

# Light requirements and depth zonation of marine macroalgae

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**ABSTRACT:** Light compensation points ( $I_c$ ) for growth were low ( $0.3$  to  $2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) for the temperate marine macroalgae *Chondrus crispus*, *Fucus serratus*, *Petalonia fascia*, *Porphyra purpurea* and *Ulva lactuca* measured at  $7^\circ\text{C}$ . These  $I_c$ -values corresponded to those estimated by a physiological model including light absorption and quantum yield for growth to describe carbon gain, and weight specific dark respiration, dark loss rate and thallus specific carbon ( $\text{mol C m}^{-2}$  thallus) to describe carbon loss. Absorption and quantum yield were close to the theoretical maximum for all species and could not explain differences in  $I_c$ . Respiration and thallus specific carbon varied more than 15-fold and were the main factors responsible for variations in  $I_c$ . Experimental  $I_c$ -values correspond to 0.12 to 0.61 % of the yearly surface light dose in Denmark ( $56^\circ\text{N}$ ). These values agree with the % of surface light (%SI) available at the depth limits of leathery and foliose macroalgae at different latitudes. Hence, there is no surplus of energy to balance grazing and mechanical losses, and these factors must be of minor importance for macroalgae growing at great depths. A literature review of depth limits for marine macroalgae reveals an upper zone of mainly leathery algae with depth limits of about 0.5 % SI, an intermediate zone of foliose and delicate algae with depth limits at about 0.10 % SI, and a lower zone of encrusted algae extending down to about 0.01 % SI. This zonation pattern is accompanied by a decrease in thallus specific carbon (i.e. thinner thalli) with increasing depth. The inverse relationship between growth rate at low light and thallus specific carbon suggests that a thin thallus is essential for growth and survival of marine macroalgae at great depths.

## INTRODUCTION

The light compensation point ( $I_c$ ) for growth of marine macroalgae is a central parameter in coastal ecology. Attached macroalgae are important in many coastal ecosystems as primary producers (Mann 1973, 1982) and structural components with a rich macrofauna. The light compensation point sets the physiological constraints for the depth limit of attached macroalgae and affects the ability of macroalgae to grow in shaded habitats, below rocks or canopies of other algae, and to sustain epiphyte loads. Despite the importance, however, few determinations of  $I_c$  for growth of marine macroalgae are available (Chapman

& Lindley 1980, Schonbeck & Norton 1980, Maggs & Guiry 1987, Sand-Jensen 1988a). Here we determine  $I_c$ -values of marine red, brown and green macroalgae displaying a range of thallus thicknesses.

The minimum light requirement for a plant is reached when captured light provides just enough ATP and reducing equivalents to balance loss processes within the tissue. Both the ability to capture and utilize light and the loss processes in the plant depend on several physiological parameters which, accordingly, affect the light compensation point. The common method to determine  $I_c$  for growth is to plot growth rates ( $y$ ) vs light ( $x$ ) for low light intensities. This method only allows judgement of the relative importance of the  $y$ -axis intercept (loss rate in the dark) and the slope of the line (light utilization efficiency) for the regulation of  $I_c$  ( $x$ -axis intercept), and parameters which influence the dark loss rate and the light utilization efficiency cannot be evaluated. In this paper we examine how the  $I_c$ -level of macroalgae depends on

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the basic physiological parameters: weight specific respiration, thallus specific carbon content (carbon per thallus area, analogous to 'leaf specific mass'; Witkowski & Lamont 1991), light absorption and quantum yield for growth.

Light compensation points measured in laboratory experiments and depth limits in nature are difficult to compare. Laboratory measurements of  $I_c$  represent the absolute (or physiological) minimum light requirements. In nature, macroalgae may need a surplus of energy to balance grazing and mechanical damage and to allow physiological adjustments to environmental changes. The natural light climate is very variable and light intensities above saturation are utilized less efficiently than low light. A surplus of energy is also needed to form new biomass and reproductive units. The mean light intensity at the depth limit is, therefore, expected to be significantly higher than laboratory measurements of  $I_c$  and differences between the two may quantify the extra energy needed to balance losses in the field. Here we compare our experimental  $I_c$ -values with literature values of light availability at the maximum depth of macroalgal growth.

