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Photoperiod and temperature as triggers in the seasonality of *Delesseria sanguinea*

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ABSTRACT: The red alga *Delesseria sanguinea* is strongly seasonal, producing gametangia in early tetrasporangia in mid- and new blades in late winter. A lamp was installed in the shallow subtidal off the Isle of Man, illuminating about 40 plants of *Delesseria* for one hour in the night or day. Single blades from separate plants were held in laboratory tanks at different temperatures and in short days, long days and with a night-break. In the sea, the night-break prevented fertility in tetrasporophytes but some gametophytes became fertile. New blades were stimulated, arising 6 weeks early. Their lengths indicated a saturation level of about 10 μmol m^{-2} s^{-1} for one hour in 24. Growth rate calculations suggested a delay in stimulation until the ambient sea temperature dropped to 13 °C. Tetrasporangia were formed after the night-break ceased in December but not January. In day-addition of light there was slight, if any, stimulation of blade production. In the laboratory, gametogenesis occurred readily in short days but not in long days or with a night-break. There was little or no effect of temperature between 8 and 14 °C. Tetraspores were rarely formed in the laboratory. The timing of gametogenesis suggested a critical daylength of about 14 h. New blades were clearly stimulated by lower temperatures in the laboratory, few forming at 14 °C and many at 7–10 °C. They appeared mainly in long days or with a night-break but formed in short days after gametangia production. It is concluded that both gamete and tetraspore production are under photoperiodic control but require different conditions, possibly gametogenesis needing fewer cycles. There is some evidence for antagonism between new blade and reproductive structure initiation. The critical daylength could involve a timing differential of a month over the species' geographical range. On the other hand it is suggested that its southern limit could be determined by the winter isotherm of 13 °C, warmer than which might not allow blade initiation.

INTRODUCTION

Delesseria sanguinea (Huds.) Lamour. is a strongly seasonal perennial subtidal red alga. New blades are apparent by February and grow to full size by July (Kain, 1984). Only the midribs of these blades usually survive into autumn and winter and these bear spermatangia from September to December and cystocarps and tetrasporangia from December to February or March (Kain, 1982). Clearly this pattern must be triggered by environmental factors and its precision suggested that daylength might be one of these.

In a review of photoperiodism in algae, Dring (1984) pointed out that no member of the Ceramiales had yet been shown to have a true photoperiodic response. As the Delesseriaceae is in this order, the results that follow should rectify this situation.

A justifiable criticism levelled at laboratory experiments aimed at answering ecological questions is that too many of the conditions are artificial and the response of an organism is partly conditioned by factors other than that under consideration. The only satisfactory solution to these problems is to carry out experiments in situ, altering only

one factor. Thence a decision was made to influence subtidal *Delesseria* plants by introducing a daylength (in the form of a night- or light-break) inappropriate to the season. This could be accomplished by installing a lamp in the sea. Unfortunately, tampering with the other important factor, temperature, in situ was clearly impracticable. Hence, laboratory experiments were made to supplement those in the field.

METHODS

A lamp was installed at 1.2 m below lowest astronomical tide (LAT) on a vertical concrete face of a block which was part of a ruined jetty (4°46.3W, 54°5.1N) inside the also ruined breakwater at the mouth of Port Erin Bay, Isle of Man. The lamp consisted of a 24-volt 72-watt tungsten halogen bulb (a heavy vehicle headlamp) with a parabolic reflector. It was housed in a waterproof 12 mm thick acrylic case. The transformer was also housed in the case which was supplied with mains voltage because it was found that the length of cable necessary caused an unacceptable power loss at the lower voltage. The supply cable of 90 m length was 1.5 mm^2 3-core, protected by being encased in heavy duty 2.5 cm diam PVC pipe. It passed through an 0-ring seal into the case. The live side was protected with an earth leakage circuit breaker. For most of the time, a small current passed through a 240 V 15 W bulb in series with the transformer. This was inadequate to operate the 100 W transformer but the small generation of heat protected the transformer against dampness. When the time switch was on, this bulb was shorted out and the transformer activated, supplying 24 V to the lamp. When this was on, current also passed through a 0.5 ohm resistor and to a light emitting diode at the source end of the cable which could only light when the underwater lamp was on: a useful check, particularly in rough weather. A full description of the system is available on request.

The light output of the underwater light was not measured in situ but at night in a seawater pond where an underwater quantum sensor was held at a series of distances from it. The photon flux densities were measured with a Crump Model 550 quantum meter and values corrected after calibration against a Li-Cor LI-1000 Datalogger.

On the (north-facing) vertical face below and around the lamp there were about 40 plants of *Delesseria* as well as occasional laminarian and smaller species. The positions of the plants were sketched and distance measurements made; most of them were recognisable on subsequent dives though there were losses and additions each year. The edges of the light beam were observed at night and markers fixed in the concrete. Plants on the east-facing side of the same block and on boulders close by at the same depth were observed as controls. For observations on fertility a short length of midrib was removed from each plant, placed in a numbered specimen tube, taken to the laboratory and examined under a dissecting microscope. Control plants were treated in the same way.

