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Photoperiodic and temperature responses in the reproduction of north-eastern Atlantic *Gigartina acicularis* (Rhodophyta: Gigartinales)

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Gigartina acicularis (Roth) Lamour., a predominantly intertidal red alga, has only rarely been found with reproductive structures in the British Isles and northern France. Elsewhere in the north-eastern Atlantic, reports of cystocarpic plants are largely from November to February while those of tetrasporangial plants are from July to October. Male and female plants formed gametangia only at daylengths of 12 h or less and at temperatures of 14–18°C. Photon exposures ≥ 1.5 mmol m^{-2} of incandescent light, given in the middle of a 16 h dark period at 16°C, completely inhibited cystocarp formation, although some carpogonial branches were formed at up to 3.34 mmol m^{-2}. Five photoperiodic cycles of $8:\overline{16}$ h at 16°C were the minimum necessary to induce the formation of carpogonial branches and cystocarps. Carpospores gave rise to plants which formed tetrasporangia at daylengths of 16, 12, 10 and 8 h at 16°C. The precise photoperiodic and temperature requirements for gametangial reproduction in *G. acicularis* result in gamete formation being limited to autumn in north-eastern Atlantic populations. It is suggested that, in the northern part of its range, populations of *G. acicularis* are largely maintained by vegetative propagation. As one goes further south the gametangial reproductive 'window' gradually enlarges due to higher ambient temperatures in the autumn. The paucity of records of tetrasporangial plants in the British Isles, however, needs further investigation. This is the first report of photoperiodic control of gametogenesis in the Rhodophyta and the response would appear to be true and absolute.

INTRODUCTION

Gigartina acicularis (Roth) Lamouroux [see Dixon and Irvine (1977) for change in nomenclature] (Rhodophyta) is a narrow, terete to slightly flattened, sparingly branched species found in intertidal or shallow subtidal habitats in the Atlantic and the Mediterranean. It grows most commonly on rocks in sheltered, silty situations, where it often forms conspicuous turfs. In the Atlantic the species has been reported from the British Isles south to Cameroun and from North Carolina south to Uruguay (Dixon & Irvine 1977). Some difficulties have been experienced in distinguishing between certain forms of this species and *G. teedii* (Roth) Lamouroux, a species with a similar geographical distribution in the north-eastern Atlantic. Forms intermediate in morphology have frequently been reported (Harvey 1833; Gayral 1958; Hoek & Donze 1966; Dixon & Irvine 1977), but Guiry (1984) has shown that cultured plants of these two species from the Atlantic will not hybridize. These difficulties of identification have been compounded by the virtual absence of reports of reproductive material of *G. acicularis,* particularly in the north-eastern Atlantic. In the British Isles cystocarpic plants have apparently been found only once (Devon in January 1829; material in BM) and records of tetrasporangial plants are also very rare (Galway Bay, November 1966; material in GALW). Elsewhere in the eastern Atlantic reproductive records for *G. acicularis* are as follows: Gayral (1966) reported cystocarpic plants from November to February on the north coast of France; Seoane-Camba (1965) found cystocarpic plants in January and February on the north coast of Spain, and tetrasporangial plants in July, August and September; in Portugal, Ardré (1969) collected tetrasporangial plants in October but did not report any other reproduction; Gayral (1958) reported cystocarpic plants from August to March on the coast of Morocco. In the British Isles, casual examination of populations by one of us

(M.D.G.) over the past decade has revealed not a single fertile plant. Cystocarpic and tetrasporangial plants were, however, common at Sines and Sagres, Portugal in January 1977, and cystocarpic plants were abundant at La Toja, Galicia, Spain in January 1978. The available phenological data on the formation of cystocarps in *G. acicularis* suggested a photoperiodic response similar to that described by Lüning (1980, 1981a, 1981b) for the formation of tetrasporangia in the *Trailliella*-phase of *Bonnemaisonia hamifera* Hariot. Using cultured plants isolated from the north coast of France and from the south coast of England we here attempt to explain the reproductive periodicity of *G. acicularis* and the lack of records of reproductive plants from the British Isles. A preliminary account of this study was given in Guiry and Cunningham (1983).

MATERIALS AND METHODS

Initial attempts to isolate *Gigartina acicularis* into culture using plants collected in January in Portugal (1977) and Spain (1978) were unsuccessful owing to necrosis (cf. West & Guiry 1982, p. 206), which is enhanced by the use of full-strength, enriched seawater media. Tetrasporangial plants of *Gigartina acicularis* were collected in the lower intertidal at Santec, a few kilometres west of Roscoff, on the north coast of France on 15 September 1981. Cultures (isolate 382) were established from tetraspores released overnight at room temperature (approx. 15°C) and inoculated onto glass slides using a fine Pasteur pipette. The plants were initially grown in a north-facing window at the Station Biologique de Roscoff with frequent changes of unenriched sterile seawater. The resulting sporelings were transported to Ireland in a cooled container. Additionally, plants were isolated vegetatively from *G. acicularis* populations from mid-intertidal pools at Kimmeridge Ledges, Dorset, UK in April 1981 (isolate 371). Whole plants were transported to Ireland in sterilized seawater in a cooled container. Growing tips were excised and cultured in enriched seawater at low photon flux densities (3–5 μmol m^{-2} s^{-1}) at 16 ± 1°C, 16:$\bar{8}$ h until the plants were free of algal contaminants.

