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Effect of blue light on indoor seedling culture of *Saccharina japonica* (Phaeophyta)

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Abstract *Saccharina japonica* is a brown alga that has been commercially cultured on a large scale in China. Integrating the light condition under seawater and the adaptation of *Saccharina* to this condition, it is expected that blue light would be beneficial to *Saccharina* culture system. Consequently, the detailed effect of blue light on the key stages during indoor seedling culture of *S. japonica* was investigated in this study. Irradiances and light qualities had little effect on zoospore attachment and germination. Egg formation occurred sooner under blue light than white light. Under optimum irradiances, 95±4% female gametophytes gave rise to eggs in 6 d under blue light, while it took 12 d for over 90% formation of eggs under white light. Over a culture period of 3 weeks, mean sporeling length and width under blue light was 1.39 and 1.56 times of that under white light, respectively, while the mean sporeling size obtained under red light was only 25% of that under white light. The higher growth rate under blue light was largely due to higher photosynthetic efficiency, as indicated by chlorophyll fluorescence of photosystem II. In addition, the mean ratio of sporeling width to length under blue light was significantly higher than that under white light. These results suggest that blue light would be superior to white light for indoor seedling culture of *S. japonica*. Based on these findings, an improved *S. japonica* seedling culture system is discussed.

Keywords Chlorophyll fluorescence · Gametophyte · Photosynthesis · Sporophyte · Zoospore

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Introduction

Saccharina (kelp) is the first commercially cultured seaweed. Nowadays, the culture area and output of *Saccharina* is the highest among all cultivated seaweeds in the world (Tseng 2001). *Saccharina japonica* (Aresch.) Lane et al. (2006) is the major cultured species along the coast of Lianjiang (24° 59′ N, 118° 48′ E), Yantai (37° 53′ N, 121° 31′ E), Weihai (36° 41′ N, 122° 42′ E), and Dalian (40° 10′ N, 123° 31′ E) in China.

The cultivation process of *S. japonica* is divided into two stages: indoor cultivation of seedlings and outdoor cultivation of mature plants. The indoor seedling culture process takes about 3 months, including zoospore collection and development, gametophyte development and reproduction, and sporeling growth. Although many key techniques involved in *Saccharina* seedling culture have been established and successfully implemented in practice, problems are still present. Firstly, temperatures should be controlled at lower than 10°C by a cooling system throughout the indoor culture process, which is 8–15°C

lower than the air temperature. During the late stage of seedling culture, the dissolved CO_2 becomes deficient as the growing sporelings consume a large amount of CO_2. Seawater is renewed more frequently or CO_2 is bubbled into the culture tanks to maintain enough CO_2 for the rapidly growing seedlings. Consequently, reducing the high cost of water cooling, water renewing, and CO_2 bubbling is one of the major problems to be settled. Secondly, the light source is sunlight from roof windows and side windows, resulting in an uneven distribution of light and limited irradiance. Improving the light conditions is another problem to be settled.

Plants of *Saccharina* grow naturally in the sublittoral zone where blue light (400–500 nm) is predominant (Dring 1981). They have fucoxanthin as one of the major light-harvesting pigments. The absorption spectrum of fucoxanthin has major peaks in the blue region of the spectrum (Wang et al. 2005). Previous findings have revealed that both gametophyte reproduction (Lüning and Dring 1972; Lüning 1975) and sporophyte photosynthesis are stimulated by blue light (Dring 1989; Forster and Dring 1992, 1994). Thus, blue light plays an important role in the lives of *Saccharina* that may be beneficial to the culture system.

Although the physiological functions of blue light on *Saccharina* have been reported decades ago, the extent of the blue light effect has not been assessed. In this study, characteristics of *S. japonica* zoospore attachment and germination, gametophyte reproduction, and sporeling growth under blue light were compared with those under white and red light. An improved indoor seedling culture system is proposed based on the findings of the present and previous studies.

Materials and methods

Light sources Blue light-emitting diodes (LEDs) of wavelength 460–475 nm, red LEDs of wavelength 620–635 nm, and white LEDs with a color temperature of 5,000–7,000 K (Honglixiang, Shenzhen, China) were used as light sources. Irradiances were measured using a quantum photometer (LI-COR, USA).

