

Seasonal changes in growth and photosynthesis-light curves of *Sargassum horneri* (Fucales, Phaeophyta) in Oura Bay on the Pacific coast of central Honshu, Japan

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Abstract: We investigated seasonal changes in the growth, photosynthesis-light curves, and chlorophyll *a* content of *Sargassum horneri* (Turner) C. Agardh in Oura Bay on the Pacific coast of central Honshu, Japan, and also characterized the physical environment, including PAR and water temperature. During monthly scuba dives, we tracked the growth of main stems and observed the growth stage of eight to ten individual *S. horneri* that had been marked when their main stems were >10 cm until they disappeared from the substratum after maturity. In addition, we measured the rates of net photosynthesis and dark respiration in upper and lower leaves of four individual *S. horneri* collected monthly with a differential gas volumeter at the monthly mean water temperature, also measuring the weight and chlorophyll *a* content of the leaves. The seasonal changes in the photosynthetic activity of upper leaves based on wet weight and chlorophyll *a* had different peaks : the former was positively correlated with the length and growth rate of the main stems, and the latter was negatively correlated with plant age. Moreover, the pattern of seasonal changes in photosynthetic activity based on weight was synchronized with changes in the nutrient content of the seawater.

Keywords: *Sargassum horneri* (Turner) C. Agardh, photosynthesis-light curve, growth, seasonal change.

Sargassum horneri (Turner) C. Agardh, an annual species, is distributed on rocky coasts throughout the Japanese archipelago, except the eastern part of Hokkaido and Okinawa, the Korean Peninsula, and China, and is one of the most common species in Japan (UMEZAKI, 1984a ; YOSHIDA, 1998). It grows on rocks at water depths of 1 to 5 m (rarely 10 m). Its length can reach several meters, extending to the sea surface in the luxury growth season. Typically, *S. horneri* forms a mixed species forest with other *Sargassum* species, and *Sargassum* forests oc-

cupy about 30% of the surface area (85,682 ha) of all seagrass and seaweed beds in Japan (Environment Agency of Japan, 1994). These forests play important roles as both primary producers and habitat in coastal ecosystems due to their great biomass. Around maturation, when the main stem of *S. horneri* attains its maximum length, the plant detaches from the substratum, and the next generation emerges and grows (UMEZAKI, 1984b). Therefore, the biomass of *S. horneri* varies seasonally according to the annual life cycle. Recently, *S. horneri* has become commercially exploited as a food resource because it contains biologically active agents, and elucidating its ecology is of major importance.

The seasonal change in the photosynthetic activity of *Sargassum* species may be related to their growth, physiology, and physical condition (PRINCE, 1980 ; DAWES, 1987 ; HONDA and OKUDA, 1989 ; 1990 ; GAO, 1990b), although

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this has not been evaluated in detail. For example, GAO (1990a) found seasonal changes in the photosynthetic rate of *S. horneri* measured monthly at 20° C and 600 $\mu\text{E m}^{-2} \text{s}^{-1}$ for one year, excluding September, and concluded that temperature, growth stage, and nutrient conditions in the sea accounted for the seasonal photosynthetic variability. PRINCE (1980) reported that a significant decline in the photosynthetic rate of *Sargassum pteropleuron* Grunow was synchronous with leaf senescence and decreased water temperatures in winter. HONDA and OKUDA (1989, 1990) demonstrated that the maximum photosynthesis rates of vernal and autumnal *S. horneri* and *Sargassum micracanthum* (Kützing) Endlicher differed depending on their stage of maturity.

Several studies in different areas have reported seasonal changes in the growth of *S. horneri* in terms of its biomass and length (UMEZAKI, 1984b ; TANIGUCHI and YAMADA, 1988 ; YOKOYAMA *et al.* 1999), but few studies have examined the seasonal changes in both photosynthetic activity and growth, except a study conducted in Wakasa Bay on the coast of the Sea of Japan (GAO, 1990b). Investigating the seasonal change in photosynthetic activity, which is the basis of growth, helps to understand the relationship between growth and the external environment or internal condition of the plants. In addition, investigations of the same species in a variety of areas that have different physical environments would help to understand these relationships more clearly.

