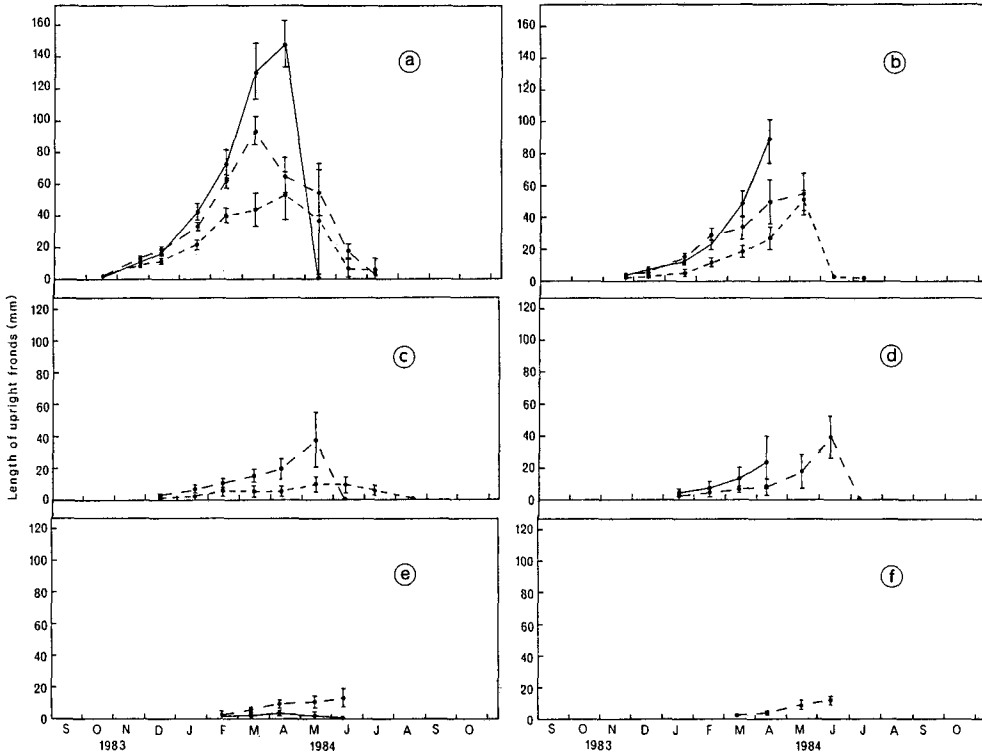


Fig. 3. *Dumontia contorta*. Mean lengths of fronds on crusts transferred to the field in September 1983 to a depth of 0.5 m (solid line), 1.5 m (long dashed line) and 2.5 m (short dashed line) initiated in consecutive months. Fig. 3a. Fronds initiated in October (from October '83 to April '84: $36 < n < 161$, from April '84 to May '84: $15 < n < 25$ and in July $n = 2$). Fig. 3b. Fronds initiated in November (from November '83 to April '84: $3 < n < 7$ and thereafter $1 < n < 5$). Fig. 3c. *Dumontia contorta*. Fronds initiated in December ($1 < n < 6$). Fig. 3d. Fronds initiated in January ($1 < n < 3$). Fig. 3e. Fronds initiated in February ($1 < n < 5$). Fig. 3f. Fronds initiated in March ($1 < n < 12$). Bars indicate standard errors

DISCUSSION

According to Rietema (1982), the formation in *Dumontia contorta* of upright fronds from crusts involves two separate steps: (1) formation of frond initials, (2) further development of these initials into young fronds. The first step is triggered by short photoperiods (< 13 h) alone, whilst the second step is brought about by short photoperiods in conjunction with a temperature below 20°C . In the present study, the initiation of fronds from crusts is reflected by the number of fronds per crust (Fig. 1) and this parameter can therefore be expected to reflect both the influence of photoperiod and temperature.

With regard to the influence of daylength, we expected initiation of fronds from crusts to take place between mid-September and mid-March when daylength (between sunrise and sunset plus civil twilight) is less than 13 h, the critical daylength (see however