Plants were grown in several types of enriched-seawater media throughout this study but for each experiment the medium type was standard. Initially, plants were grown in quarter-strength Provasoli's Enriched Seawater [PES; West's modification in McLachlan (1973) except that the disodium glycerophosphate concentration was reduced by half]. Due to a bacterial contaminant, a spore-forming *Bacillus* species which now seems to be common in many laboratories culturing marine algae, and which is resistant to a wide range of antibiotics (West & Guiry unpubl. data), plants were later grown in a modification of Von Stosch's medium (VS). Our VS is composed of equal volumes of the following stock solutions (all in 500 ml glass-distilled water): 21.26 g $NaNO_3$; 2.68 g Na_2 DL-beta-glycerophosphate; 0.139 g $FeSO_4 \cdot 7H_2O$; 0.98 g Mn $Cl_2 \cdot 4H_2O$; 1.86 g Na_2 EDTA$\cdot 2H_2O$; 0.05 g Biotin; and 0.1 g Aneurine HCl and 0.2 mg Vitamin B_{12}. Two media types are made up from this stock solution: half-strength VS, to which 10 ml of VS solution is added to each litre of sterilized seawater and quarter-strength, to which 5 ml is added. The absence of a TRIS buffer in VS may help to reduce bacterial contamination (cf. van der Meer 1982).

Photon flux densities were measured using a LI-COR Model 185-B meter and a LI-190SB quantum sensor. Light sources were directly above the cultures and reflected light from the sides and bases of the culture cabinets was taken into account in all measurements. Fluorescent light was provided by cool-white 65/80 W tubes; incandescent light was provided by 60 W household tungsten bulbs. Temperature was measured using nickel-chromium/nickel-aluminium thermocouples immersed in 250 ml distilled water. (This was the volume of the culture medium used in the temperature experiments.) In all studies temperature is expressed as the variation found in these volumes of water.

A preliminary study of a field population of *Gigartina acicularis* at New Quay, Co. Clare, Ireland (53°09.5'N, 9°05'W) was carried out from September 1982 through April 1983. The site was visited at fortnightly intervals. Plants were sampled haphazardly within a 0.025 m^2 fixed quadrat. These samples were examined microscopically in the laboratory for reproduction. Seawater temperatures were taken at the turn of the tide.

Seawater temperatures for the period 1974–1981 were obtained from the Shellfish Research Laboratory, Carna, Co. Galway, which is about 75 km due west of the New Quay site. Temperature is continuously recorded at the intake point for the Laboratory's seawater pumps. Daylength readings were obtained for Shannon Airport, Co.

Clare which is about 70 km south of the study site.

RESULTS

Growth of plants in culture

Vegetative plants from Britain (isolate 371) grown in full-strength media became green distally and ultimately died. Eventually, it was found that quarter-strength PES or VS would support growth. A single vegetative plant was isolated which when 25–30 mm long grew at 5–7 mm per week at 16 ± 1°C, 16:$\bar{8}$ h, 20–25 μmol m^{-2} s^{-1}. Plants grown from this isolate did not reproduce over a period of 8 months under these conditions. On transferring some of these plants to 16 ± 1°C, 8:$\overline{16}$ h, 20 μmol m^{-2} s^{-1}, spermatangia were formed after 8 days whereas plants retained at 16:$\bar{8}$ h remained sterile. Growth was slower under this short-day regime, only 1–3 mm of new tissue being formed each week on plants 25–30 mm long. These plants resembled the French isolate described below but had a lighter colour (Figs 4a–c).

Tetraspores released from field plants from France (isolate 382) had formed small discs about 100 μm in diameter on arrival in our laboratory. After 15 days at 16 ± 1°C, 16:$\bar{8}$ h, 25 μmol m^{-2} s^{-1} in quarter-strength PES, discs about 150 μm in diameter had single upright fronds up to 200 μm long and both discs and uprights had a few hyaline hairs up to 250 μm long. Upright fronds grew rapidly, reaching 4 mm long (discs to 400 μm) after 29 days. At 57 days the plants were about 17 mm long but no reproduction had taken place. Some plants were then transferred to 16 ± 1°C, 8:$\overline{16}$ h, 20 μmol m^{-2} s^{-1}. After 13 days under this regime spermatangia and carpogonial branches were apparent on separate plants but plants retained at 16 ± 1°C, 16:$\bar{8}$ h, 25 μmol m^{-2} s^{-1} remained sterile. Carpogonial branches were formed on new tissue at the apices of the main axes and the lateral branches; the fertile area was often distinctly swollen (Figs 1a, b). Trichogynes were easily observed as very large numbers were formed and they protruded 150–350 μm beyond the surface of the thallus. Spermatia could be clearly seen adhering to the trichogynes, even under a dissecting microscope. Spermatangia were formed in a continuous sorus 4–5 mm below the apices (Figs 2a, b) which, after the cuticle had been shed, released spermatia continuously. Male and female plants were isolated into separate culture for further investigation of the photoperiodic response.