Here we describe the ecological influences on photosynthesis in *S. horneri* under monthly mean water temperature conditions *in situ*. We measured the photosynthesis-light curves based on both weight and chlorophyll *a* (chl.*a*) content of leaves monthly. Growth was assessed from measures of main stem length made while scuba diving to observe the growth stage. We investigated the relationships among seasonal changes in the photosynthetic activity, growth, physiological condition, and abiotic environment of the species. Moreover, based on comparisons with the results from another area (GAO, 1990), we examined the factors causing the seasonal changes in photosynthetic activity and growth.

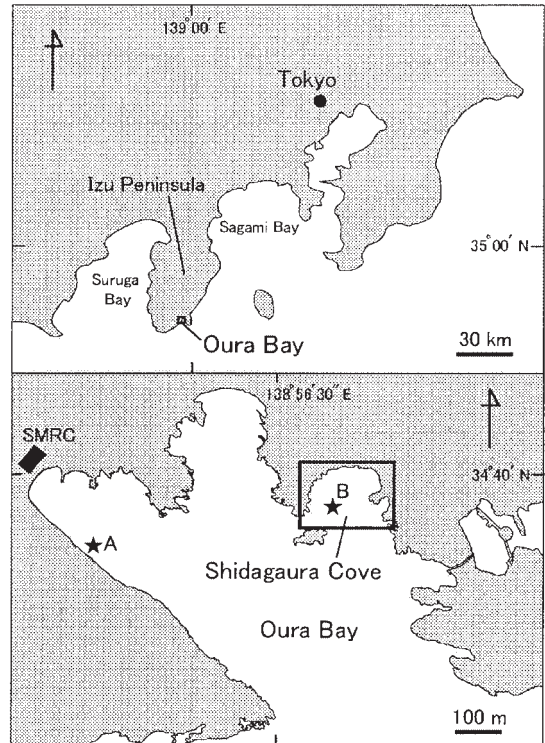


Fig.1 Map showing the study site in Shidagaura Cove, Oura Bay, located near the tip of the Izu Peninsula on the Pacific coast of central Honshu, Japan, and the Shimoda Marine Research Center (SMRC), University of Tsukuba. In the lower panel, A and B indicate the measurement locations for water temperature and PAR, respectively.

2. Materials and Methods

2.1. Study site

Sargassum horneri was collected from Shidagaura Cove in Oura Bay, located near the tip of the Izu Peninsula on the Pacific coast of central Honshu, Japan (Fig. 1). A *Sargassum* forest exists in the subtidal zone consisting of rocks and rock plates at depths of 1 to 5 m with horizontal dimensions of about 100×100 m ; *S. horneri* was a dominant species at the study site.

2.2. Measurement of *in situ* PAR and water temperature

The photosynthetically active radiation (PAR) in Shidagaura Cove was measured at 10-min intervals from December 2001 to December 2002 with light intensity sensors (MDS

Mark 5/L ; Alec Electronics, Japan) fixed on the sea floor at depths of 1, 2, and 3 m. Surface water temperatures in Oura Bay (Fig. 1) were measured daily by personnel from the Shimoda Marine Research Center of the University of Tsukuba at 10 : 00 h. The monthly mean surface water temperature was then determined and used for the experiment.

2.3. Measurement of growth

Sargassum horneri has one main stem that grows from the holdfast and lateral branches that grow from the main stem (Fig. 2). The length of the main stem serves as an index of individual plant growth. Therefore, ten individuals of *S. horneri* at depths of 2 to 3 m in Shidagaura Cove were selected randomly and marked with tags fixed to the base of the main stem in December 2001. Scuba divers measured the main stem lengths of the marked individuals each month from December 2001 to December 2002, from the time the main stem length exceeded 10 cm until the individual detached from the substratum after maturity. When a marked individual detached, the divers marked a new individual and continued their measurements. The main stem typically grows the longest, although when it is cut off due to wave action or other factors, a lateral branch can grow longer than the main stem. In cases where the lateral branch was longer than the main stem, the lateral branch length was measured. Sprouting and maturity were also examined in situ during the underwater measurements of the main stems. In addition, approximately four individuals were collected for measuring photosynthesis and respiration.

