Comparative studies on critical light conditions for young *Eisenia bicyclis* and *Ecklonia cava*

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Ecklonia cava KJELLMAN usually occupies deeper water than does *Eisenia bicyclis* SETCHELL in sublittoral rocky areas. Young fronds of these species are growing under considerably low light condition on the community floor. Critical light intensity for young *Ei. bicyclis* and *Ec. cava* observed on the community floor was respectively 1.0–1.5% and 0.5–1.0% of the light intensity at water surface. Photosynthetic rate of young fronds of both species was saturated at 200 μE/m^2/s, and the saturated rate was higher in *Ei. bicyclis* than in *Ec. cava*. Under light lower than 50 μE/m^2/s the net photosynthetic rate was higher in *Ec. cava* than in *Ei. bicyclis*, and the compensation light intensity was 4.8 μE/m^2/s for the former and 8.2 μE/m^2/s for the latter. Daily net production was calculated with the mathematical model based on photosynthesis-light equations and natural light conditions. The estimated daily compensation light of young *Ec. cava* was 0.6% (0.24 E/m^2/day) and that of young *Ei. bicyclis* was 1.1% (0.42 E/m^2/day) of the water surface light intensity on the day of average solar radiation for the period of the present study (April-July). The estimated daily compensation light intensity agreed well with the observed critical light intensity for both species on the community floor. It is clear that young *Ec. caua* fronds can grow under the lower *in situ* light intensity in deeper water as compared with young *Ei. bicyclis* fronds.

Key Index Words: compensation point—critical light intensity—Ecklonia cava—Eisenia bicyclis—Phaeophyta—photosynthesis—seaweed.

The two species of brown algae, *Eisenia bicyclis* SETCHELL and *Ecklonia cava* KJELLMAN, are widely distributed along the Pacific coast of central Japan, and are important algae both ecologically and economically. *Ei. bicyclis* usually grows in shallow water down to 5 m in the sublittoral zone, while *Ec. cava* occupies deeper water of 3–25 m or more, both species forming dense marine forests. A considerable knowledge has been accumulated on their distribution and population structure from the ecological point of view (HAYASHIDA

1977, IWAHASHI 1968, IWAHASHI *et al.* 1979, KIDA and MAEGAWA 1982, 1983, 1985, OHNO and ISHIKAWA 1982, TANIGUCHI and KATO 1984, MAEGAWA and KIDA 1984a, b). There are, however, few studies on their photosynthesis and respiration which are important for estimating the primary production (SAKANISHI *et al.* 1988a, b) and for production ecology (MAEGAWA *et al.* 1987).

A large part of the biomass and production of *Ei. bicyclis* and *Ec. cava* is accounted for by the adult fronds forming the canopy (HAYASHIDA 1986, TANAKA *et al.* 1984, YOKOHAMA *et al.* 1987, MAEGAWA and KIDA 1987). However, young fronds on

the community floor play an important role as major constituents of the coming generation. The main external factor influencing the productivity of the algal communities might be an incident solar radiation. On their community floor, however, light intensity is very low (HAYASHIDA 1986, MAEGAWA and KIDA 1987), because the light is absorbed by the blades in the canopy and by water column. It is necessary for young fronds of these species to receive light greater than their compensation light intensity for their growth. Thus, the light condition in the communities is the most important factor allowing young fronds to survive and grow up to adults. In addition, it is important to know accurately the photosynthetic rate at light levels near the compensation point for estimating the daily light requirements. Furthermore, the distribution and diurnal changes in solar radiation are important for determining daily net production and daily compensation point.

The present study was undertaken to determine the critical light conditions for young fronds of *Ei. bicyclis* and *Ec. cava* with reference to the characteristics of photosynthesis and the natural light conditions in the communities, following the previous study (MAEGAWA *et al.* 1987). This kind of information will be useful in determining the factors governing the difference in vertical distributions of the two species.

