

## An Estimation of the Algal Production of *Sargassum confusum* (Phaeophyta) on the Coast of Ohori, East Sea, Korea, by Mathematical Models Based on Photosynthetic Rates and Biomass Changes

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### 광합성율과 생물량에 기초한 *Sargassum confusum*의 생산성 계산 모델

고철환 · 조성억

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A production model was constructed by combining the production rate and biomass of *Sargassum confusum* measured at monthly intervals on the coast of Ohori, Korea, to estimate the algal production for a given period. The production for a certain period, e.g., for a year ( $P_{yr}$ ), was calculated from the equation:  $P_{yr} = \int P_t \cdot B_t dt$ , where  $P_t$  and  $B_t$  are the production rate and biomass at time  $t$ .  $P_t$  was considered as a function of temperature and light. Photosynthesis-Irradiance curves obtained from the *in situ* experiments were applied for  $P_t$ . Temperature and light intensity can be expressed as periodic functions of time ( $T, L = f(t)$ ). Diurnal values of water temperature and light intensity at 3 m depth where *S. confusum* mainly found were substituted into the equation of  $P_t$ .

Simulations using our models show that temperature was one of the most sensitive factors operating on the primary production. Thirty percent decrease of light intensity by cloud cover was estimated to decrease the annual production by 5%.

동해안 오후리에 서식하는 *Sargassum confusum*을 대상으로 광합성율과 생물량의 시간에 따른 변화를 조사하여 해조류의 년생산성을 예측하는 모델을 구성하였다. 즉 년생산량  $P_{yr}$ 를  $P_{yr} = \int P_t \cdot B_t dt$  (이때  $P_t$ 와  $B_t$ 는 주어진 시간에서의 광합성율과 생물량을 나타낸다)의 식을 설정하여 구하였다.  $P_t$ 는 수온과 광량의 함수로 보아 서로 다른 수온과 광도의 조건에서 광합성율 측정하여  $P_t$ 에 대입하였다. 수온과 광량은 년변화를 보이므로 오후리에서 1년 동안 기록된 값들을 이에 대입하였다. 이 때 이 값들은 *Sargassum confusum*이 서식하는 수심 3m를 기준으로 하였다. 모델에 의한 모의 결과는 수온이 일차생산량을 결정하는 가장 중요한 요인임을 보여주었다. 구름을 가정하여 30%의 광량을 무작위로 감소시켰을 때 해조류의 년생산량은 5% 감소하였다.

### INTRODUCTION

The present study estimates the algal production using a numerical model which couples sets of photosynthetic data obtained from *in situ* experiments with seasonal standing crops. The estimate obtained from the model is 'crop productivity'

*sensu* Charles-Edwards (1981). Until now, longterm estimates of macroalgal production have been largely calculated from biomass changes (Vollenweider, 1969; Bach and Josselyn, 1979; Rice and Chapman, 1982). Calculation from a set of temporal biomass measurements, however, underestimates the algal production due to the loss of the product

via exudation, shedding of algae and grazing by herbivorous animals. The oxygen and isotope methods give us more accurate values of the primary production. The values are, however, of short-term duration and therefore could be an inadequate estimate of the primary production of a prolonged period.

In extrapolating photosynthetic rates ( $P_t$ ) to an annual production ( $P_{yr}$ ), the equation  $P_{yr} = \int^yr P_t \cdot B_t dt$  is used in the present study.  $P_t$  was considered as a function of temperature and light. However, more factors must be regarded to calculate the annual production accurately. For example,  $P_t$  could correlate rather with physiological conditions of algae than with environmental factors such as temperature and light intensity. Curves of diurnal photosynthetic performance of seaweeds have demonstrated a morning maximum, afternoon depression and late afternoon recovery (Ramus and Rosenberg, 1980). The metabolic potential for photosynthesis per unit biomass varies seasonally (King and Schramm, 1976b; Brinkhius, 1977a; Littler *et al.*, 1979; Littler and Arnold, 1980). In order to make the extrapolated production estimates reliable, it is necessary to measure  $P_t$  by short time spacing. Production rates varied also considerably from the base to the apex of the thallus (King and Schramm, 1976a; Gao and Umezaki, 1989). In many cases, however, the application of improved methods and frequent *in situ* experimentation would be technically difficult and expensive.