2.4. Measurement of net photosynthesis and dark respiration

Between December 2001 and December 2002, the net photosynthetic and dark respiratory rates of *S. horneri* were measured from October to April when the main stem length exceeded 10 cm. During the experiment, the water temperature was set at the monthly mean from Oura Bay in the previous year. Leaves were measured because they are the primary organ for net primary production of the plant (GAO and UMEZAKI, 1989a ; GAO, 1991). Since the photo-

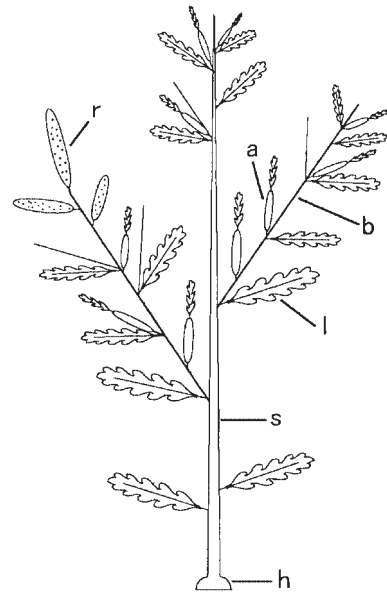


Fig. 2 Diagram of an individual *Sargassum horneri*. h, holdfast ; s, main stem ; b, lateral branch ; l, leaf ; a, air - vesicle ; r, receptacle.

synthetic rate of leaves depends on their position, namely the upper or lower portion of the plant (GAO and UMEZAKI, 1988, 1989a ; GAO, 1991 ; MURASE *et al.* 2000), eight cuttings of leaves (about 5 cm⁻² per cutting) were selected randomly from each portion of the plant for the four individuals collected monthly from Shidagaura Cove. The net photosynthetic and dark respiratory rates for a total of 16 cuttings were measured using the following method.

We used a differential gas volumeter (DGV ; Productmeter ; Nikko-Kagaku, Japan), which measured the increase or decrease in the rate of oxygen (μ) produced or consumed by the cuttings placed in a small flask (YOKOHAMA and ICHIMURA, 1969 ; YOKOHAMA *et al.*, 1986). The DGV has often been used to measure the net photosynthetic and respiratory rates of macroalgae (YOKOHAMA, 1973 ; GAO and UMEZAKI, 1988 ; SAKANISHI *et al.*, 1989 ; GAO and NAKAHARA, 1990 ; GAO, 1991 ; SERISAWA *et al.*, 2001b). Cuttings were identified by cubicle (mesh case) and kept in an aquarium (5000 ml) with filtered running seawater for about 24 h in the laboratory before measuring the net photosynthetic and dark respiratory rates to avoid effects associated with the trauma of

cutting (SAKANISHI *et al.*, 1988). The net photosynthetic and dark respiratory rates of *Sargassum* species exhibited apparent day-night rhythms independent of daytime exposures to various intensities of solar radiation (GAO and UMEZAKI, 1989b ; GAO, 1990a). Based on this pattern, a series of experiments was started at 13 : 00 h, and the flasks were shaken by motor for 1 h at a constant light intensity of $400 \mu\text{E m}^{-2} \text{s}^{-1}$ just before the experiment. A 30ml conical reaction flask with a cutting and 10 ml of filtered seawater, and a compensation flask with $^{-1} 0$ ml of filtered seawater only were attached to the DVG. The flasks were put in a water bath ($30 \times 70 \times 30$ cm) at a thermostat-regulated temperature matching the monthly mean water temperature measured the previous year. The flasks were irradiated by a lamp (KP-10S 100V-300W ; Philips, Japan) and the light reflected from mirrors placed under the water bath. Seven light intensities ($800, 400, 200, 100, 50, 25, 0 \mu\text{E m}^{-2} \text{s}^{-1}$) were applied using neutral density glass filters (TND-50, 25, 12.5 ; Toshiba, Japan). The PAR of the various light intensities was measured with a quantum photon meter (LI-189 ; LI-COR, USA). Oxygen evolution or consumption in the reaction flask was monitored every 3 min for about 20 min per light intensity with continual shaking (amplitude about 2.5 cm, frequency about 130 lap m^{-1} intervals) in the water bath.