For laboratory experiments, plants were collected between June and September, when blades had reached almost their maximum size and before reproduction took place in the field. The sites of collection were on the open coast of the south end of the Isle of Man at 2–8 m below LAT. Single blades, usually the largest, were collected, each from a separate plant. The blades were held, four in each, in the clips-sets used for *Plocamium* (Kain, 1987). Up to 13 clip-sets were placed in 43 l of seawater in each tank (60 × 30 × 30 cm deep) of black polyethylene held in controlled temperature water baths in light-proof rooms. Seawater pumped daily into storage and header tanks was filtered

through polyester wool and allowed to equilibrate in a tank in the water bath at least overnight before receiving plants. It was changed weekly. Twice-weekly a nutrient addition of KNO_3 and $NaHPO_4$ was made, to give a concentration of 7 μmol dm^{-3} N and 0.7 μmol dm^{-3} P. There was continuous aeration through two stones in each tank. Irradiance was supplied by 4 or 8 7-W fluorescent lamps, 3 or 6 green and 1 or 2 white. These provided about 37 μmol m^{-2} s^{-1} in short days (8:$\overline{16}$) and 21 μmol m^{-2} s^{-1} in long days (16:$\overline{8}$). When conditions were changed, care was taken to transfer equal numbers of "plants" (blades of midribs) from each set of old conditions to each set of new conditions so that in any comparisons the plants' history was balanced.

Plants were examined by removing one clip-set at a time into a glass dish of seawater, swivelling the clips so that they lay almost in one plane and would therefore lie on their sides, and viewing the midribs under a stereo microscope using photo-optic light sources. Both sides of each midrib were completely scanned. As each clip-set was numbered and the clips were in order on the holder, each midrib was identifiable.

Unless otherwise stated, the significance of differences between percentages was tested using a 2 × 2 test of independence (G-statistic) (Sokal & Rohlf, 1981).

Estimates of daylength in the shallow subtidal region were obtained from chart recordings from photocells maintained at 3 m below LAT in Port Erin Bay in 1967–9 (Kain, 1971). The sensitivity of the system varied between 0.2 and 4 μmol m^{-2} s^{-1}.

RESULTS

Surface seawater temperatures for the sea near Port Erin (Slinn & Eastham, 1984) together with the daylength (sunrise to sunset) for 54°N are shown in Figure 1. Also

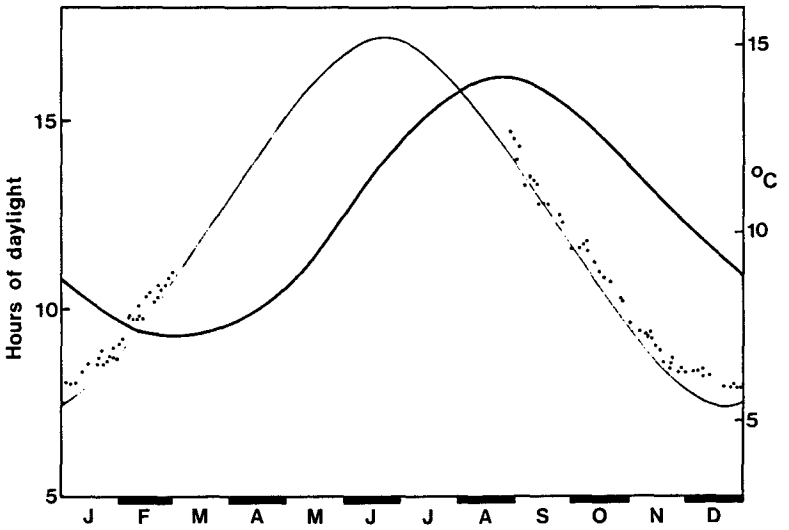

Fig. 1. Mean surface sea temperature off Port Erin, Isle of Man (Slinn & Eastham, 1984) (thick line) and daylength from sunrise to sunset (with upper rim of the sun apparently at the horizon) for 54 °N (Admiralty, 1955) (thin line). Also shown are daylengths recorded from an underwater cell at 3 m below LAT in Port Erin Bay in 1967–1969 (dots)

shown are hours per day at 3 m below LAT when irradiance was above about 1 μmol $m^{-2} s^{-1}$.

From 5 September 1983 to 4 January 1984, the underwater lamp was on for one hour in the middle of the night period. On 20 December, it was observed that most of the illuminated plants had produced new blades (Fig. 2), not normally visible in natural populations before February. In January, parts of the plants were sampled and examined for reproductive structures (Fig. 2). Of 17 plants within the beam and at less than 1 m from the lamp only one was fertile (cystocarpic). Of 46 control plants similarly observed 27 were tetrasporic and 3 cystocarpic, a highly significant ($P \leq 0.001$) difference. Male plants are not fertile in January (Kain, 1982). One month later another plant near the edge of the beam was found to be cystocarpic but no others became fertile that season although they were subjected to short days from mid-January until March.