The present model gives an estimate of the production for a prolonged period, e.g., the annual production, by combining photosynthetic rates observed with the seasonal change of biomass. Most of the previous experiments measured the production rates but did not use the rates to estimate the productivity for a prolonged duration (King and Schramm, 1976b; Peterson *et al.*, 1987). A simple method integrating production data measured at certain intervals has been proposed (Brinkhius, 1977b; Hatcher *et al.*, 1977). Drew (1983) applied a mathematical model incorporating both temperature and light intensity into the calculation of annual carbon budget of *Laminaria*. The present mo-

del differs from the Drew's model in the algorithm structure, especially in the incorporation of temperature. The calculation presented in this paper might be improved by using more accurate  $P_t$  values through frequent experimentations. A brown alga, *Sargassum confusum* Agardh, was selected for this study, since subtidal zones of the east coast of Korea were dominated mainly by rockweeds, especially the species of *Sargassum*.

## MATERIALS AND METHODS

Experiments on photosynthetic rates were conducted in June of 1986 at Ohori on the east coast of Korea (38°20'N, 128°33'E). The study area has a small tidal range of 0.3 m during the spring tide. The bottom substrata of the coast of Ohori are mainly composed of fine sand. However, the study site including the subtidal zone to the depth of 10 m is composed of rocks. Species of *Sargassum* are the main component of the vegetation to the depth of 5-6 m from February to August (Koh, 1983).

The oxygen light-dark bottle method was applied for the measurements of photosynthetic activity. The apical fronds of *S. confusum*, collected at the depth of 3 m by SCUBA diving, were cut to 0.5-1.0 gram of wet weight, freed of epibionts, and placed in 300 mL BOD bottles filled with the local sea water filtered through 0.45  $\mu$ m GF/C filter. The bottles were incubated outdoors at 10°C and 23°C in a temperature regulated tank. Light intensities were controlled by shielding the bottles with nylon screens of various densities (Arnold and Murray, 1980). Incubations at 3 m depth where the species *S. confusum* was mostly found were performed for comparison. The whole process was repeated three times and the mean values for each temperature were taken for the model calculation. Solar irradiances were measured with Kahlsico Model No. 268 WA 310 submarine photometer.

After incubation for about an hour, changes in oxygen concentration due to algal photosynthesis and respiration were measured using the Winkler method (Strickland and Parsons, 1972). Production

estimates based on oxygen evolution were converted to calories after Brower and Zar (1977), using a photosynthetic quotient of 1.2 and respiratory quotient of 1.0. All values are expressed per gram dry weight. Biomass data measured at the experiment site (Koh and Ahn, 1985) were converted to units of energy content using the caloric content values of samples determined by a Parr 1241 adiabatic calorimeter.

Based on the Photosynthesis-Irradiance (P-I) relationships and biomass changes, expressed as calories, a mathematical model estimating the annual production was constructed. The following is a brief description of our model: Photosynthetic responses of *S. confusum* to light intensities at different water temperatures were expressed using the Jassby and Platt (1976) and Chalker (1980) model. The annual variation of sea water temperature was mathematically formulated by least-square fitting of measured values once a month from 1983 to 1985 at Ohori. Solar insulations for photosynthesis of *S. confusum* at 3 m depth were obtained by putting the extinction coefficient determined *in situ* to a insolation equation. Temperatures and light intensities obtained from these models were then inserted into the photosynthesis versus irradiance curves for the calculation of production rate at given times. The annual production was calculated as an integral by multiplying production rates determined from the above P-I curves to the biomass. The computer program, MAPP, written in Pascal for IBM PC-compatibles, was applied in calculating the annual production.