The net photosynthetic and dark respiratory rates under the seven light intensities were fitted to the following approximation of photosynthesis-light curves proposed by Eilers and Peeters (1988) :

$$P = I / (aI^2 + bI + c) - R_d, \quad (1)$$

$$P_m = I / (b + 2\sqrt{ac}), \quad (2)$$

$$s = I/c, \quad (3)$$

where P , I , and R_d are the photosynthetic rate, light intensity, and dark respiratory rate, respectively ; a , b , and c are constants ; P_m is the maximum net photosynthetic rate ; and s is the initial slope.

After the experiment, the wet weights of the cuttings were measured with an electronic balance (EB-330S ; Shimadzu, Japan). To quantify photosynthetic pigments, the cutting was

placed in 10 ml of N,N-dimethyl-formamide (DMF) solution at -25°C for at least 1 day. The absorbances of the extract at 663.8 nm and 750 nm were measured with a spectrophotometer (UV-3000 ; Shimadzu), and the chl.*a* levels were calculated using the formula proposed by PORRA *et al.* (1989).

3. Results

3.1. Water temperature and daily PAR

Figure 3 (a) shows the monthly mean of water temperature and mean daily PAR averaged per month measured at a depth of 1 m in the survey area from December 2001 to December 2002. The monthly mean water temperature increased from February to August and decreased from September to February. A

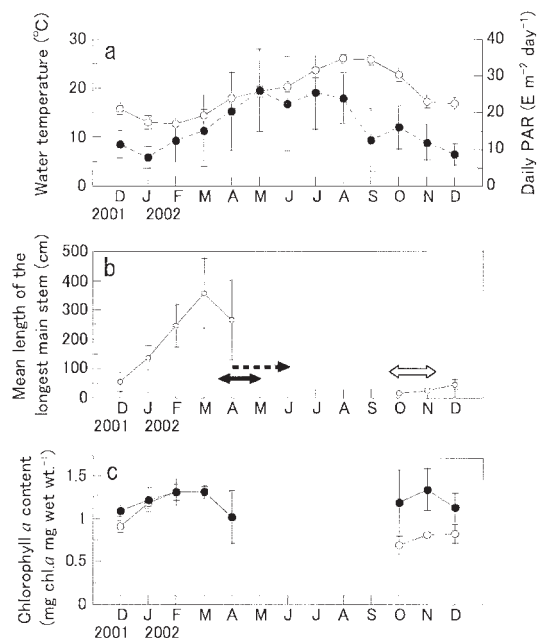


Fig. 3 **a**, Monthly means of water temperature and daily PAR at a depth of 1 m at the study site. Open and solid circles represent the water temperature and daily PAR, respectively. **b**, Seasonal growth patterns of *S. horneri*. The mean length of the longest main stem (open circle) and maturation period (solid arrow), early stage of growth (open arrow), and period of plant detachment of (dotted arrow) are shown by season. **c**, Chlorophyll *a* contents of the upper (open circle) and lower (solid circle) leaves of *S. horneri* for months when photosynthesis was measured.

Table 1 Mean growth rate (cm month⁻¹) of main stems of *S. horneri* marked and measured by a diver.

Period	Mean growth rate (cm month ⁻¹)	S.D.
Dec 2001 - Jan 2002	64.8	17.9
Jan 2002 - Feb 2002	142.7	75.3
Feb 2002 - Mar 2002	151.3	25.3
Mar 2002 - Apr 2002	18.8	8.0
Apr 2002 - May 2002	-	-
Oct 2002 - Nov 2002	12.7	5.5
Nov 2002 - Dec 2002	23.4	15.5

minimum temperature of 13° C was attained in February and a maximum of 26° C was reached in August and September. The mean daily PAR depended on day length ; it was high from May to August and low from November to February. The minimum and maximum values of the mean daily PAR were 7.8 E m⁻² day⁻¹ in January and 26.1 E m⁻² day⁻¹ in May, respectively.