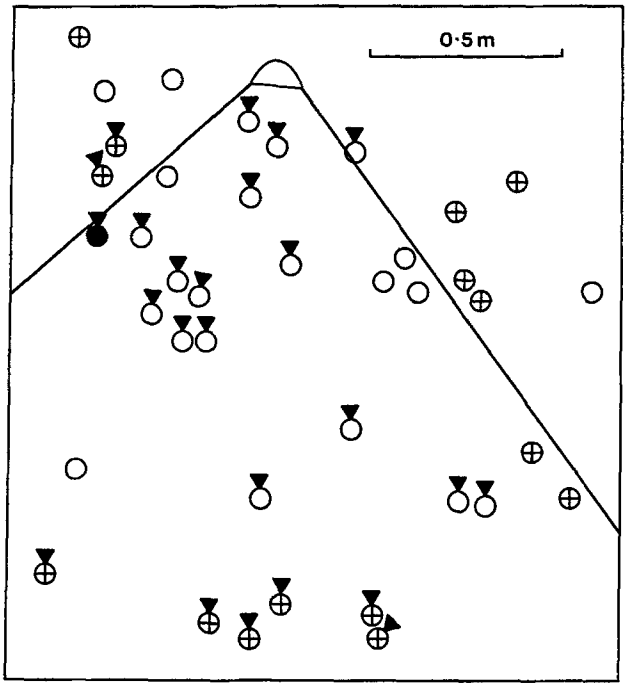

Fig. 2. Diagram of the vertical face with the underwater lamp (top) attached, showing the limits of the main light beam (lines). The lamp had caused a night-break from 5 Sept. 1983. Each circle represents an attached plant of *Delesseria*. ▼ = new blades by 20 Dec. 1983. Reproductive structures on 24 Jan. 1984: ○ = none; ● = cystocarps; crossed circles = tetraspores

During the following season the lamp was on somewhat intermittently, because of technical difficulties, but only late during the day or near dusk. In January, fertility was spread more or less evenly amongst the plants and clearly not influenced by the beam from the lamp (Fig. 3). The individual shown as cystocarpic in Figure 2 was now apparently tetrasporic. Close examination revealed a complex holdfast which could have

been formed by two plants. At this time there were new blades on many of the illuminated plants (Fig. 3).

In the 1985–6 season the lamp was on for one hour during daylight from 11 October to 29 January. Again most plants were fertile in January and about half bore new blades.

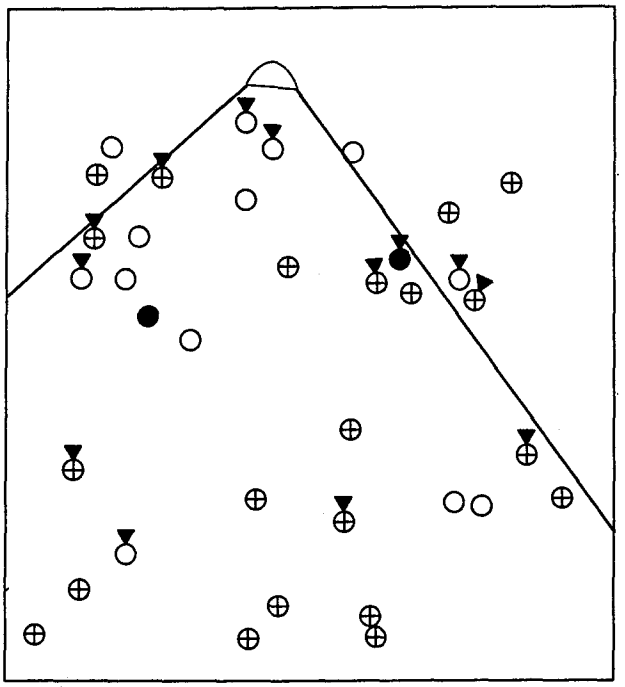

Fig. 3. As Figure 2, observed on 2 Jan. 1985, after the lamp had caused day-addition of light

During the final season, the night-break was re-introduced, the lamp being on from 20 August to 12 December 1986. In November, there were new blades on five plants close to the lamp (Fig. 4). In December, there were no fertile tetrasporophytes within the beam (Fig. 4), unlike control plants in which 23 out of 35 bore tetrasporangia. There were, however, several fertile gametophytes within the beam. Seven weeks after the lamp was switched off, 17 plants within the beam bore bladelets with developing tetrasporangia (Fig. 5), almost uniformly unripe. Control tetrasporophytes and those outside the beam, however, had by this time shed about half their tetraspores.

The numbers of plants with new blades, within the beam from the lamp and outside as controls, are given for various times in Table 1. After exposure to the night-break there was clear stimulation of blade production; after day-addition of light there may have been stimulation but the significance is marginal.

The new blades produced in response to the night-break in December 1983 were measured in situ and the largest on each plant was plotted in Figure 6 against the estimated photon irradiance received from the lamp. In spite of considerable scatter there is some evidence of the lowest irradiances resulting in smaller blades, but above about

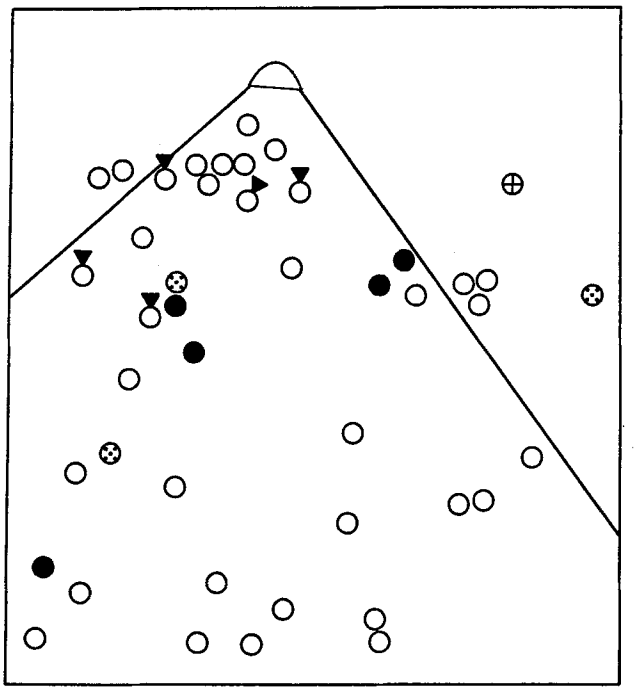

Fig. 4. As Figure 2, blades observed on 21 Nov., reproduction on 12 Dec. 1986, after a night-break from 20 Aug. 1986. dotted circles = spermatangia

