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Interaction of photoperiod and temperature in the development of conchocelis of *Porphyra purpurea* (Rhodophyta: Bangiales)

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Abstract The indoor cultivation of the free-living conchocelis of a *Porphyra purpurea* (Roth) C. Ag. strain, isolated from Long Island Sound, was established, and the effects of both photoperiod and cultural temperature on conchosporangia development were studied. Statistical analysis revealed that temperatures between 10°C and 15°C and light phases between 12 and 16 h per day comprised an ideal growth "window" for both the vegetative growth and reproductive development of conchocelis. For vegetative growth, there was a significant interaction between temperature and photoperiod. Conchospores were released from mature conchosporangia under both neutral (12/12 h) and long (16/8 h) day lengths. Different seawater supplements, such as full- and half-strength Von Stosch enrichment, showed no significantly different effects on growth or development. This work provides a guideline for maintaining conchocelis cultures of *P. purpurea*, which is a type of the *Porphyra* genus.

Keywords *Porphyra purpurea* · Conchocelis · Development · Photoperiod · Temperature

Introduction

In 1949, Drew (1949) proved that *Conchocelis rosea* was the diploid phase of *Porphyra umbilicalis*; it was then discovered that plants of the genus *Porphyra* alternate their generations between a leafy gametophyte (monostromatic or distromatic, monoecious or dioecious) and a filamentous sporophyte. In the wild, the conchocelis phase only grows in shells. There, they develop into conchosporangia and release conchospores. Under suitable conditions, conchospores germinate into leafy blades after meiosis (Mitman and van der Meer 1994). In 1961, Iwasaki (1961) produced free-living conchocelis in the laboratory. This provided a controllable, indoor strategy to investigate the development of conchosporangia and the release of conchospores.

For both biological and economical purposes, great effort has been expended to determine how the development of the *Porphyra* conchocelis is regulated, especially through light and temperature. In 1956, Tseng and Chang (1956) demonstrated that for *Porphyra tenera*, the formation of conchosporangia required stimulation by raising the cultural temperature. In 1967, Dring (1967) discovered that the vegetative growth of conchocelis was correlated with a certain photoperiod range (8- to 16-h light), whereas the formation of conchosporangia was inhibited by a light period of more than 12 h. Chen et al. (1970) also proved that both photoperiod and temperature had effects on the initiation and discharge of conchospores in *Porphyra miniata*. A series of observations made by Waaland et al. (1987, 1990) on *Porphyra abbottae*, *Porphyra perforara*, and other related species also supported the effects of a decreased temperature stimulus on conchospore maturation and of a short light period on the release of conchospores.

As the type of *Porphyra* (Irvine and Brodie 1997), the leafy blade of *P. purpurea* is monoecious, but the male and female parts are divided by a straight line. Because the suitable condition for conchosporangia formation has been shown to be 12–16 h of light, sporophytes are usually visible in the spring and summer (Conway and Cole 1977).

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However, taxonomic research on this species and its relatives is still murky (Brodie et al. 1996; Brodie and Irvine 1996). From cytological observations, there have been different reports of *P. purpurea* chromosome numbers, such as $n=4$ (Kito et al. 1971) or $n=5$ (Mitman and van der Meer 1994), which might result either from the somatic pairing of different chromosome sets (Cole et al. 1983; Zhou et al. 2008) or from the mistaken study of close relatives of the species, which are not easily distinguishable based on morphological characters (Bray et al. 2006, 2007).

As for the growth and development of *P. purpurea*, Mitman and van der Meer (1994) reported work from their Nova Scotia isolation. Under conditions of 16/8 h (light/dark) and 40 μmol photons m^{-2} s^{-1}, 13–15°C was the optimal range for conchocelis growth. They used 15°C as the standard condition for conchospore formation, and a decrease from that temperature to 13°C was regarded as an essential trigger for the release of conchospores.

In the summer of 1996, Yarish et al. collected a *Porphyra* strain from Long Island Sound. This material was repeatedly discovered in the following years. Observations of its chromosome number showed that $n=5$, as in *P. purpurea*. Further molecular identification also proved this to be a *P. purpurea* strain, as described by Bray et al. (2006, 2007).

