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Citation	北海道大学水産科学研究彙報, 52(2), 103-109
Issue Date	2001-09
Doc URL	http://hdl.handle.net/2115/21949
Type	bulletin (article)
File Information	52(2)_P103-109.pdf



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Effects of Irradiance and Water Temperature on the Photosynthesis and Growth of the Crustose Coralline Alga *Lithophyllum yessoense* Foslie (Corallinales, Rhodophyceae)

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Abstract

The effects of irradiance and water temperature on the photosynthesis and growth of *Lithophyllum yessoense*, which is extensively dominant in the sublittoral zone in southwestern Hokkaido, Japan, were examined in the laboratory. The maximum net photosynthesis rate ($P_{n,max}$) was about $16 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ at 15–25°C. The compensation irradiance (I_c) and saturating irradiance (I_k) of *L. yessoense* were considerably reduced as the water temperature decreased, and initial slope (α) was highest at 5°C. The net photosynthesis was relatively high at low water temperatures under any irradiance except in the dark. This physiological adaptability to low irradiance at low water temperatures would allow this alga to grow in the severe limitation of irradiance of winter and early spring in southwestern Hokkaido. However, the I_c and I_k increased at high water temperature, showing a strong dependence on a high irradiance. The results indicate that *L. yessoense* is not adapted to grow in a dim environment, such as a macroalgal canopy.

Key words: Crustose coralline alga, *Lithophyllum yessoense*, Photosynthesis, Growth

Introduction

Lithophyllum yessoense grows extensively in the sublittoral zone of southwestern Hokkaido, Japan (Adey et al., 1976; Masaki, 1984). The total coverage of this alga is 79% at Taisei in this area (Fujita, 1989). An extensive area covered with a large amount of crustose corallines without fleshy macroalgae is generally referred to as a Coralline flat (Ayling, 1981). The predominance of crustose corallines prevents the recruitment of other macroalgae, such as *Laminaria* Lamouroux and *Undaria* Suringar by its epithallial sloughing (Masaki et al., 1981, 1984) and its released allelochemicals (Denbo et al., 1997; Suzuki et al., 1998). Studying the adaptability of crustose corallines to light and water temperature is necessary to prevent the decrease in macroalgae in southern Hokkaido (Tamura, 1951).

The photosynthesis rate has been studied in many crustose corallines to estimate the carbon production (Johansen, 1981). Fujita (1988) showed seasonal changes in photosynthesis and respiratory rates of *L. yessoense* at four seasons. However, no information exists on specific photosynthesis characteristics of *L. yessoense* in a laboratory culture, nor on the relationships between the photosynthesis rate and the environmental conditions, such as irradiance and water temperature.

The presence or absence of coralline algae, as well as

the characteristics of their growth, are largely influenced by environmental conditions (Johansen, 1981). The effects of irradiance and water temperature on the growth of sporelings of *L. yessoense* have been examined (Notoya, 1978; Fujita, 1986; Ichiki et al., 2000). Fujita et al. (1992) observed the regenerating growth of *L. yessoense*. However, no report exists of the effects of irradiance and water temperature on the growth of adult thalli of this alga.

Here, we describe the effects of irradiance and water temperature on the photosynthesis and growth of adult thalli of *L. yessoense* in a laboratory culture, and we discuss the relationships among photosynthesis, growth and environmental conditions (water temperature and irradiance).

Materials and Methods

Lithophyllum yessoense for the photosynthesis experiment was collected in the sublittoral zone at Kumaishi in December 1999 and for the growth experiment in April and May 2000, when the water temperatures were about 10°C. The water temperature along the coast of the Japan Sea ranges from 4°C to 23°C (Hokkaido Aquaculture Development Authority, 1999). The plants for photosynthesis experiment were pre-cultured at 15°C using bubbling under $83 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (14L : 10D) with a white fluorescent lamp for 6–9 days