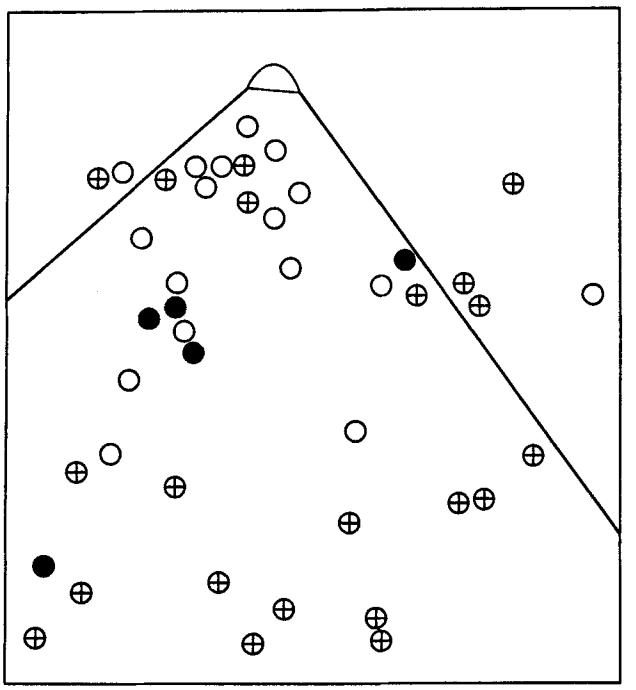

Fig. 5. As Figure 2, observed on 30 Jan. 1987, after natural daylight only from 12 Dec. 1986

Table 1. The number of plants of *Delesseria* within the beam of the underwater light and of control plants which bore new blades on the dates shown together with the significance of the difference between them. The light was on at night (N) or in the day (D)

Date	Light on	In light beam		Controls		Significance of difference
		n	With new blades	n	With new blades	$P \leq$
20. 12. 83	N	24	21	20	0	0.000*
02. 01. 85	D	29	11	27	2	0.02**
12. 01. 86	D	22	11	27	6	0.05**
21. 11. 86	N	38	5	25	0	0.004*

* Tested according to Sokal & Rohlf (1969, p. 608)
** Tested with G-test of independence

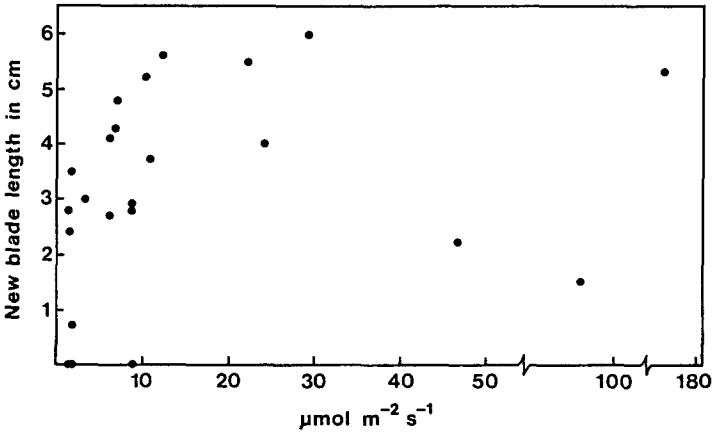

Fig. 6. Length of the longest new blade on plants of *Delesseria* within the beam of the underwater lamp on 20 Dec. 1983 plotted against the photon flux density from the lamp for one hour each night

10 µmol m^{-2} s^{-1} irradiance had no effect. This is equivalent to 36 mmol m^{-2} day^{-1}. A calculation from the data of Kain et al. (1976) gives the mean daylight at 3 m LAT in November/December as 583 $mmol^{-2}$ day^{-1}.

In attempting to establish when new blades were stimulated in the field, measurements were made of their growth rate. On a few occasions new blades were identifiable, both in the field and in the laboratory, over a period of about a month. The relative growth rate in length of each of these blades is plotted against the mean length (calculated using logarithms of the lengths) in Figure 7. As would be expected, there was a significant ($P \leq 0.05$) decrease in growth rate with size. A regression equation was used to predict the growth of a new blade from the size of 1.9 mm, the mean size of blades after 28 days under laboratory conditions favouring blade production (see later) following culture in non-favouring conditions. The growth curve is plotted in Figure 8, following a presumed triggering, arbitrarily, at the time the lamp was switched on in 1983.