Effects of temperature on cystocarp formation

Stock cultures of male plants of isolate 382 from France were maintained at 16 ± 1°C, 8:$\overline{16}$ h, 20 μmol m^{-2} s^{-1}, and female plants were grown at 16 ± 1°C, 16:$\bar{8}$ h, 20 μmol m^{-2} s^{-1}, for at least one month beforehand. Under these conditions the males formed an abundance of spermatia and the females did not form carpogonial branches. Each experimental culture dish contained one pretreated male and five pretreated female plants. The dishes were then placed at 8:$\overline{16}$ h, 20–30 μmol m^{-2} s^{-1}, at each of the temperatures shown in Table 1. Plants were examined at regular intervals with a dissecting microscope; cystocarps were deemed to have formed when a noticeable bulge was apparent on the thallus surface. After 17 days all cultures were transferred to 13 ± 1°C, 16:$\bar{8}$ h, 20 μmol m^{-2} s^{-1}, to await the development of cystocarps, at which time the male plant was also removed. Cystocarps (Figs 3a, b) were formed only in cultures maintained at 14–18°C inclusive (Table 1), and were formed most rapidly, 7–9 days after the start of the cross, at 16°C. Carpospores were not released in most instances although carposporophytes were present in all cystocarps sectioned. A transfer to 10°C is generally necessary for carpospore release. A replicate experiment at 1°C intervals from 16 to 20°C gave similar results. Controls maintained at 16:$\bar{8}$ h at 16 and 10°C did not form cystocarps.

Effects of daylength and night-breaks on formation of gametangia

Plants (isolate 382) were preconditioned as described in the previous section. One male and five female plants were placed in each dish and were then grown at 16 ± 1°C, 20–30 μmol m^{-2} s^{-1}, at the photoperiods shown in Table 2. The cultures were monitored at regular intervals and were removed to non-inducing conditions (16 ± 1°C, 16:$\bar{8}$ h, 20 μmol m^{-2} s^{-1}) after 17 days. Cystocarps were formed only on female plants subjected to daylengths of 12 h and less (Table 2). Cystocarps were formed most rapidly, and in larger numbers, at daylengths of 8 h. There would seem to be a gradual increase in the time necessary for formation and a reduction in the number of fertile plants with increasing daylength

Table 1. Effects of temperature on cystocarp formation in *Gigartina acicularis* (strain 382 from France). Numbers indicate number of plants forming cystocarps in a dish of five plants. All cultures were given an 8:$\overline{16}$ h photoperiod at 20–30 μmol m^{-2} s^{-1} for 17 days at the temperatures shown and were then transferred to 16 ± 1°C, 16:$\overline{8}$ h, 25 μmol m^{-2} s^{-1}

Temperature (±1°C)	No. of days from start of cross											
	3	5	7	9	11	13	15	17	25	32	39	46
24	–	–	–	–	–	–	–	–	–	–	–	–
23	–	–	–	–	–	–	–	–	–	–	–	–
22	–	–	–	–	–	–	–	–	–	–	–	–
20	–	–	–	–	–	–	–	–	–	–	–	–
19	–	–	–	–	–	–	–	–	–	–	–	–
18	–	–	–	–	1	2	4	5	5	5	5	5
16	–	–	–	2	4	5	5	5	5	5	5	5
16*	–	–	1	4	5	5	5	5	5	5	5	5
14	–	–	–	–	1	2	3	5	5	5	5	5
13	–	–	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	–	–	–	–
10*	–	–	–	–	–	–	–	–	–	–	–	–