A culture of this strain that was initiated from a single carpospore was maintained and recently adopted by the Community Sequencing Project of the Joint Genome Institute. In this paper, we describe how the photoperiod, temperature, and nutrients regulate the growth and development of this species at the conchocelis stage, which may help standardize further research work.

Materials and methods

The original leafy blades were collected from Long Island Sound, Connecticut. The conchocelis culture was initiated from a single carpospore released and maintained as a unialgal line in the Marine Biology Laboratory of the University of Connecticut at Stamford.

Tufts of free-living conchocelis were blended (Osterizer Blender) twice for 30 s each, with an interval of 30 s, and then filtered through two meshes with pore sizes of 70 and 35 μm, respectively. The fragments collected between these two meshes were rinsed and suspended in fresh seawater as a starting material for the experiment. Approximately 40 fragments were inoculated in 6-cm diameter Petri dishes containing 16 mL of growth medium. To compare the effects of nutrient supply, seawater supplemented with full- (VSE) or half-strength (VSE/2) Von Stosch enrichment (Von Stosch 1964) was used. Preparative experiments showed that photon flux density in the range of 20–40 μmol photons m^{-2} s^{-1} had similar effects on the growth and development of conchocelis. Thus, the dishes were maintained under 28.5–32.5 μmol photons m^{-2} s^{-1}, provided by high output cool white fluorescent lamps and measured with a PAR quanta meter (LI COR).

Table 1 Comparison of the effects of VSE- and VSE/2-enriched seawater on the growth of free-living conchocelis of *P. purpurea* under different combinations of photoperiod and temperature (one-way ANOVA)

Week	1	2	3	4	5	6	7	8	9	10	11
5°C, LD	-	-	-	-	*	-	**	-	-	**	-
5°C, ND	*	-	-	-	-	-	**	-	-	-	**
5°C, SD	-	-	-	-	-	-	-	-	-	**	-
10°C, LD	-	-	-	-	-	-	-	-	-	-	-
10°C, ND	-	-	-	-	-	-	-	-	**	*	-
10°C, SD	-	-	-	-	-	-	**	-	-	-	-
15°C, LD	-	-	-	-	-	-	-	-	-	-	-
15°C, ND	-	-	-	-	**	-	-	*	-	-	-
15°C, SD	-	*	-	-	**	-	-	-	*	-	-
20°C, LD	**	**	-	-	**	**	-	-	-	-	-
20°C, ND	-	*	-	-	**	-	-	**	-	*	**
20°C, SD	-	*	-	**	**	-	-	-	-	*	-

Shadow: groups that grew well (the "window")

LD: 16/8 h (L/D); ND: 12/12 h (L/D); SD: 8/16 h (L/D)

–: not significantly different; *: $p<0.05$ (significantly different); **: $p<0.01$ (significantly different)

The cultures with either VSE or VSE/2 were incubated at four different temperatures (5°C, 10°C, 15°C, and 20°C) and three photoperiods (LD, long day length at 16/8 h; ND, neutral day length at 12/12 h; and SD, short day length at 8/16 h, light/dark regimes). The media were changed weekly by gentle pipetting. Each experimental condition had six replicates for statistical analysis.

Observations and measurements were made weekly with an Olympus CK-2 inverted microscope. Ten observations of each replicate were made, and the projected area of each conchocelis filament/tuft was calculated. The results are expressed as the mean ± standard deviation.

The growth rate (GR%) was calculated by the equation: $GR\% = [(A_t/A_0) - 1]/t \times 100\%$ where A_0 and A_t represent the average projected areas measured before and after each 1-week cultivation period, respectively, when t (day) was set at 7 for a week.

The main and combined effects of the medium, temperature, and photoperiod were tested by analysis of variance (ANOVA; Sokal and Rohlf 1981).

