15 Control of Algal Life-history by Daylength and Temperature

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Abstract: How are the characteristic patterns of seasonal growth and reproduction in benthic marine algae controlled by the environment? From what is known of higher plants, which are much better understood at present than algae, it can be expected that photoperiod and temperature are the main controlling factors. A culture system was developed in which various benthic algae were cultivated at 12 combinations of temperature and photoperiod. A night-break regime was included to test for genuine photoperiodic responses. New photoperiodic reactions were found in the *Trailliella*-phase of the red alga *Bonnemaisonia hamifera* Hariot, which formed tetrasporangia only in short days, at 15°C, as well as in the *Codiolum*-stage of the green alga *Monostroma grevillei* (Thur.) Wittr., which became reproductive again only under short-day conditions, at lower temperatures. In the brown alga *Scytosiphon lomentaria* (Lyngb.) Link, which forms erect thalli under short-day conditions, various photoperiodic ecotypes exist, all with different critical daylengths and obviously adapted to the latitudes at which they are growing. Two species of *Petalonia* also exhibited genuine photoperiodic responses. Various stages of other algae were found to react definitely to temperature, not to photoperiod. Among these are the gametophytes of several representatives of the Desmarestiales and Laminariales, which mature only in a certain range of lower temperatures. The ecological significance of these reactions, which enable the plants to occupy a niche in space and time, is discussed.

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INTRODUCTION

Since the beginning of this century phycologists have devoted much energy to clarifying the life histories of benthic marine algae, a task which is still not completed but which was fulfilled for many terrestrial plants during the last century. This lagging behind may explain why the question of by what means algal life-histories are regulated by external factors in order to fit the local environment has thus far found few answers for marine algal species. Hundreds of photoperiodic responses have been discovered and analyzed in higher, terrestrial plants, since Garner and Allard (1920) discovered photoperiodism in plants (Vince-Prue, 1975). But until 1967 no photoperiodic response had been convincingly demonstrated to occur in benthic marine algae; it therefore seemed plausible until that time to assume that the seasonal development of algae is regulated exclusively by temperature, which is of course a much more reliable indicator of season under water than on land. The first clear-cut proof of a photoperiodic response in marine algae was demonstrated in the *Conchocelis*-phases of *Porphyra tenera* Kjellm. (Dring, 1967a,b; Rentschler, 1967) and *Bangia atropurpurea** (Richardson and Dixon, 1968; Richardson, 1970), where the formation of fertile cell rows is promoted by short days and where phytochrome is the likely candidate as the photomorphogenetic pigment. A second photoperiodic response, which is however triggered by a blue UV-absorbing pigment and is also light-saturated at extremely low levels as in many phytochrome-mediated responses, was found to be involved in the formation of erect thalli from the prostrate crusts of *Scytosiphon lomentaria* (Dring and Lüning, 1975). From the culture work of various authors, some few more cases are known in which photoperiod may control the algal life-histories, but these still have to be analyzed in detail (see reviews by Dring, 1970, 1974). Recently, Mayhoub (1976) reported that a genuine photoperiodic response controls tetrasporangial formation in the *Hymenoclonium*-stage of the red alga *Calosiphonia vermicularis*. It is to be expected that further detailed investigations of the environmental regulation of algal life-histories will soon reveal more

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*As *Bangia fuscopurpurea* in the previous literature cited; all following mentions of all benthic macroalgae that are covered by the British check-list (Parke and Dixon, 1976) employ nomenclature presented in that list.

cases of genuine photoperiodism – indeed, some new examples will be provided in this chapter – but on the other hand such studies will also reveal those cases wherein certain algae in fact detect the ambient season exclusively by temperature. The present investigation is intended to contribute towards this goal, although of the multitude of species and stages which still have to be investigated in this respect, only a very small number can be treated here.

MATERIAL AND METHODS

Throughout this study algal cultures were grown in white fluorescent light (Osram 65 W/19, Daylight 5000 De Luxe), at photon flux densities of 15–20 $\mu E/m^2/s$ (as measured with a Lambda quanta meter; equivalent to an irradiance of about 3–4 W/m^2, or an illuminance of about 750–1000 lux). Unialgal cultures were established by growing spores which had been released from wild material in plastic petri dishes (90 mm diameter, 15 mm high) filled with enriched sea water (PES; Provasoli, 1968). Young stages which had developed from the spores were isolated at an age of 2–3 weeks with forceps under a dissecting microscope. During the first weeks, a medium containing germanium dioxide (2 ml of a saturated solution of GeO_2 in distilled water, added to 1 litre of PES) was used to eliminate diatoms. Afterwards normal PES was used and changed weekly.

Treatments at different daylengths were carried out in a culture system consisting of boxes made of black plastic (8 mm thick PVC; 40 x 25 cm, 12 cm high) equipped with an automatically opening or shutting cover (Fig. 1). An electric time switch triggered a pneumatically operated lever (operating pressure 6–7 bar) which opened or closed the lid instantaneously. In addition, the light-dark status of a box was monitored by a photoelement situated in the interior of the box, which registered continuously on a multi-channel recorder. Two fluorescent lamps (or 3–4 at lower temperatures) were mounted at 40 cm from the top of the boxes, so that the photon flux density given above was obtained.

For basic experiments four systems, each consisting of three boxes (light regimes $8:\overline{16}$, $16:\overline{8}$, and $8:\overline{7.5}:1:\overline{7.5}$), were operated in different constant temperature rooms (± 1°C), at 5, 10, 15, and 20°C. Temperatures were measured continuously by resistance

Fig. 1. Culture system used for photobiological experiments. The unit, consisting of three boxes each equipped with automatically opening or shutting cover, is operated in a constant temperature room.

thermoprobes and registered on a multi-channel recorder. For the determination of critical daylength, a set of 9 (or 12) boxes was used in one constant temperature room. The advantage of this system is to be seen in the fact that the lamps are not included in the light-tight cabinet, which makes it less difficult to maintain a constant temperature within the cabinet.

The following culture scheme was used with representatives of the Scytosiphonales. For establishing unialgal stock cultures the zoospores, released by erect thalli which had been collected at various locations in the field (Table I), were transferred to continuous light, at 15°C. The crusts developing from the germinated spores were isolated as stock cultures. For induction of erect thalli, the crusts were transferred into a short-day regime ($8:\overline{16}$) for 6 weeks (15°C, or 10°C, according to species). Once the formation of the erect thalli had been induced, the latter were allowed to continue growth also in continuous light. At the age of 6 weeks, 20–30 erect thalli (of 5–10 mm length) were transferred into big glass culture vessels (22 cm diameter; 10 cm high; closed with a glass lid; filled with 1.5 l of PES) and cultivated in continuous light for a further 6 weeks (without change of medium). After this time, the erect thalli had reached a length of 5–15 cm and were usually sporogenous. For spore release, the erect thalli were blotted briefly with filter paper, exposed in a dry petri dish for 2–3 h, and then re-immersed in PES. The zoospores, which were released due to this procedure within a few minutes, were seeded into plastic petri dishes (90 or 55 mm diameter; 15 mm high) at such a density that at least 150 (small dish) or 250 plants (large dish) grew in one dish. The bottom of the plastic petri dishes had been scraped with a hot needle prior to filling with PES in order to ensure firm contact of the prostrate system of the plants.