## RESULTS

### Photosynthesis-Irradiance curves

P-I curves were made using the data on photo-

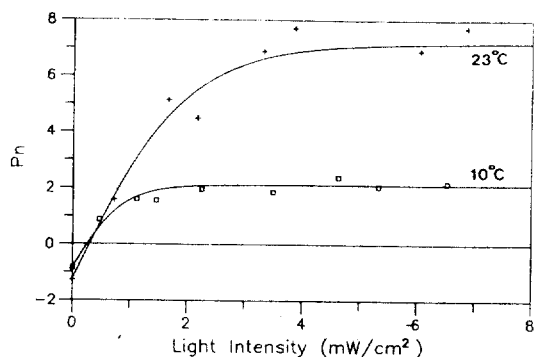


Fig. 1. Photosynthesis-Irradiance curves of *Sargassum confusum* obtained from experiments at Ohori in June ( $P_n$  = Net photosynthesis in  $\text{mgO}_2 \text{ g DW}^{-1} \text{ h}^{-1}$ ).

synthetic activities of *Sargassum confusum* measured at the study site in different light and temperature conditions. Fig. 1 shows the P-I curves at two temperature conditions of 10°C and 23°C. Photosynthesis showed basically a hyperbola-shaped response to light intensity at both temperatures. Photosynthesis increased with increasing light intensities up to some asymptotic value. Photoinhibition was not observed over about one hour incubation. Table 1 shows some important properties for P-I curves. There was a great difference of maximum  $P_n$  between both temperatures. The P-I relations of *S. confusum* at each temperature could be described by the following hyperbolic tangent function slightly modified from Jassby and Platt (1976) and Chalker (1980):

$$P_n = (P_m + R) \tanh[\alpha I / (P_m + R)] - R \quad (1)$$

where  $P_n$  is net photosynthetic rate ( $\text{mgO}_2 \text{ g}^{-1} \text{ h}^{-1}$ ),  $P_m$  is maximum net photosynthesis,  $R$  is respiration rate,  $\alpha$  is initial slope, and  $I$  is light intensity ( $\text{mW cm}^{-2}$ ). Fig. 1 shows the measured  $P_n$  in different light intensities and the fitted curves of eqn (1). The coefficient of determination ( $r^2$ ) were

Table 1. Photosynthetic parameters and  $Q_{10}$  values of *Sargassum confusum*

	Maximum $P_n$	$R$ ( $\text{mgO}_2 \text{ g DW}^{-1} \text{ h}^{-1}$ )	Maximum $P_z$	$I_k$ ( $\text{mW cm}^{-2}$ )	$\alpha$ ( $\text{mgO}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ mW}^{-1} \text{ cm}^{-2}$ )
23°C	7.18	-1.28	8.46	1.98	4.28
10°C	2.12	-0.85	2.96	0.88	3.38
$Q_{10}$	2.56	1.37	2.56	-	1.20