## MATERIALS AND METHODS

Laboratory growth experiments were described in detail by Markager (in press). Briefly, attached individuals of 5 marine macroalgae were collected in Århus Bay, Denmark, (salinity about 20 ‰) and cut into discs (*Ulva lactuca*, *Petalonia fascia*, *Porphyra purpurea*) or 2 to 4 cm apical shoots (*Fucus serratus*, *Chondrus crispus*). After 7 to 14 d acclimation, thallus pieces were grown at 7 °C at 5 to 8 different light intensities and in the dark for 13 to 41 d. The growth medium was GF/C filtered seawater enriched with 500  $\mu\text{g NH}_4\text{-N l}^{-1}$ , 500  $\mu\text{g NO}_3\text{-N l}^{-1}$  and 100  $\mu\text{g PO}_4\text{-P l}^{-1}$ . The experiment was repeated 6 times with 1 to 3 species each time. Growth rates ( $\mu$ ) were determined from changes in carbon content of the tissue over time ( $t$ ). Thallus specific carbon ( $D$ ) and dark respiration ( $R_d$ ) were measured at the end of the experiments on all thalli from the dark and from each light intensity. Dark respiration was measured as oxygen consumption in closed bottles over 14 h at 7 °C and converted to carbon units assuming RQ of 0.8 mol  $\text{CO}_2 \text{ mol}^{-1} \text{ O}_2$ . Fractional light absorption ( $A$ ) was measured every week as 1 minus fractional transmission (Vermaat & Sand-Jensen 1987) on all thalli.

The light compensation point was estimated from the relationship between growth rate and light (e.g. Fig. 1), by (1) selecting a light intensity below which the points show a linear relationship and then calculating  $I_c$  by regression analysis, and (2) calculating the parameters for one of the common  $\mu$ -I or P-I functions

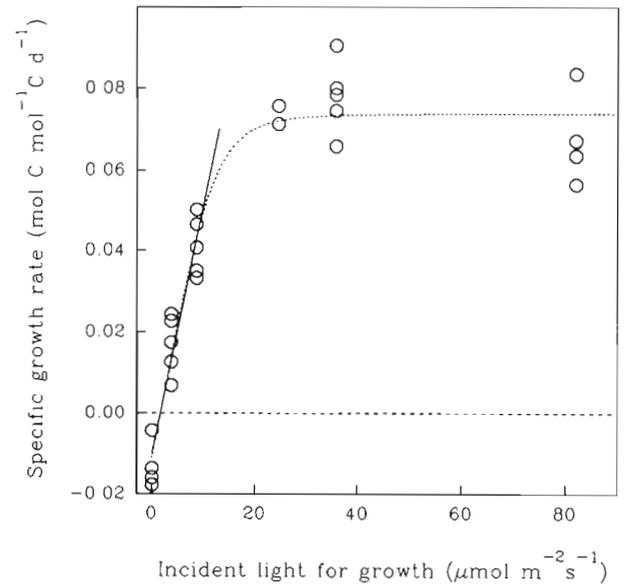


Fig. 1. *Petalonia fascia*. Specific growth rate vs incident light at 7 °C. (—) Linear relationship calculated by linear regression for points below 10  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ; (.....) Eq. 1 fitted to all data points

(Bannister 1979, Jassby & Platt 1976) and then calculating  $I_c$ . Method 1 is objective, apart from the selection of the appropriate light range, and allows calculation of confidence limits for  $I_c$ . Method 2 seems objective, but the selection of  $\mu$ -I equation can bias the estimate of  $I_c$  (Geider et al. 1985), and this method does not provide confidence limits for  $I_c$ . For Method 2 we used the equation of Bannister (1979) which has a shape parameter ( $m$ ) which should minimize the influence of curve shape on  $I_c$ :

$$\mu = \frac{\alpha I \mu_m}{((\mu_m)^m + (\alpha I)^m)^{1/m}} + \mu_d \quad (1)$$

where  $\mu$  = net growth rate;  $\alpha$  = initial slope of growth rate vs light;  $\mu_m$  = maximal growth rate; and  $(-\mu_d)$  = loss rate in the dark. The difference between  $I_c$ -values determined by the linear regression (Method 1) and the  $\mu$ -I curve (Method 2) was 0 to 1.2  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  (mean value 0.35  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and 2.7 times less than the 95 % confidence limits found by the linear regression method (mean values  $\pm 0.95 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ; Table 1). Thus, the uncertainty related to the choice of calculation method was small compared to the uncertainty of growth measurements of  $I_c$ . We subsequently chose the linear regression method because it provides confidence limits for  $I_c$ .

Light-limited net growth rate of macroalgae with a flat thallus can be expressed by

$$\mu = I \phi_g A - (R_m + k \mu_g) D \quad (2)$$

Symbols and units are defined in Table 1. The product  $I \phi_g A$  represents the area specific carbon gain per unit