Material for experimentation on the *Trailliella*-phase of *Bonnemaisonia hamifera* was obtained by fragmenting tufts (about 5 mm diameter), which had been pre-cultivated in PES, by means of forceps into units which consisted of 2–3 branches, each with 10–20 cells. For each treatment, 150 units were used in one glass dish (90 mm diameter; 55 mm high) filled with sea water to which less than normal Provasoli enrichment had been added (see below).

Monostroma grevillei was isolated from field samples (containing also *M. arcticum* Wittr.) according to the methods described by Kornmann (1962a) and Kornmann and Sahling (1962, 1977). Negatively phototactic swarmers represent the zoospores of *M. arcticum* and were directly transferred into the treatments at different temperatures and daylengths. Positively phototactic swarmers represent the gametes of *M. grevillei*. The life history of this species was routinely completed in the laboratory within 20 weeks in the following way. The zygotes derived from copulation of the anisogamous gametes were cultivated for 6 weeks in continuous light ($20\,\mu E/m^2/s$), at 15°C. During this time, the diameter of the resultant *Codiolum*-stage increased to a diameter of about 70 μm. For induction of spore formation the *Codiolum*-stages, fixed to glass slides, were transferred to short-day conditions (8 h light per day, photon flux density as before), at 5°C. Zoospores were produced, and blades of 2–5 mm length had grown from these by 12 weeks after the transfer. Subsequently, the blades were grown to fertility for 2 weeks at 15°C, in continuous light.

In all experiments 150 plants (250 in the case of experiments on critical daylength) were counted for the determination of the percentage of plants which had reacted in a specific way. Further details of material and methods are included in the sections below.

RESULTS AND DISCUSSION

In the following, three cases of photoperiodic control will be treated: (1) the formation of erect thalli in the brown algal order Scytosiphonales, with special emphasis on the occurrence of photoperiodic ecotypes in *Scytosiphon lomentaria*; (2) the induction of tetrasporangia in the *Trailliella*-phase of the red alga *Bonnemaisonia hamifera*; (3) the induction of spore formation in the *Codiolum*-stage of the green alga *Monostroma grevillei*. Afterwards several cases will be treated where it has been established that the control of performance of the life history is exerted definitely not by daylength, but by temperature.

1. Photoperiodism in the Scytosiphonales

Scytosiphon lomentaria (Lyngb.) Link grows in all boreal-temperate seas, but does not enter the tropics. In the North Atlantic it has been found from Spitsbergen (78°N; Svendsen, 1959) to the Canaries (28°N; Price *et al.*, 1978), and from Labrador (60°N; Wilce, 1959) to the Bermudas (32°N; Taylor, 1960). On the Pacific side of North America the species occurs from the Bering Sea to Baja California (Abbott and Hollenberg, 1976).

The question of whether the erect thalli are gametophytes or sporophytes has been raised since the beginning of the century (e.g. Kuckuck, 1912; Kylin, 1933) and answered in various ways, depending on whether fusion of the swarmers had been observed or not. Clayton (1979) discussed the problems involved in this differentiation. If no fusion occurs, one may be dealing with only one mating type, and another difficulty for observation of the mating reaction may lie in the "elusive nature of the mating reaction in these algae" (Clayton, 1979). Additonal support for the interpretation of the erect thalli as gametophytes (Kuckuck, 1912; Feldmann, 1949) was supplied by the discovery that a crustose sporophyte bearing unilocular sporangia is involved in the life histories of several Scytosiphonales (see summary of literature in Wynne and Loiseaux, 1976). According to the results of the exhaustive work of Nakamura and Tatewaki (1975), the life history of *Scytosiphon lomentaria* is characterized by a heteromorphic alternation between the erect thalli as gametophytes and the crustose sporophytes. Strains in which the swarmers released by the erect thalli do not fuse are consequently interpreted as following only a parthenogametic type of life history, according to the authors cited. The work of Clayton (1976, 1978, 1979) demonstrates both the complexity of life histories in the Scytosiphonales and the need for further experimental work.

The present study deals only with strains of *Scytosiphon lomentaria* in which no fusion of swarmers was observed. Furthermore, it was not the aim of this study to follow the development of the crusts (or the filamentous prostrate systems, where no firm contact was achieved by the young germling with the bottom of the petri dish) over a period long enough to find the appropriate conditions for obtaining sporangia in the prostrate system.

Several authors (Tatewaki, 1966; Wynne, 1969; Rhodes and Connell, 1973) have reported that from the swarmers released by the erect thalli crusts develop under long-day conditions and crusts bearing erect thalli under short-day conditions as seen in Fig. 2 in the case of the Helgoland strain. Subsequently it was established that, in the case of a strain from Helgoland, genuine photoperiodism is involved in this response (Dring and Lüning, 1975). The critical daylength, as determined at 15°C, was found to lie between 12 and 13 h, and a 1-min light break with a very low irradiance of blue light, given in the middle of a dark period of 16 h, inhibited completely the formation of erect thalli.

Table I (Nos 1–9) shows the results which were obtained with nine photoperiodically active isolates of *Scytosiphon lomentaria* from different localities, the extremes ranging from 32°N (Mexico) to 69°N (Northern Norway). There is a clear relationship between the geographical latitude at which a strain was sampled and the temperature range in which erect thalli were produced under short-day conditions ($8:\overline{16}$). The isolates from 32–48°N (Nos 1–4) produced erect thalli at all temperatures from 5 to 20°C. In the upper interval of this range, it took 3–4 weeks after seeding the zoospores before the erect thalli were visible emerging from the prostrate system; in the lower interval, it required 6–8 weeks. In the isolates from 54–58°N (Helgoland to southern Norway, Nos 5–7), the production of erect thalli was partially prevented at 20°C, but still functioned perfectly at 15°C. The strain from Iceland (66°N, No. 8) was fully blocked in this respect already from 15°C upwards, and the isolate from Tromsö (69°N, No. 9) from 10°C upwards. With increasing

Table I. Development of isolates from different geographical latitudes of *Scytosiphon lomentaria* (S), *Petalonia fascia* (F), and *P. zosterifolia* (Z) at 8 or 16 h light per day, and in a night-break regime (B; $8:\overline{7.5}:1:\overline{7.5}$) at four temperatures. Treatments covered a duration of 4–8 weeks, and percentage of plants which had formed erect thalli from prostrate systems (crustose or filamentous) was determined in 150–250 plants: + = 100–95% with erect thalli; – = 0–5% with erect thalli. Numbers in brackets give percentage of plants with erect thalli, if in the range 5–95%.