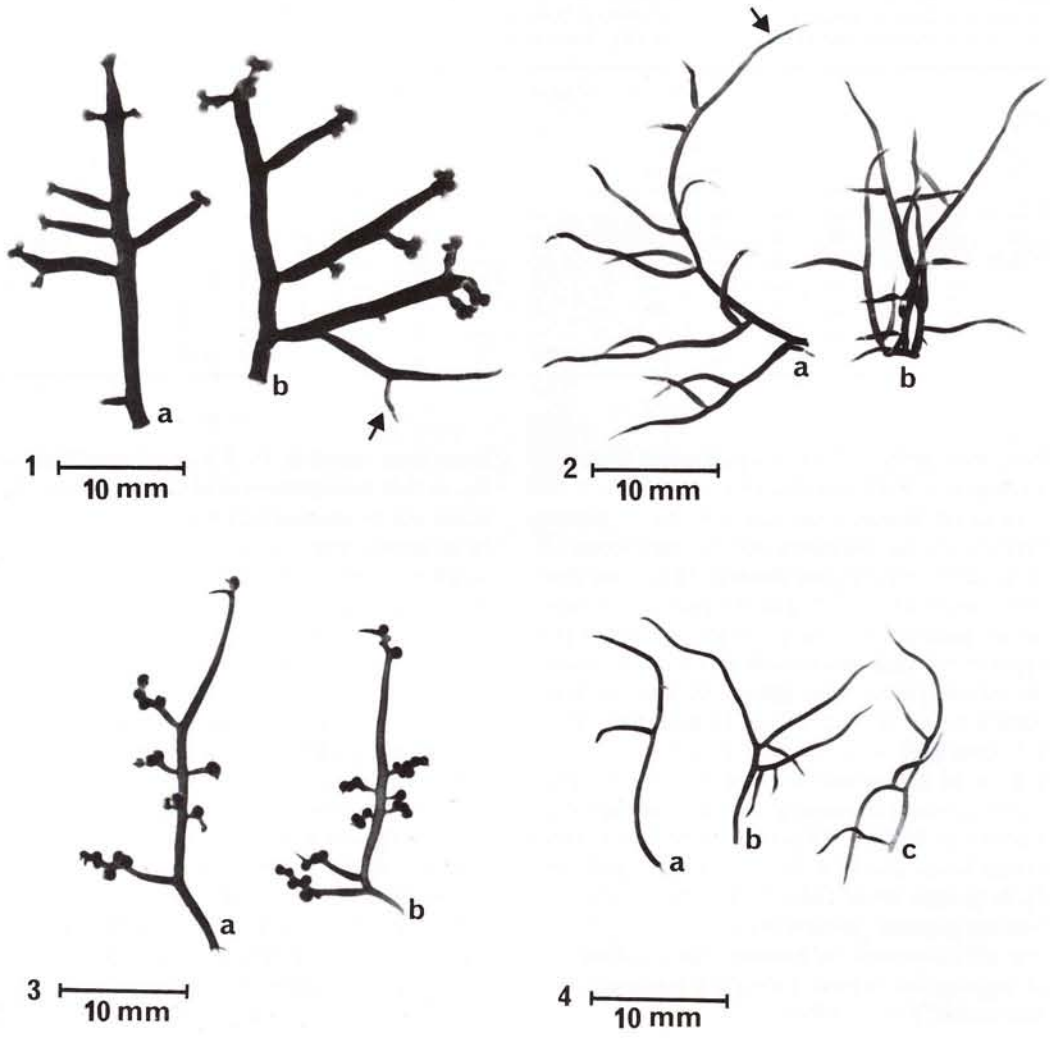
* Repeat.

(Table 2). Night-breaks in the middle of a 16 h night blocked reproduction, even when they consisted of only 10 min of incandescent light at 20 μmol m^{-2} s^{-1}. However, in one of three replicate experiments carried out at different times using a 1 h night-break with fluorescent light at 30 μmol m^{-2} s^{-1} a single cystocarp was formed after 39 days (Table 2); this cystocarp did not release spores, despite having being maintained at 15 and 10°C for 14 weeks after the conclusion of the experiment, and eventually degenerated without releasing spores. Trichogynes were not apparent on any of the plants grown at daylengths of >12 h, however, increasingly larger numbers were formed at daylengths of ≤12 h. It, unfortunately, proved impossible to quantify this effect. How-

Table 2. Effects of photoperiod on cystocarp formation in *Gigartina acicularis* (strain 382 from France). All cultures were grown at 16 ± 1°C. Numbers indicate number of plants per dish of five plants forming cystocarps after the specified period

Photoperiod (h) (light: dark)	Night break	No. of days from start of cross											
		3	5	7	9	11	13	15	17	25	32	39	46
16:8	–	–	–	–	–		–	–	–	–	–	–	–
16:8*	–	–	–	–	–	–	–	–	–	–	–	–	–
14:10	–	–	–	–	–	–	–	–	–	–	–	–	–
12:12	–	–	–	–	–	–	1	1	1	2	4	4	4
12:12*	–	–	–	–	–	–	1	1	1	1	1	1	1
10:14	–	–	–	–	–	1	3	4	4	5	5	5	5
10:14	–	–	–	–	–	–	3	4	5	5	5	5	5
8:16	–	–	–	–	–	2	4	5	5	5	5	5	5
8:16*	–	–	–	–	1	4	5	5	5	5	5	5	5
8:16	1 h	–	–	–	–	–	–	–	–	–	–	–	–
8:16	1 h*†	–	–	–	–	–	–	–	–	–	–	1	1
8:16	1 h*†	–	–	–	–	–	–	–	–	–	–	–	–
8:16	30 min‡	–	–	–	–	–	–	–	–	–	–	–	–
8:16	10 min‡	–	–	–	–	–	–	–	–	–	–	–	–

* Repeat.
† Fluorescent light at 30 μmol m^{-2} s^{-1} used as the night break.
‡ Incandescent light at 20 μmol m^{-2} s^{-1} used as the night break.