Estimation of zoospore attachment and germination under different light qualities Mature sporophytes of *S. japonica* were collected from the Guanwu breeding center for *Saccharina* in Lianjiang (24° 59′ N, 118° 48′ E), China. The parts with sori were cut from the plants, rinsed in sterilized seawater to remove contaminants, air-dried in darkness at 6–8°C for 2–4 h, and then immersed in filtered sterile seawater at 10–12°C. Zoospores were released soon and allowed to settle on glass slides under blue, red, and white light provided by LEDs. Irradiances are shown in Table 1, and the photoperiod was 10:14 h L:D. Twelve hours later, five glass slides were selected randomly from each treatment, rinsed with sterile seawater to remove spores that were not firmly attached. Then, the number of zoospores that had attached to the glass slides was determined using a microscope with eyepiece graticule. Three fields of view were checked at random on each selected glass slide. Germination of zoospores was observed using the microscope 5 d later.

Measurement of the optimum irradiance of each light quality for gametophyte reproduction and sporeling growth Zoospores as obtained above were cultured at 12°C under a 8:16 h L:D photoperiod with 10 μmol photons $m^{-2}s^{-1}$ white light. Seven days later, zoospores developed into male and female gametophytes. They were then cultured at 12°C under a 8:16 h L:D photoperiod with varying irradiances (Table 1) under blue, red, or white light. After 7 d, five glass slides were selected randomly from each treatment and three microscopic fields of view were checked at random on each glass slide. Egg and sporeling formation rate was obtained as the formula: (eggs + sporelings)/(eggs + sporelings + undeveloped female gametophytes).

Sporelings were obtained by culturing the gametophytes at 12°C under a 10:14 h L:D photoperiod with 40 μmol photons $m^{-2}s^{-1}$ white light for 7 d. Then they were cultured at 12°C under a 8:16 h L:D photoperiod with varying irradiances (Table 1) of blue, red, and white light, respectively. After 7 d, lengths of 50 randomly selected sporelings were recorded.

Percent of sporeling formation rose to the maximum under 40 μmol photons $m^{-2}s^{-1}$ blue light and white light and 30 μmol photons $m^{-2}s^{-1}$ red light. The mean length of the sporelings peaked at around 40 μmol photons $m^{-2}s^{-1}$ red light, 60 μmol photons $m^{-2}s^{-1}$ blue light, and 80 μmol photons $m^{-2}s^{-1}$ white light. Taken together, the optimum irradiances for both *S. japonica* gametophyte reproduction and sporophyte growth were set as 40 μmol photons $m^{-2}s^{-1}$ under red light, 60 μmol photons $m^{-2}s^{-1}$ under blue light, and 80 μmol photons $m^{-2}s^{-1}$ under white light.

Table 1 Irradiances of blue, white, and red light used in this study

Light quality	Irradiance (μmol photon $m^{-2}s^{-1}$)				
Blue light	16	30	40	60	120
White light	20	40	80	120	160
Red light	10	20	30	40	50

Assessment of the effect of light quality on S. japonica gametophyte reproduction Gametophytes as obtained above were cultured under 60 μmol photons $m^{-2}s^{-1}$ blue light, 40 μmol photons $m^{-2}s^{-1}$ red light, or 80 μmol photons $m^{-2}s^{-1}$ white light. Percent of the female gametophytes that had developed into eggs/sporelings was checked every 3 d as described above.

Assessment of the effect of light qualities on S. japonica sporeling growth Three hundred sporelings with the size of three to five cells were cultured under 60 μmol photons $m^{-2}s^{-1}$ blue light, 40 μmol photon $m^{-2}s^{-1}$ red light, or 80 μmol photons $m^{-2}s^{-1}$ white light. The length, width, and ratio of width to length of 50 randomly selected sporelings were recorded every 7 d.