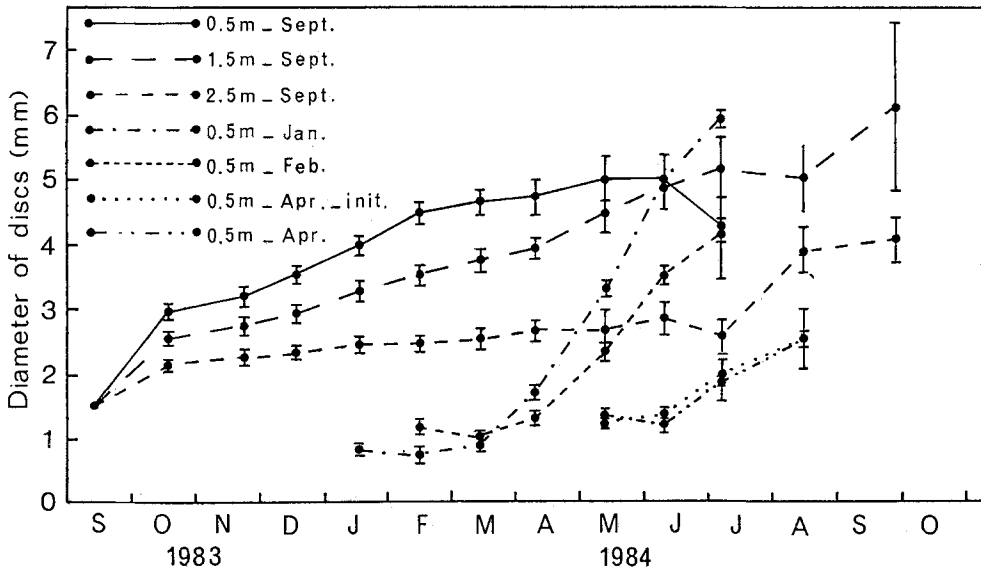


Fig. 4. *Dumontia contorta*. Mean diameter of crusts transferred to different depths and on different dates as mentioned in the legend of Fig. 1 (for n see legend of Fig. 1).

the discussion in Breeman et al. [1984] on "effective daylength"). This expectation is clearly supported by the results of the present field study. Fronds are initiated on crusts transferred to the field in September, January, February and on pretreated crusts transferred to the field in April (Fig. 1) but not on non-pretreated crusts transferred to the field in April. Also crusts transferred to the field in September continue to give off new fronds until March (Fig. 3f) but not in April. High temperature could not be expected in the period of investigation to block initiation of uprights completely, as it was always lower than 20 °C in the period September-March (Fig. 5). However, the period of optimum temperatures for upright thallus formation (i.e. 10–20 °C; Rietema & Breeman, 1982), coinciding with short days, is limited to autumn (September to early November). Consequently, maximum initiation of fronds from crusts would be expected in early autumn; this was actually the case (Fig. 1). After November, the number of fronds per crust hardly increased. New fronds were still being formed, but they replaced fronds which had disappeared. This is in contrast with observations in Brittany. Here the total number of uprights per crust increased up to February (Klein, 1987).

The bulk of the fronds which constitute the spring flush of *D. contorta* is apparently initiated in the preceding early autumn (October). In autumn, the fronds are still tiny (only a few mm high) but their exponential growth (approximately one doubling/month; see Fig. 3a) ensures that they reach their adult length (up to 34.5 cm) in early spring (April) within a period of about 5–6 months. These large, adult plants usually become fertile (they form tetraspores) and decay after shedding of the spores from their tips downwards until the last basal stumps disappear in summer.

Interestingly, the progressively smaller number of fronds initiated in later months (November, December, January; Figs 3b–d) also need a period of about 5–6 months to

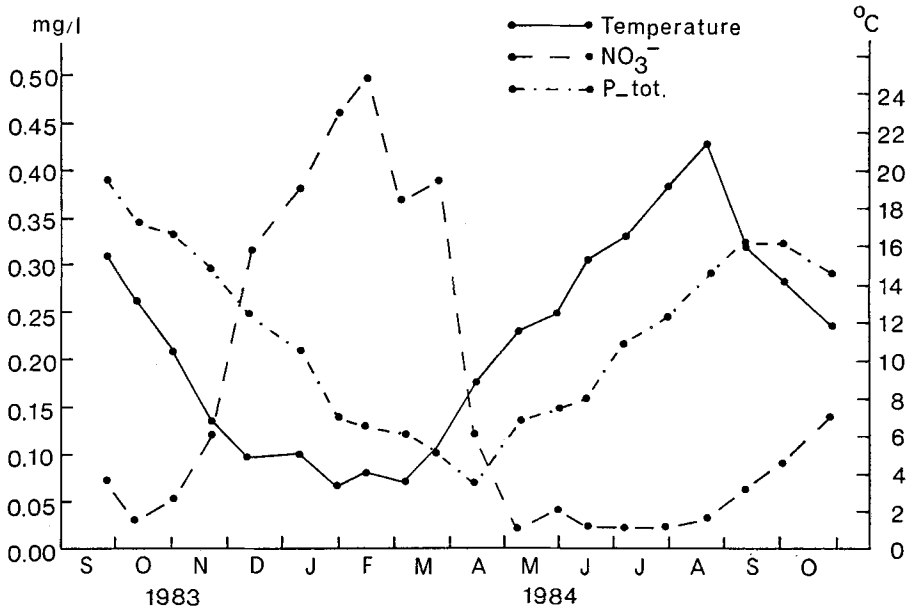


Fig. 5. Water temperature, total phosphorus and nitrate concentrations in Lake Grevelingen in the experimental period (data from DIHO)