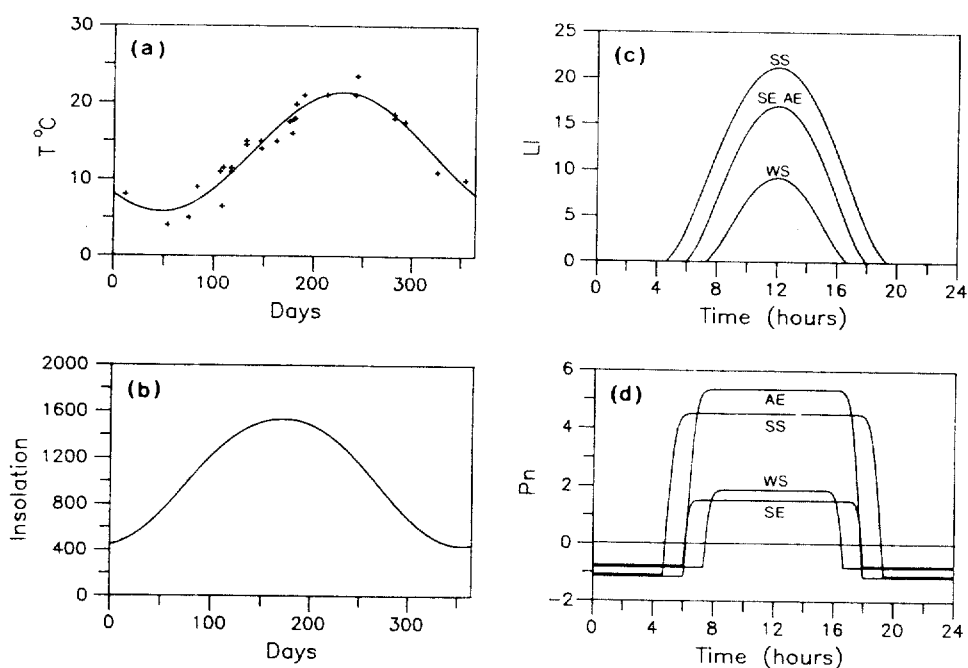


Fig. 2. (a) Annual change of water temperature ( $^{\circ}\text{C}$ ) and (b) insolation ( $\text{Kcal m}^{-2} \text{day}^{-1}$ ). (c) Diurnal variations of the light intensity, LI ( $\text{mW cm}^{-2}$ ), at different seasons. (d) Daily net production,  $P_n$ , in  $\text{mgO}_2 \text{g DW}^{-1} \text{h}^{-1}$  of *S. confusum* at different seasons (SS=summer solstice, SE=summer equinox, AE=autumn equinox, WS=winter solstice).

0.97 at  $23^{\circ}\text{C}$  and 0.95 at  $10^{\circ}\text{C}$ .

#### Variations of water temperature and light intensity

The seasonal change of water temperature at Ohori closely approximated a sinusoidal curve. A cosine curve was fitted to the observed temperatures of 1983 to 1985. Nonlinear regression analysis gave us the constant and coefficient values written in the following cosine eqn (2):

$$T = 13.6 - 7.8 \cos[2\pi(\text{day} - 46.6)/365] \quad (2)$$

where  $T$  is water temperature ( $^{\circ}\text{C}$ ) on a Julian day.

The coefficient of determination ( $r^2$ ) of eqn (2) was 0.92 ( $p < 0.001$ ). The observed temperatures and a fitted curve are plotted in Fig. 2a. The temperature oscillated around the mean of  $13.6^{\circ}\text{C}$  with an amplitude of  $7.8^{\circ}\text{C}$ . The highest temperature was  $21.4^{\circ}\text{C}$  on day 229 (mid-August) and the lowest was  $5.8^{\circ}\text{C}$  on day 47 (mid-February).

The incident light intensity at any depth would be a function of solar radiation and water clarity.

The extinction coefficient reflecting water clarity was determined to be  $0.48 \text{ m}^{-1}$  from the data measured *in situ* during the experiments. The transmittance portion at 3 m water depth where *S. confusum* mainly inhabited was therefore 23.4% of the surface irradiance.

The amount of light on the surface of the water varies daily and seasonally. One of the major causes of the variation is the change of sun angle which depends on time, date and latitude. So the following model adopted from KIER (1982) was applied to predict the intensity of light available for *S. confusum* at a given time on a given day.

$$I = S_i [1 + 0.033 \cos(360 \text{ day}/365)] \cos\theta_z (T_d + T_f) T_r \quad (3)$$

$$\cos\theta_z = \cos\delta \cdot \cos\phi \cdot \cos\Omega + \sin\delta \cdot \sin\phi$$

where  $I$  is incident light intensity in  $\text{mWcm}^{-2}$ ,  $S_i$  (solar constant) is  $135.3 \text{ mWcm}^{-2}$ ,  $\cos\theta_z$  is the cosine of solar zenith angle,  $\delta = 23.45 \sin[360(284 +$

day)/365].  $\phi$  (latitude) is  $38^{\circ}20'N$  in Ohori,  $\Omega$  is the angle of hour,  $T_r$  (water transmittance) is 23.4%.  $T_d$  is the atmosphere transmittance coefficient of the direct radiation and determined as  $T_d = 0.1233 + 0.7559 \exp(-0.3878/\cos\theta_z)$ ,  $T_f$  is atmosphere transmittance coefficient of diffuse radiation and determined as  $T_f = 0.2710 - 0.2939 T_d$ .