Results

In preparative experiments, there were a large number of sizeable tufts and long filaments of conchocelis after a single 30-s blending, and subsequent filtration did not provide sufficiently identical starting conchocelis fragments. Additionally, with a blending time of more than 60 s, the identity of the conchocelis fragments could not be improved. After being blended and filtered, the conchocelis fragments that remained between the two layers of nytex meshes were identical in size. The average length was 105.5±1.9 μm, and the average diameter was 3.4±0.3 μm ($p<0.01$, $n=100$). All of the collected materials were vegetative conchocelis (thin filaments). In suspensions of

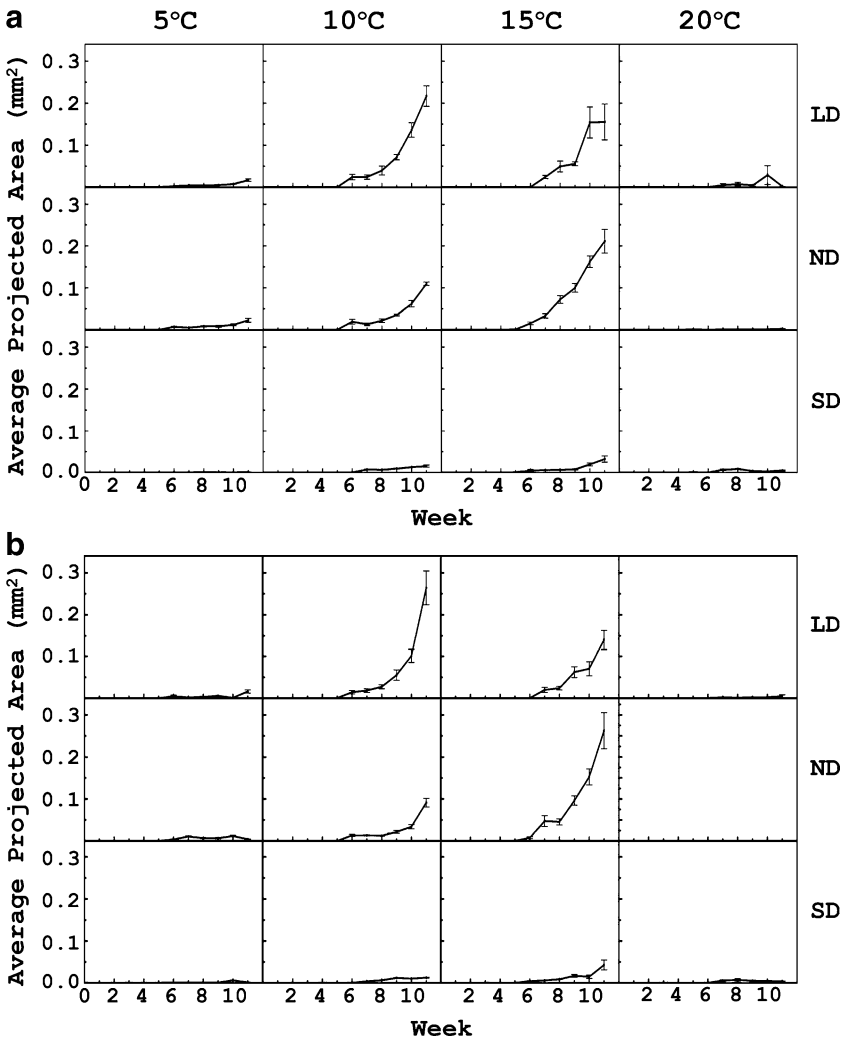

Fig. 1 Vegetative growth of *P. purpurea* conchocelis in Von Stosch (VSE)- (**a**) and 1/2 Von Stosch (1/2 VSE)-enriched (**b**) seawater under different combinations of temperature and photoperiod. The photoperiods were 8/16-h (SD), 12/12-h (ND), and 16/8-h (LD) light/dark regimes. The average projected area was calculated as the mean ± standard deviation ($n=60$)

cultured conchocelis, the length of a single cell was ~40 μm. The criterion for a length of 105.5±1.9 μm helped ensure that all material was initiated from a fragment with two normal growing cells. An interval of 30 s between two blends was essential to increase the percentage of surviving fragments (85%/60%, with/without a 30-s rest). After 1 week of cultivation, the declining conchocelis fragments were removed by changing the culture medium. The active fragments adhered to the Petri dish via secreted gel components.