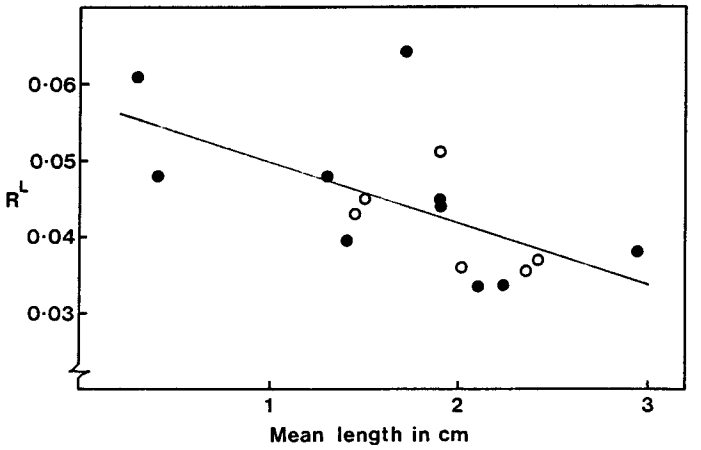

Fig. 7. The relative growth rate in length (R^L) of single new blades of *Delesseria* plotted against the mean (calculated from the logarithms of the initial and final lengths) of each blade. ● = in the laboratory; ○ = in the field

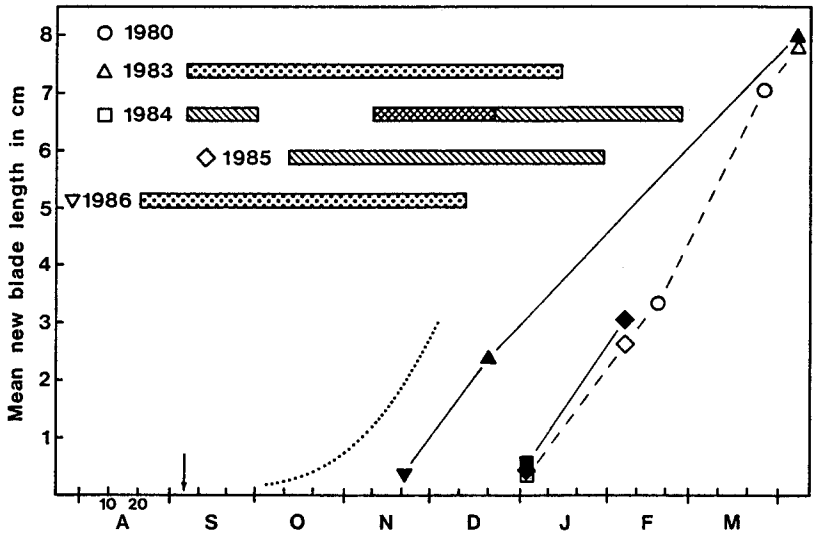

Fig. 8. The mean of the largest new blade on each plant (calculated from logarithms) in the field in the winter, the symbols corresponding to the years shown. Bars: duration of irradiance from underwater lamp; stippled: one hour in the night; single hatching: one hour in the day; cross hatching: two hours in the day. Filled symbols: within lamp beam; open symbols: not in beam. Dotted line: growth of a hypothetical blade arising at time of arrow (see text). 1980 observations from Kain (1984)

Figure 8 mainly shows the observed mean blade sizes on in situ plants during four winter seasons, relative to the periods when the lamp was on, together with data from previous observations on Port Erin breakwater (Kain, 1984). Within each condition, the observations from different years agree quite closely, night-break blades reaching a

Table 2. The numbers of midribs bearing male or female gametangia and new blades in tanks under various conditions at various times together with significant differences (G-test of independence). NB = new blades; gam = gametangial midribs

Experiment No.	Start Date	°C	Photoperiod (light:dark)	n	Time (Days)	♂	♀	New blades	Time (Days)	New blades	Difference*	Significance P ≤
1	08. 08. 84	10	16 : $\overline{8}$	56	70	0	0	46			More NB	0.000
		14	16 : $\overline{8}$	40	70	0	0	5				
		14	8 : $\overline{16}$	56	70	6	5	3				
2	09. 09. 85	10	8 : $\overline{7.5}$: 1 : $\overline{7.5}$	52	46	0	0	28	66	36	More NB (46d)	0.001
		12	8 : $\overline{7.5}$: 1 : $\overline{7.5}$	52	46	1	0	11	66	21		
		10	8 : $\overline{16}$	52	46	8	2	1	66	22	More NB (66d)	0.000
		12	8 : $\overline{16}$	52	46	16	3	1	66	0	More gam	0.05
3	15. 07. 86	10	8 : $\overline{16}$	140	50	33	12	8				n.s.
		12	8 : $\overline{16}$	139	50	21	32	8				
4	01. 09. 86	14	16 : $\overline{8}$	103	71	0	1	1				
5	11. 11. 86	8	8 : $\overline{16}$	78	50	12	21	11			More gam	0.000
(from 4)		14	8 : $\overline{16}$	70	50	0	3	4				

* From adjacent condition within experiment

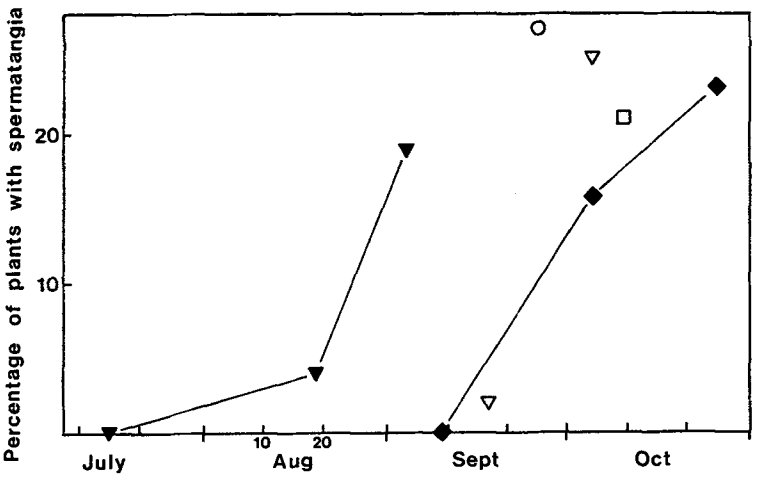

Fig. 9. The percentage of blades or midribs bearing spermatangia at different times of year. Filled symbols: in the laboratory in short days; open symbols; in the field in natural daylength. ▲ = Experiment 3; ◆ = Experiment 2; □ = 1979; ○ = 1980; ▽ = 1986