Cloud coverage was not considered in the above equation. Fig. 2b shows the annual variation of the daily insolation according to the equation. Highest insolation at 3 m depth was  $1,540 \text{ Kcal m}^{-2} \text{ day}^{-1}$  on day 171, the day of summer solstice; the lowest was  $440 \text{ Kcal m}^{-2} \text{ day}^{-1}$  on day 348, the day of winter solstice. The predicted light intensities at a given time were then integrated for the estimation of the total insolation during the daylight hours. Diurnal changes of the incident light intensity calculated from the eqn (3) for the 3 m depth on solstice and equinox are shown in Fig. 2c. The total insolation at the sea surface during a whole year was  $1.57 \times 10^6 \text{ Kcal m}^{-2} \text{ yr}^{-1}$  and the amount provided to *S. confusum* for photosynthesis at 3 m depth was  $3.68 \times 10^5 \text{ Kcal m}^{-2} \text{ yr}^{-1}$ ; that is 23.4% of the surface insolation.

#### Daily photosynthesis rates

The effects of irradiance and temperature which are subjected to diurnal variation should be considered together in predicting the daily photosynthetic rates. The eqn (1) given in the previous section was therefore modified to combine the P-I curves and temperature conditions. The eqn (4) made it possible to calculate the gross photosynthesis and the respiration in any light and temperature conditions at a given time of a fine day.

$$\begin{aligned} P_g &= P_m \tanh[\alpha I / P_m] \\ P_m &= P_{23} Q_p^{(T-23)/10} \\ R &= R_{23} Q_r^{(T-23)/10} \\ \alpha &= \alpha_{23} Q_a^{(T-23)/10} \\ P_n &= P_g - R \end{aligned} \quad (4)$$

where  $P_g$  is the gross photosynthetic rate ( $\text{mgO}_2 \text{ g}^{-1} \text{ h}^{-1}$ ),  $P_m$  is maximum  $P_g$ ,  $R$  is respiration rate,  $P_n$  is net photosynthetic rate,  $P_{23}$  is  $P_m$  at  $23^{\circ}\text{C}$ ,  $R_{23}$  is  $R$  at  $23^{\circ}\text{C}$ ,  $Q_p$  is  $Q_{10}$  of  $P_m$ ,  $Q_r$  is  $Q_{10}$  of

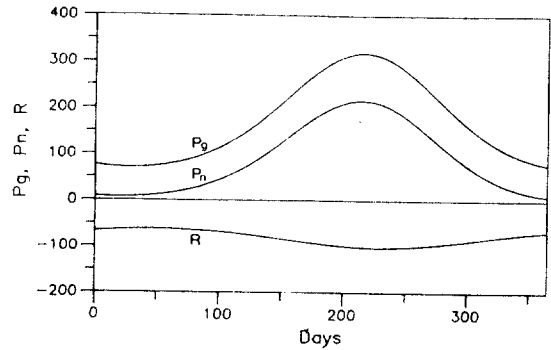


Fig. 3. Annual changes of photosynthetic and respiration rates ( $\text{cal g DW}^{-1} \text{ day}^{-1}$ ) of *Sargassum confusum* ( $P_g$ =gross production,  $P_n$ =net production,  $R$ =respiration).

$R$ ,  $Q_a$  is  $Q_{10}$  of  $\alpha$ ,  $I$  is the light intensity ( $\text{mW cm}^{-2}$ ),  $T$  is temperature,  $\alpha$  is initial slope,  $\alpha_{23}$  is  $\alpha$  at  $23^{\circ}\text{C}$ .

The influences of temperature on the photosynthesis were reflected in the above equation by means of  $Q_{10}$  values determined from the photosynthetic activity. The values measured at  $10^{\circ}\text{C}$  and  $23^{\circ}\text{C}$  (Table 1) were chosen for the model calculation. It was assumed that the  $Q_{10}$  values obtained from the experiment could be applied also to temperatures under  $10^{\circ}\text{C}$ . Diurnal changes of photosynthetic rates shown in Fig. 2d are examples calculated by the eqn (4) under the light conditions given in Fig. 2c and temperatures predicted by the eqn (2). The results shown in Fig. 2d share one important feature that there is a rapid increase and decrease in net photosynthesis just after sunrise and before sunset respectively. Exclusive of these times, photosynthesis during the daytime stayed at a constant level despite different light intensities.