During cultivation, VSE and VSE/2 only showed significantly different effects on conchocelis growth in limited stages (Table 1), especially when the conchocelis were growing in suboptimal conditions. When the conchocelis were growing in suitable conditions, such as 10°C or 15°C under ND or LD, nutrient supplement did not show significant effects.

A long lag phase in the growth of conchocelis was found in each of the combined conditions, with a daily growth rate usually <5%. For any combination that involved VSE and for 5 and 10°C with VSE/2, the lag phase took 5 weeks, and in conditions of 15 and 20°C combined with VSE/2, it took 4 weeks (Fig. 1). This result suggested that the higher temperature might produce some advantage in initiating the vegetative growth of conchocelis. From the sixth week, all groups with ND or LD incubated at 10°C approached the exponential growth phase. The growth rate was 60.53% (LD) and 62.34% (ND) in VSE/2 and 71.72% (LD) and 67.80% (ND) in VSE (Fig. 2). Meanwhile, groups incubated at 5°C and 15°C with ND reached growth rates of 48.75% (5°C) and 45.07% (15°C) in VSE, respectively, slightly higher than those in VSE/2 (36.91% and 40.11% at 5°C and 15°C, respectively; Fig. 2).

At the seventh week, the growth rate of each aforementioned group underwent an obvious decrease; most groups exited the exponential phase. Only those incubated at 15°C with ND and VSE/2 maintained a