Isolate No.	Species	Origin of isolate	Latitude	5°C			10°C			15°C			20°C		
				8	B	16	8	B	16	8	B	16	8	B	16
1	S	Punta Banda (Mexico)	32°N	+	–	–	+	–	–	+	–	–	+	–	–
2	S	Halifax (Nova Scotia)	45°N	+	–	–	+	–	–	+	–	–	+	–	–
3	S	Rovinj (Yugoslavia)	45°N	+	–	–	+	–	–	+	–	–	+	–	–
4	S	Seattle (Washington)	48°N	+	–	–	+	–	–	+	–	–	+	–	–
5	S	Helgoland (Germany)	54°N	+	–	–	+	–	–	+	–	–	(14)	–	–
6	S	Port Erin (Isle of Man)	54°N	+	–	–	+	–	–	+	–	–	(34)	–	–
7	S	Lindesnes (Norway)	58°N	+	–	–	+	–	–	+	–	–	(16)	–	–
8	S	Tjörnes (Iceland)	66°N	+	–	–	+	–	–	–	–	–	–	–	–
9	S	Tromsö (Norway)	69°N	+	–	–	–	–	–	–	–	–	–	–	–
10	S	Flinders, Vict. (Australia)	38°S	+	+	+	+	+	+	+	+	+	+	+	+
11	F	Helgoland (Germany)	54°N	+	(44)	(52)	+	(51)	(34)	+	(48)	(35)	(48)	(16)	(93)
12	Z	Helgoland (Germany)	54°N	+	–	–	(46)	–	–	(38)	–	–	–	–	–

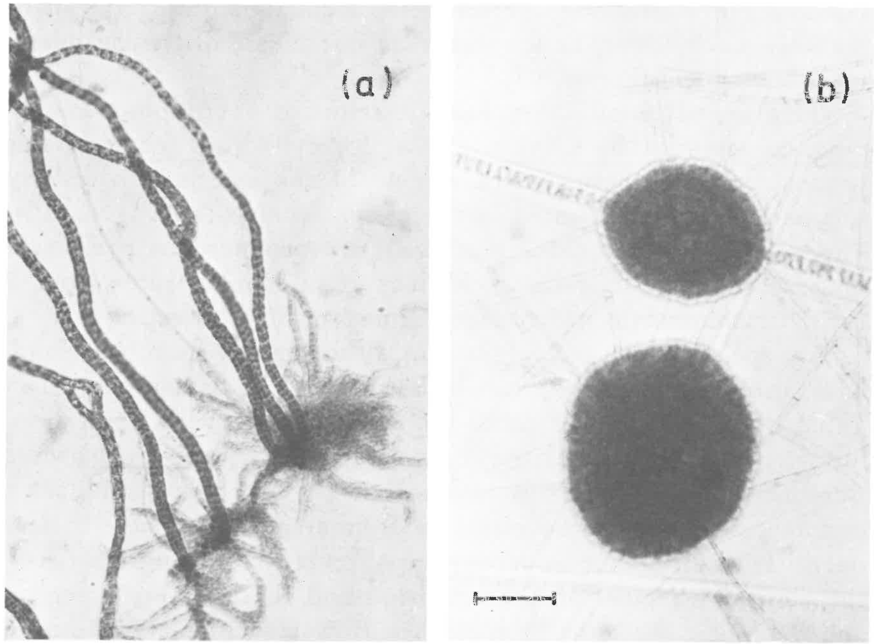

Fig. 2. *Scytosiphon lomentaria* (Helgoland) cultured for 4 weeks at 8 h (a) or 16 h (b) white fluorescent light per day. Scale represents 100 μm.

latitude, there is thus apparently a temperature block preventing the formation of erect thalli at concomitantly lower temperatures. The finding of Rhodes and Connell (1973) that a strain of *S. lomentaria* collected on the Atlantic coast of Virginia (37°N) still formed erect thalli in culture at 21°C at 9 h light per day (but not at 14 h) is in accordance with the reactions of the presently investigated strains originated from 32–48°N (Table I, Nos 1–4).

Another important feature, which is evident from Table I, is the effectiveness of the night-break regime. This fact characterizes all nine strains as showing absolute photoperiodic responses (in the sense of Vince-Prue, 1975), with an induction of almost 100% of the plants by short days, and an inhibition of almost 100% by long days or by an interruption of the long night. In the present study 1 h of white light of comparatively high irradiance (3–4 W/m^2) was used as the night interruption. It seems likely, however, that the energy required for inhibition of erect thalli formation during the night break is much lower, as found earlier in the case of the Helgoland strain (Dring and Lüning, 1975).

There are also non-photoperiodic strains of *Scytosiphon lomentaria*, as reported by Clayton (1978) for cylindrical forms of this species from southern Australia. One of the strains provided by this author has been tested in the present study (Table I, No. 10). The results confirm that erect thalli are produced in this strain under short- and long-day conditions at all temperatures from 5 to 20°C, and that the night-break regime is also not effective.

Two species of the genus *Petalonia*, although only from Helgoland, have also been tested. It can be seen from the data presented in Table I (No. 11) that *P. fascia* (O. F. Müll.) O. Kuntze is not absolutely, but only quantitatively, a photoperiodic plant (in the sense of Vince-Prue, 1975); this means that daylength only induces a certain percentage of the plants to form erect thalli. There is clear quantitative difference in percentage of erect thalli formed between the short-day regime on the one hand and the night-break regime and the long-day regime on the other. However, complete inhibition by short nights is not possible, as was also found to be the case in a strain of this species from the Netherlands (Roeleveld *et al.*, 1974). In contrast to *P. fascia* the second species occurring on Helgoland, *P. zosterifolia* (Reinke) O. Kuntze (Table I, No. 12), shows an absolute photoperiodic response, as in *Scytosiphon lomentaria*. Induction of erect thalli is only partially possible from 10°C onwards and is completely blocked at 20°C.

In order to determine the critical daylength, cultures of the various strains of *Scytosiphon lomentaria* were grown at intervals of 0.5–2.0 h within the range 8–18 h light per day. Figure 3 shows the results for seven strains of this species investigated at 10°C, and for four strains investigated at 15°C. It is obvious that the isolates must be all genetically different as regards the daylength range in which erect thalli can be formed. For example, the Mexican strain produced erect thalli at daylengths up to 11 h, the Helgoland strain up to 12 h, and the Iceland strain up to 14 h light per day (all at 10°C). It is well-known from studies in higher plants (see Hillman, 1962; Cumming, 1969; McMillan, 1974) and also in many insect species (e.g. regarding diapause determination; Beck, 1968) that northern ecotypes have a lower absolute requirement for darkness