Assessment of the effect of light qualities on photosynthesis After 45 days, the photosynthetic parameters of photosystem II (PS II) of the sporelings were measured by chlorophyll fluorescence assay using an imaging pulse-amplitude-modulation fluorometer (Walz, Germany). Six sporelings were selected at random from each treatment. The samples were dark-adapted for 15 min; then the fluorescence yield (F′) and the maximum light-adapted fluorescence yield (F_m') were measured after 20 s of illumination. Fifteen records of F′ and F_m' were made for each measurement. The effective quantum yield of PS II (Φ_{PSII}) was calculated as $\Delta F/F_m' = (F_m'-F')/F_m'$. After measurement of Φ_{PSII}, samples were illuminated at 12 increasing irradiance levels, from 7 to 1,200 μmol photons $m^{-2}s^{-1}$. Under each irradiance level, F′ and F_m' were measured each 20 s, from which the relative electron transport rate (rETR) was obtained. Rapid light curves were fitted to rETR versus the photosynthetically active radiation (E_{PAR}) curve according to the procedure of Jassby and Platt (1976): $rETR = rETR_{max} \cdot \tanh(\alpha \cdot E_{PAR}/rETR_{max})$ using Statistica 7.0 (StatSoft, USA). Alpha represents the initial slope, and $rETR_{max}$ is the maximum relative electron transport rate. Irradiance at onset of light saturation (E_k) was calculated according to the formula: $E_k = rETR_{max}/\alpha$. The fluorescence terminology is consistent with Cosgrove and Borowitzka (2010).

Culture medium All cultures in this study were performed in still seawater with gravity 1.019 and pH8.1–8.2. Seawater was fertilized with 4 mg L^{-1} $NaNO_3$ and 0.4 mg L^{-1} KH_2PO_4 and renewed every 3 d.

Statistical analysis The statistical significance of differences was tested by one-way ANOVA. This was followed by Tukey's test when appropriate. Statistical analyses were conducted using SPSS 17.0, and $P<0.01$ was considered to indicate significance. All data are reported as means ± SD.

Results

Effect of blue light on *S. japonica* zoospore attachment and germination

After 12 h, it was observed that all zoospores stopped swimming. There was no significant variation in the number of attached zoospores under the varying irradiances and light qualities ($F=1.132$, $P=0.355$; Fig. 1). After 5 days, almost all zoospores germinated into gametophytes under all irradiances and light qualities (Fig. 2).

Effect of blue light on gametophyte reproduction

Formation of eggs was observed on the first day under 60 μmol photons $m^{-2}s^{-1}$ blue light, the fourth day under 80 μmol photons $m^{-2}s^{-1}$ white light, and the sixth day under 40 μmol photons $m^{-2}s^{-1}$ red light. After 6 days, 95±4% female gametophytes gave rise to eggs under blue light. It took 12 d for over 90% formation of eggs under white light. The percent of egg formation reached 45±5% on the twelfth day under red light while no significant increase in the number of eggs and sporelings was observed in the following 6 days (Fig. 3). The female gametophytes that had not transformed into eggs developed into filamentous thalli with several vegetative cells (Fig. 4).

It has been reported that the reproduction of *Saccharina* gametophytes occurs only under sufficient blue light illumination, which serves as a morphogenetic response to blue light (Lüning 1975; Shi et al. 2005). In this study, the gametophytes were first cultured under white light for 7 d. We hypothesised that morphogenetic responses might have occurred in some gametophytes during this period so that they gave rise to eggs even when transferred to red light illumination. A supplementary experiment was carried out

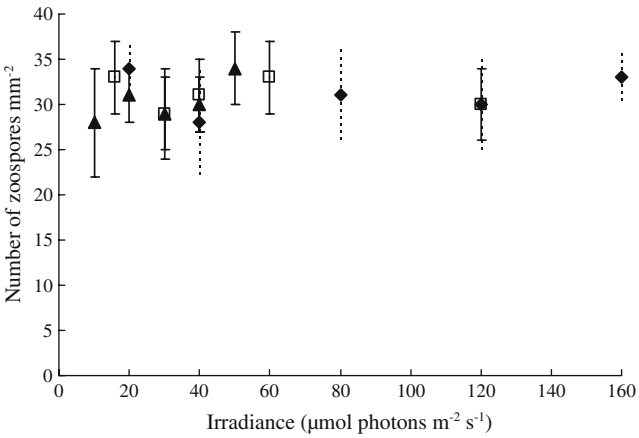

Fig. 1 Number of zoospores attached onto glass slides under different irradiances and light qualities. Symbols: *solid diamonds* = white light, *hollow squares* = blue light, *solid triangles* = red light. Data are mean ± SD ($n=15$)