3.2. Seasonal change in growth

Figure 3 (b) and Table 1 show the monthly mean length and monthly mean growth rate (cm month⁻¹) of main stems standardized using a month of 30 days. The monthly mean length of the main stems reached a maximum of 358 cm in March, and then decreased in April. Field observation revealed that *S. horneri* matured from mid-March to April (Fig. 3 (b)). Entire plants of *S. horneri* detached from the substrata, without residual parts, from April to May (Fig. 3 (b)). Sprouts of new plants were observed on rocks from the beginning of October until the end of November. The monthly mean growth rate of the main stems ranged from 64.8 to 151.3 cm month⁻¹ from December to March. Growth was highest (151.3 cm month⁻¹) from February to March and lowest (12.7 cm month⁻¹) from October to November.

3.3. Chlorophyll a content by wet weight

The chl. *a* content in the upper leaves ranged from 0.69 to 1.32 mg chl. *a* g wet wt.⁻¹ (Fig. 3

(c)), and increased with main stem growth (Fig. 3 (b)). However, the values for the lower leaves remained constant between 1.09 and 1.34 mg chl. *a* g wet wt.⁻¹ throughout the experiment. The chl. *a* content of the lower leaves was greater than that of the upper leaves from October to December (*t*-test, *P* < 0.05). The chl. *a* content of the upper leaves approached that of the lower leaves as the plants grew and matured.

3.4. Seasonal change in the photosynthesis-light curves

3.4.1. Maximum net photosynthetic rate

Figure 4 shows the photosynthesis-light curves based on wet weight. The maximum net photosynthetic rate of upper leaves based on wet weight reached a maximum of 3.9 μl O₂ mg wet wt.⁻¹ h⁻¹ in March and a minimum of 2.3 μl O₂ mg wet wt.⁻¹ h⁻¹ in December (Fig. 5 (a)). The maximum net photosynthetic rate of upper leaves based on the chl. *a* content reached a maximum of 3.6 μl O₂ μg chl. *a*⁻¹ h⁻¹ in October and a minimum of 2.0 μl O₂ μg chl. *a*⁻¹ h⁻¹ in February (Fig. 5 (b)). The net photosynthetic rate of the upper leaves exceeded that of the lower leaves, except in March and April (*t*-test, *P* < 0.05 ; cf. GAO, 1990b). The differences in the maximum net photosynthetic rates between the upper and lower leaves were substantial during the young stage of growth (October-December), but decreased as the plants grew. At maturation, from March to April, the maximum net photosynthetic rates were similar between the upper and lower leaves.

The maximum net photosynthetic rates of the upper leaves based on wet weight at the mature stage were greater than in the young stage. By contrast, the rates based on the chl. *a* content at the young stage exceeded those at the mature stage. The chl. *a* content of leaves increased as the individuals grew, although the photosynthetic activity of the chl. *a* in leaves decreased as the individuals became older.

3.4.2. Dark respiratory rate

The monthly dark respiratory rates (*R_d*) of the upper and lower leaves of *S. horneri* based on wet weight are given in Fig. 5 (c). The dark respiratory rate of the upper and lower leaves

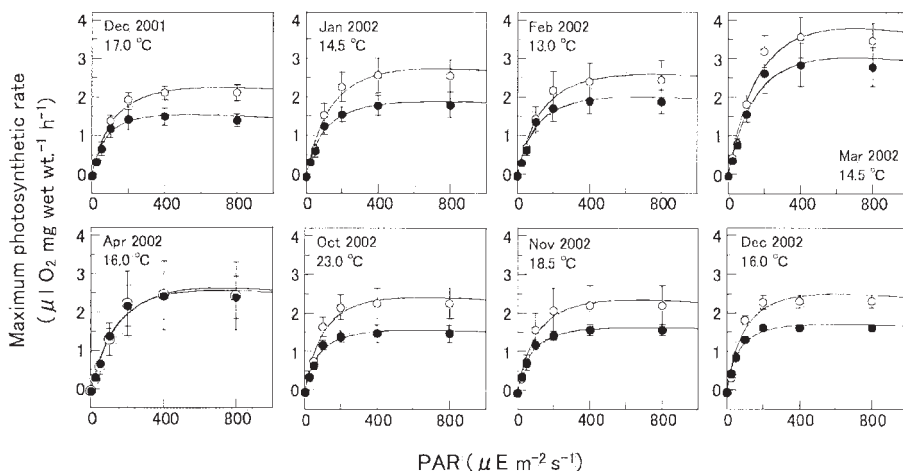


Fig. 4 Photosynthesis - light curves of the upper and lower leaves of *S. horneri* from December 2001 to December 2002. Open and solid circles indicate results for the upper and lower leaves, respectively. The bars represent the standard deviation (\pm S.D.) of samples. Temperatures in the panel represent *in situ* water temperatures during measurement of net photosynthetic and dark respiratory rates.