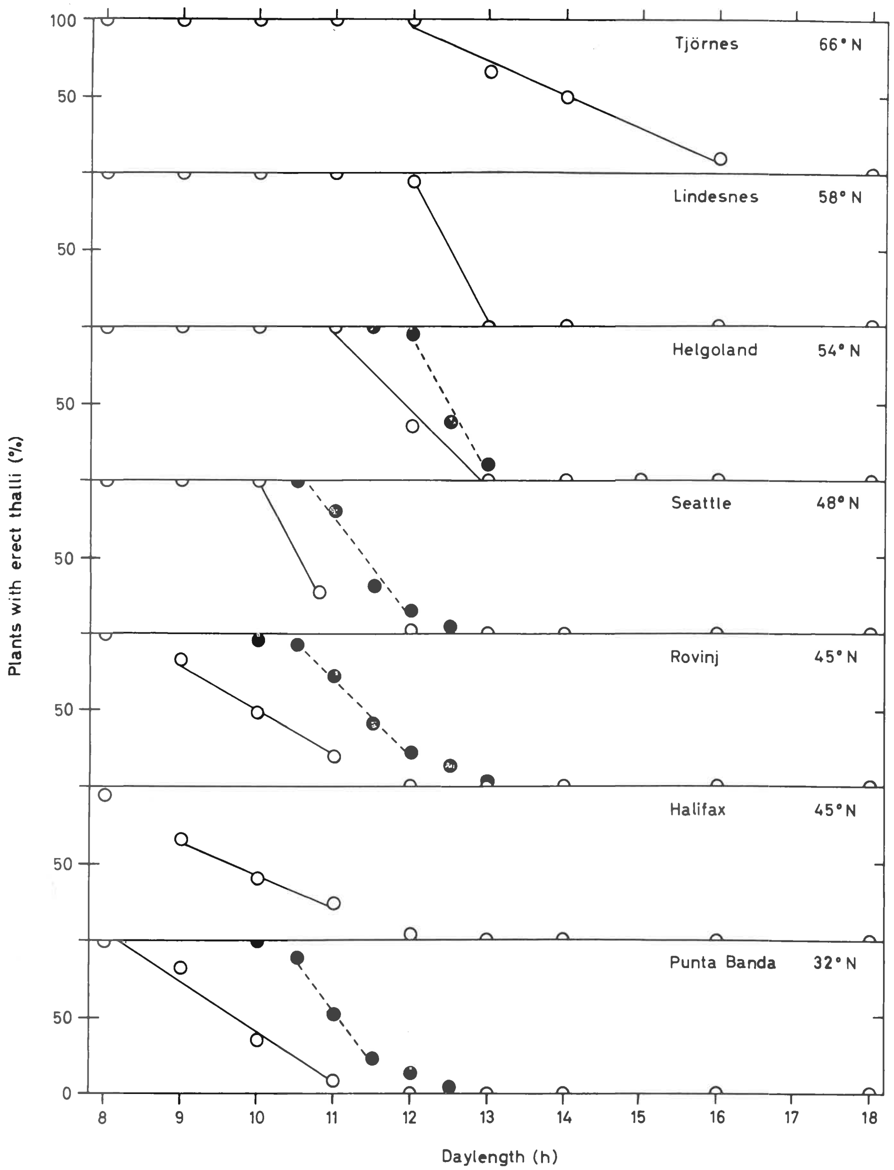

Fig. 3. Effect of daylength on erect thallus formation by different geographical strains of *Scytosiphon lomentaria* at 10°C (open circles) or 15°C (filled circles). Each value is based on a count of 250 plants.

than southern ecotypes of the same species. This accords with the fact that night length from April to August decreases progressively towards north, as pointed out by Cumming (1969). The same phenomenon is encountered again in the case of *Scytosiphon lomentaria*, and one may safely regard the different geographical isolates of this alga, although morphologically similar, as genetically distinct latitudinal or photoperiodic ecotypes. It is furthermore obvious from Fig. 3 that the critical daylength increases with temperature. From 10 to 15°C, the 50% response increased by 1.4 h in the Mexican and Mediterranean strains, by 0.9 h in the strain from Seattle, and by 0.6 h in the Helgoland strain. Such temperature-dependent shifts of the critical daylength are again also known from higher plants (Hillman, 1962).

Since the critical daylength for induction of erect thallus formation decreases from north to south, the period in which only crusts are formed becomes extended along the same gradient, as shown in Table II, where predictions about seasonal development have been based on the results obtained in the laboratory at 10°C and also local temperatures are tabulated. The picture would change slightly if predictions were based on the locally prevailing temperatures, e.g. on an autumn temperature of 5°C in the north (no laboratory data available for this temperature so far), or on autumn temperatures of 15–20° C in the south. Regarding the results available to date on temperature-dependent shifts of critical daylength (Fig. 3) one may predict that the periods of exclusive formation of crusts would be shortened in the south by about a month, but hardly lengthened appreciably in the north, since the change in daylength is so rapid in spring and autumn at high latitudes (Table II).

In all experiments described so far, the swarmers of the erect thalli were transferred immediately into the different regimes of daylength and temperature. Thus the induction of erect thalli formation was possible under short-day conditions right from the beginning. One effect of this kind of treatment was that no symmetrical crusts were formed under short-day conditions, as reported earlier (Dring and Lüning, 1975). Instead, rhizoidal outgrowths appeared early at the margins of the prostrate systems, probably to be interpreted as a means by which the plant fixes the developing erect thalli to the substratum with a widespread attachment system

Table II. Daylength required for induction of 100, 50, and 0% of plants to form erect thalli in isolates of *Scytosiphon lomentaria* from different geographical latitudes. Values were derived from experiments conducted at 10°C. Values enclosed by lines indicate the months in which no induction of erect thallus formation is possible.

Isolate No.	Origin	Latitude	Daylength for induction of erect thalli (h light/day) 100%	50%	0%	Daylength[a] on 21 of month and local water temperatures[b] J	F	M	A	M	J	J	A	S	O	N	D	
1	Punta Banda	32°N	< 8	9.7	> 12	10.4	11.3	12.2	13.1	13.9	14.3	13.9	13.1	12.2	11.3	10.4	10.0	h light/d
2	Halifax	45°N	< 8	9.6	> 12	9.3	10.8	12.2	13.8	15.0	15.6	15.0	13.8	12.2	10.8	99.3	8.8	h light/d
						2	1	1	3	6	10	13	15	14	12	8	5	°C
3	Rovinj	45°N	< 8	10.0	> 12	9.3	10.8	12.2	13.8	15.0	15.6	15.0	13.8	12.2	10.8	9.3	8.8	h light/d
						11	9	10	13	17	23	24	23	23	21	18	12	°C
4	Seattle	48°N	< 9	10.5	> 12	9.0	10.6	12.2	14.0	15.4	16.0	15.4	14.0	12.2	10.6	9.0	8.3	h light/d
						9	8	8	9	10	13	14	14	13	12	11	10	°C
5	Helgoland	54°N	< 11	11.9	> 13	8.2	10.3	12.2	14.4	16.3	17.1	16.3	14.4	12.2	10.3	8.2	7.4	h light/d
						5	4	4	6	9	13	16	17	16	14	10	7	°C
7	Lindesnes	58°N	< 12	12.5	> 13	7.6	9.9	12.3	14.8	17.0	18.2	17.0	14.8	12.3	9.9	7.6	6.5	h light/d
						5	4	4	5	8	11	13	16	14	12	9	7	°C
9	Tjörnes	66°N	< 12	14.0	> 17	5.0	9.0	12.3	16.1	20.3	24.0	20.3	16.1	12.3	9.0	5.0	2.8	h light/d
						3	2	2	2	3	7	9	9	7	6	5	4	°C

[a] Daylength according to Smithsonian Meteorological Tables.

[b] Water temperatures according to the following sources: Chapman (Halifax; personal communication); Zavodnik, 1973 (Rovinj); Weigel, 1978 (Helgoland); Waaland, 1976 (Seattle); Tomczak and Goedecke, 1962 (Lindesnes); Stefánsson, 1969 (Tjörnes). Water temperatures for Punta Banda are not available.