Annual variation of daily photosynthetic rates estimated by integrating the eqn (4) is illustrated in Fig. 3. Photosynthesis and respiration rates expressed in terms of energy units showed peaks in the summer. It was also observed from Fig. 3 that photosynthetic rates changed more rapidly than respiration rates. The highest net production was  $216 \text{ cal g DW}^{-1} \text{ day}^{-1}$  on day 214, and the lowest was  $6.3 \text{ cal g DW}^{-1} \text{ day}^{-1}$  on day 22.

#### Annual production

Table 2. Comparison of the net production (Kcal m<sup>-2</sup>) during a given period from standard run with alternative simulations under modified conditions

Condition	Date	1983						1984			Sum (%)
		3/27	4/16	5/26	6/24	9/1	10/20	12/21	2/23	3/16	
1. Net production (original run)		507	3,007	4,641	9,232	854	364	95	45	84	18,829 (100.0)
2. 30% diminished irradiance by cloud cover		482	2,891	4,439	8,814	805	324	75	41	80	17,952 (95.3)
3. Temperature increase of +2.5°C		733	4,031	5,997	11,763	1,105	539	214	77	130	24,589 (130.5)
4. Temperature decrease of -2.5°C		328	2,184	3,540	7,165	649	224	3	20	49	14,161 (75.2)
5. Distinguishing holdfasts from apical leaves		207	1,688	4,106	8,716	504	130	-47	3	24	15,331 (81.4)
6. Conditions 2 and 5		192	1,611	3,924	8,318	472	106	-58	1	21	14,588 (77.5)

Diurnal photosynthesis obtained from the above eqn (4) was the diurnal rate which was expressed on the basis of unit biomass in gram dry weight. The annual production could be calculated therefore by an integration of the daily photosynthetic performance for a given biomass on an *i*-th day. The equation for this calculation was:

$$P_g = \sum_{i=1}^{365} [B_i \cdot P_i] \quad (5)$$

$$R = \sum_{i=1}^{365} [B_i \cdot P_i]$$

$$P_n = P_g - R$$

where  $P_g$  is annual gross production,  $P_n$  is annual net production,  $R$  is annual respiration in Kcal m<sup>-2</sup> yr<sup>-1</sup>,  $B_i$  is the biomass on *i*-th day (Kcal m<sup>-2</sup>),  $P_i$  is gross production on *i*-th day (cal g DW<sup>-1</sup> day<sup>-1</sup>),  $R_i$  is respiration on *i*-th day (cal g DW<sup>-1</sup> day<sup>-1</sup>).

The annual production obtained from the eqn (5) reveals total organic materials in caloric units produced by the photosynthetic activity. Biomass values ( $B_i$ ) for the eqn (5) are actual standing crops harvested at Ohori in 1983-84 at monthly intervals by Koh and Ahn (1985). The net production in terms of photosynthesis for each sampling period are depicted in Table 2. The relative proportion of the production in May-September was about 75% of the net annual production. The annual gross production from the present model

amounted to  $3.24 \times 10^4$  Kcal m<sup>-2</sup> yr<sup>-1</sup>; it was 8.8% of the insolation reached at 3 m depth. The net production was  $1.9 \times 10^4$  Kcal m<sup>-2</sup> yr<sup>-1</sup>, 5.2% of the *in situ* insolation.

## DISCUSSION

The first step for constructing our production model was to determine how *S. confusum* responded to changes in light intensity and temperature. Physiological parameters such as maximum photosynthetic rate, respiration rate, initial slope, and saturation irradiance ( $I_k$ ) were, therefore, determined in different temperature conditions through *in situ* experiments at Ohori (Table 1). Rates of the maximum photosynthesis and dark respiration were comparable with the published data of other *Sargassum* spp. under similar temperature conditions. Maximum photosynthetic rates of *S. confusum* were lower than the rates recorded for tropical *S. filipendula* (Peckol and Ramus, 1985), but greater than those of *S. pteropleuron* on the South Florida coast (Prince, 1980) and pelagic *Sargassum* (Lapointe, 1986). Rates of dark respiration of *S. confusum* were slightly greater than those of *S. echinocarpum*, *S. obtusifolium*, and *S. pteropleuron* in Prince (1980).