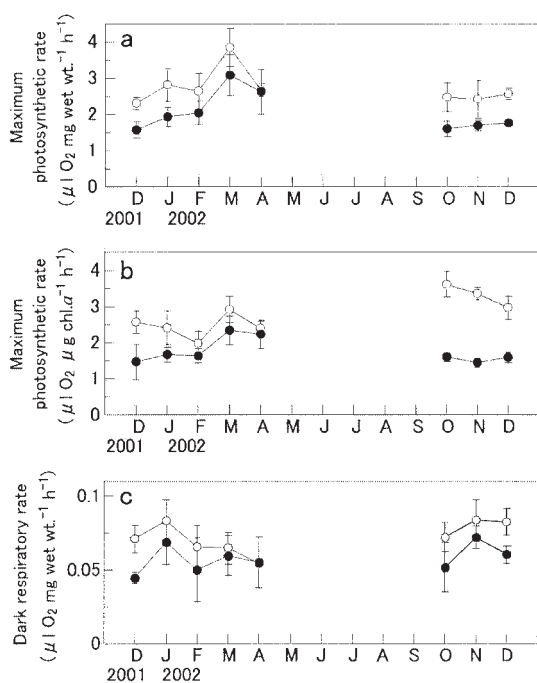


Fig. 5 Seasonal changes in the maximum net photosynthetic rates of *S. horneri* based on the wet weight (a) and chlorophyll *a* content (b). Seasonal changes in dark respiratory rates of *S. horneri* on a wet weight basis (c). Open and solid circles represent the upper and lower leaves, respectively.

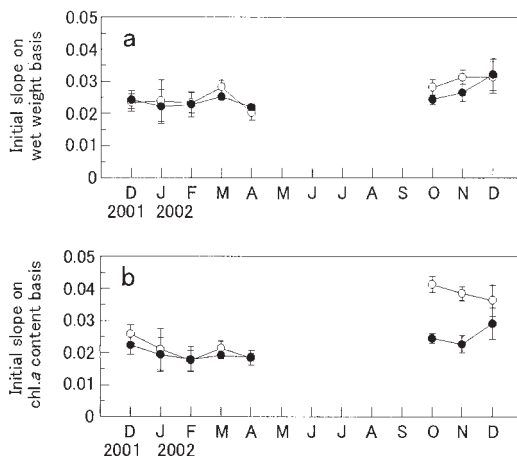


Fig. 6 Seasonal changes in the initial slopes on a wet weight (a) and chlorophyll *a* basis (b). Open and solid circles represent the upper and lower leaves, respectively.

ranged from 0.05–0.08 and 0.04–0.07 $\mu\text{l O}_2 \text{ mg wet wt.}^{-1} \text{ h}^{-1}$, respectively, and the maximum dark respiratory rate of upper leaves based on wet weight reached a maximum in January and November and a minimum in April (Fig. 5 (c)). In addition, there was no significant difference in respiratory rates between the upper and lower leaves (*t*-test, $P > 0.05$), except in December, and the difference decreased during the maturation stage (February–April; cf. GAO, 1990b).

3.4.3. Initial slope

The initial slopes of the photosynthesis-light curves based on wet weight and the chl.*a* content of upper leaves of showed seasonal variation similar to that of the maximum net photosynthetic rate, P_m . Depending on the P_m in this study, the initial slopes from October to December were higher than those from January to April (Fig. 6 (a, b)). There was little difference in the initial slopes between the upper and lower leaves, except for values based on the chl.*a* content from October to December.