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to arrange the amount of pigments (Ramus and Zimmerman, 1977) and for the growth experiment for 20–38 days to lessen influences of the rapid growth by the regeneration (Fujita et al., 1992). 1/4 concentration of PES medium without vitamins was used for the culture and photosynthesis measurements, and $0.25 \text{ mg} \cdot \text{l}^{-1}$ GeO_2 and $1 \text{ ml} \cdot \text{l}^{-1}$ antibiotic mixture (Tatewaki et al., 1989) were added to this medium to inhibit the growth of diatoms and bacteria. The medium was changed every 10 days. Seawater was filtered through a glass fiber filter (Whatman GF/C $0.44 \mu\text{m}$, Whatman, Maidstone, UK) and was autoclaved at 120°C for 15 minutes.

Photosynthesis

The algal size was adjusted to ca. 1.5 cm^2 at 3 days before the photosynthesis measurements. Photosynthesis was measured using the dissolved oxygen method with an oxygen electrode (Model 57, YSI). After 30 minutes of acclimatization, the fluctuation of dissolved oxygen in a glass bottle (25 ml) agitated with a stirrer was monitored for 30 minutes. The water temperature was adjusted to 5, 10, 15, 20, 25 and 30°C using a Cool-nics (Komatsu-yamato) under 0, 16.6, 83, 166, 415 and $830 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ of a tungsten lamp, and 36 conditions were set for the different combinations of water temperature and irradiance. The photosynthesis parameters were expressed from photosynthesis-irradiance (P-I) curves using the equation (Gómez et al., 1998),

$$P(I) = P_{n \max} \tanh(\alpha I / P_{n \max}) + R,$$

where $P(I)$ is the gross photosynthesis rate expressed in $\mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$; $P_{n \max}$ is the maximum net photosynthesis; \tanh is the hyperbolic tangent; α is the initial slope estimated by the least square method using six to nine data at limiting irradiance; I is the irradiance and R is the respiration in the dark. The saturating irradiance (I_k) was calculated from the intersection between the $P_{n \max}$ and α . The compensation irradiance (I_c) corresponded to the intersection between the curve and x-axis ($y=0$).

Growth

The effect of irradiance was examined under 8.3, 16.6, 41.5, 83, 166 and $332 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (14L : 10D) at 15°C . The effect of water temperature was examined at 5, 10, 15, 20 and 25°C under $83 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (12L : 12D). The plants were acclimated by culture for 10 days at each experimental condition with bubbling. The culture medium was changed every 10 days.

Microscopic pictures were taken to record the thallus growth in vertical section on the first and on the 40th day of culture, so that the same part of a thallus could be

traced. The length from the edge of section to thallus margin was measured. The marginal growth rate was calculated using the equation,

$$\text{Marginal growth rate} = 100 \cdot (L_2 - L_1) / (t_2 - t_1)$$

where L_1 and L_2 are the length at times t_1 and t_2 , respectively.

The least square method was used to estimate the coefficient correlation (r^2) between the water temperature and the photosynthesis characteristics and between the marginal growth rate and the photosynthesis characteristics.

Results

Photosynthesis

Fig. 1 shows net photosynthesis-irradiance relationships at $5\text{--}30^\circ\text{C}$. The photosynthesis rates increased with increase in irradiance and were saturated at $166\text{--}415 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Photoinhibition did not occur even at $830 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at all water temperatures.

Table 1 summarizes the photosynthesis characteristics. The maximum gross photosynthesis rate ($P_{g \max}$) increased with the increase in water temperature up to 25°C , reaching $45.9 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$, about 3.5 times that at 5°C . The respiration rate (R) increased with increase in water temperature, showing a significant correlation ($p < 0.01$) between water temperature and R (Table 2); it was $32.6 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ at 30°C , about 11 times that at 5°C . The maximum net photosynthesis rate ($P_{n \max}$) at 15°C was $17.1 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$, the highest of all the conditions, although it was similar to those at 20°C and 25°C ; it was $10.1 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ at 5°C , about 7 times that at 30°C . The compensation irradiance (I_c) increased with increase in water temperature, showing a significant correlation ($p < 0.01$) between water temperature and I_c (Table 2). It was $121 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at 30°C , about 23 times that at 5°C . The saturating irradiance (I_k) at 20°C was $172.8 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, the highest of all the conditions, and was 7.4 times that at 5°C . The photosynthesis efficiency (α) was 0.56 at 5°C , and was less than 0.28 at other water temperatures.