Figs 1-4. Morphology of fertile plants of *Gigartina acicularis* from France and England in culture.

Figs 1a, b. Female plants of isolate 382 from France. The plants were grown for several months at 16 + 1°C, 16:$\overline{8}$ h and then transferred to 16 ± 1°C, 8:$\overline{16}$ h; carpogonial branches are forming in large numbers in the swollen areas present at most of the tips. These branches more or less cease elongation and swollen tissue is formed continuously. Some branches resume growth and become acicular (arrow); these have smaller numbers of carpogonial branches.

Figs 2a, b. Male plants of isolate 382 from France. Spermatangial sori are forming at the tips (arrow). These plants were grown continuously under 16 ± 1°C, 8:$\overline{16}$ h; plants grown under long-day regimes are generally broader.

Figs 3a, b. Female plant of isolate 382 from France forming cystocarps at 16 ± 1°C, 8:$\overline{16}$ h. The female plants were grown under a photoregime of 8:$\overline{16}$ h prior to the introduction of a male plant, note the difference in morphology between these plants and those shown in Figs 1a, b, which were initially grown at 16:$\overline{8}$ h.

Figs 4a-c. Male plants of isolate 371 from England grown continuously at 16 ± 1°C, 8:$\overline{16}$ h; spermatangial sori are forming at the tips.

Table 3. Number of cycles of 8:$\overline{16}$ h photoperiod necessary to induce cystocarp formation in *Gigartina acicularis* (isolate 382 from France). Plants were transferred from an 8:$\overline{16}$ h photoregime at 16 ± 1°C after periods varying from 1 to 9 days (⊖ indicates time of transfer). Numbers of plants (of five) forming cystocarps are indicated

Number of days from start of cross																	
1	2	3	4	5	6	7	8	9	11	13	15	17	18	25	32	39	46
⊖	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	⊖	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	⊖	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	⊖	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	⊖	–	–	–	–	–	–	–	–	2	5	5	5	5
–	–	–	–	–	⊖	–	–	–	–	–	–	1	3	5	5	5	5
–	–	–	–	–	–	⊖	–	–	–	–	–	1	3	5	5	5	5
–	–	–	–	–	–	–	⊖	–	–	1	2	3	5	5	5	5	5
–	–	–	–	–	–	–	–	⊖	1	2	3	5	5	5	5	5	5

ever, the number of cystocarps formed is clearly a reflection of the number of trichogynes.

In order to determine the number of photoperiodic cycles necessary for the formation of cystocarps, male plants (isolate 382) were preconditioned as described in the previous section for at least two months prior to the start of the experiment. One fertile male plant and five sterile female plants were placed in each of nine culture dishes at 16 ± 1°C, 8:$\overline{16}$ h, 20 μmol m^{-2} s^{-1}. One dish was removed to 13 ± 1°C, 16:$\bar{8}$ h, at 24 h intervals for nine successive days. Cultures were examined at regular intervals over a period of 46 days. All plants formed cystocarps except those kept at 8:$\overline{16}$ h for 1–4 days (Table 3). It is clear from Table 3 that the greater the number of photo-inductive cycles, the more rapidly the cystocarps are formed. Again, inhibition of carpogonial branch formation seemed to be responsible for the effect.

In an attempt to determine the number of cycles necessary for the formation of spermatangia, male plants (isolate 382) were preconditioned for two months under non-inducing conditions at 16 ± 1°C, 16:$\bar{8}$ h, 20 μmol m^{-2} s^{-1}. Female plants were also preconditioned for two months under the same temperature and irradiance levels as the males but at 8:$\overline{16}$ h. At the end of this time, the female plants were forming numerous carpogonial branches in swollen areas at the tips of the branches. The experiment consisted of three male plants and three female plants placed in each of six dishes at 16 ± 1°C, 8:$\overline{16}$ h, 20 μmol m^{-2} s^{-1}, with one dish removed to non-inducing conditions every 24 h for 6 days. The male plants were removed after 14 days, at which time no spermatangia were apparent. The female plants exhibited a high degree of necrosis shortly after being transferred to 16:$\bar{8}$ h and fragmented easily, so that the numbers of plants with cystocarps could not be assessed. Cystocarps were apparent in all dishes after 14 days; they were formed in small numbers (1–3 per dish), and there was no pattern to their frequency of occurrence.

It seems likely from these results that despite the preconditioning of the male plants at 16:$\bar{8}$ h for two months prior to the start of the experiment, spermatangia were forming from spermatangial mother cells induced prior to this. Spermatangia in *Gigartina* species are difficult to detect, especially when present in small quantities. Although none were seen when the plants were examined at the beginning of the experiment, we are inclined towards the opinion that some were forming as there was no pattern in the frequency of occurrence of cystocarps as was found in the reciprocal experiment (Table 3).