Table 1. Observed and calculated light compensation points ( $I_c$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and the parameters that determine the calculated  $I_c$  in different experiments with 5 species of marine macroalgae. Thallus specific carbon at  $I_c$  ( $D$ ,  $\text{mol C m}^{-2}$  thallus area, one side), weight specific dark respiration ( $R_m$ ,  $\text{mmol C mol}^{-1} \text{ cell C d}^{-1}$ ), dark loss rates ( $\mu_d$ ,  $\text{mmol C mol}^{-1} \text{ cell C d}^{-1}$ ) and fractional light absorption ( $A$ , dimensionless) are mean values of 10 to 14 individuals (Markager in press). Gross quantum yield for growth ( $\phi_g$ ,  $\text{mmol C mol}^{-1}$  absorbed photons) is the mean value of individuals at limiting light (Markager in press).  $k$  (dimensionless) = slope of the linear relationship between parallel measurements of dark respiration and specific growth rate for 25 to 90 individuals. Thallus specific carbon and absorption at  $I_c$  were calculated by interpolation between values in the dark and at low light. Area specific respiration at  $I_c$  was calculated as  $(R_m + k\mu_d)D$ , ( $\text{mmol C m}^{-2} \text{ d}^{-1}$ ). Photosynthetic efficiency ( $\alpha$ ) is calculated as  $A\phi_g$ , [ $\text{mmol C m}^{-2} \text{ d}^{-1}$  ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )<sup>-1</sup>]. CL: minimum estimates (see text) of confidence limits ( $p > 0.95$ ); CV: coefficient of variation (SD/mean)

	<i>Ulva lactuca</i>				<i>Petalonia fascia</i>				<i>Fucus serratus</i>	<i>Porphyra purpurea</i>	<i>Chondrus crispus</i>	
	Light:dark cycle:	24:0	24:0	14:10	24:0 <sup>a</sup>	24:0	24:0	14:10	14:10	14:10	24:0	14:10
$\phi_g$		83	70	92	56	86	74	100	95	98	73	99
Absorption at $I_c$		0.63	0.63	0.65	0.40	0.58	0.60	0.59	0.68	0.89	0.48	0.88
$\alpha$ ( $\phi_g A$ )		4.5	3.8	5.2	1.9	4.3	3.8	5.1	5.6	7.5	3.0	7.5
$D$ at $I_c$		0.46	0.59	0.58	0.36	0.30	0.45	0.35	0.35	2.46	0.38	4.38
Dark respiration		6.0	5.1	3.5	13.0	24.0	21.6	18.6	30.6	2.7	2.9	0.47
Dark loss rate		12.0	1.3	9.3	12.0	35.0	5.8	13.0	11.9	1.2	8.5	0.32
$k$		0.11	0.07	0.16	0.10	0.19	-0.03	0.17	0.00	0.06	0.18	0.03
Respiration at $I_c$		3.3	3.0	2.9	5.1	9.0	9.7	7.2	10.7	6.8	1.7	2.1
Observed $I_c$		1.87	0.33	1.37	2.47	2.20	1.61	1.61	2.45	1.12	1.28	0.44
Calculated $I_c$		0.73	0.80	0.56	2.65	2.10	2.53	1.42	1.92	0.90	0.55	0.28
CL of observed $I_c$		0.3	1.73	1.35	0.97	1.21	1.50	0.89	1.02	3.55	0.89	6.75
CV of calculated $I_c$		-	0.12	0.35	-	-	0.13	0.29	0.41	0.16	-	0.27

<sup>a</sup> Data from Sand-Jensen (1988a, b)

time. The basic loss process is the carbon specific maintenance respiration ( $R_m$ ), equivalent to the respiration of individuals kept in the dark for a long time. However, because the respiration rate increases linearly with the growth rate with the slope  $k$  (Langdon 1988, Sand-Jensen 1988a, Geider & Osborn 1989, Sand-Jensen & Madsen 1991, Markager & Sand-Jensen unpubl.), the term  $k\mu_g$  is added to  $R_m$ . Here  $\mu_g$  represents the gross growth rate defined as the observed growth rate ( $\mu$ ) plus the dark loss rate ( $-\mu_d$ ). To obtain the loss rate per unit area of the thallus, the carbon specific respiration rate is multiplied by the thallus specific carbon ( $D$ ). Eq. 2 is rearranged to yield the light compensation point ( $I_c$ ) at zero growth ( $\mu = 0$ ):

$$I_c = \frac{(R_m - k\mu_d) D}{\phi_g A} \quad (3)$$

For  $\mu = 0$ ,  $\mu_g$  is equal to the dark loss rate which is inserted in Eq. 3.  $I_c$ -values calculated from Eq. 3 are hereafter denoted calculated  $I_c$ -values and the  $I_c$ -values estimated by linear regression from  $\mu$ -I plot are denoted observed values, because they (though calculated) are derived directly from measured growth rates.