Materials and Methods

Measurements of light distribution on the community floor were carried out at 5 m depth in Nabeta Bay, Izu Peninsula, Shizuoka Prefecture, on June 21, 1985, for *Ec. cava* community, and at 4 m depth off Iwaizaki, Shima Peninsula, Mie Prefecture, on June 13, 1986, for *Ei. bicyclis* community. To determine the light distribution on the community floor where young fronds were growing, light intensity was measured at 121 points 10 cm apart from each other

in the community with a quantum meter (LI-COR 185B/192SB). Light in the community and on the sea surface was simultaneously monitored by a recorder (TOA EPR-152A) on a boat, and the relative light intensity was calculated.

Photosynthesis and respiration of young *Ei. bicyclis* and *Ec. cava* were measured from April to July 1986. Intact young fronds less than one year old (cf. MAEGAWA and KIDA 1984a, b) with frond area of 15–35 cm^2 and dry weight of 60–250 g were collected from the communities at depths of 3–4 m for *Ei. bicyclis* and 7–10 m for *Ec. cava* around the coast of Shima Peninsula, Mie Prefecture. When samples were collected light intensity at the growing site was measured. The collected samples were transported to the Fisheries Research Laboratory of Mie University and were rinsed with seawater to make them free of obvious epiphytes with careful handlings not to wound the fronds. After keeping the sample fronds in running seawater overnight, photosynthesis and respiration were measured with a differential gas-volumeter (YOKOHAMA and ICHIMURA 1969, YOKOHAMA *et al.* 1986, YOKOHAMA and MAEGAWA 1988). Twenty-one fronds of *Ei. bicyclis* and thirteen fronds of *Ec. cava* were used for photosynthesis and respiration measurements. The methods of measuring photosynthesis and respiration were essentially the same as those described in the previous paper (MAEGAWA *et al.* 1987).

Photosynthetically active radiation (PAR) on the horizontal plane was measured with a quantum meter (LI-COR 192SB) from April to July 1986 at the campus of Mie University about 70 km to the north of the sampling site. Values were integrated every 0.5 sec. and recorded at 10 min. intervals to the data-logger (LI-COR LI-1000).

Results

Fig. 1 shows the distribution of relative light intensity on the community floor as
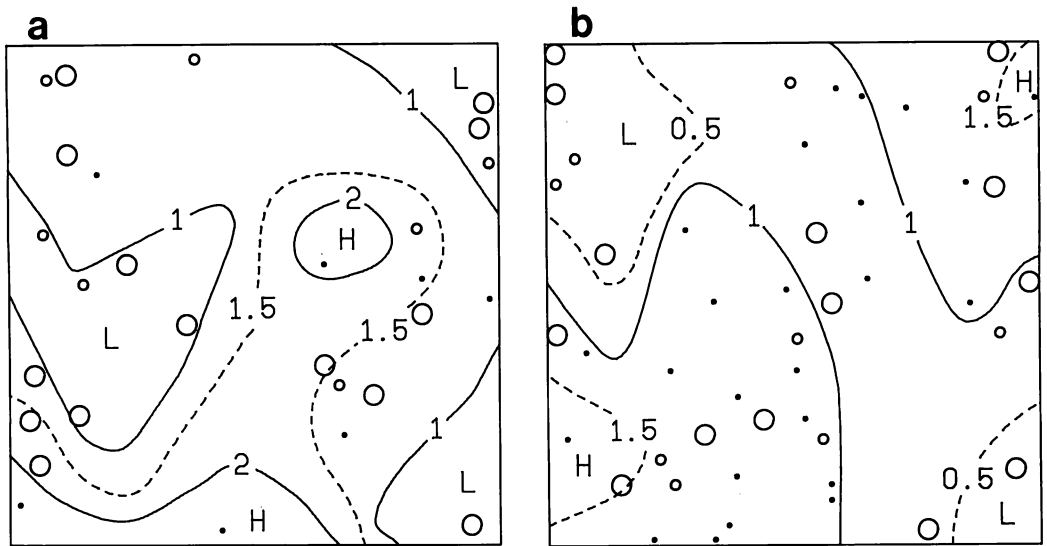
Fig. 1. Distributions of the relative light intensity (isopleths, % of the water surface value) and of individuals on the community floor of *Eisenia bicyclis* (a) and *Ecklonia cava* (b). The size of circles indicates the length of stipes: large open circles, >30 cm; small open circles, 10–30 cm; small solid circles, <10 cm. H, higher; L, lower.