Night-break photon exposure effects

Two male plants forming spermatangia and five preconditioned sterile female plants (isolate 382) were placed under a 8:$\overline{16}$ h photoregime with a 1 h light break in the middle of the 16 h dark period. The main 8 h light period was provided by cool-white fluorescent light at 16–25 μmol m^{-2} s^{-1} but the light break was given by an incandescent bulb at photon flux densities of 0.09–20 μmol m^{-2} s^{-1} (Table 4).

Cystocarps were formed only at the lowest photon exposures of 0.64 and 0.32 mmol m^{-2}; at the former exposure only one plant formed cystocarps and only two were produced on this plant; at the latter four plants eventually formed cystocarps but only a few were produced on each plant. The control, which did not receive any

Table 4. Night break photon exposures necessary for the inhibition of carpogonial branch and cystocarp formation in *Gigartina acicularis* (strain 382 from France). Two male plants forming spermatia and five sterile female plants were placed at 16 ± 1°C, with a 1 h light break in the middle of a 16 h night. The light break was provided by a tungsten bulb at the irradiances shown. The males were removed after 17 days and the female plants transferred to 13 ± 1°C, 16:$\overline{8}$ h, 25 μmol m^{-2} s^{-1}. Numbers indicate the number of plants forming cystocarps; t = trichogynes observed

Photon flux density (μmol m^{-2} s^{-1})	Photon exposures (mmol m^{-2})	No. of days from start of cross						
		13	15	19	23	26	30	42
20	72	—	—	—	—	—	—	—
10	36	—	—	—	—	—	—	—
5	18	—	—	—	—	—	—	—
2	7.2	—	—	—	—	—	—	—
0.93	3.34	—	—	—	t	t	t	t
0.42	1.51	—	—	—	t	t	t	t
0.18	0.64	—	t	t	1	1	1	1
0.09	0.32	—	t	t	1	3	4	4
Control	0	3	5	5	5	5	5	5

night-break, formed numerous cystocarps rapidly on all plants. Trichogynes were formed in small numbers on plants receiving photon exposures of 3.34 and 1.51 mmol m^{-2} (Table 4) but no cystocarps were formed on these plants; presumably the incidence of occurrence was too low to allow fertilization to take place. At photon exposures of 7.2 mmol m^{-2} and above, neither trichogynes nor cystocarps were formed. Unfortunately, it is impossible to count trichogyne numbers because they are clustered too closely together and the terete nature of the plant makes microscopic examination difficult.

Effects of daylength and temperature on tetrasporogenesis

Female plants of *Gigartina acicularis* from France (isolate 382) crossed to male plants from England (isolate 371) formed cystocarps which released carpospores at 10 but not at 15 or 20°C. These spores gave rise to plants similar in morphology to the gametangial plants except that they were darker in colour and less frequently branched. Initially plants were grown at 16 ± 1°C, 16:$\overline{8}$ h, 20–25 μmol m^{-2} s^{-1}. On reaching 11 mm long at 74 days, three plants were transferred to 16 ± 1°C, 8:$\overline{16}$ h, 20–25 μmol m^{-2} s^{-1}; tetrasporangia were formed on plants 14.5 mm long after 15 days. Plants retained at 16:$\overline{8}$ h did not, however, form tetrasporangia for a further 49 days and only one plant formed tetrasporangia on this occasion. Sterile plants from this culture were transferred to a variety of photoregimes at 16 ± 1°C (Table 5). Tetrasporangia were formed under all conditions tested, including a night-break regime. Shorter daylengths did tend to result in more rapid reproduction but the differences in timing for these mature plants were slight (Table 5). Plants forming tetrasporangia were transferred to 10 ± 1°C at 16:$\overline{8}$ h and 8:$\overline{16}$ h. The short-day regime caused almost immediate cessation of tetrasporogenesis but under the long-day regime the plants continued to form and release numerous tetraspores for about 6 weeks and then ceased.

Preliminary field studies

At the New Quay study site, a large population of *G. acicularis* occurs on silty rocks, boulders and stones at mean low water neap tides down to extreme low water spring tides in the area of a rapids system. No reproduction of *G. acicularis* was observed during October 1982 through April 1983. Temperature and daylength measure-

Table 5. Number of days to tetraspore release in mature tetrasporangial plants of *Gigartina acicularis*, grown under different photoregimes at 16 ± 1°C

Photoregime (h)	Number of days				
	3	5	7	9	11
16:$\overline{8}$	—	—	—	1	3
12:$\overline{12}$	—	—	3	3	3
10:$\overline{14}$	—	1	3	3	3
8:$\overline{16}$	—	1	3	3	3
8:$\overline{7.5}$:1:$\overline{7.5}$	—	—	3	3	3