Values for  $R_m$  and  $\mu_d$  were attained for individuals kept in the dark for at least 25 d, and  $k$  was determined from the relationship between respiration rate and growth rate for all individuals in each experiment. Gross quantum yield for growth ( $\phi_g$ ) was calcu-

lated individually for each thalli from the increase in biomass ( $x_t - x_0$ ) and dark respiration ( $R_d$ ), both converted to carbon units, and measurements of absorbed light ( $I_a$ )

$$\phi_g = \frac{(x_t - x_0) + R_d t}{I_a} \quad (4)$$

The measured values for absorbed light also include reflection and absorption by non photosynthetic active compounds, and the calculated  $\phi_g$ -values, therefore, underestimate the true quantum yield (Markager in press). Quantum yield is known to decrease as the light intensity approaches saturation. Therefore, only values for light-limited individuals were used to calculate  $\phi_g$ -values.

## RESULTS

### Light compensation points

Observed  $I_c$ -values were between 0.33 and 2.45  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and averaged 1.52 (Table 1). Three experiments with *Ulva lactuca* (a foliose green alga) yielded 0.33, 1.37 and 1.87  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , slightly lower than 2.47  $\mu\text{mol m}^{-2} \text{s}^{-1}$  found by Sand-Jensen (1988a). In 4 experiments with the foliose brown alga *Petalonia fascia*,  $I_c$ -values were from 1.61 to 2.45, and the

$I_c$ -value was lower,  $1.12 \mu\text{mol m}^{-2} \text{s}^{-1}$ , for the leathery brown alga *Fucus serratus*. The foliose red alga *Porphyra purpurea* had an  $I_c$ -value of  $1.28 \mu\text{mol m}^{-2} \text{s}^{-1}$  and the leathery red alga *Chondrus crispus* showed the lowest value of  $0.44 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The small range (Table 1) means that none of the differences between species were statistically significant, given the uncertainty of the estimates.

The reported  $I_c$ -values represent intensities during the light period. For *Ulva lactuca* and *Petalonia fascia*, where experiments were performed in continuous light or a 14:10 light:dark cycle,  $I_c$ -values were relatively unaffected by the length of the light period (Table 1). Thus, the 24 h light dose to reach  $I_c$  was lower for individuals kept in a light:dark cycle.

The  $I_c$ -values calculated from Eq. 3 ranged from 0.28 to  $2.53 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Table 1) and show a significant correlation ( $r = 0.71$ ,  $p = 0.013$ ;  $t$ -test) to observed values (Fig. 2). Assuming that differences exceeding 2 SD are significant, *Chondrus crispus* has significantly lower calculated  $I_c$ -values than *Ulva lactuca* and *Fucus serratus* in 1 experiment and than *Petalonia fascia* in 2 experiments.

### Regulation of $I_c$

Light absorption was higher in *Fucus serratus* and *Chondrus crispus* than in the other species with lower thallus specific carbon (Table 1). There was no signifi-

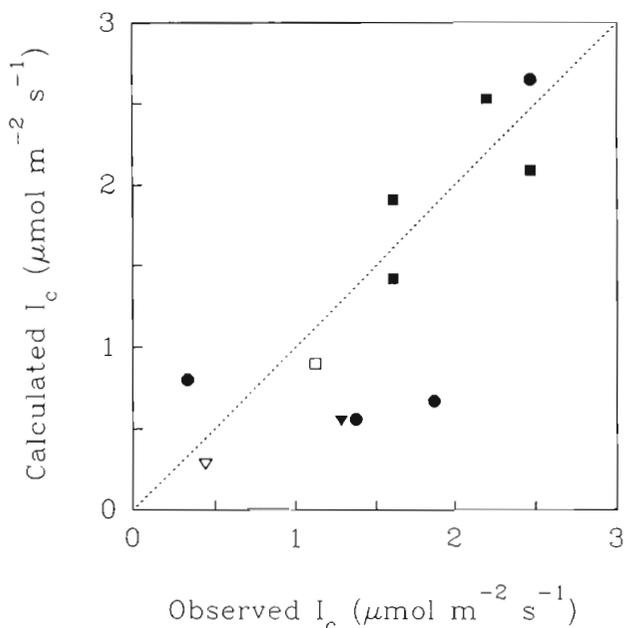


Fig. 2. Calculated (Eq. 3) versus observed values of the light compensation point for growth at  $7^\circ\text{C}$ ; (●) *Ulva lactuca*; (■) *Petalonia fascia*; (□) *Fucus serratus*; (▽) *Chondrus crispus*; (▼) *Porphyra purpurea*

cant difference in gross quantum yield between species. Mean dark respiration was high for *Petalonia fascia* (mean  $23.8 \text{ mmol C mol cell}^{-1} \text{ d}^{-1}$ ), intermediate for *Ulva lactuca*, *F. serratus* and *Porphyra purpurea* ( $2.7$  to  $6.0 \text{ mmol C mol cell}^{-1} \text{ d}^{-1}$ ) and low for *C. crispus* ( $0.47 \text{ mmol C mol cell}^{-1} \text{ d}^{-1}$ ). No systematic variations in  $k$  and dark loss rate could be detected. However, for all 3 parameters ( $R_m$ ,  $k$  and  $\mu_d$ ) values were particularly low for *C. crispus*, indicating very low weight specific loss rates.