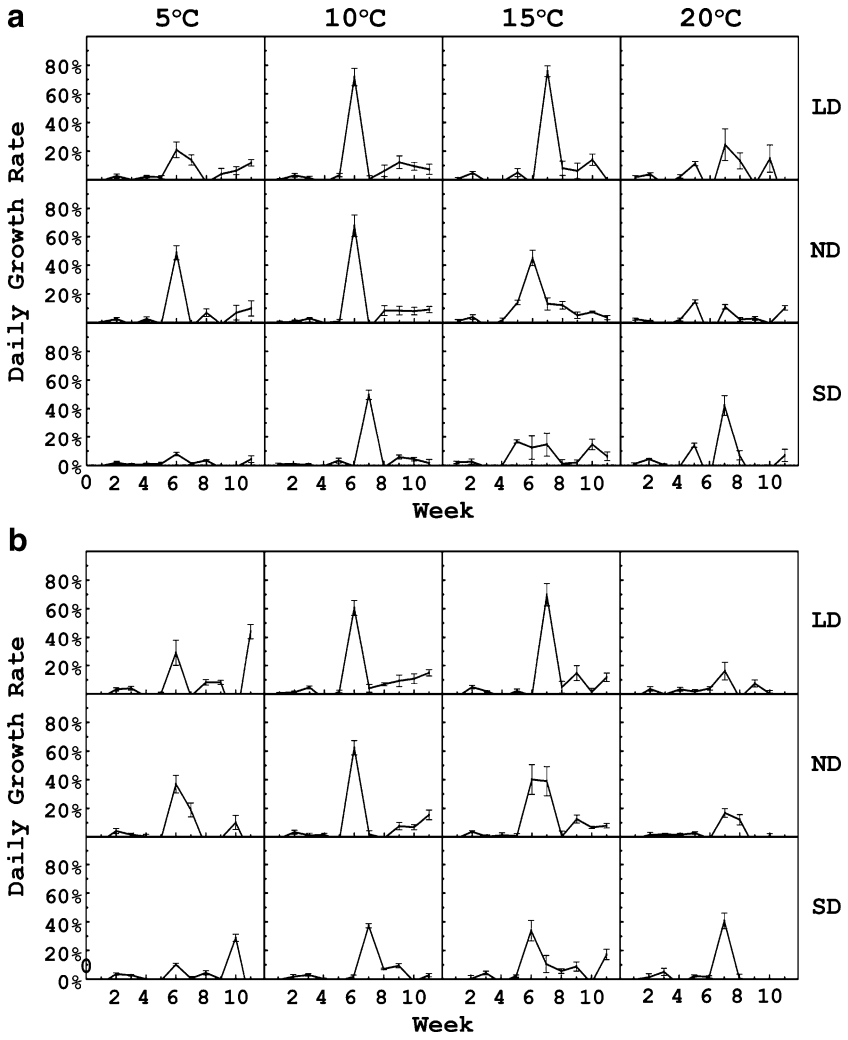

Fig. 2 Daily growth rate of *P. purpurea* conchocelis in Von Stosch (VSE)- (**a**) and 1/2 Von Stosch (1/2 VSE)-enriched (**b**) seawater under different combinations of temperature and photoperiod. The photoperiods were 8/16-h (SD), 12/12-h (ND), and 16/8-h (LD) light/dark regimes. The average projected area was calculated as the mean ± standard deviation (n=60)

daily growth rate of 38.97%, whereas those at 10°C, SD and VSE/2 fell to a 37.22% growth rate. Similarly, in VSE/2, the conchocelis growing in the 10°C SD, 15°C LD, and 20°C SD groups entered their exponential phases, with daily growth rates of 37.22%, 69.73%, and 40.70%, respectively. These values were still lower than their counterparts in VSE (49.60%, 75.78%, and 42.25%, respectively; Fig. 2).

From the analysis of biomass increases, it was simple to determine that the growth conditions of 10°C and 15°C and ND and LD encompassed a "window" for the ideal growth of free-living conchocelis whether in VSE or VSE/2. The growth showed typical sigmoid curves, with a plateau between two fast-growing phases (Fig. 1). By comparing the growth curves and developmental stages under different cultivation conditions (Figs. 3 and 4), it appears that the first phase of the curve resulted from the exponential growth of the free-living conchocelis and the third phase was from the vegetative growth of the conchosporangia that developed from the conchocelis. The transition phase (plateau) between them was just before conchosporangia could be observed. This phase was shortest in the 15°C with ND condition as new conchosporangia were forming and growing from the sixth week throughout the tenth week (Figs. 3 and 4). But for conchocelis growing in other conditions, the transit phase took longer. From the projected area measured under a microscope, it looked like that the growth was suspended during this transit phase until conchosporagia were observed from most branches of the conchocelis (Fig. 3).

Although a high daily growth rate was also observed round the six and seventh weeks at 5 or 20°C with SD, the growth on the whole was very low, mostly because of the poor growth in the first 5 weeks of the cultivation. Undoubtedly, the combination of SD and these temperatures was not ideal for conchocelis growth (Fig. 3).

The ANOVA showed that the interaction between the photoperiod and the temperature had a significant effect on growth. In the fifth week, this interaction was not yet significant for those combinations in VSE/2. However, starting with the sixth week in both media, the effects were significant at the $p<0.01$ level. Furthermore, the effects of temperature or photoperiod alone were significant at the level of $p<0.01$ (Table 2).

In comparison with vegetative growth, development was also interesting. As the developmental scheme in Fig. 4 shows, conchosporangia were not initiated in the 20°C at LD group with both media and a neutral day length with