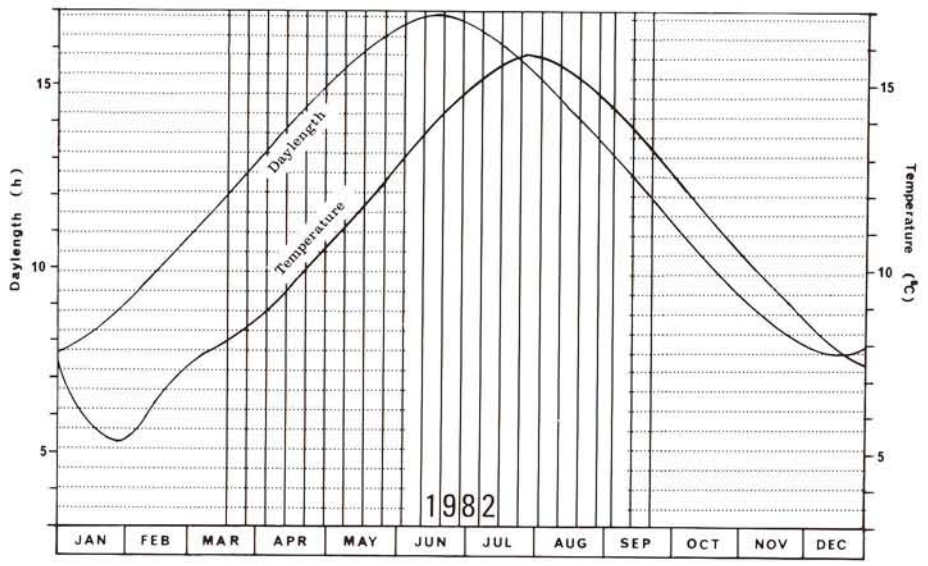


Fig. 5. Temperature and daylength curves for Galway Bay in 1982. Data from temperature readings taken at the Shellfish Research Laboratory, Carna, Co. Galway and from the field study site at New Quay (Sept.–Dec.). Vertical unbroken lines indicate inhibition of gametangial reproduction in *Gigartina acicularis* by daylengths of >12 h; horizontal broken lines indicate inhibition by temperature <14°C.

ments show (Fig. 5) that in the autumn of 1982 water temperatures fell too rapidly for the formation of gametangia.

DISCUSSION

Gigartina acicularis is yet another marine alga which shows a clear photoperiodic response. It is the first red alga reported to show a combination of photoperiodic and temperature control of gamete formation; all previously reported instances have been in the formation either of meiosporangia or of erect fronds. In the few instances where short-day induction of gametogenesis has been reported it has not been established whether these are true photoperiodic responses. The only other marine red alga with an isomorphic life history for which a true photoperiodic response has been shown is *Halymenia latifolia* Kützing (Maggs & Guiry 1982). The response in *G. acicularis* is clearly a true photoperiodic one, and is similar to that found in many flowering plants. This is confirmed principally by three features:

(1) Five cycles of inducing conditions are sufficient for a clear-cut response in the formation of cystocarps. Some short-day flowering plants require only a single inductive cycle, however, most require a minimum of 12 inductive cycles (Vince-Prue 1975). Photoperiodic algae reported to date, all of which have been short-day plants, require 5–12 inductive cycles (Dring & West 1983).

(2) A low-energy night-break in the middle of a long night inhibits the response. Because of problems with handling large numbers of *G. acicularis* plants it is difficult to pinpoint the 50% inhibition point accurately; it is, however, clear from Table 4 that a night-break photon exposure of 1.15 mmol m^{-2} of tungsten white light causes inhibition of cystocarp formation.

(3) Once the initial response has been induced, removal to non-inducing conditions does not inhibit further development. This is principally shown by the experiments in which plants forming cystocarps continue to develop under long-day conditions. Furthermore, spermatangial formation continues in sori induced under short-days although no new sori are formed. Similarly, carpogonial branches are only formed on tissue produced under short-day conditions; no new carpogonial branches are formed when a transfer to long-days is effected.

Table 6. Seawater temperatures at the intake point of the Shellfish Research Laboratory, Carna, Ireland for the period 1974–81. Readings represent means of temperatures taken in the last two weeks of September and the first two weeks of October; standard deviations of the means are also given (SD)

	September				October			
	$\bar{x}$	SD	Max.	Min.	$\bar{x}$	SD	Max.	Min.
1974	13.0	0.8	14.8	12.1	11.5	0.5	12.5	11.0
1975	13.9	0.6	14.6	12.7	13.2	0.7	13.8	11.6
1976	13.7	0.6	14.4	12.6	12.8	0.8	14.4	11.5
1977	12.8	0.8	14.1	11.7	10.5	0.4	11.4	10.2
1978	14.8	1.3	16.5	12.5	13.4	0.5	14.5	13.0
1979	13.8	0.7	15.0	12.4	14.1	0.4	14.8	13.5
1980	14.9	0.5	15.7	14.0	12.0	1.6	14.7	10.5
1981	14.1	0.5	15.1	13.3	11.6	1.3	14.5	10.4

Although we have shown that five cycles of 8:$\overline{16}$ h photoperiod at 16 ± 1°C is the minimum number of cycles necessary for the formation of mature, receptive carpogonial branches, we have not been able to work out the number of cycles necessary for the formation of spermatangia. It seems likely that spermatangial *sorus* formation is under photoperiodic control but sori induced under short-day conditions continue to form spermatangia when transferred to long-day conditions.