We can identify the sensitivity of  $I_c$  to variations in the parameters affecting  $I_c$ . Light absorption and quantum yield varied about 2-fold among the 5 species whereas the 4 parameters affecting the area specific respiration rate varied 15-fold or more (Table 2). The sensitivity of  $I_c$  to variation of each parameter in Eq. 3 was calculated from the first partial derivative which has the unit  $\mu\text{mol m}^{-2} \text{s}^{-1} (\text{parameter unit})^{-1}$  (Table 2). The product of the first derivative and the range of variation for the specific parameter yields the potential contribution to the variation in  $I_c$  caused by that parameter. We calculated the contribution to the variability in  $I_c$  for the entire range of values observed in our experiments (Table 1). Calculations identified  $D$  (60 to 70 % of the potential variation) and  $R_m$  (ca 25 % of the variation in  $I_c$ ) as the main parameters influencing  $I_c$  (Table 3). Absorption and quantum yield had, because of low variability, negligible effects on  $I_c$ , and  $I_c$  was relatively unaffected by variations of  $k$  and dark loss rate (Table 3). These results, based on the entire range observed for each parameter, refer to the total variability in  $I_c$  for all 5 species. Within-species variability was, however, smaller than that among species particularly for  $D$ . Variability in  $I_c$  was, for *Ulva lactuca*, mainly dependent on  $R_m$  and to a smaller extent on  $A$  and  $D$ . For *Petalonia fascia* the main parameters controlling  $I_c$  were  $D$  and  $R_m$  (Table 3). The sum of variation in  $I_c$  for each parameter (Table 3) represents a maximum estimate of  $I_c$  variability. Any positive relationship between gain ( $A$  and  $\phi_g$ ) and loss parameters ( $R_m$ ,  $\mu_d$ ,  $k$  and  $D$ ), or negative relations within gain or loss parameters, will reduce the actual variation in  $I_c$ . For the loss parameters we did find a negative correlation between  $R_m$  and  $D$ . Hence, the actual variation of areal specific respiration was smaller (6.3-fold) than the sum of variation in each of the loss parameters.

## DISCUSSION

### Minimum light requirements

Observed and calculated  $I_c$ -values ranged between  $0.3$  and  $2.7 \mu\text{mol m}^{-2} \text{s}^{-1}$  for the 5 species acclimated to low light at  $7^\circ\text{C}$ . Because the species represent

Table 2. First partial derivatives of the parameters in the equations for  $I_c$  (Eq. 3) and the mean values for the 11 experiments in Table 1, using a 14 : 10 h light : dark cycle for all experiments. The range and variability of the parameters are given. Units as in Table 1

Parameter	$\frac{dI_c}{dx}$	Mean of 1st partial derivative	Minimum	Maximum	Range	Factor of variation
Quantum yield	$\frac{dI_c}{d\phi} = -\frac{(R_m - k\mu_d)D}{A\phi^2}$	-0.029	56	100	44	1.8
Absorption	$\frac{dI_c}{dA} = -\frac{(R_m - k\mu_d)D}{A^2\phi}$	-3.97	0.40	0.89	0.49	2.2
Thallus specific carbon	$\frac{dI_c}{dD} = \frac{(R_m - k\mu_d)}{A\phi}$	5.52	0.295	4.38	4.09	14.9
Dark respiration	$\frac{dI_c}{dR_m} = \frac{D}{A\phi}$	0.297	0.47	30.6	30.1	65.1
$k$	$\frac{dI_c}{dk} = \frac{\mu_d D}{A\phi}$	1.72	-0.03	0.19	0.22	$\infty$
Dark loss rate	$\frac{dI_c}{d\mu_d} = \frac{kD}{A\phi}$	0.021	0.32	35.0	34.7	109

different taxonomic groups and thallus thicknesses, this interval may, overall, be a realistic range for foliose and leathery marine macroalgae grown at 7 °C. Literature data for these thallus types support this conclusion. Values between 2.2 and 3.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in *Ascophyllum nodosum* and *Pelvetia canaliculata* can be calculated from growth data (10 °C) presented by Schonbeck & Norton (1980). Chapman & Lindley (1980) found 0.64  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (0 to 1 °C) in *Laminaria solidungula* and Maggs & Guiry (1987) obtained very low values (0.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , 15 °C) for a filamentous red alga. Low values (0.3 to 0.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , 10 °C)

were also found for 3 *Laminaria* species and *Saccorhiza polyschides* (Kain 1966). However, some of these values may be underestimated because they are based on changes in surface area or fresh weight. Some species are able to increase their area or fresh weight at low light and in the dark, at the expense of their carbon reserves (Chapman & Lindley 1980, Sand-Jensen 1988a, Markager & Sand-Jensen unpubl.).