Fig. 2 shows net photosynthesis-temperature relationships at irradiances between 0 and $830 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The optimum water temperatures for photosynthesis were 25°C under $830 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 15°C under $415 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 10°C under $166 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, $5\text{--}15^\circ\text{C}$ under $83 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and 5°C under $16.6 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The net photosynthesis rate at 5°C was about a half that at 25°C under $830 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The net

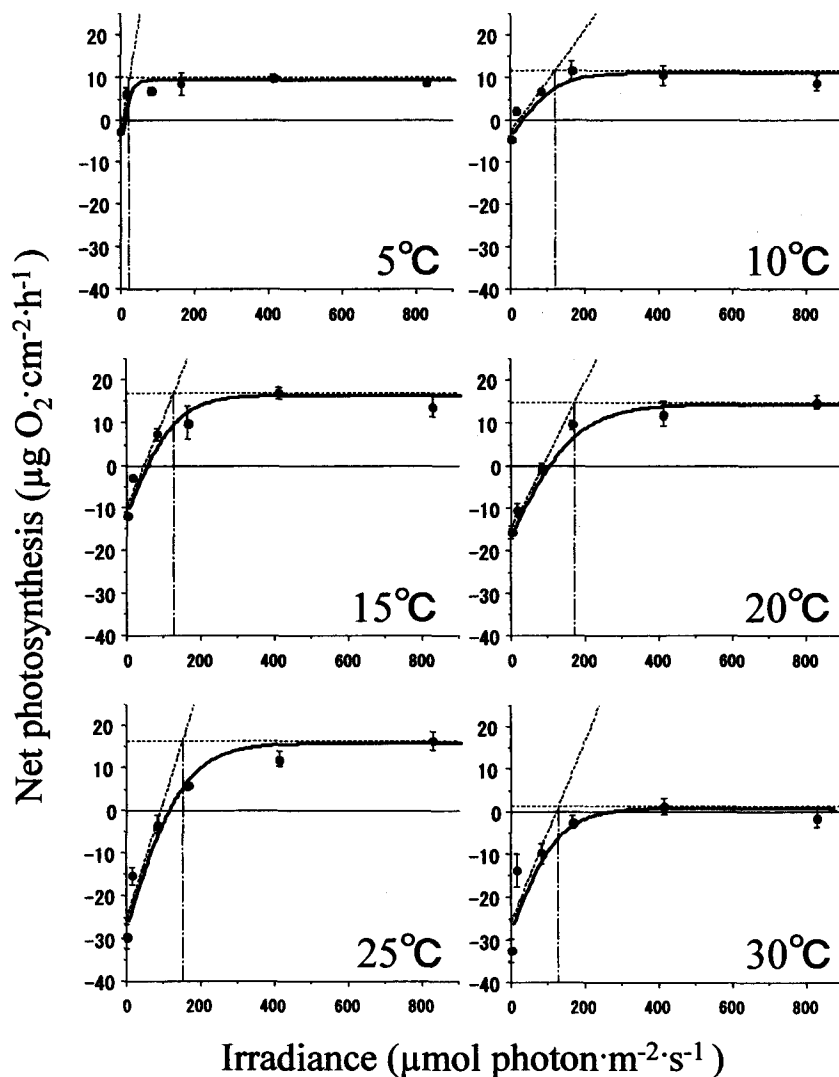


Fig. 1. Photosynthesis-irradiance relationships of *Lithophyllum yessoense* at 5°C to 30°C. Symbols represent mean values ($n=3$). Vertical bars indicate standard errors.