SMITH *et al.* (1983) reported that the initial slopes of young and mature disks of *Macrocystis integrifolia* were similar on an area basis, whereas the initial slopes of young disks on a pigment basis were generally higher than those of mature disks. This was also true in our study, suggesting that the chl.*a* of young leaves adapts to low light intensities.

4. Discussion

The growth rate and maturation of *S. horneri* in the Shidagaura Cove study differed from those in other areas. UMEZAKI (1984b) examined the growth in *S. horneri* off sheltered shores in Obama Bay, a branch bay of Wakasa Bay, in the Sea of Japan, and reported a maximum mean main stem length of 161.0 cm in May and a daily rate of increase in length ranging from 0.054 to 1.96 cm day⁻¹ (1.6 to 58.8 cm month⁻¹) from September to May. The mean length and growth rate of *S. horneri* main stems in Shidagaura Cove were more than twice those in Wakasa Bay. The maturation period took place from late March to April in Shidagaura Cove, while it occurred from April to May (UMEZAKI, 1984b) or May to June (GAO, 1990b ; GAO and HUA, 1997) in Wakasa Bay. The winter water temperature in Wakasa Bay (10° C in February ; UMEZAKI, 1984b ; GAO, 1990b) was lower than that in Shidagaura Cove (13° C in February ; Shimoda Marine Research Center ; SMRC). *Sargassum horneri* in Shidagaura Cove, which faces the Pacific Ocean, grew faster, attained larger sizes, and matured earlier than those in Wakasa Bay since water temperature had a positive effect on the growth rate and maturation of plants (DE WREEDE, 1976 ; PRINCE and

O'NEAL, 1979 ; OGAWA, 1982, 1983). The duration of monthly total sunlight in Maizuru (66.1–96.8 h from December to February) near Obama Bay in winter was less than that in Irouzaki (161.5–189.3 h from December to February) near Shidagaura Cove (Japan Meteorological Agency, 2002). Presumably, the daily total PAR also had a positive effect on growth through photosynthetic activity (LÜNING, 1993 ; UCHIDA, 1993). Therefore, in Shidagaura Cove, the warmer water temperature in winter and the greater solar radiation promoted relatively rapid growth and early maturation of *S. horneri*.

Younger leaves of *Laminaria* and *Fucus* species contain less pigment than those of older leaves (KÜPPERS and KREMER, 1978 ; HENLEY and DUNTON, 1995). The chl.*a* content of the lower leaves of *Sargassum* species was higher than that of upper leaves (GAO and UMEZAKI, 1988 ; GAO, 1990b, 1991). This study also showed that the chl.*a* content of the lower (older) leaves of *S. horneri* was greater than in the upper (younger) leaves. However, the chl.*a* content was similar between these leaf types from January to April, which occurred because the condition of the upper leaves approached that of the lower leaves as they aged. The main stem of *S. horneri* grows not only at the apical part, but also throughout as growth progresses (UMEZAKI, 1984b) ; therefore, the average properties of the upper and lower leaves converge. Accordingly, the differences in the photosynthetic rate, respiratory rate, and initial slope between upper and lower leaves diminished as the plants grew. The chl.*a* content decreased in April, which is the maturation period (cf. WHEELER, 1980 ; GAO, 1990b). Degradation of chl.*a* was responsible for this phenomenon because the plants began to senesce after maturation.

The maximum photosynthetic rates based on wet weight were positively correlated with the increases in main stem length. GAO (1990b) studied the photosynthetic ability of *S. horneri* leaves in Wakasa Bay and reported that their net photosynthetic rates based on dry weight exhibited two peaks annually : one in November and another in March. UMEZAKI (1984b) stated that these peaks in photosynthetic

activity roughly corresponded to peaks in the growth rate. In general, annual seaweeds utilize energy produced during a single growing season. It may not be possible for such seaweeds to grow rapidly without high photosynthetic rates.