Reported  $I_c$ -values for photosynthesis are usually higher than  $I_c$ -values for growth. Mean values for 22 species of marine macroalgae were 6.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 5 °C and 7.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 10 °C (King & Schramm

Table 3. Mean values of the product  $dI_c/dx (x_{\max} - x_{\min})$  ( $dI_c/dx$  = mean of the first partial derivative; and  $(x_{\max} - x_{\min})$  = range of the parameter for individuals grown at  $I_c$ ) for the 6 parameters in Eq. 3. Values are shown for all experiments together, for 4 experiments with *Ulva lactuca*, and for 4 experiments with *Petalonia fasciata*. Units are  $\mu\text{mol m}^{-2} \text{s}^{-1}$

Parameter	All experiments		<i>Ulva lactuca</i>		<i>Petalonia fasciata</i>	
	Mean	% of sum of means	Mean	% of sum of means	Mean	% of sum of means
Quantum yield ( $\phi_g$ )	-0.11	0.32	-0.10	2.0	-0.09	2.0
Absorption	-1.94	5.6	-1.06	21.4	-0.56	12.4
Thallus specific carbon	22.58	65.1	1.12	22.5	1.51	33.5
Dark respiration	8.94	25.8	2.25	45.2	1.63	36.3
$k$	0.38	1.1	0.18	3.6	0.44	9.9
Dark loss rate	0.74	2.1	0.27	5.4	0.26	5.9
Sum of absolute values	34.7	100.0	4.97	100.0	4.50	100.0

1976). Dunton & Jodwalis (1988) estimated  $I_c$  for photosynthesis to be about  $3 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *Laminaria solidungula* (2 °C) and Matta & Chapman (1991) found  $26.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *Colpomenia peregrina* (15 to 20 °C). Apart from methodological differences, a possible explanation for the discrepancy is that respiration rates increase with growth rates (Langdon 1988, Sand-Jensen 1988b, Markager & Sand-Jensen unpubl.).  $I_c$ -values obtained in photosynthesis experiments with plants grown at normal light intensities (King & Schramm 1976, Matta & Chapman 1991) will, therefore, be higher than  $I_c$ -values for growth with plants acclimated to low light conditions (Sand-Jensen 1988b). Consequently, photosynthetic measurements of  $I_c$  do not allow estimates of minimum light requirements for growth and maximum depth penetration, unless experiments are performed with individuals acclimated to light intensities about the  $I_c$ -value. This aspect is frequently overlooked.

#### Factors affecting minimum light requirements

The  $I_c$ -model (Eq. 3) is a combination of well-known relationships between light intensity and carbon gain, and between growth rate and respiration. The model is able to explain most of the variation in the observed  $I_c$ -values, despite the large confidence limits relative to the small range of  $I_c$ -values. Furthermore, no systematic deviation from a 1:1 relationship was found (Fig. 2) and the mean values were in close agreement. Hence, the model developed here should provide a useful basis for the analysis of variations in  $I_c$ .

The sensitivity analysis showed that the 9-fold variation in  $I_c$  observed over the 11 experiments (Table 1) was primarily attributable to differences in weight specific dark respiration rate and thallus specific carbon whereas the influence of light absorption and quantum yield was much smaller. To appreciate this difference in variability of gain and loss processes of organic carbon, we must consider the physical constraints on the parameters.

The gain parameters ( $A$  and  $\phi$ ) have well defined upper limits (1 for  $A$  and  $125 \text{ mmol C mol}^{-1}$  photons for  $\phi$ ; Raven 1984), and the observed values are within about 50 % of these values and consequently vary less than 2-fold. For quantum yield the differences between the observed and the theoretical values were mainly due to reflection and absorption by structural components (Markager in press). Furthermore, all values below  $92 \text{ mmol C mol}^{-1}$  photons were found in experiments with continuous light suggesting that this represents a stress which reduces quantum yield. We therefore conclude that about  $95 \text{ mmol C mol}^{-1}$  photons is a realistic value for all species in a natural light cli-

mate. A detailed analysis of quantum yield for growth for the species treated here is provided by Markager (in press). Light absorption varies more than quantum yield but was closely correlated with the log thallus specific carbon (Markager in press), probably because absorption in thin species is limited by the maximum possible pigment content per unit area (Markager in press) and package effects (Rabinowitch 1951, Britz & Briggs 1987). Overall, carbon gain in individuals adapted to low light is close to the maximum attainable provided that nutrients and growth conditions otherwise are adequate. The low values for absorption and quantum yield for *Ulva lactuca* included in Table 1 ( $A = 0.4$ ,  $\phi_g = 56 \text{ mmol C mol}^{-1}$  photons) from Sand-Jensen (1988a, b) are presumably due to nitrogen limitation and high light levels in the field at collection of plants for experiments.