Table 1. Photosynthetic characteristics of *Lithophyllum yessoense*. Units: $P_{g \max}$ (maximum gross photosynthetic rate), R (respiration), $P_{n \max}$ (maximum net photosynthetic rate), I_c (compensation irradiance), I_k (saturating irradiance) and α (initial slope). \pm shows SE.

	5°C	10°C	15°C	20°C	25°C	30°C
$P_{g \max}$ ($\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$)	13.0	16.5	28.9	30.7	45.9	34.0
R ($\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$)	2.9 ± 0.1	4.7 ± 0.7	11.9 ± 0.9	15.7 ± 1.5	29.4 ± 2.8	32.6 ± 2.7
$P_{n \max}$ ($\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$)	10.1 ± 0.8	11.8 ± 2.3	17.1 ± 1.3	14.9 ± 1.6	16.5 ± 2.1	1.4 ± 1.9
I_c ($\mu\text{mol Photon m}^{-2} \text{ s}^{-1}$)	5.2 ± 0.6	21.7 ± 3.5	44.9 ± 5.5	85.5 ± 10.1	91.3 ± 15.2	121.0 ± 33.3
I_k ($\mu\text{mol Photon m}^{-2} \text{ s}^{-1}$)	23.2 ± 2.9	120.2 ± 19.3	126.6 ± 15.4	172.8 ± 20.5	151.2 ± 25.1	127.4 ± 35.1
α	0.56 ± 0.08	0.12 ± 0.02	0.21 ± 0.03	0.17 ± 0.02	0.28 ± 0.06	0.21 ± 0.08

photosynthesis rates at 5°C under all irradiances ranged from $6.3 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ to $10.1 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$, but the rate was from $-15.3 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ to $16.5 \mu\text{g O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ at 25°C.

Growth

Fig. 3 shows the relationship between marginal growth rate and irradiance. The marginal growth rate increased with increase in irradiance up to $83 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, under which it was $16.2 \mu\text{m} \cdot \text{day}^{-1}$, the

Table 2. Coefficient correlations (r^2) of photosynthetic characteristics to water temperature ($n=6$) and marginal growth rate ($n=5$) in *Lithophyllum yessoense*.

	$P_{g \max}$	R	$P_{n \max}$	I_c	I_k	α
Temperature	*0.753	**0.950	0.084	**0.977	0.471	0.199
Growth rate	0.243	0.173	0.441	0.474	*0.901	*0.828

A significant correlation : * ($p < 0.05$), ** ($p < 0.01$).

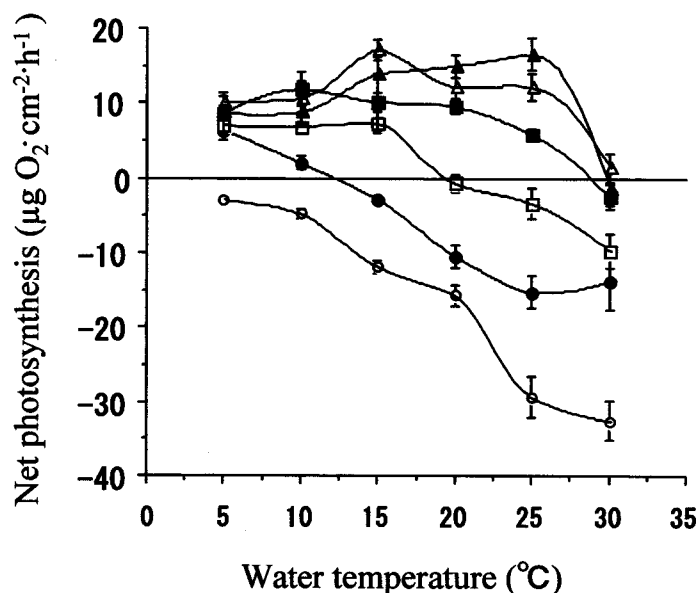


Fig. 2. Photosynthesis-temperature relationships of *Lithophyllum yessoense*. Symbols represent mean values ($n=3$). Vertical bars indicate standard errors.