well as the distribution of individual fronds for both species. Relative light intensity varied from 0.6 to 2.2% for *Ei. bicyclis,* and from 0.2 to 1.8% for *Ec. cava.* Most of the young fronds less than 10 cm of stipe length were found growing in the places where light intensity was higher than 1.0% for *Ei. bicyclis* and 0.5% for *Ec. cava.* It should be noticed that the critical light condition for survival and growth is between 1.0 and 1.5% for the former and between 0.5 and 1.0% for the latter. It is thus clear that young fronds of the two species were growing under very low light intensity on the community floor. Relative light intensity of 1% corresponds to about 20 $\mu E/m^2/s$ at local noon on a fine day from April to July in the region investigated.

Photosynthesis-light curves on frond area basis of young *Ei. bicyclis* and *Ec. cava* are shown in Fig. 2. Photosynthetic rate of both species was almost saturated at 200 $\mu E/m^2/s$, and the saturated rate was higher in *Ei. bicyclis* than in *Ec. cava.* Under light intensities lower than 50 $\mu E/m^2/s$, however, the net photosynthetic rate was higher in *Ec. cava* than in *Ei. bicyclis* and it increased
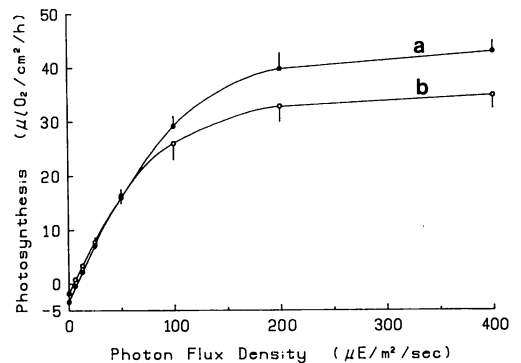

Fig. 2. Photosynthesis-light curves at 20°C of young *Eisenia bicyclis* (a) and *Ecklonia cava* (b). Vertical bars indicate SD.

Table 1. Photosynthesis-light equations on frond area basis, weight basis and chl. *a* basis in young *Eisenia bicyclis* and *Ecklonia cava.* P, net photosynthetic rate; I, photosynthetically active radiation ($0 \leqq I \leqq 25$ $\mu E/m^2/s$).

Basis	*Ei. bicyclis*	*Ec. cava*
Area	P=0.41 I−3.38	P=0.38 I−1.82
Dry weight	P=0.059 I−0.50	P=0.063 I−0.29
Chl. *a*	P=0.29 I−2.48	P=0.32 I−1.56

linearly with increase in light intensity in both of the species. Table 1 shows the
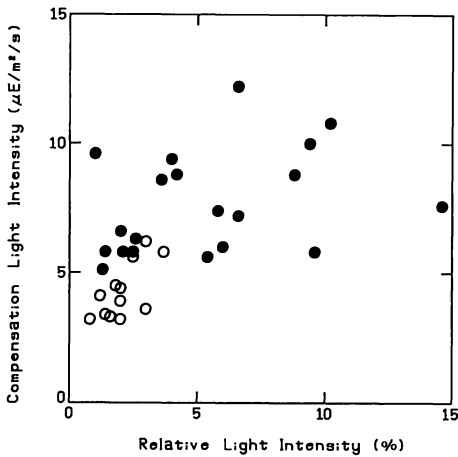
Fig. 3. Relationships between the relative light intensity at growing site and the compensation light intensity for young *Eisenia bicyclis* (●) and *Ecklonia cava* (○).
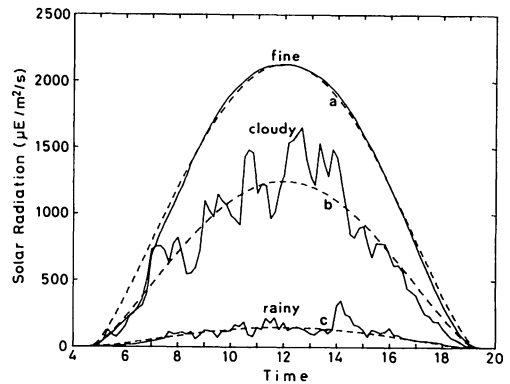