The carbon specific respiration rate varied considerably, and in contrast to the upper limits for  $A$  and  $\phi$ , the physical constraints on lower limits of  $R_m$  are not quantified in the literature. Consequently, we are unable to determine a theoretical lower limit for  $I_c$ . *Fucus serratus*, *Chondrus crispus* and *Porphyra purpurea* had low rates of dark respiration which, in *C. crispus*, more than compensated for the high thallus specific carbon. *C. crispus* and *P. purpurea* had the lowest area specific respiration rates among the 5 species. If this is a general phenomenon among red algae, it could explain their common dominance at great depths (Sears & Cooper 1978, Dring 1981, Mathieson et al. 1981), but further experiments are needed to test this hypothesis.

#### Experimental $I_c$ -values and depth limits

Subtidal vegetation of macroalgae can be divided into 3 zones (Vadas & Steneck 1988). An uppermost zone dominated by large brown algae with an understory of other algae; an intermediate zone where foliose and delicately-branched species dominate, still with an understory of crustose algae; and a deep community where vegetation consists only of crustose, often calcified algae (Norton et al. 1977, Littler et al. 1985, Vadas & Steneck 1988). The vertical extension of these zones is set by light attenuation in the water column and is, therefore, best described by the percent of surface light (% SI) reaching their maximum depth of growth. Reported extinction depths for these 3 zones range from 0.12 to 1.5 % SI (mean 0.48 % SI) for the upper zone, where large brown algae dominate, from 0.02 to 0.22 % SI (mean 0.12 % SI) for that dominated by foliose algae, and from 0.003 to 0.05 % SI (mean 0.012 % SI) for the deepest zone dominated by crustose algae, with the extremely low values of 0.0005 % SI (Littler et al. 1985) and 0.00023 % SI (Agegian & Abbott 1985) as apparent

exceptions (Table 4). The value of Littler et al. (1985) was found by extrapolation of a light attenuation curve between 0 and 120 m (Fig. 1 in Littler et al. 1986) down to 268 m and Agegian & Abbott (1985) only provided a mean attenuation coefficient of  $0.052 \text{ m}^{-1}$  for the entire water column. Direct light measurements are needed to confirm the exact light levels as % SI for these deepest records of macroalgae.

If these depth limits corresponded to a fixed light dose, then depth limits as % SI are expected to be shallower at higher latitudes due to less incoming surface light. This expectation is not supported by the data (Table 4) for leathery and foliose algae. In fact, the deepest growing large brown algae were found in the arctic (Chapman & Lindley 1980, Dunton 1990), where the annual light dose at the maximum depth of *Laminaria solidungula* was 45 to  $50 \text{ mol m}^{-2} \text{ yr}^{-1}$  (Dunton 1990), which is lower than  $71 \text{ mol m}^{-2} \text{ yr}^{-1}$  for *Laminaria hyperborea* at Helgoland (North Sea) (Lüning & Dring 1979). Perhaps reduced metabolic rates associated with lower temperature at higher latitudes compensate for the lower surface light there, so that depth limits, given as % SI, are relatively independent of latitude. Data for crustose species from temperate and especially from arctic regions are needed before a general statement can be made for this group.

Our experimental  $I_c$ -values ( $0.3$  to  $2.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) in a 14:10 h light:dark cycle correspond to  $5.5$  to  $46 \text{ mol m}^{-2} \text{ yr}^{-1}$  or about  $0.12$  to  $0.61$  % SI in Denmark ( $56^\circ \text{ N}$ ), where mean water temperatures are close to the experimental temperature ( $7^\circ \text{ C}$ ). These values agree with % SI values in Table 4 for leathery and foliose algae. The correspondence suggests that algae living at depths with % SI in the lower part of the ranges in Table 4 have no surplus energy to cover grazing or mechanical losses. This is supported by observations of particularly deep growth when grazing is insignificant. For example, Vadas & Steneck (1988) found lower depth limits ( $0.4$  % SI) for large brown algae when herbivores were few, which is lower than that reported for *Laminaria hyperborea* ( $1.5$  % SI) on a location subjected to grazing by *Echinus esculentus* (Kain 1971, 1976). It therefore appears that the greatest depth limits in Table 4 are set directly by the physiological light compensation point for growth.