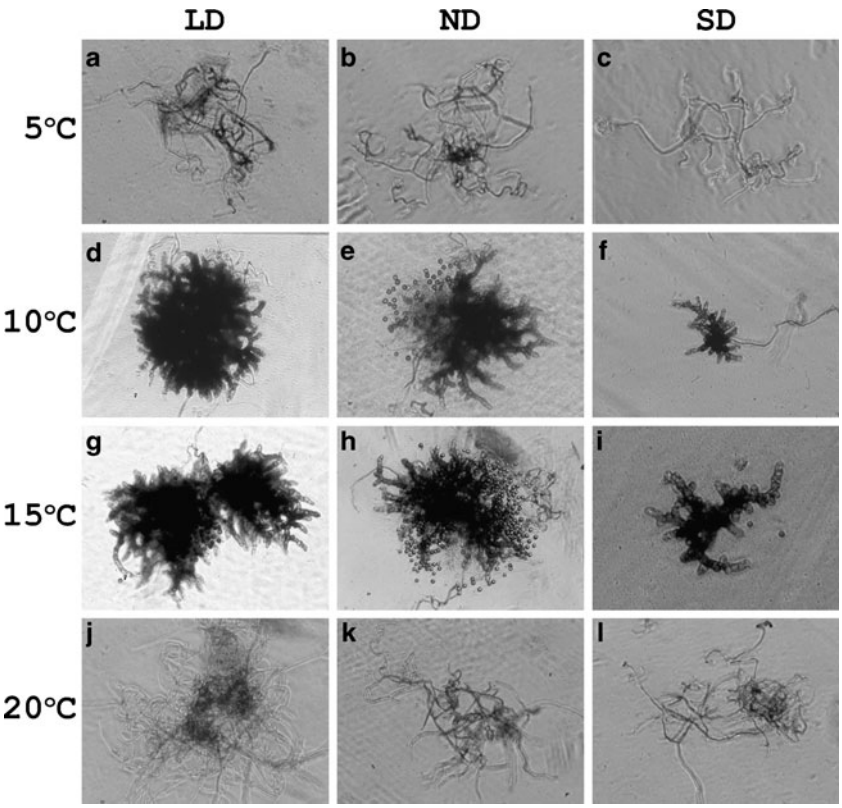

Fig. 3 *P. purpurea* conchocelis cultures after 11 weeks under different conditions in Von Stosch-enriched seawater (VSE). The photoperiods were 8/16-h (SD), 12/12-h (ND), and 16/8-h (LD) light/dark regimes

VSE or at SD with VSE/2. There was also no conchosporangia at 5°C SD with VSE. In the preferred "window," we observed that the conchospores were released and germinating by the end of the study. Although some conchosporangia were produced at 5°C and 20°C, no maturation was found (Fig. 3).

It is important to note that under 10°C LD with VSE, some conchocelis were able to complete all of the steps of transformation from a free-living conchocelis to a mature conchosporangia, and the conchospores were released and germinated within a single week. Spores were also released and found to be germinating in the following weeks. Conversely, in both the ND and LD at 15°C groups, the conchospores were not released until the tenth week. However, the number of conchospores and their germination rates were higher at 15°C than at 10°C (data not shown).

Discussion

In 1971, Iwasaki and Sasaki (1971) concluded that there were three essential requirements for conchospore release: high light intensity, a drop in the temperature, and short daytime. With the increase of material used in such research, Bird and McLachlan (1992) further found that the ability to release conchospores varied by strain.

Concerning the growth and development of conchocelis, although many reports verified the effects of light intensity, photoperiod, and temperature, statistical analyses were not widely adopted in addition to qualitative observations. In 1980, Chiang and Wang's work on *Porphyra angusta* used ANOVA and showed that the photoperiod did not have a significant effect on the formation of conchosporangia, while both light intensity and temperature did ($p<0.05$).