Fig. 4. Diurnal changes in photosynthetically active radiation (PAR) under 3 types of weather conditions. The broken lines show the sine curves fitted. (a) $I_0 = 2130 \times \sin^{1.3} (\pi \cdot t/D)$; (b) $I_0 = 1250 \times \sin^{1.3} (\pi \cdot t/D)$, and (c) $I_0 = 150 \times \sin^{1.3} (\pi \cdot t/D)$.

linear photosynthesis-light equations represented on frond area basis, dry weight basis and chl. *a* basis, which were calculated by the squares linear regression method in the light intensity range lower than $25 \, \mu E/m^2/s$. Photosynthetic rate was clearly different between the species, but the slope of each line was almost the same (no significant difference at 95% confidence level). Average respiratory rate of *Ec. cava* ($1.82 \, \mu l \, O_2/cm^2/h$) was almost half that of *Ei. bicyclis* ($3.38 \, \mu l \, O_2/cm^2/h$). The compensation light intensity was $8.2 \, \mu E/m^2/s$ for *Ei. bicyclis* and $4.8 \, \mu E/m^2/s$ for *Ec. cava*.

Fig. 3 shows the relationships between the light condition (relative light intensity) at growing sites and the compensation light intensity of young *Ei. bicyclis* and *Ec. cava*. The compensation light intensity was calculated from each photosynthesis-light equation in the range lower than $25 \, \mu E/m^2/s$. There are no significant correlations between the light condition at growing sites and the compensation light intensity in both species, although the compensation light intensity of both species is clearly different.

Fig. 4 shows the diurnal changes in photosynthetically active radiation (PAR) under 3 types of weather conditions, fine, cloudy and rainy day. Solar radiation on

the water surface (I_0, $\mu E/m^2/s$) at a given time t hours after sunrise is approximately given by:

$$I_0 = I_{max} \sin^{1.3} (\pi \cdot t/D), \qquad (1)$$

where I_{max} is the maximum I_0 during the daytime and D is the length of daytime (from sunrise to sunset). Table 2 summarizes the results obtained in April, May, June and July. The average I_{max} in this period was $1440 \, \mu E/m^2/s$, which was 65.8% of the maximum solar radiation on fine day. The average length of daytime was 13.9 hours.

The photosynthetic rate of young *Ei. bicyclis* and *Ec. cava* when irradiated from both sides of the blade was twice as high as that when irradiated from one side of the blade in the laboratory (MAEGAWA et al. 1987). In addition, the relative light intensity on the blade was 80% of that of the horizontal plane immediately above the blade tip in the community (MAEGAWA et al. 1987). Thus, the gross photosynthetic rate (P_g, $\mu l O_2/cm^2/h$) on a frond area basis in the community can be written as follows:

$$P_g = 2 \times 0.8 \times 0.41 \times I$$
$$\text{(for *Ei. bicyclis*)}, \qquad (2)$$

$$P_g = 2 \times 0.8 \times 0.38 \times I$$
$$\text{(for *Ec. cava*)}, \qquad (3)$$

where I is the light intensity (μE/m^2/s) measured on the horizontal plane above the young frond tip in the range lower than 25 μE/m^2/s.

Based on the above equations, the daily production and daily compensation light level of young *Ei. bicyclis* fronds were estimated as follows. The light intensity on the water surface at a given time t hours after sunrise can be calculated by eq. (1). Relative light intensity on the community floor (Z) is given by:

$$Z = I/I_0.$$

Hence, the gross photosynthetic rate (P_g, eq. (2)) at a given time t hours after sunrise is given by:

$$P_g = 0.66 \times Z \times I_{max} \times \sin^{1.3}(\pi \cdot t/D). \quad (4)$$

Thus, the daily gross production (Q_g, μl O$_2$/cm^2/day) is given by:

$$Q_g = \int_0^D \{0.66 \times Z \times I_{max} \times \sin^{1.3} (\pi \cdot t/D)\} dt$$

$$\doteqdot 1.21 \times Z \times I_{max} \times D/\pi \quad (5)$$

as a function of 3 parameters, the relative light intensity on the community floor (Z), maximum light intensity during the daytime (I_{max}) and the length of daytime (D, 13.9 h in the present case).
The daily net production (Q_n, μl O$_2$/cm^2/day) is also given by:

$$Q_n = 1.21 \times Z \times I_{max} \times D/\pi - 3.38 \times 24. \quad (6)$$

The daily compensation light level ($Z_{c.d}$) is given by:

$$Z_{c.d} = (3.38 \times 24 \times \pi)/(1.21 \times I_{max} \times D). \quad (7)$$