certain size about 6 weeks earlier than controls. Day addition blades were barely ahead of controls, though in February 1986 they were just significantly longer (Mann-Whitney U-test, $P \leq 0.05$).

The results of some of the tank experiments carried out during three successive seasons are summarized in Table 2. With two exceptions midribs produced gametangia in short days only: a night-break was effective in preventing their formation. The two exceptions were both blades collected in September.

The timing of development of ripe spermatangia in Experiments 2 and 3 (10° and 12 °C pooled) together with similar observations on field material is plotted in Figure 9. There were significantly ($P \leq 0.005$) fewer midribs with spermatia after 35 short days in July/August (Expt. 3) than after 25 short days in September/October (Expt. 2). Ripe male plants were observed in the field from mid-September onwards.

The percentages of the midribs developing gametangia and new blades in Experiments 1–5 are plotted against temperature in Figures 10 and 11 respectively. There was no systematic effect of temperature on the production of gametangia (Fig. 10). New blade production, however, was clearly stimulated at lower temperatures (Table 2), particularly in long days or with a night-break (Fig. 11). In short days, some new blades developed at 10 °C after the production of gametangia (Table 2, Expt. 2, Fig. 11). When plants were transferred from short days to long days or night-break, new blades were stimulated (Table 3, Fig. 11).

The blade lengths produced in Experiment 1 are shown in Figure 12. In short days, even in the prolonged exposure, no blades grew to more than 4 mm at 14 °C. In long days at this temperature, a few did but the majority remained as 'spikes' of less than 1 mm. Only at the lower temperature of 10 °C in long days did most of the blades exceed 4 mm.

Tetrasporangia were observed on plants held in the laboratory only in three instances. These were on plants that had been in short days for two months.

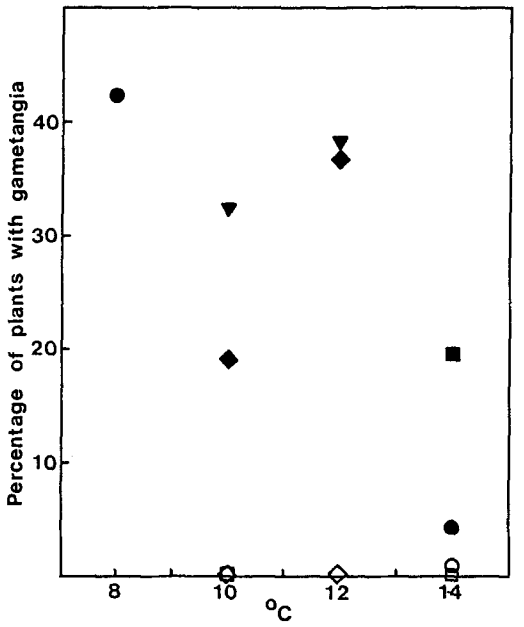

Fig. 10. The percentage of blades or midribs bearing gametangia at different temperatures in the laboratory. Filled symbols: in short days; open symbols: in long days. □ = Experiment 1; ◇ = Experiment 2; ▽ = Experiment 3; ○ = Experiments 4 & 5

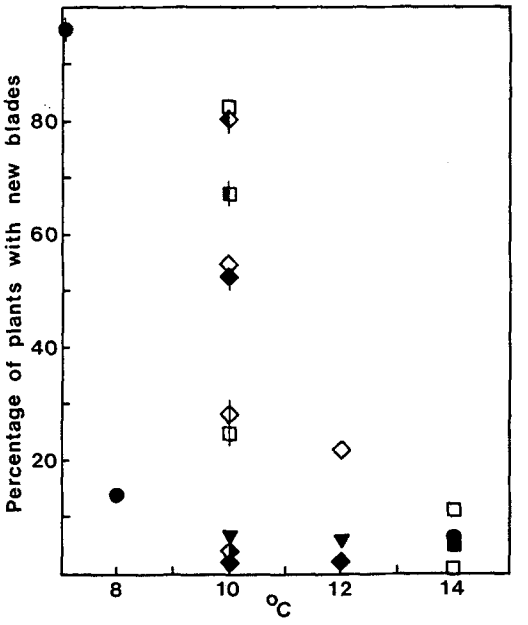

Fig. 11. The percentage of midribs bearing new blades at different temperatures in the laboratory. ◧ = Experiment 1a from short days (SD); ◨ = Experiment 1a, from long days (LD); ◆ = Experiment 2a, SD to SD; ◈ = Experiment 2a, SD to night-break (NB); ◇ = Experiment 2a, NB to SD; ◈ = Experiment 5a; others as in fig. 10