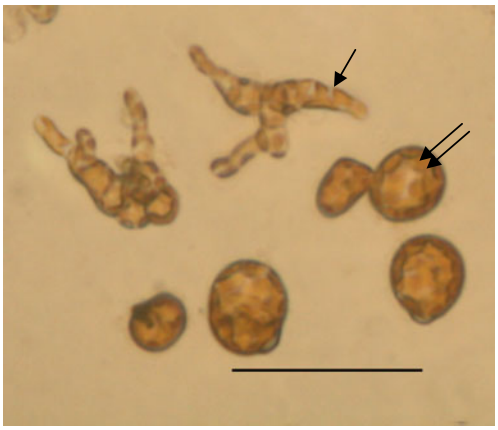

Fig. 2 Zoospores germinating into gametophytes. *Single arrow* points to the male gametophyte; *double arrows* indicate the female gametophyte. *Scale bar* = 20 μm

to test this hypothesis. Gametophytes were cultured under red light from the beginning of zoospore collection and blue light was absent throughout. No sporelings were observed during a culture period of 45 d, and all female gametophytes grew into vegetative filaments.

Effect of blue light on sporeling growth

At the end of the 1st week, mean length of the sporelings under blue and white light was similar (F=0.358, P=0.566; Fig. 5a) while mean width of the sporelings under blue light was significantly larger than that under white light (F= 10.730, P=0.011; Fig. 5b). Both sporeling length and width under red light were significantly lower than those under white and blue light (P=0.000). After 2 weeks of treatment, the mean length of sporelings under blue light became significantly higher than that under white light (F=88.567, P=0.000). Variations in sporeling size, measured as both

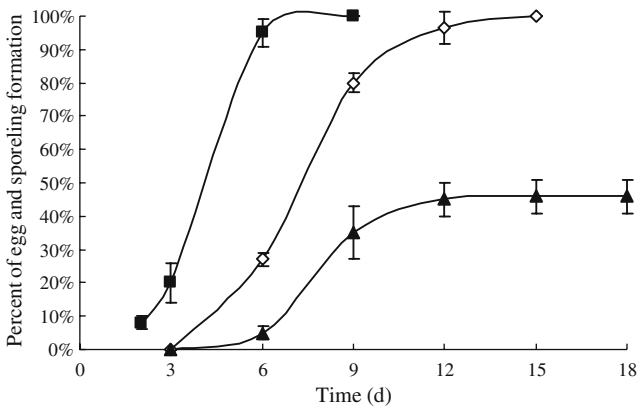

Fig. 3 Percent of egg and sporeling formation under 80 μmol photons $m^{-2}s^{-1}$ white light, 40 μmol photons $m^{-2}s^{-1}$ red light, and 60 μmol photons $m^{-2}s^{-1}$ blue light. Symbols: *hollow diamonds* = white light, *solid squares* = blue light, *solid triangles* = red light. Data are mean ± SD (n=15)

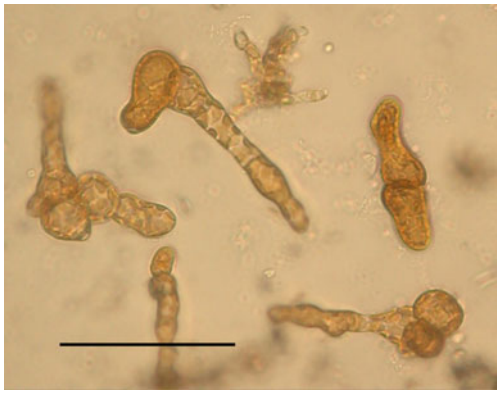

Fig. 4 Female gametophytes developing vegetatively into filamentous thalli under red light. *Scale bar* = 40 μm

length and width, under the three light qualities increased as the culture period was lengthened. At the end of the third week, mean sporeling length and width under blue light were 1.39 and 1.56 times of that under white light, respectively, while the mean sporeling size obtained under red light was only 25% of that under white light (Fig. 5a, b).

Mean ratios of sporeling width to length under blue light were significantly higher than those under white light (on the eighth day: F=224.133, P=0.000; on the 21st day: F= 43.97, P=0.003). There was no significant variation in the ratios under red and white light (F=6.868, P=0.059).