The daily production and daily compensation light level of young *Ec. cava* was calculated in the same way starting with eq. (1) and eq. (3). The gross photosynthetic rate (P_g) at a given time t hours after sunrise is given by:

$$P_g = 0.61 \times Z \times I_{max} \times \sin^{1.3}(\pi \cdot t/D). \quad (8)$$

The daily gross production (Q_g, μl O$_2$/cm^2/day) is given by:

$$Q_g = \int_0^D \{0.61 \times Z \times I_{max} \times \sin^{1.3} (\pi \cdot t/D)\} dt$$

$$\doteqdot 1.12 \times Z \times I_{max} \times D/\pi. \quad (9)$$

The daily net production (Q_n, μl O$_2$/cm^2/day) is also gien by:

$$Q_n = 1.12 \times Z \times I_{max} \times D/\pi - 1.82 \times 24. \quad (10)$$

The daily compensation light level ($Z_{c.d}$) is given by:

$$Z_{c.d} = (1.82 \times 24 \times \pi)/(1.12 \times I_{max} \times D). \quad (11)$$

The relationships between daily net production (Q_n) and light condition (Z and/or I_{max}) of both species were examined in Fig. 5. Values of I_{max} represent weather conditions; e.g. 2190 μE/m^2/s on fine day, lower than 150 μE/m^2/s on rainy day and 1440 μE/m^2/s on the day with average solar radiation (Table 2). Net production will equal zero at a particular daily light compensation point which depends on the relative light intensity. It is expected that young fronds of *Ei. bicyclis* and *Ec. cava* can grow when their net production exceeds the daily respiratory loss at light intensities greater than their compensation point, 1.1 % (*Ei. bicyclis*) or 0.6% (*Ec. cava*) at 1440 μE/m^2/s of I_{max} on an average day during the present study (Fig. 5). These values agree well with the observed critical light for the species on the community floor (Fig. 1).

Table 2. The monthly maximum (I_{max}) of photosynthetically active solar radiation (PAR) on fine and average days, and the average length of daytime in April, May, June and July 1986.

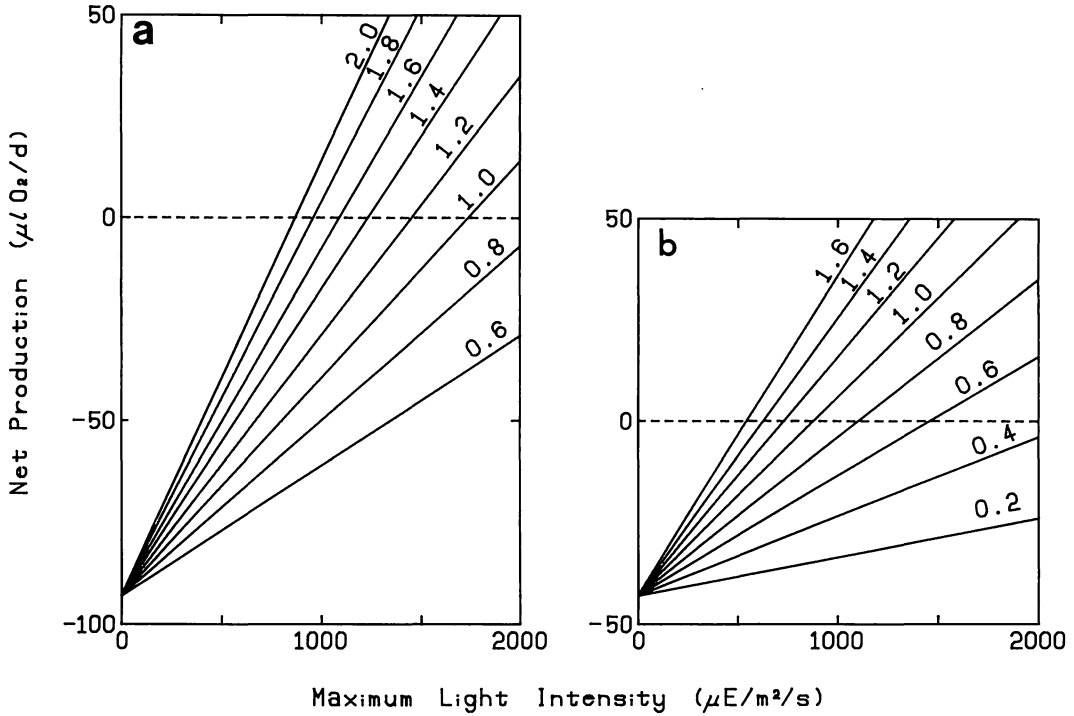| Month	I_{max} (μE/m^2/s)		Daytime (h)
	fine day	average day	
April	2066	1350	13.1
May	2193	1600	14.0
June	2235	1430	14.4
July	2217	1380	14.2
Mean	2178	1440	13.9