reach their maximum length. These are, however, progressively shorter at reproductive maturity than the fronds initiated earlier. Similarly, the lengths of the fronds initiated in February and March (Figs 3e, f) are extremely small before senescence. The cause of this difference might be the higher growth rate of the young fronds in early autumn, possibly by a combination of higher temperatures and light levels. This is confirmed by the fact that the growth rate of the fronds at 0.5 m is higher than that of the fronds at 1.5 and 2.5 m, which indicates that their growth is light limited. The optimum temperature for growth of macrothalli is ca 16 °C (Fortes & Lüning, 1980; Rietema, 1982).

The overall phenology of *D. contorta* fronds (cf. Fig. 2) suggests the existence of an external cause for the end of the *Dumontia* flush in April. The most likely cause would seem to be the almost complete depletion of nitrates and/or phosphates in April (Fig. 5). This nutrient depletion reflects the nutrient needs of the spring bloom of planktonic and benthic algae. According to this interpretation, nutrient depletion would be the cause of the cessation of growth of the *Dumontia* fronds, possibly also of their becoming reproductive and the reason for their subsequent decay. However, when considering the growth and development of the decreasing numbers of fronds which are initiated later on in autumn and winter, these have life spans of ca. 5–6 months which are similar to those of the earliest initiated fronds. They reach their maximum sizes as late as May or June (Figs 3c, 3d) when the ambient nutrient concentrations are at their lowest levels (Fig. 5). Possibly these low nutrient levels are responsible for the smaller maximum sizes of these fronds. It is, however, unlikely that the low nutrient levels are the direct cause of the reproduction and subsequent decay of the bulk of the *D. contorta* fronds in April. More probably, the massive induction of fronds from crusts in early autumn by a combination of

short days and high autumnal temperature ensures an almost precise timing, in April, of the maximum frond biomass and consequently of maximum reproduction. In this way, *D. contorta* profits by the high nutrient levels in early spring and does not have to compete with other benthic algae in Lake Grevelingen which display a maximum development later in the season. In this context it is interesting that the recently introduced *Sargassum muticum* seems to cause the complete disappearance of *D. contorta* including its crust from the 0.5 m sites. Here it reappears, however, in the period of absence of *Sargassum* (September–May).

Recently, the blooming of the *D. contorta* fronds in spring and its withdrawal into crusts in summer was interpreted as a strategy to avoid grazing by periwinkles (*Littorina litorea* L.) which are particularly active in summer (Lubchenco & Cubit, 1980). Crusts were thought to be resistant to grazing. However, the dense populations of *L. litorea* in Lake Grevelingen were not observed to graze on *Dumontia* fronds. Other invertebrates using the fronds for the construction of dwellings were much more destructive. Accordingly we think it quite unlikely that the occurrence of two heteromorphic life forms in both the gametophytic and sporophytic stages of *D. contorta* (uprights and crusts) is primarily an adaptation to avoid grazing pressure.

The fronds that are induced later in autumn (on crusts transferred into the field in September) and that reach their maximum sizes in May and June do decay subsequently, however, often without becoming reproductive. In studies on the phenology of natural *D. contorta* populations along the coasts of New Hampshire (Kilar & Mathieson, 1978) and Brittany (Klein, 1987) it was also found that maximum frond biomass was reached in April and declined afterwards through the decay of reproductive plants. A limited number of essentially smaller plants survived, however, until July and these were still reproductive. Only in August and September were upright fronds entirely lacking. These observations agree with the results of the present study apart from the summer fronds being reproductive.

At present, one can only hypothesize about the direct cause of the reproductive maturation of the upright fronds and their subsequent decay. It may be that an upright frond, once initiated, needs a more or less fixed period of time (5–6 months as suggested by the present field observations) to become reproductive, irrespective of its final size. Another possibility is that rising temperature, light level or daylength in spring might induce reproductive structures. However, if this were true then the critical levels of these parameters should be lower for the earlier induced fronds. So far, the causative factors for the induction of reproduction have not been investigated in laboratory.

There can be no doubt that *D. contorta* crusts transferred in September 1983 did "oversummer" in 1984 (Fig. 4), and started to form upright fronds again in October 1984 (Fig. 1). This is in accordance with observations on the "oversummering" function of the crusts, made already in 1889 by Reinke (in Brebner, 1895).

Acknowledgements. We would like to thank the director and staff of the Delta Institute for Hydrobiological Research (DIHO) at Yerseke for the use of the laboratory facilities and for providing us with data on temperature and nutrient load in Lake Grevelingen. R. P. and B. K. gratefully acknowledge the hospitality of Drs. A. W. Fortuin.

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