○: $0 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, ●: $16.6 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$,
 □: $83 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, ■: $166 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$,
 △: $415 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, ▲: $830 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$

highest of all irradiances.

Fig. 4 shows the relationship between the marginal growth rate and water temperature. The marginal growth rate increased with increase in water temperature from 5°C to 20°C, reaching $23.5 \mu\text{m}\cdot\text{day}^{-1}$ at 20°C, about 10 times that at 5°C; it was $15.1 \mu\text{m}\cdot\text{day}^{-1}$ at 25°C. The marginal growth rate was correlated significantly with I_k positively ($p < 0.05$) and with α negatively ($p < 0.05$, Table 2).

Discussion

Productivity

The $P_{n \max}$ of *L. yessoense* acclimated in a laboratory culture was similar to that obtained by Fujita (1988). The maximum $P_{n \max}$ of this alga was one to three times those of other crustose corallines (e.g. *Porolithon onkodes* (Heydrich) Foslie, *Neogoniolithon solubile* (Foslie et Howe) Setch. & Mason) in coral reefs (Littler and Doty, 1975; Wanders, 1976). However, the marginal and accretive growth rates of crustose corallines in coral

reefs (Finckh, 1904; Adey and Vassar, 1975; Matsuda, 1989) are more than five times those of *L. yessoense* (Fujita, 1990; Ichiki, 2001). The results show that the yields of photosynthates do not always reflect the growth rates in crustose corallines. The maximum $P_{n \max}$ of *L. yessoense* was about a half that of *Laminaria religiosa* Miyabe, which dominates in southwestern Hokkaido (Matsuyama, 1985).

Saturated irradiance for photosynthesis and growth

Growth and photosynthesis were saturated under $83 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $415 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 15°C, respectively. The discrepancies of these saturated irradiances between growth and photosynthesis have been reported for many macroalgae (Lüning, 1981). The saturated irradiance for the growth of adult thalli was about one-third that of the sporelings of this alga (Ichiki et al., 2000), indicating that the growth of adult thalli is less dependent on the higher irradiance than the sporelings.

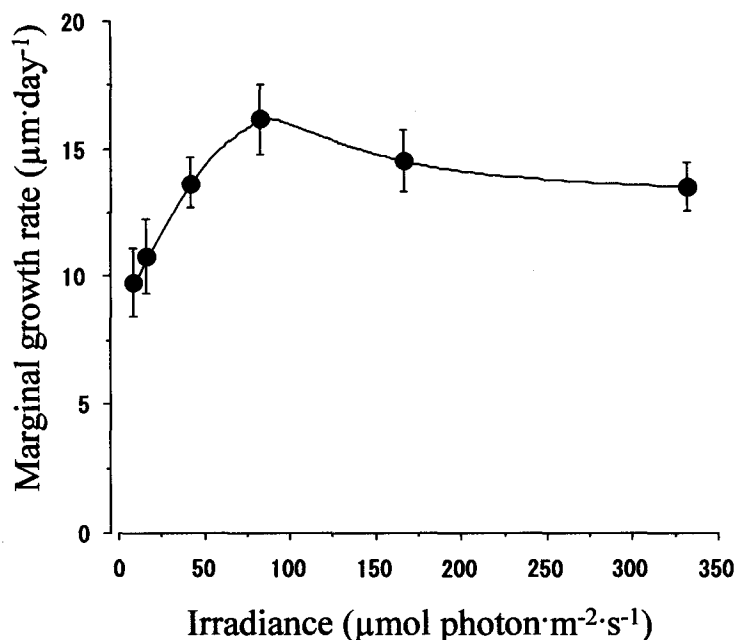


Fig. 3. Relationships between marginal growth rate of *Lithophyllum yessoense* and irradiance. Symbols represent mean values ($n=8$). Vertical bars indicate standard errors.