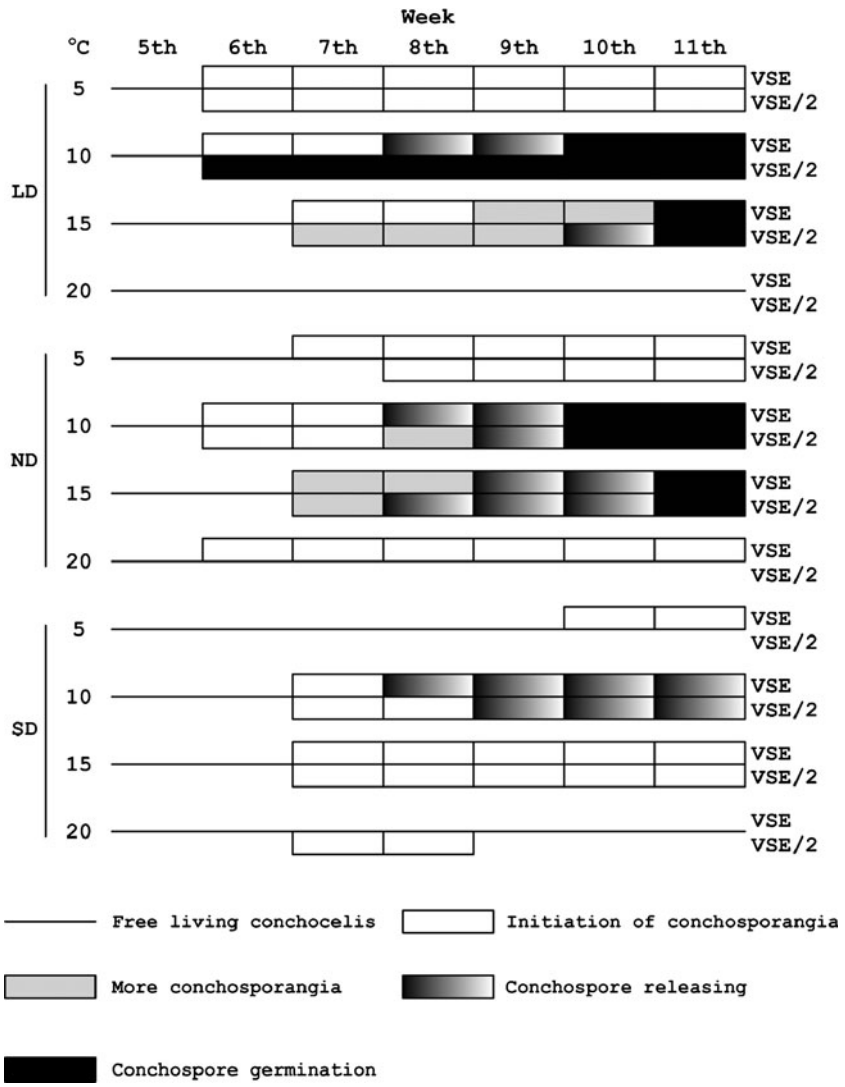

Fig. 4 Scheme showing the developmental stages of *P. purpurea* conchocelis in Von Stosch (VSE)- (**a**) and 1/2 Von Stosch (1/2 VSE)-enriched (**b**) seawater under different combinations of temperature and photoperiod. The photoperiods were 8/16-h (SD), 12/12-h (ND), and 16/8-h (LD) light/dark regimes

Table 2 ANOVA showing the effects of photoperiod, temperature, and their interaction on the growth of free-living *P. purpurea* conchocelis for each week

F	VSE			VSE/2		
	Photoperiod (*df*=2)	Temp. (*df*=3)	Interaction (*df*=6)	Photoperiod (*df*=2)	Temp. (*df*=3)	Interaction (*df*=6)
Week						
5	10.88**	97.53**	9.08**	4.47*	8.36**	1.03
6	10.34**	14.03**	6.04**	7.70**	12.36**	5.17**

From the sixth week, the effects were all significant at $p<0.01$ level

*$p<0.05$; **$p<0.01$

In our work on *P. purpurea*, statistical analysis did not suggest that VSE was more suitable than VSE/2 for conchocelis growth, although the raw data in each group did appear higher in VSE than in VSE/2. Table 1 shows that there was no significant difference in their effects under normal growing conditions.

The interaction analyses led to some results that were different from the work of Chiang and Wang (1980), and this is reasonable due to the different species used. Starting with the exponential growth found in the sixth week, both temperature and photoperiod showed very significant effects on growth ($p<0.01$), and their interaction was significant at the $p<0.05$ level. This result suggested the presence of a two-dimensional "operating window" for controlling the growth of *P. purpurea* conchocelis.

The initial growth rate of the free-living conchocelis stage of this strain was lower than those reported earlier in the same species or genus (Mitman and van der Meer 1994; Waaland et al. 1987, 1990). The conchocelis required 5 weeks to enter the exponential phase. This difference may be due to different cultivation designs (e.g., with or without aeration) or because of the damage from mechanical blending used in this study. Furthermore, the conchocelis could not be maintained at the transition phase (from free-living conchocelis to conchosporangia) for long periods. Once the suitable conditions were reached, free-living conchocelis began to transform into conchosporangia and started to release conchospores.