Table 3. The numbers of midribs bearing new blades after being transferred from different conditions of temperature or photoperiod together with the significance of differences (G-test of independence)

Experiment	Date of transfer	Original conditions		New conditions		Time (days)	n	New blades	Significant differences $P \leq$
		°C	Photoperiod (LD)	°C	Photoperiod (LD)				
1a	14. 02. 85	10	$8:\overline{16}$	10	$16:\overline{8}$	53	49	33	0.001
		10	$16:\overline{8}$	10	$16:\overline{8}$	53	48	12	
2a	14. 11. 85	10	$8:\overline{16}$	10	$8:\overline{16}$	46	52	28	0.005
		10	$8:\overline{16}$	10	$8:\overline{7.5}:1:\overline{7.5}$	46	52	42	
		10	$8:\overline{7.5}:1:\overline{7.5}$	10	$8:\overline{16}$	46	52	2	0.001
		10	$8:\overline{7.5}:1:\overline{7.5}$	10	$8:\overline{7.5}:1:\overline{7.5}$	46	52	14	
5a	02. 01. 87	8	$8:\overline{16}$	7	$8:\overline{16}$	50	54	53	ns
		14	$8:\overline{16}$	7	$8:\overline{16}$	50	74	71	

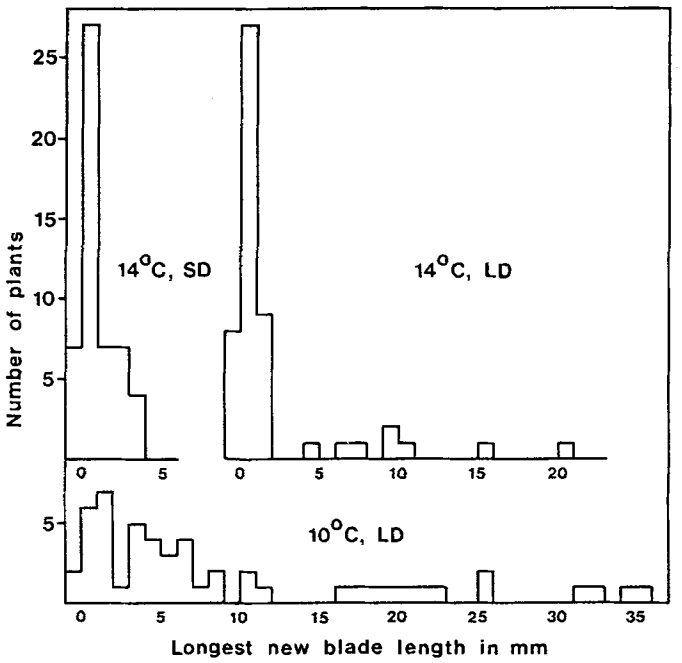

Fig. 12. The numbers of midribs with the largest new blade in various size classes in Experiment 1 in the laboratory. The class below zero is the number with no new blades

DISCUSSION

From the field data it is clear that the night-break afforded by the lamp in the sea prevented (1983–4) or delayed (1986–7) fertility in tetrasporophytes. Although this result has not been reproduced in the laboratory there can be little doubt that tetraspore production is under photoperiodic control. From the laboratory experiments it is also clear that gametangia production is similarly stimulated by short days (long nights) and inhibited by a night-break.

Male gametangia have been observed in the field in mid-September and it is likely that the less obvious carpogonia develop at a similar time (Table 2, Expt. 6). The critical daylength must therefore be longer than 12 h; perhaps it is of the order of 14 h (Fig. 1) if triggering begins in late-August, which seems possible. This would explain the two cases of fertility in long days or with a night-break (Table 2). On the other hand, sufficient cycles have not been received by 9 September to stimulate the vast majority of plants. The faster development of gametangia in the laboratory in September/October compared with July/August (Fig. 9) could be due to the blades having gone through some maturing process or, more likely, to the fact that they had already received some of the necessary number of cycles in the sea before transfer to the laboratory.

The population of *Delesseria* inhabiting the western side of Port Erin breakwater showed a reasonable balance betweeen the phases with possibly a slightly greater proportion of tetrasporophytes (Kain, 1982). The other (exposed) sites from which labora-

tory material was collected presumably support a similar balance as up to 40 % of the blades developed gametangia under short day conditions (Fig. 10). The sheltered site of the underwater light, however, seemed to favour tetrasporophytes.

It seems that the requirements for fertility in tetrasporophytes differ from those for gametophytes. Laboratory conditions favoured the latter but not the former. Some plants developed gametangia within the beam of the light creating a night-break in the field whereas tetrasporangia were inhibited. Also, under natural conditions, tetrasporangia develop considerably later than gametangia (Kain, 1982). Carpospores and tetraspores are both first dehisced in December but carposporophyte development is preceded by carpogonia 2–3 months earlier. If this involves a difference in time of triggering, rather than rate of development, there are three likely mechanisms. Tetrasporangia might require (a) a shorter daylength, (b) more cycles or (c) a lower temperature than gametangia. It is difficult to understand how one of these might have operated in allowing gametangia and not tetrasporangia to develop near the underwater light. One possibility is, if (b) operates, that stormy conditions might have rendered the water highly turbid for some days, cutting down the irradiance from the light to below the detectable threshold and allowing the required number of short day cycles for gametogenesis.