Fig. 5. Relationships of the daily net production to the maximum light intensity of daytime for young *Eisenia bicyclis* (a) and *Ecklonia cava* (b) in relation to different relative light intensities (figures on the lines).

Discussion

Solar radiation is an ultimate source of biological production which is initiated in the conversion of its radiant energy into chemical energy in organic matter through photosynthesis of plants, the primary producers. Primary production in the coastal areas of the sea is carried out mainly by macroalgae. Distribution and diurnal changes of the solar radiation, especially of the photosynthetically active radiation (PAR), are important for algal photosynthesis in the sea (RYTHER 1956, RYTHER and YENTSCH 1957, ICHIMURA et al. 1962). In spite of its important ecological significance, only a little attention has so far been paid to the light distribution within underwater plant communities (IKUSIMA 1965, 1966, GERARD 1984, 1986, HAYASHIDA 1986, MAEGAWA and KIDA 1987), probably because of the difficulty of light measurements under natural conditions. On the

community floor of *Ei. bicyclis* and *Ec. cava* the light intensity is critical for the survival and growth of young fronds. Photosynthetic characteristics of young fronds of seaweed species under dim light condition will provide a key to understand the difference in vertical distributions of the species.

In the present study the improved differential gas-volumeter (YOKOHAMA and MAEGAWA 1988) with large reaction and compensation vessels (250 ml) was used to measure photosynthesis and respiration in intact young fronds of comparatively large area (15–35 cm^2) of *Ei. bicyclis* and *Ec. cava*, and it was possible to obtain detailed photosynthetic oxygen changes even near the compensation light level. The saturated light intensity, light compensation point and respiratory rate of young *Ei. bicyclis* and *Ec. cava* in the present study were well in agreement with those of adult fronds (SAKANISHI et al. 1988a, b) and almost the same as reported in a previous paper (MAEGAWA et al. 1987). The light com-

pensation point estimated by the linear photosynthesis-light relationship of young fronds irradiated from one side was 8.2 $\mu E/m^2/s$ for *Ei. bicyclis* and 4.8 $\mu E/m^2/s$ for *Ec. cava*. These values were higher than those of adult or young *Macrocystis pyrifera* (CLENDENNING 1971, FAIN and MURRAY, 1982) and young *Laminaria japonica* (NIIHARA 1980), although the saturated light intensity was almost similar.

It was reported that mature blades of *Macrocystis pyrifera* from different depths exhibited different photosynthetic characteristics; i.e. the photosynthetic capacity of canopy blades was higher under saturating irradiance and their photosynthetic efficiency was higher at low irradiance as compared with those of deeper blades (GERARD 1986). These differences in photosynthetic characteristics of blades collected from different depths were primarily attributable to acclimation to light conditions. For young *Ei. bicyclis* and *Ec. cava* in the present study, the compensation light intensity varied with various light conditions of the growing sites from where they were collected, even though no significant correlations were found between the light condition at growing sites and the compenastion light intensity (Fig. 3). However, the level of compensation light intensity was distinguishable between the two species. The photosynthetic capacity under saturating irradiance could also be distinguished clearly between young *Ei. bicyclis* and *Ec. cava* regardless of the light conditions at their growing sites in the present study as well as in the previous study (MAEGAWA *et al.* 1987).