Gametogenesis in *G. acicularis* is confined to a relatively narrow temperature and photoperiod range (14–18°C inclusive; night lengths ≥12 h) which has interesting seasonal effects. This combination of conditions confines the formation of gametangia to the autumn. As one goes further north in the Atlantic this reproductive 'window' becomes progressively smaller, eventually reaching a point where reproduction in a population may take place only when higher-than-average autumn temperatures allow induction. This assumes, of course, that latitudinal ecotypes do not exist, a possibility that should not be discounted as such ecotypes are now known in two red algae [*Dumontia contorta* (S.G. Gmelin) Ruprecht; Rietema & Breeman 1982 and *Halymenia latifolia* Kützing; Maggs & Guiry unpubl. data]. Analysis of autumn temperature data taken near the known northern limit of *Gigartina acicularis* in the Atlantic (Roundstone, Co. Galway) for the period 1974–81 (Table 6) suggests that sexual reproduction was theoretically possible only in the autumns of 1978, 1979 and, perhaps, 1980; in all other years for which data are available, temperatures dropped below 14°C before daylengths of 12 h were achieved (late September; Fig. 5). In 1982, sea temperatures dropped below 14°C before the end of September, thus blocking any gametangial reproduction. Our field observations at New Quay indicated that no reproduction took place in a large field population. The available phenological data on the reproduction of this species in the British Isles since it was first found in 1811 suggest that reproduction has been extremely rare. One must, however, bear in mind that *G. acicularis* is a relatively uncommon plant which is confined to south and south-western coasts, and that field phycological activity tends to be at its lowest ebb in December to February.

The virtual absence of reports of tetrasporangial plants from the British Isles is more difficult to explain because the formation of tetrasporangia does not seem to be limited by daylength. No tetrasporangial plants were found at the New Quay study site during the period September 1982 to April 1983. Tetrasporangial plants do occur in this population as plants isolated vegetatively into culture formed tetrasporangia; these tetrasporangia released viable tetraspores that developed into male and female plants which have more or less the same photoperiodic response as that described in this paper for plants from Brittany (Guiry unpubl. data). Further studies are needed to elucidate the conditions (particularly temperature) necessary for the formation of tetrasporangia in field and cultured plants.

Lüning (1980, 1981a, 1981b) has shown a photoperiodic/temperature response in the formation of tetrasporangia in the *Trailliella*-phase of *Bonnemaisonia hamifera* which is very similar to the control of gametogenesis in *G. acicularis*. In *B. hamifera* tetrasporogenesis is confined to daylengths of 11 h and less and to temperatures of 15–17°C inclusive. [No tetrasporangia were formed at 10, 12, 20 or 23°C (Lüning 1981b).] At Helgoland, in the North Sea, gametophytes of *B. hamifera* are only found sporadically in the wild (Kornmann & Sahling 1977); in 1968 and

1969 they were common and Lüning (1980) points out that in 1966 and 1967, September water temperatures at Helgoland were higher by 0.7–0.8°C than the 10 year mean for this month. Lüning (1980), citing Feldmann (1957), stated that only tetrasporophytes of *B. hamifera* have been found on Scandinavian coasts. Rueness (1977), however, records the occurrence of gametophytes in Norway; presumably these occur sporadically on Scandinavian coasts in the same way that they do at Helgoland. In this regard it is interesting to note that although the shell-boring phases of *Helminthocladia calvadosii* (Lamouroux) Setchell and *Scinaia forcellata* Bivona-Bernardi were found recently by Kormann and Sahling (1980), the gametophytes have not been collected there since the beginning of the present century.

Dixon (1965, 1973) has pointed out that a number of algae near the northern limits of their distribution in the British Isles are unknown in a reproductive state, notably *Pterocladia capillacea* (S.G. Gmelin) Bornet et Thuret and *Bornetia secundiflora* (J. Agardh) Thuret. Both of these algae appear to maintain populations by vegetative fragmentation. A population of *Pterocladia capillacea* in a pool on Anglesey, Wales has been monitored since 1929 without any reproduction being observed (Dixon 1965, unpubl. data). Some of the other algae thought to be long-term non-reproductive clones in the British Isles (Dixon 1965) have since been found with reproductive structures; for example *Pterosiphonia complanata* (Clemente) Falkenberg (Norton & Parkes 1972; Cullinane *et al* 1980). It is, however, clear that some populations of algae can be maintained by vegetative reproduction and/or fragmentation over very long periods with or without occasional reproduction. In British Isles *Gigartina acicularis* it is probable that reproduction takes place only very infrequently and that populations are largely maintained by perennation of basal portions. It is possible that other species, currently maintaining populations by perennation/fragmentation, may, with a change in ambient temperatures, be able to reproduce.

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