With ND or LD, those conchocelis incubated at 10°C began exponential growth and released conchospores earlier than those at 15°C, but this earlier maturation inhibited vegetative growth. The growth rate was slowed in all groups when conchosporangia were initiated.

Under the preferred conditions, 15°C ND, nutrient supplementation became a limiting factor for growth. Although conchospores were not released and germinating until the tenth week, both the number of spores released and the germination speed were higher than those incubated at 10°C where the release of conchospores began at the sixth week.

In the experiments on this Long Island Sound *P. purpurea* strain, although both photoperiod and temperature had significant effects on the vegetative growth of conchocelis, they showed a much looser control of the formation and maturation of conchosporangia. In the "window" encompassed by a 10–15°C incubation and a 12- to 16-h light period, conchocelis were released at a low speed even if the conditions were not ideal. Thus, *P. purpurea* appears to be a "generalist" (Mumford 1980). We found that the course of conchocelis development was correlated with the annual temperature change in Long Island Sound (Fig. 5). In the wild, the temperature reached 10°C in April when the leafy blades were visible. The indoor cultivation proved that the presence of a leafy blade at this time was a characteristic of *P. purpurea* as a "generalist." Although neither conchocelis nor conchospore release was found at this time in the natural locations, we assume that conchospores were released and germinated starting this time on at a low rate. In May and June, the mass discharging of conchospores was initiated, and there were more leafy blades observed in the field from late June through early October (Kraemer and Yarish 1999).

Considering the development of leafy blades, there was only a small difference between the temperature tolerance

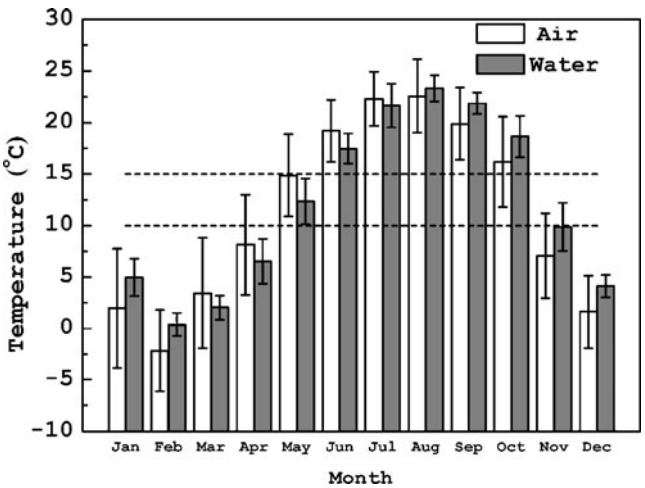

Fig. 5 Year-round fluctuation of air and seawater temperature in Long Island Sound (data from the National Data Buoy Center of National Oceanic and Atmospheric Administration, www.ndbc.noaa.gov)

of *P. purpurea* from Nova Scotia (Mitman and van der Meer 1994) and this Long Island Sound strain. The former died at 20°C and grew well at 13°C under LD, while the latter barely survived at 20°C and preferred 15°C under ND for optimal growth and development. At 10°C, the growth of the Long Island Sound strain was only slightly suppressed, whereas the strain from Nova Scotia grew much more poorly when comparing their growth at 15°C. However, under the harsher conditions of 5°C with SD and dim light (5 μmoL photons m^{-2} s^{-1}), the Nova Scotia strain maintained a slow growth (Mitman and van der Meer 1994), while the Long Island Sound strain barely grow under similar circumstances.

There were also some differences between these two strains in the release and germination of conchospores. No release was observed at 15°C, and no leafy blades were found at SD or ND, for Nova Scotia *P. purpurea*. However, similar results were not detected with the Long Island Sound plant. Conchospores were released at 10°C and even greater quantities at 15°C. Furthermore, even under a 12-h light period, conchospores could germinate.

Morphological and developmental studies have shown an obvious variation among the Northwest Atlantic monostromatic *Porphyra* species. Molecular information, such as *rbc*L sequences, provides helpful information for identifying different *Porphyra* collections (Bray et al. 2006, 2007), but it has yet to be determined if the differences in plant development are the result of genetic differences or ecological adaptation.

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