The difference of photosynthesis-light curve in relation to light quality was remarkable in green and red algae (YOKOHAMA 1973a, b). However, KAGEYAMA and YOKOHAMA (1974) reported that the photosynthesis-light curve was slightly different with the light quality in three species of Phaeophyta, *Ishige sinicola*, *Sargassum ringgoldianum* and *Undaria pinnatifida*, collected from shallow water, but was not different in *Undaria peterseniana* from deeper water.

In the present study it was assumed that there is no significant difference in photosynthetic rate of *Ei. bicyclis* and *Ec. cava* in relation to light quality.

The estimation of the critical light intensity for young *Ei. bicyclis* and *Ec. cava* was carried out in the present study with special reference to the mathematical model of community photosynthesis for submerged aquatic plants by IKUSIMA (1970). In his report the light intensity on the water surface (I, klx) at a given time t hours after sunrise was approximately given by:

$$I = I_{max} \sin^2(\pi \cdot t/D),$$

where I_{max} is the maximum I during the daytime and D is the length of daytime (hr). In the present study, however, the diurnal change in solar radiation (I, $\mu E/m^2/s$) is represented by:

$$I = I_{max} \sin^{1.3}(\pi \cdot t/D).$$

It is thought that the discrepancy among the equations may be due to the difference of measuring methods and units which are illuminance (lx) in the former and photon flux density ($\mu E/m^2/s$) of PAR in the latter.

The estimated critical light level was 1.1% for *Ei. bicyclis* and 0.6% for *Ec. cava* in reference to the light intensity at the water surface (Fig. 5). These values correspond to about 0.42 $E/m^2/day$ and 0.24 $E/m^2/day$ respectively, which are almost the same as the daily compensation light of phytoplankton (PARSONS *et al.* 1984). Photosynthetic characteristics of *Ei. bicyclis* and *Ec. cava* respectively represent characters of the sun and shade types of photosynthesis in terrestrial plants (BOARDMAN 1977). It is clear that young *Ec. cava* fronds can grow under the lower *in situ* light intensity in deeper water as compared with young *Ei. bicyclis* fronds. This difference in critical light cnodition is considered to be one of the most important factors to determine the difference in their vertical distributions, particularly the lower limit of distribution of the two species. The estimated daily compensation light of both species agreed well with the observed critical light condi-

tions on the community floor. This indicates that the present measurements of light conditions in the field and photosynthetic rate in the laboratory were accurately carried out.

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前川行幸*・喜田和四郎*・横浜康継**・有賀祐勝***：褐藻アラメおよびカジメ幼体の光要因からみた生育限界の比較

三重県志摩半島沿岸および静岡県伊豆下田鍋田湾のアラメ・カジメ群落について，生育場所の光環境，幼体の光合成―光関係，日射の日変化等を測定し，日補償点を推定するためのモデル式を作り，両種幼体の光環境からみた生育限界の解明を試みた。さまざまの場所から採取されたアラメ幼体21個体，カジメ幼体13個体について光合成―光曲線を求めた。光合成―光関係，生育場所の相対光強度，日射の日変化等から1日の純生産量を求めるモデル式を作り，日補償点を推定した。得られた日補償光強度は，海面に対する相対光強度で表わされ，アラメ幼体では約1.1%，カジメ幼体では約0.6%であった。また，幼体の生育する現場での光環境を知るため群落底部の光分布を測定した結果，アラメ幼体は1.0―1.5%，カジメ幼体は0.5―1.0%相対光強度の場所に生育しており，モデル式からの推定値とよく一致した。以上の結果から，カジメはアラメに比べより深所に分布することが説明される。両種の水深の違いを，光合成の面から日補償点の差として明らかにすることができた。（*514　三重県津市江戸橋2―80　三重大学生物資源学部藻類増殖学研究室，**415　静岡県下田市5―10―1　筑波大学下田臨海実験センター，***108　東京都港区港南4―5―7　東京水産大学藻類学研究室）