(Fig. 2a). In one experiment with the Helgoland strain, 6-week-old crusts, which had been grown to a diameter of about 1 mm in continuous light, were transferred to short-day conditions ($8:\overline{16}$) at 15°C. Seven weeks later, all crusts had formed erect thalli. From this it is clear that the short-day response takes place in both young germlings and established crusts. In another experiment, swarmers released by the erect thalli of the Helgoland strain were seeded on to scratched Plexiglas slides and transferred to an underwater station at 2 m depth below MLWS in June. The developing crusts survived on the slides when the zoospores, from which they had originated, had settled near or on the scratches. The crusts continued to grow throughout the summer and reached a diameter of about 2 mm by the end of November. In winter, there is little light at this depth near Helgoland due to very turbid water (Lüning and Dring, 1979), and there was practically no further development in the crusts. At the beginning of March, however, numerous erect thalli of up to 5 mm length had developed from the crusts. It thus seems likely that the crusts are perennial stages. It should be noted that the species is mainly to be found in the lower eulittoral region, near Helgoland. However, in the upper sublittoral region, where the field experiment took place, erect thalli of considerable length also occur in late spring and early summer.

The main ecological significance of the photoperiodic response in *Scytosiphon lomentaria* seems to lie in the fact that the swarmers released by the erect fronds are forced to develop first into a solid crust on the rocky substratum; they are prevented from producing a new generation of erect thalli right away, which is possible in the laboratory 2–4 weeks after seeding of the swarmers, under short-day conditions. If one assumed that 2–3 months are required from germination of a swarmer until the formation of a fertile erect thallus under short-day conditions in the field, then it is evident from Table II that by the time new swarmers are produced, daylength has already reached the range which allows only formation of crusts. As a result of the photoperiodic response, a new generation of erect thalli can be produced only from autumn onwards, either by direct vegetative formation from the crusts or by their zoospores, where these exist at this time. At low latitudes, the fact that the induction of erect thallus formation is still possible at high water

temperatures in southern strains (Table I) becomes important in autumn, when water temperatures above 20°C occur in the south (Table II). At high latitudes, the "short-day interval" in late autumn and winter can hardly be used by the plants for the formation of erect thalli due to lack of light; the "short-day interval" in spring has to be used instead, since this is followed by a period of increasing light availability. It should be stressed that the induction of erect thallus formation may require a very low irradiance, but for the subsequent formation of the erect thalli sufficient light to support photosynthesis is needed. However, even in March when the induction of erect thallus formation is already prevented by daylength in the south (Table II), total solar radiation at 75° is only 18% of the corresponding value which can be measured at 30°N; only by June are equal amounts of light received at both latitudes (Perl, 1935). For strains which live at high latitudes, it is therefore essential that the induction of erect thalli is not prevented at such short daylengths as in strains living at medium or low latitudes. Another reason for the phenomenon of increasing critical daylength in northern strains may be seen in the fact that the medium daylengths occupy a comparatively short period in spring in the high north, so that there is no need for a sharp critical daylength in the medium range of daylengths.

Obviously, the probably perennial crust represents the growth form best-adapted to survive both severe winter conditions, especially at northern latitudes, and high summer temperatures in the south. The erect thalli of *Scytosiphon lomentaria* disappear in the field during May in the Adriatic Sea (Munda, 1973); by July in the North Sea, at Helgoland; but can still be found in August in Iceland (Munda, 1972). These geographical differences, which are evident again in the phenological pattern of *Petalonia fascia* (Roeleveld *et al.*, 1974), may simply reflect the fact that the erect thalli appear later in the year from south to north and disappear after a certain time interval due to complete disintegration after sporulation. However, it remains to be established whether or not there is also a differential resistance in the crust and the erect thallus towards high temperatures. If it could be demonstrated that the erect thalli do not withstand temperatures as high as do the crusts, it might be understood why the induction of erect thalli is restricted to a comparatively short period in winter in strains living near the southern limit of the species. For instance, based on the present determinations of critical daylength (at 10 and 15°C, Fig. 2), a substantial percentage (more than 50%) of the Mexican plants is induced to form erect thalli only in December and January (Table II).

2. *Photoperiodism in* Bonnemaisonia hamifera

The heteromorphic life-history of *Bonnemaisonia hamifera*, which as the gametophyte alternates with the tetrasporangial phase sometime known as *Trailliella intricata*, was discovered by Koch (1950) in the following way: "At the end of November 1946 tetrasporangia developed in the cultures, which had been standing on the north-east window of the laboratory since summer". From released tetraspores, the gametophytes developed; this life history therefore emerged as previously predicted by Feldmann and Feldmann (1941), who had already clarified the life history of *Asparagopsis armata* and its tetrasporophyte, *Falkenbergia rufolanosa*. Afterwards, Koch was not able to induce tetrasporangia when he continued the culture of the *Trailliella*-phase in a constant temperature room (personal communication). This same difficulty was experienced later on by Shevlin and Polanshek (1978), who cultured the tetrasporangial phase of the Pacific *Bonnemaisonia geniculata*, but could only obtain vegetative growth.

In the course of the present study three isolates of the *Trailliella*-phase, which had been isolated from Helgoland material in 1944 (W. Koch), 1959 (D. Müller), and 1961 (P. Kornmann) and thereafter propagated vegetatively in different laboratories, were cultured at four temperatures and three different daylength regimes. Tetrasporangia were formed in all three isolates in only one set of the 12 possible sets of conditions, that of 8 h light per day and at a temperature of 15°C (Table III, expts 1–3; Fig. 4). Since sporangia were formed neither at 16 h light per day nor in the night-break regime, this response is genuinely photoperiodic, occurring over a narrow temperature range. However, up to 10% only of the tufts had formed sporangia in the short-day regime (15°C), and this only after a long treatment under inductive conditions. Obviously, secondary factors inhibited the expression of the response. When the photon flux density was raised to 20 μE/m^2/s and – more importantly – the

Table III. Formation of tetrasporangia in different isolates of the *Trailliella*-phase of *Bonnemaisonia hamifera* at 8 or 16 h light per day, and in a night-break regime (B; 8:$\overline{7.5}$:1:$\overline{7.5}$), at four temperatures (expts 1–3) as well as at different nutrient concentrations (expt 4, modified PES). T: Tetrasporangia were formed (percentage in brackets); v: plants remained vegetative.

Expt No.	Strain	Medium	Duration of expt (weeks)	Photon flux density (μE/m^2/s)	5°C			10°C			15°C			20°C		
					8	B	16	8	B	16	8	B	16	8	B	16
1	2080[a]	PES	18	12	v	v	v	v	v	v	T (<10)	v	v	v	v	v
2	2089[b]	PES	18	12	v	v	v	v	v	v	T (<10)	v	v	v	v	v
3	2123[c]	PES	12	12	v	v	v	v	v	v	T (<10)	v	v	v	v	v
					ml of Provasoli enrichment[d] added to 1 litre of sea water[e]											
					0		0.02		0.1		0.2	1	2			20
4	2080[a]	mod. PES	4	20	T(80)		T(96)		T(75)		T(51)	T(52)	T(50)			T(29)

[a] isolated by P. Kornmann in 1961. [b] isolated by D. Müller in 1959. [c] isolated by W. Koch in 1944. [d] 1 ml contained 28 μm NO_3–N. [e] 1 litre contained 16 μm NO_3–N.