Effect of blue light on sporeling photosynthesis

Φ_{PSII}, $rETR_{max}$, α, and E_k were all highest under blue light and lowest under red light (Table 2). The variations were extremely significant among the three light qualities (P< 0.01). Alpha qualifies the efficiency of light capturing (Serôdio et al. 2006). *S. japonica* has the chlorophyll a/ fucoxanthin protein complex as the major light-harvesting complex. The major absorption peaks of fucoxanthin are in the blue light region (Wang et al. 2005). Consequently, the light-harvesting complex is highly efficient in capturing blue light, resulting in the highest α among the three light qualities. Mean E_k of sporelings under blue light was about 470 μmol photons $m^{-2}s^{-1}$ higher than that under white light. While mean E_k under red light was only 60 μmol photons $m^{-2}s^{-1}$ lower than that under white light. The light saturation parameter E_k is regularly used as an indication of the photoacclimation state of photosynthetic organisms and describes the optimum irradiance for balance between the light and dark reactions of photosynthesis (Henley 1993). The much higher E_k under blue light indicated that the stimulation of the enzymes participating in photosynthetic dark reactions was in concert with stimulation of the efficiency of light capturing. Good balance between the light and dark reactions led to the significantly higher capacity of photoacclimation under

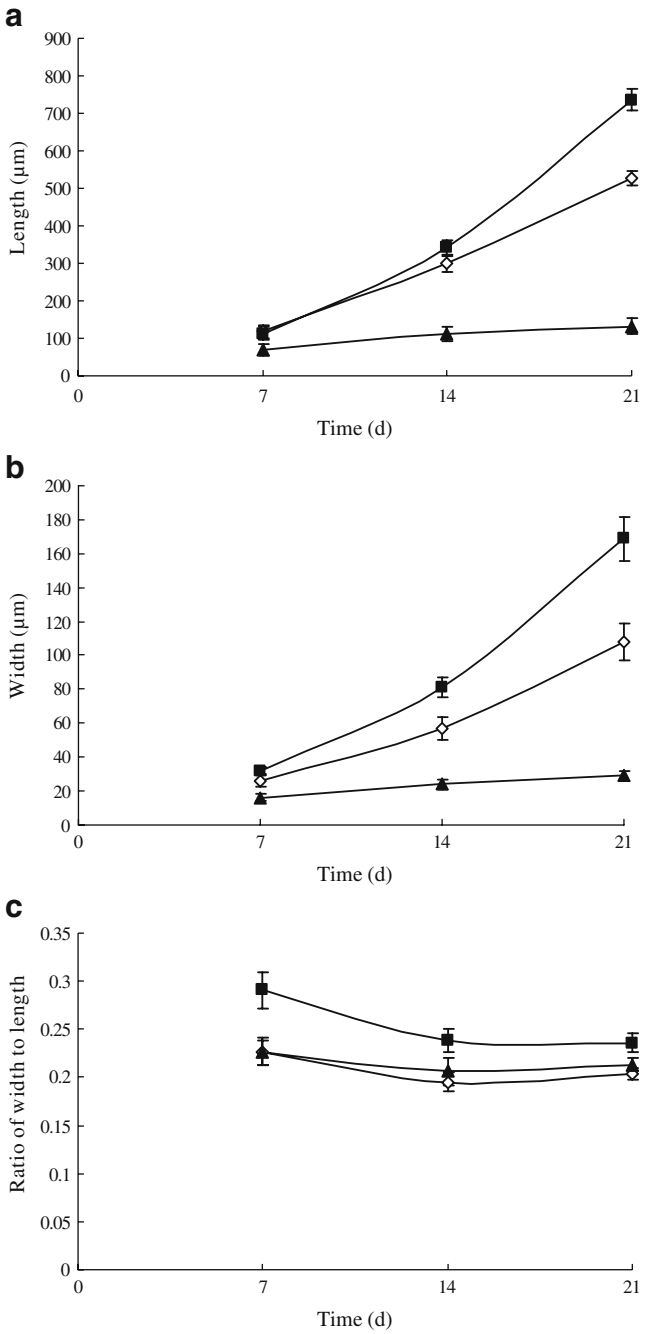

Fig. 5 Growth of sporelings under white, red, and blue light. **a** Length of sporelings; **b** width of sporelings; **c** ratio of width to length of sporelings. Symbols: *hollow diamonds* = white light, *solid squares* = blue light, *solid triangles* = red light. Data are mean ± SD (n=50)