Rates of photosynthesis of *S. confusum* were regulated mainly by temperature, but the effect of temperature on respiration rates was not significant. Prince (1980) reported that photosynthetic rates of *S. pteropleuron* showed a seasonal variation,

whereas the respiration rates showed no significant variation. High primary production of *S. confusum* at Ohori in summer calculated from the model appeared to result from the more active response of temperature on photosynthetic rates than on respiration rates.

Although our physiological parameters are comparable to other results, the annual production calculated from the model remains still uncertain. This uncertainty is expected if we consider the large amount of physiological and temporal variability in the algal production of the natural environment. Simulation runs can be made to get a feeling for the possible implications of this uncertainty and to determine the effect of varying parameters.

To evaluate the extent to which temperature influences the primary production, an arbitrary increase and decrease of the annual mean could be employed. When the temperature was raised or even lowered by 2.5°C, the simulated annual production increased or decreased by about 30% and 25% from the standard run, respectively (Table 2). A significant factor which might change the amount of the annual production which is poorly demonstrated in the present model is the cloud cover. It is, however, apparent from Table 2 that the effect of cloud cover on the annual net production integrated by using a stochastic cloudiness scheme is not substantial. The annual production decreased only about 5%, when 30% decrease of light intensity by cloud cover was entered (Table 2). These differences indicate the relative importance of temperature rather than the light intensity in determining the photosynthetic rate of *S. confusum*.

To test the sensitivity of different photosynthetic capacity of different part of plants to the annual production, production rates of apical leaves and holdfasts are substituted into a simulation process. The net production described in the condition 5 of Table 2 are obtained by replacing the production rates with partially reduced rates determined from production measurements of holdfasts in summer (unpublished data). The photosynthetic rates of holdfasts were about 25.2% lower than

those of apical blades and these values were comparable with Gao and Umezaki's result (1989). It was supposed from the field observation that holdfasts, in the fast-growing phase, constituted less than 20% of the whole thallus in weight, and in other periods, 70-90%. The result of regarding these coefficients described in Table 2 indicates that the estimate of production declines to 81.4% of that calculated from the standard run. The condition 6 in Table 2 seems to be more theoretically improved, because the cloud cover and different metabolic responses of the thallus are included. This estimation of 14.6 Kcal m<sup>-2</sup> yr<sup>-1</sup> was seven times the annual production estimated from the biomass change alone.

Further improvements are possible, however, the variety of responses in biological processes of the algal production is extreme. For example, the photosynthetic activity was known to have diurnal fluctuations. The changing activity was not reflected in our model in detail, for such fine curves could not be fitted through the necessary simplification used in the model construction. If diurnal fluctuations are mainly regulated by the light history as pointed out by Knoop and Bate (1988), the simplification would be more difficult. The seasonal characteristics of P-I curves should be considered in the present model as well, for the photosynthetic activity,  $P_i$  in a given day, was multiplied by the biomass for the annual integration (eqn 5). Photosynthesis-temperature responses can be analysed more in detail in order to get substantial information on the production for a long period (Knoop and Bate, 1990). To cover this deficiency, experiments on P-I relationships at closer time intervals are necessary.

Radiant environment within the community can be changed spatially and temporally. We applied an extinction coefficient obtained during the experiment period for the whole year, however, extinction coefficient is a physical parameter which is difficult to describe with any one value. Spatial difference of the light intensity caused by the canopy effect is another factor to be determined for the production model. Field experiments with whole plants in an open, continuously recording

flow-through system provides more compensated value. (Schramm, 1973). The accuracy of the estimation largely depends on the information about production rates in different environments. Our model must be therefore improved by modifying the algorithm with the data obtained from more frequent and sophisticated experiments.

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