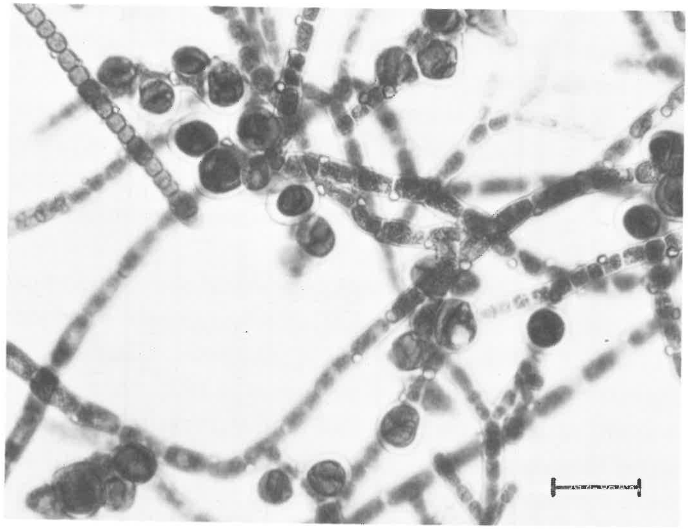

Fig. 4. *Trailliella*-phase of *Bonnemaisonia hamifera* with tetrasporangia, cultured at 8 h light per day and 15°C. Scale represents 100 μm.

plants were cultured during the treatments in sea water, to which had been added either none at all or only 0.02–0.1 ml per litre of Provasoli enrichment, instead of the 20 ml of the original formula (Provasoli, 1968), more than 75% of the tufts formed sporangia at $8:\overline{16}$ and 15°C; the controls in the night-break regime remained solely vegetative (Table III, expt 4). If it is nitrate which at too high a concentration inhibits the onset of reproduction, as is known in the case of several unicellular algae (see Dring, 1974) and also in the *Falkenbergia*-phase of *Asparagopsis armata* (Oza, 1976), significant inhibition of tetrasporangium formation would occur in the *Trailliella*-phase from about 20 μm NO_3–N onwards, corresponding to an addition of 0.2 ml Provasoli enrichment to 1 litre of sea water (containing already 16 μm NO_3–N, Table III). Although the media were changed twice a week in this experiment, in plain sea water there was a tendency for the plants to bleach out. In further experiments, a medium was used which contained 0.1 ml Provasoli enrichment added to 1 litre of sea water, so that in spite of the nutrients added a high percentage reaction could still be obtained (Table III).

From the tetraspores, some of which had already been released 4 weeks after the beginning of the inductive treatment, male and female gametophytes developed; these became fertile after 3–4 months when cultured in continuous white fluorescent light (20 $\mu E/m^2/s$), at 15°C.

In another experiment, the critical daylength for formation of tetrasporangia was determined at 15°C. After 4 weeks at 8–16 h light per day (hourly intervals) the following percentages of plants bearing tetrasporangia were obtained: more than 92% at 8 and 9 h; 48% at 10 h; 6% at 11 h; 0% from 12 h onwards. Since daylength at Helgoland is still 12.2 h on 21 September (Table II), one may infer that the *Trailliella*-phase must remain vegetative until about this time. In fact, tetrasporangia are found in this plant at Helgoland only from October to December (Kornmann and Sahling, 1977). However, the species invaded the Atlantic only at the end of the last century, originating probably from Japan (see Koch, 1951); one is perhaps more justified in comparing its photoperiodic behaviour with the environmental conditions prevailing at the original locations. In Japan (Fukuoka-Prefecture, Kyushu; 34°N), the *Trailliella*-phase of *Bonnemaisonia hamifera* forms tetrasporangia in the field also from October onwards (daylength < 12 h; see Table II), tetraspores being released in November and December, according to Chihara (1961). The same author reported that the gametophytes in the field in November (17°C), grow throughout the winter (temperature minimum in February, 13°C), attain their maximum size and fertility in late spring (May: 15°C), and disappear soon after release of the carpospores, by mid-summer. At this time the temperature at the Japanese locality begins to rise from 20 to 25°C, so that the species seems to persist through the summer in the form of the *Trailliella*-phase, a similar phenomenon to that seen in *Porphyra tenera*, which passes the summer as the *Conchocelis*-phase (Kurogi, 1959). Chihara (1961) already suspected that daylength might control the onset of sporulation in the *Trailliella*-phase and the present results, which show the effectiveness of the night-break, confirm this hypothesis.

Clearly, the *Trailliella*-phase is able to distinguish between autumn and spring, since formation of tetrasporangia does not occur under short-day conditions when water temperature is 5 or 10°C (Table III). It will be necessary to determine the exact temperature interval which permits induction by a short photoperiod to take place. As to the temperature regime at the original locations, one may predict that the temperature optimum for photoperiodic induction will more probably occur between 15 and 20°C than between 10 and 15°C. Furthermore, the fact that gametophytes are present on the coasts of France and of the British Isles, but that only tetrasporophytes have been found on Scandinavian coasts (Feldman, 1956), may here find explanation. At northern latitudes, temperature may be too low in those autumn months in which daylength has become short enough for photoperiodic induction of sporangium formation (Table II). At Helgoland, where the gametophytes have only been found sporadically in the field (Kornmann and Sahling, 1977), an additional difficulty for their survival may exist in the extremely low light available because of turbid water during the winter months. Nevertheless, gametophytes were very common in the field on Helgoland in 1968 and 1969 (Kornmann and Sahling, 1977), and it is interesting to note that in 1966 and 1967 water temperatures in September were higher by 0.7–0.8°C than the 10-year mean for this month (1965–1975; Weigel, 1978). By contrast, in 1965 and from 1970 onwards, when no gametophytes of *Bonnemaisonia hamifera* were observed in the field, September temperatures have been below the 10-year mean (Treutner, personal communication).

The combination of a short-day regime and high temperatures required for tetrasporangia formation in this alga is unusual in normal culture conditions, where at most "spring" (short days and low temperatures) is imitated, not "autumn", as required here. This explains why other workers (e.g. Koch, Kornmann, Müller; personal communication) failed to obtain tetrasporangia in the *Trailliella* isolates which they cultured for many years in growth chambers with artificial illumination.