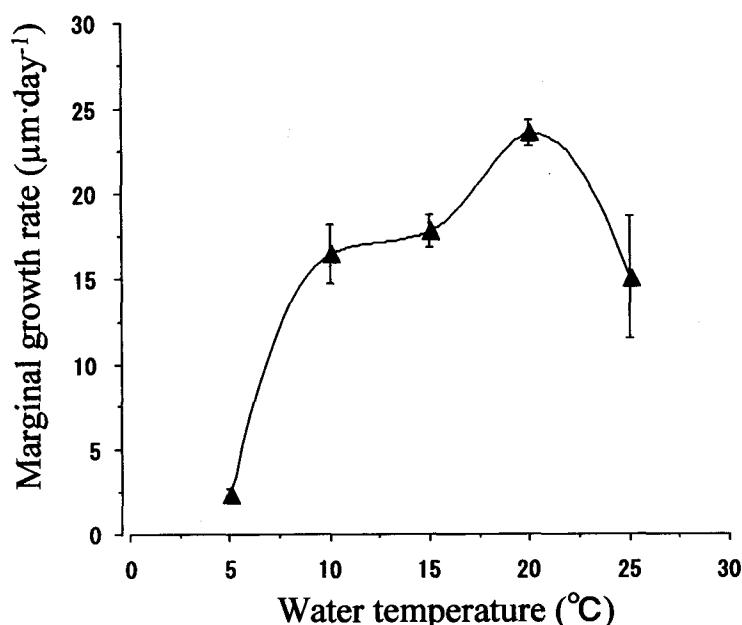


Fig. 4. Relationships between marginal growth rate of *Lithophyllum yessoense* and water temperature. Symbols represent mean values ($n=8$). Vertical bars indicate standard errors.

Optimum water temperature for photosynthesis and growth

The optimum water temperature for the growth of *L. yessoense* was 20°C, which was similar to that of the sporelings of this alga reported by Ichiki et al. (2000). The growth of this alga was inhibited at 25°C, similar to the results for sporelings of this alga found by Fujita (1986) and Ichiki et al. (2000). However, the optimum

water temperature for gross photosynthesis was recorded at 25°C, showing a different optimum water temperature between the gross photosynthesis and the growth. The optimum water temperature for photosynthesis disagrees with that for growth in some arctic seaweeds (Healey, 1972). However, the optimum water temperature for the growth in this study agreed with that for I_k in *L. yessoense*, showing a significant positive correlation between the marginal growth rate and I_k . Such results

suggest that the degree of dependence on the irradiance reflects the growth of *L. yessoense*. Difficulties in measuring the extreme slow growth of crustose corallines cause a lack of data on the growth rate (Garrabou and Ballesteros, 2000). Accordingly, we think that the I_k is a useful indicator of the growth activity of crustose corallines.

Adaptability to water temperature and irradiance

I_k shows some correlation with algal habitat, and α is a useful indicator of the light quantum yield (Lobban and Harrison, 1994). The I_c and I_k of *L. yessoense* were considerably reduced as the water temperature decreased, and α was highest at 5°C. The net photosynthesis was relatively high at low water temperatures under any irradiance except in the dark. This physiological adaptability to low irradiance at low water temperature would allow this species to grow in the severe limitation of irradiance, such as at low sun irradiation, short photoperiods and enormous epiphytes, such as diatoms, to grow on this alga (per. obs.), which all occur during winter and early spring in southwestern Hokkaido. However, the I_k and I_c increased at high water temperature, showing a strong dependence on high irradiance. In southwestern Hokkaido, the irradiance under a sparse *L. religiosa* canopy on a solstitial day, when the water temperature is about 15°C (Hokkaido Aquaculture Development Authority, 1999), is about 80 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fujita, 1988), which is less than I_k (126.6–172.8 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and similar to I_c (44.9–91.3 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at 15–25°C for *L. yessoense*. Accordingly, these facts support the suggestions by Fujita (1988) that *L. yessoense* is not adapted to grow under a *L. religiosa* canopy formed from late spring to autumn in southwestern Hokkaido.

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