The estimated photosynthetic rates of upper leaves of *S. horneri* at the monthly mean water temperature and $600 \mu\text{E m}^{-2} \text{s}^{-1}$ in Wakasa Bay (GAO, 1990b) varied from $2\text{--}20 \text{ ml O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$ (average $10 \text{ ml O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$) and reached a peak in November, while the maximum photosynthetic rates of upper leaves in this study varied from $13\text{--}22 \text{ ml O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$ (average $16 \text{ ml O}_2 \text{ g dry wt.}^{-1} \text{ h}^{-1}$) and reached a peak in March. The mean photosynthetic rates in our study area was 1.6 times greater than in Wakasa Bay, reflecting the larger plant size and high growth speed in our study area. The difference in the peak times of the seasonal changes in the photosynthetic rates at the two localities was probably influenced by changes in nutrient conditions. Seasonal changes in nutrient conditions influence photosynthetic variability and growth in some macroalgae (CHAPMAN and CRAIGIE, 1977 ; CHAPMAN *et al.*, 1978 ; GAO, 1990b ; SERISAWA *et al.*, 2001a). According to GAO (1990b), the highest photosynthetic rate of *S. horneri* in Wakasa Bay occurred during months with high nitrate and phosphate concentrations, ranging from 0.6 to $7.0 \mu\text{M}$ and from 0.15 to $0.4 \mu\text{M}$, respectively. At our study site (Oura Bay), $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ were high from February to April (8.0 and $0.6 \mu\text{M}$, respectively) and low from May to November (2.0 and $0.3 \mu\text{M}$, respectively ; SERISAWA *et al.*, 2001a). Therefore, high nutrient levels in spring may elevate the photosynthetic rate in March. When light and temperature are not limiting factors, nutrient conditions, especially nitrate, constitute a limiting factor for the photosynthetic rate of seagrass and seaweed (KIRK, 1994). Thus, regarding the seasonal changes in the photosynthetic rate based on wet weight observed in this study, the limiting factor may not be light and temperature, but nutrient conditions.

High growth rates and productivity of several *Sargassum* species during periods of low water temperature have been noted

(CARPENTER and COX, 1974 ; DE WREEDE, 1976). This was also true for *S. horneri* in Shidagaura Cove. It has been reported that the optimum temperature for photosynthetic activity of several macroalgae acclimated to the environmental temperature during a year (YOKOHAMA, 1973 ; LEE and BRINKHUIS, 1988 ; GAO, 1990b). Although the photosynthesis-temperature curves obtained in short-term experiments (<1 day) indicated a strong influence of temperature (YOKOHAMA, 1973 ; GAO, 1990b), the results of our study suggest that photosynthetic activity is not strongly influenced by environmental temperature over the long term (>1 month).

The maximum net photosynthetic rates of the upper leaves based on the chl.*a* content in this study (2.0 and $3.6 \mu\text{l O}_2 \mu\text{g chl.}a^{-1} \text{ h}^{-1}$) were comparable to those of *Sargassum patens* ($2.5 \mu\text{l O}_2 \mu\text{g chl.}a^{-1} \text{ h}^{-1}$) measured by GAO and UMEZAKI (1988) and *S. horneri* ($1.8\text{--}3.5 \mu\text{l O}_2 \mu\text{g chl.}a^{-1} \text{ h}^{-1}$) by GAO and UMEZAKI (1988) and GAO (1991). The rates for *Sargassum* species were much higher than those of *Ecklonia cava* Kjellman (Laminariales, Phaeophyta) ($1.0\text{--}1.9 \mu\text{l O}_2 \mu\text{g chl.}a^{-1} \text{ h}^{-1}$, SERISAWA *et al.*, 2001b). The maximum net photosynthetic rates based on the chl.*a* content should be synchronous with the age of the plant.

Temperature, nutrients, and light intensity are factors that affect the growth rate of plants. The seasonal change in the net photosynthetic rates based on wet weight was synchronous with the length and growth rate of the plant, whereas the change based on chl.*a* content was synchronous with its age. This suggests that photosynthetic rates determined from wet weight measurements reflect external controls. Contrasting estimates of the photosynthetic rate from chl.*a* measurements may reflect the internal condition (age) of plants.

Acknowledgment

We thank Y. TSUCHIYA, T. SATO, and H. SHINAGAWA, on the staff of the Shimoda Marine Research Center, University of Tsukuba, for their help with the underwater measurements and sampling.

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Received October 3, 2006
Accepted October 23, 2006