3. Photoperiodism in Monostroma grevillei

Monostroma grevillei has a heteromorphic life-history, the blades representing the dioecious gametophytes and the *Codiolum*-stage, which develops after copulation of the anisogamous biflagellate gametes, the sporophyte; this latter reproduces the blades again by means of quadriflagellate zoospores (Kornmann, 1962a; Kornmann

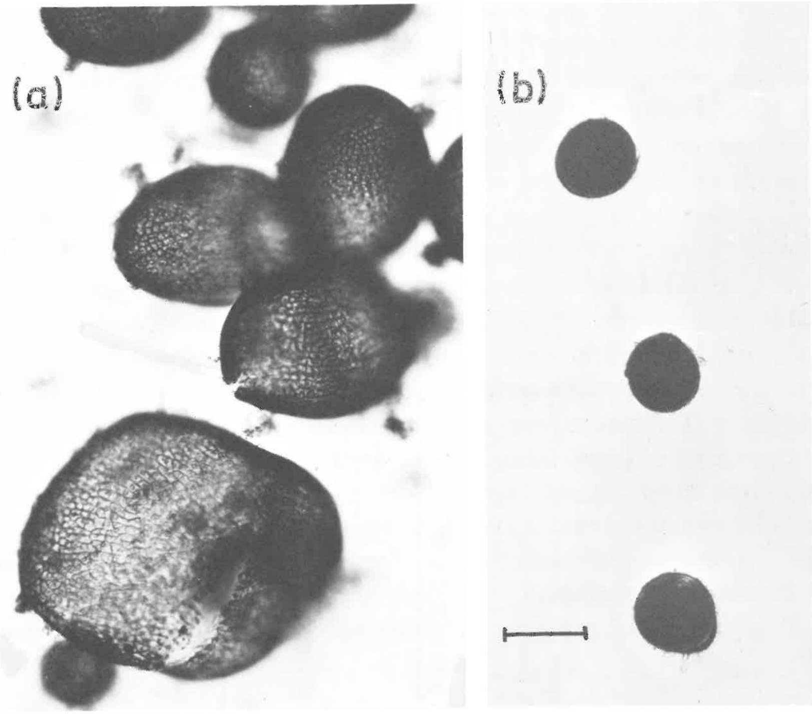

Fig. 5. *Monostroma grevillei* cultured for 20 weeks from zygotes at 5°C and 8 h (a) or 16 h (b) light per day. (a) Saccate thalli have been formed from prostrate systems developed from zoospores which were released by *Codiolum*-stage. (b) *Codiolum*-stage has remained vegetative since start of experiment. Scale represents 100 μm.

and Sahling, 1962, 1977). As can be seen from Table IV (expt 1), the *Codiolum*-stage became sporogenous only in short days (8:16) and at temperatures from 5–15°C (with a low percentage at the uppermost temperature). From the zoospores prostrate discs developed, and from these the saccate fronds arose (Fig. 5a). Under long-day conditions, however, the *Codiolum*-stage remained vegetative for at least 20 weeks (Fig. 5b). Since the same reaction occurred also in the night-break regime at all temperatures (Table IV), the induction of zoospore formation is obviously due to a genuine photoperiodic response in this alga. In three *Monostroma* spp. occurring in Japan, Tatewaki (1972) also found that the *Codiolum*-

Table IV. Development of *Codiolum*-stages and gametophytes of *Monostroma grevillei* at 8 or 16 h light per day, and in a night-break regime (B; $8:\overline{7.5}:1:\overline{7.5}$) at four temperatures. *Codiolum*-stages were grown from zygotes, gametophytes from germlings derived from zoospores of *Codiolum*-stages. S: > 60% of *Codiolum*-stages sporogenous; (S): < 10% of *Codiolum*-stages sporogenous; v: all *Codiolum*-stages vegetative; D: prostrate disc of gametophyte only; E: erect, saccate fronds formed from all prostrate discs.

Expt No.	Stage	Duration of expt (weeks)	5°C			10°C			15°C			20°C		
			8	B	16	8	B	16	8	B	16	8	B	16
1	*Codiolum*	10	S	v	v	S	v	v	(S)	v	v	v	v	v
2	Gametophyte	7	E	E	E	E	E	E	D	D	D	D	D	D

stages ("cysts") involved in the life histories require short days (10:$\overline{14}$) and lower temperatures for spore formation.

Once the zoospores have been released and have germinated into small discs, the erect, saccate fronds (later splitting into blades) are formed irrespective of daylength, but only at lower temperatures (Table IV, expt 2). This again has already been stressed in the case of several species by Tatewaki (1972) and in the case of *Monostroma grevillei* by Kornmann (1962).

On Helgoland, the species occurs in form of the blades only from March to May (Kornmann and Sahling, 1977). Although the critical daylength for spore formation still has to be determined, one may postulate that the seasonal cycle of *Monostroma grevillei* is regulated in the following way by daylength and temperature. The zygotes derived from gametes released by the blades in spring remain vegetative and survive the summer as the *Codiolum*-stage, since daylength is too long. In autumn, daylength becomes suitable for induction of spore formation, but temperature is too high in many locations. Only in late winter and early spring does the temperature become low enough to allow photoperiodic induction of spore formation, as long as the days are short enough.

4. Regulation by Temperature

Although it is clear from the foregoing that in true photoperiodic responses induction is possible only in a definite although often rather broad temperature range, the actual triggering factor in such reactions is daylength, or better, nightlength. On the other hand, there are clear-cut cases in which daylength is not involved at all in triggering the formation of a certain stage in the life history of a certain alga; temperature or other environmental phenomena, such as light quality (e.g. induction of fertility by blue light and UV in laminarian gametophytes; Lüning and Dring, 1975), are their primary factors.

Table V summarizes the results found on the development of specific stages of various algae not influenced by daylength.

In the life history of *Monostroma arcticum* no sexual stages are involved; the blades reproduce themselves by biflagellate zoospores giving rise to a prostrate disc, from which the blades develop as saccate thalli at low temperature (Kornmann and Sahling, 1962).

Table V. Development of specific stages of various algae at 8 or 16 h light per day, and in a night-break regime (B; $8:\overline{7.5}:1:\overline{7.5}$) at four temperatures. P: prostrate system; E: erect thalli arise from prostrate system (> 50%); F: fertile (> 50%); v: all plants vegetative; C: conchosporangia formed; R: released; N: not released. Symbols in brackets: < 10% of plants formed stage indicated by symbol; –: no survival.

Species	Duration of expt (weeks)	5°C			10°C			15°C			20°C		
		8	B	16	8	B	16	8	B	16	8	B	16
Monostroma arcticum[a, b]	18	E	E	E	E	E	E	P	P	P	P	P	P
Acrosiphonia arcta[a, c]	5	E	E	E	E	E	E	E	E	E	P	P	P
Desmarestia viridis[a, d]	5	F	F	F	(F)	(F)	(F)	v	v	v	v	v	v
Desmarestia aculeata[a, b]	5	F	F	F	F	F	F	v	v	v	v	v	v
Chorda filum[d, e, f]	5	F	F	F	F	F	F	v	v	v	v	v	v
Laminaria digitata[a, d, e]	5	F	F	F	F	F	F	F	F	F	v	v	v
Laminaria hyperborea[a, d, e]	5	F	F	F	F	F	F	F	F	F	v	v	v
Laminaria saccharina[a, d, e]	5	F	F	F	F	F	F	F	F	F	v	v	v
Laminaria japonica Areschoug[d, e, g]	5	F	F	F	F	F	F	F	F	F	v	v	v
Macrocystis pyrifera (L.) C.Ag.[d, e, h]	5	F	F	F	F	F	F	F	F	F	v	v	v
Porphyra miniata[i]	10	C	C	C	C	C	C	C	C	C	–	–	–
Porphyra miniata[i]	20	R	R	R	N	N	N	N	N	N	N	N	N
Lomentaria orcadensis[j]	8	–	–	–	E	E	E	E	E	E	E	E	E

[a] Origin: Helgoland, Germany.
[b] Grown from zoospores of field material.
[c] Grown from gametes of field material.
[d] Started from unialgal culture of filamentous gametophytes.
[e] Male and female gametophytes mixed together. F applies to both sexes.
[f] Origin: Tromsö, Norway.
[g] Origin: Yoishi, Japan; isolated by Y. Sanbonsuga.
[h] Origin: Santa Barbara, California.
[i] Origin: Halifax, Nova Scotia; isolated by L. C. -M. Chen.
[j] Grown from tetraspores of plant from unialgal culture.