The production of new blades in response to the night-break was a considerable surprise. It is unlikely that it was due to there being extra light for photosynthesis for the following reasons. Firstly, the threshold level for the effect was an order of magnitude lower even than mid-winter ambient light levels and certainly much lower than photosynthesis saturation: 50 μmol m^{-2} s^{-1} of continuous light (Lüning, 1979). Secondly, new blades can be initiated and grow in the dark (Lüning, 1984a). Thirdly, the day-addition of light in the sea resulted in only a very slight stimulation of blade initiation and growth. Admittedly, the timing of the day-addition was later than that of the night-break but this is unlikely to be the cause of the difference in blade initiation. The increase in lengths of blades responding to the night-break closely paralleled the growth of the theoretical blade plotted in Figure 8 in spite of the fact that this increase was determined by two observations made in two different years (1983 and 1986) when the light was switched on at different times. Also mean blade size in early January was very similar in the two day-addition years, although the timing of the lighting had again been different. Finally, if the observations from laboratory experiments and growth rate determinations are to be believed, a blade stimulated when the light was switched on in 1983 would have been 25 mm long before the end of November, 24 days before the plants in the beam in the field reached this size. All these facts point to another, combining, trigger being effective in the sea: probably temperature. The size of the night-break stimulated blades, combined with the theoretical growth curve (Fig. 8), suggests blade inception at the beginning of October. The sea temperature is then 13 °C. From the laboratory experiments this seems rather high to be stimulatory to blade production.

New blades are normally produced at about the time of the shortest day. The stimulation of their production by long days or a night-break both in the laboratory and in the sea seems unrelated to the species' seasonality. However, in nature occasional plants produce a second crop of new blades during the late summer and it is possible that this reaction developed as a response maximizing the use of increased irradiance, such as might occur when a laminarian canopy plant was removed. The normal seasonal trigger for new blade production is undoubtedly temperature: when this falls new blades are

stimulated. However, it is possible that this stimulation can be modified by the development of reproductive structures. In short days in the laboratory, new blades at 10 °C were delayed until after gametangia had developed (Table 2, Expt. 2). If the day-addition did stimulate new blade production in the field then the delay, compared with the night-break effect, could have been due to reproductive structures forming in the meantime. Followed to its conclusion, this argument would indicate that the night-break in the sea allowed new blade growth by preventing reproduction, rather than being stimulatory in itself. However, this would indicate that 13 °C is the critical temperature for blade production. Also it would leave unexplained the laboratory observations that transfer to long days stimulates blade production, even after reproduction.

Conversely, it seems likely that new blades can inhibit the development of reproductive structures. There seems no alternative explanation for the failure of short days between January and March 1984 to stimulate these, as sea temperature cannot have been the cause.

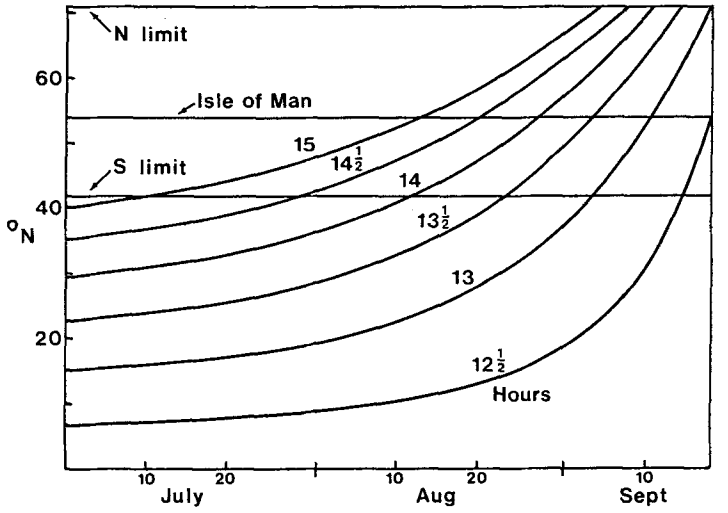

Fig. 13. The distribution of various daylengths from 12½ to 15 h duration with latitude and season. The geographical limits of *Delesseria*, together with the latitude of the Isle of Man, are shown as horizontal lines

In its geographical distribution, *Delesseria sanguinea* only occurs in the northeast Atlantic: around Iceland, the Faroes, the British Isles and on mainland Europe from northern Norway to the Bay of Biscay (Lüning, 1985). Its southern limit is probably around Galicia, northern Spain (Niell, 1978). The limiting latitudes are 42° and 71°N. At 42°N the sea surface temperature is 13 °C in winter and 19 °C in summer (Sverdrup et al., 1942). *Delesseria* has been shown to tolerate a week at 23 °C (Lüning, 1984b) so it seems unlikely that its southern limit is determined by summer temperatures. It is possible, however, that new blade production is not adequately stimulated by winter temperatures above 13 °C encountered further south than 42 °N. This must, however, remain a conjecture at present.

A critical daylength other than 12 h must involve latitudinal differences in timing. These are shown for daylengths of 12½ to 15 h in Figure 13. With a 14-h critical daylength, possibly implicated in the Isle of Man, plants at the southern limit would be triggered 16 days earlier (unless there is a genotypic difference in response). Over the whole geographical range of *Delesseria* there is a difference of a month in the timing of a 14-hour daylength.

There are clearly many unanswered questions concerning the triggers responsible for the pronounced seasonality of this species. The seasonality itself hinders experimentation by confining it to short periods of the year.

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