blue light than under white light (F=4485.228, P=0.000). Φ_{PSII} and $rETR_{max}$ obtained from *S. japonica* sporelings under blue light were both significantly higher than those under white light (Table 2; F=22.791, P=0.001; F=2331.423, P=0.000). These two parameters are closely related to the carbon fixation process. The former is suggested to be dependent on the activity of CO_2 fixation enzyme Rubisco (MacIntyre et al. 2000; Serôdio et al. 2006) and the latter is found to have strong linear relationship with the efficiency of carbon fixation under stressless conditions (Fryer et al. 1998). From the characteristics of the above photosynthetic parameters, a conclusion can be made that blue light caused a cooperative stimulation of photosynthetic light and dark reactions in *S. japonica* sporelings.

Discussion

It takes approximately 3 months for indoor seedling culture of *S. japonica* under artificial management. The culture process is composed of three stages: zoospores seeding onto the culture mats and developing into gametophytes, gametophytes developing into sporelings, and sporelings growing to several centimeters long until being transplanted to field (Scoggan et al. 1989).

Eggs of *S. japonica* have no capacity to swim and usually lie just outside the residue of the parent female gametophytes and then germinate into sporelings after fertilization. Consequently, the distribution of zoospores determines the density of sporelings. *Saccharina* zoospores swim for dozens of minutes to several hours after being released. Previous findings revealed that the swimming is not directed by light (Kawai 1988; Maier and Müller 1990). This property enables zoospores to distribute evenly in seawater regardless of light conditions. However, zoospores become floating spores prior to settlement (Fukuhara et al. 2003). Brown algal zoospore attachment is affected by many factors, such as water velocity (Pang and Shan 2008) and dose of ultraviolet B radiation (Liu et al. 2008). The attaching capacity even varies among different populations (Edding et al. 1993). So far, little is known about light effects on *Saccharina* zoospore attachment. In indoor seedling culture, the light source is sunlight from roof windows and side windows, i.e., light is unevenly distributed in the culture room. Consequently, it would be a disadvantage if the attachment of floating spores is affected by light. The present study found that there was no significant variance in zoospore attachment under different irradiances as well as light qualities. This means *S. japonica* zoospores will attach to the culture mats evenly regardless of the light conditions. Previously, Shi et al. (2005) reported that germination of *S. japonica* zoospores occurs 1 d after settlement irrespective of irradiance and light quality, while germination of *Saccharina latissima* (previously *Laminaria saccharina*; Lane et al. 2006) zoospores is slightly delayed under red light (Lüning 1975). Accordingly, light quality may have a species-specific effect on *Saccharina*/*Laminaria* zoospore germination. This study only recorded the germination of *S. japonica* zoospores 4 d after the

Table 2 Photosynthetic parameters of *S. japonica* sporelings under different light qualities

	Φ_{PSII}	$rETR_{max}$	α	E_k
Blue light	0.822±0.015	472.462±9.087	0.376±0.083	1,256.882±11.045
White light	0.781±0.018	270.556±5.290	0.343±0.069	787.874±8.975
Red light	0.690±0.013	196.880±5.562	0.270±0.052	728.107±8.230

Values are the means ± SD (n=6)

Φ_{PSII} effective quantum yield, α the initial slop, $rETR_{max}$ relative electron transport rate at light saturation, E_k (μmol photons m^{-2} s^{-1}) irradiance at onset of light saturation

settlement, and no significant variance was found under all light qualities and irradiances. Taken together, it seems that there is no specific requirement of light conditions for *S. japonica* zoospore attachment and germination.

There are only a few reports about the effect of blue light on the vegetative growth of *Saccharina* gametophytes. Growth of *S. latissima* gametophytes has been reported to be identical under blue and red light (Lüning 1975); however, growth of *S. japonica* gametophytes seems to be stimulated by blue light and delayed by red light (Shi et al. 2005). No matter whether the vegetative growth of *Saccharina* gametophytes is stimulated by blue light or not, it has been assured that their reproduction is largely affected by blue light (Lüning and Dring 1972; Lüning 1975; Shi et al. 2005). White light is the combination of all light qualities including blue light. Although the gametophytes developed similarly under white and blue light, egg formation occurred much earlier under blue light than white light (Fig. 3). The current indoor seedling culture system employs sunlight from roof and side windows as the only light source. Gametophytes start to produce eggs on the 15th to 18th day after zoospore settlement, and it takes about 15–20 d for 100% formation of eggs, leading to asynchronously aged sporelings. Based on the present findings, it is to be expected that it will take much less time for 100% formation of eggs, and then sporelings will grow more synchronously by applying blue light to the culture system.