As can be seen from Table V, the formation of saccate thalli takes place at 5–10°C, and no photoperiodism is involved, as in the development of the corresponding stage in *M. grevillei* (see above). Saccate thalli transferred to higher temperatures matured at all temperatures from 5–15°C, as already reported by Kornmann and Sahling (1962), irrespective of daylength. *M. arcticum* obviously survives the summer as a disc, and the formation of blades is exclusively induced by appropriately low temperatures in early spring.

The life history of *Acrosiphonia arcta* (Dillw.) J.Ag., in which according to Kornmann (1962b) the filamentous, erect gametophytes reproduce themselves directly from the zygote (or parthenogenetically from gametes), also seems to be regulated exclusively by temperature. From the swarmers of the erect plants, rhizoidal prostrate systems were formed at all temperatures investigated, and erect, filamentous thalli were formed in the range 5–15°C, irrespective of daylength (Table V). In late summer, the formation of erect thalli is thus blocked by high temperatures and the prostrate, rhizoidal system is formed instead; this latter represents the perennial part of the plant and is induced in winter by low temperatures to form the erect thalli again (Kornmann, 1962b).

In the Phaeophyta, the gametophytes of two species of *Desmarestia* and of six species of the Laminariales were investigated (Table V). The general result was that the gametophytes became fertile, irrespective of daylength, at temperatures from 5 to 10°C (*Desmarestia* spp., *Chorda filum*) or from 5 to 15°C (Laminariales). Hence, no photoperiodism seems to be involved in the maturation of the gametophytes, as reported earlier in the case of *Laminaria saccharina* (Lüning and Dring, 1975). Blue light is required for induction of fertility (Lüning and Dring, 1975), and the quantum dose required for induction increases with temperature (Lüning, 1980). High temperatures (e.g. 15–20°C in the case of the *Desmarestia* spp. and *Chorda filum*; 20°C in the case of the Laminariales) block reproduction completely. The fact that no photoperiodism is involved in the maturation of the gametophytes does not rule out, but makes even more likely, the possibility that the sporophytes may become sporogenous at appropriate daylengths only. However, nothing is known about this matter at present.

In the *Conchocelis*-phase of the red alga *Porphyra miniata*, higher temperatures prevent the discharge of conchosporangia which, according to Chen *et al.* (1970), are formed in a broad temperature range. In the present study, it was found that daylength is not involved in the formation of conchosporangia in this species (Table V). In accordance with the results of the authors cited, conchosporangia were formed at all temperatures and daylengths (although 20°C was not survived), but conchospore release occurred only at 5°C, again irrespective of daylength (Table V). This reaction represents a special type of regulation of seasonal development, in that the conchosporangia are formed and are present under a wide range of environmental conditions, but are released only as a result of induction by low temperatures.

The red alga *Lomentaria orcadensis* which reproduces only by tetraspores, is found in the sublittoral zone on Helgoland from May until December (Kornmann and Sahling, 1977). The spores germinate to form crusts, and from these erect plants were formed at all daylength regimes in the temperature range 10–20°C (Table V). Obviously, the erect thalli can arise from the possibly perennial crusts as soon as water temperature is high enough in summer.

CONCLUSIONS

The foregoing examples may have demonstrated that it is possible by a relatively small number of critical treatments to elucidate the developmental responses triggered either by photoperiod or by temperature. It appears crucial that the algae are cultured in different daylength regimes, over the whole temperature range which they are able to survive. Otherwise one might miss a possible photoperiodic response, where this occurs only over a narrow temperature interval, as in the *Trailliella*-phase of *Bonnemaisonia hamifera*. One also has to note the possibility that a species has segregated into various ecotypes, all with different critical daylength and all differing slightly in the temperature range in which photoperiod induction can occur, as seen in the case of *Scytosiphon lomentaria*.

The photoperiodic responses reported above are short-day reactions which occur only when daylength has fallen below a critical value. They are all inhibited by long days (short nights) or – as in many higher short-day plants (Vince-Prue, 1975) – by a night-break regime (two short nights per 24 h) which is photosynthetically almost identical with the short-day regime. However, in the crustose tetrasporophyte of the red alga *Acrosymphyton purpuriferum* (J.Ag.) Sjöst. which forms tetrasporangia only in short days, night-breaks of up to 1 h duration were not effective (Cortel-Breeman and Ten Hoopen, 1978).

In view of the great number of algal species which have still to be investigated as to the regulation of their life histories by photoperiod or temperature, it is premature to try to answer the question of whether regulation by one or the other factor is characteristic for certain ecological groups of species. For instance, the cases known in the Bangiophycidae (Dring, 1967; Rentschler, 1967; Richardson and Dixon, 1968), in the Scytosiphonales and in *Monostroma grevillei* seems to support as plausible the idea that photoperiodism will mainly be found in eulittoral species, for which water temperature is too variable an environmental signal for the detection of season. On the other hand, there are also non-photoperiodic species in the eulittoral region (Table V), and the photoperiodically active red algae *Bonnemaisonia hamifera*, *Calosiphonia vermicularis* (Mayhoub, 1976) and *Constantinea subulifera* Setchell (Powell, 1964) are all sublittoral species. There is no reason why photoperiod should not trigger the seasonal development of algae even at the lower limit of the phytal region, at 150–200 m depth in clear waters, provided that a pigment other than phytochrome transmits the photomorphogenetic stimulus. As Dring (1971) pointed out, the red/far red system (phytochrome) could theoretically still operate through much of the phytal region in coastal "green" waters, where the vertical extension of the phytal region does not reach such great depth as in clear "blue" waters. According to the same author, red and even far red light, although penetrating poorly into water, could still saturate the phytochrome system of sublittoral algae where present in these plants at moderate water depths; there, the plants would exhibit the low saturation levels which are characteristic of phytochrome. However, the finding that exclusively blue light (and probably UV) is effective as night-break in the photo-periodic response of *Scytosiphon lomentaria* suggests the possibility that several different photomorphogenetically-active pigments, independent of red or far red light, may have developed during the evolution of these algae. From both a photobiological and an ecological point of view, it will be interesting to see which pigments mediate the photoperiodic responses in the green alga *Monostroma grevillei* and in the three sublittoral red algal species mentioned above.

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