The higher growth rate of *S. japonica* sporelings under blue light was largely due to the higher photosynthetic efficiency (Table 2). It has been proven that photosynthesis of *S. latissima* or *Laminaria digitata* sporophytes in saturating irradiance of red light can be stimulated by blue light and that the degree of stimulation varies among species (Forster and Dring 1994). The $rETR_{max}$ of *S. japonica* sporelings under blue light was 140% higher than that under red light (Table 2), higher than the previous reports on sporelings of *S. latissima* as well as the adult plants of *S. latissima*, *Laminaria hyperborea*, and *L. digitata* (Dring 1989; Forster and Dring 1994). *S. japonica* seems to be more sensitive to blue light.

The above studies (Dring 1989; Forster and Dring 1994; and the present) were conducted in natural seawater. It has been further shown that stimulation of photosynthesis of brown algae by blue light is correlated with an increased inorganic carbon uptake (Klenell et al. 2002, 2004; Schmid and Dring 1993a, b, 1996a, b; Schmid et al. 1996). The degree of blue light stimulation is absolutely dependent on the CO_2 concentration of the medium (Forster and Dring 1992). At a CO_2 concentration typical of natural seawater (12.4 mmol m^{-3}, pH8.2), blue light increases oxygen exchange rates of *L. digitata* sporelings in saturating red light irradiance to about 50%. The stimulation can be increased to over 150% at CO_2 concentrations below that of natural seawater (Forster and Dring 1992). During indoor seedling culture of *S. japonica*, sporelings consume more CO_2 as they are growing and CO_2 will be deficient, especially in deep water where air–water gas exchange is limited. It can be seen that sporelings will achieve normal and even higher growth by illumination of blue light during the period of CO_2 deficiency.

The mature sporophytes of *S. japonica* used in this study were collected from a new cultivar characterized by high ratios of blade width to length. Nowadays, over 80% *Saccharina* plants are used for food in China. Plants with higher ratios of blade width to length are superior to those with lower ratios for food products processing. The growth of young sporophytes of this cultivar under blue light was on average 39% in length and 56% in width higher than that under white light (Fig. 5a, b). Blue light seemed to stimulate the latitudinal growth more than longitudinal growth. This blue light effect is likely to persist in field culture since the light condition under seawater occupied by field culture is predominated by blue light. Therefore, application of blue light to indoor culture system may be able to achieve a good crop of plants with both larger blade sizes and higher ratios of blade width to length.

LEDs have many advantages over other light sources, including high irradiance output with low heat dissipation, long lifetime, small size, and a high capacity to control the spectral composition (Lee and Palsson 1995; Morrow 2008; Olsson et al. 2007), and they have been widely adopted in

cultivation of higher plants and microalgae (Kim et al. 1991; Lee and Palsson 1995; Wang et al. 2007). In this study, blue light was provided by LEDs, and they were shown to be highly efficient for both gametophyte reproduction and sporeling growth in *S. japonica*. As a result, we propose an improved *S. japonica* seedling culture system that employs LEDs as light sources. In the improved system, every two culture mats are fixed as a unit by connecting one edge of a culture mat with that of the other culture mat at an angle of 45–90°. Then they are placed in arrays in the tank with the joints upwards so that the utilization efficiency of the culture room is at least doubled. Blue light is provided by equipping arrays of blue LEDs underwater along the linkages between two culture mat units. During the stage of zoospore collection and germination, only sunlight from windows is used since zoospore attachment and germination are not affected by irradiances and light qualities. Blue light is used 5–7 d later when zoospores have developed into male and female gametophytes. The period of blue light illumination is initially set as 12–14 h per day to achieve rapid and simultaneous reproduction of gametophytes. Six days later, the period of blue light illumination is shortened to 8–10 h per day for rapid and healthy growth of sporelings. It is expected that the use of blue light to the indoor seedling culture systems will significantly reduce the cost and increase the quality of *S. japonica* seedlings.

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