#### Thallus-specific carbon influencing macroalgal zonation

Vertical distribution of macroalgae in the 3 zones as proposed by Vadas & Steneck (1988) is supported by

Table 4. Depth limits of marine macroalgae with sheet-like thalli in metres and in percent of surface light (% SI) for localities from tropical to high arctic northern regions. Species are divided into 3 morphological types. Leathery species have a thick thallus with many cell-layers and foliose species have a thin thallus with only one or few cell-layers. In cases where the reference listed depth limits for many species, only the deepest occurring species in each group was included

Species	Latitude (°N)	Depth (m)	Leathery (% SI)	Foliose (% SI)	Crustose (% SI)	Source
<i>Cystoseira</i> sp.	27	8.5	0.2			Neushul (1971)
<i>Cystoseira</i> sp.	28	9.5	0.12			Neushul (1971)
<i>Agarum cribrosum</i>	43	40	0.44			Vadas & Steneck (1988)
<i>Laminaria hyperborea</i>	54	8	0.7			Lüning & Dring (1979)
<i>Laminaria hyperborea</i>	54	19	1.0–1.9			Kain (1971), Kain et al. (1976)
<i>Laminaria solidungula</i>	70	6.4	0.2			Dunton (1990)
<i>Laminaria solidungula</i>	69	20	0.18			Chapman & Lindley (1980)
Foliose macroalgae	11	140		0.18		Hillis-Colinvaux (1985), Colin et al. (1986)
<i>Lobophora variegata</i>	16	140		0.06		Agegian & Abbott (1985)
<i>Monostroma</i> sp.	21	118		0.22		Agegian & Abbott (1985)
<i>Johnson-Sea-linkia profunda</i>	24	157		0.02		Littler et al. (1985)
<i>Maripelta</i> sp.	28	13		0.12		Neushul (1971)
<i>Ptilota serrata</i>	43	50		0.11		Vadas & Steneck (1988)
<i>Phycodrys rubens</i>	43	50		0.11		Vadas & Steneck (1988)
Corallines	11	228			0.004	Hillis-Colinvaux (1985), Colin et al. (1986)
Crustose red algae	16	250			0.00023*	Agegian & Abbott (1985)
Crustose red algae	21	182			0.008	Agegian & Abbott (1985)
Crustose red algae	24	268			0.0005	Littler et al. (1985)
Crustose red algae	36	Cave			0.003	Larkum et al. (1967)
<i>Leptophytum laeve</i>	43	63			0.02	Vadas & Steneck (1988)
<i>Lithothamnion</i> sp.	54	15			0.05	Lüning & Dring (1979)
Overall mean			0.48	0.12	0.012	

\* calculated from a mean attenuation coefficient of  $0.052 \text{ m}^{-1}$  for the water column as stated in the paper; a lower attenuation coefficient due to the spectral changes at great depths may increase this value to about  $0.0005$  %

the data in Table 4. Algal growth forms in these zones correspond to 3 levels of thallus specific carbon ( $D$ ).  $D$ -values between 1.5 and 4.5 mol C m<sup>-2</sup> are representative for leathery species, e.g. *Fucus* or *Laminaria* species and *Chondrus crispus* (Lüning 1971, 1979, Raven et al. 1979, this study). The foliose species in this study had  $D$ -values between 0.3 and 0.6 mol C m<sup>-2</sup> at  $I_c$ , representative for 'thin algae', and the density of the deepest crustose algae in Littler et al. (1985) can be calculated to be 0.0087 mol C m<sup>-2</sup> (Littler et al. 1986).

Thallus specific carbon ( $D$ ) regulates the area specific growth rate in 2 ways. Together with the carbon specific respiration ( $R$ ) it affects the area specific respiration ( $R_a = RD$ ) which, as shown above, is a key factor for the carbon balance per unit area and thus for  $I_c$ . However,  $D$  also regulates the specific gross growth rate [net growth plus respiratory losses, mol C (mol cell C)<sup>-1</sup> d<sup>-1</sup>] attainable for a certain carbon surplus per unit area. Though light absorption, and thereby carbon fixation, increases to some extent with  $D$  (Markager in press), the specific gross growth rate will decline in direct proportion to  $D$  for a constant carbon fixation rate per unit area. This is the situation because the variation in  $D$  is much larger (15-fold in this experiment) than the variation in light absorption

(2-fold here). Therefore, macroalgae will show an inverse relationship between light limited gross growth rate and  $D$  as depicted in the 4 examples in Fig. 3. For leathery algae (1, Fig. 3) growing to a maximum depth of 0.5 % SI, calculated gross growth rate approaches 2 mmol C mol<sup>-1</sup> C d<sup>-1</sup> when the thallus specific carbon reaches 4.4 mol C m<sup>-2</sup>. This gross growth rate exceeds dark respiration rates in some thick species and allows a low, but not unrealistic, specific growth rate. For example, the dark respiration rate of *Chondrus crispus* was only 0.5 mmol C mol<sup>-1</sup> C d<sup>-1</sup>. For an alga living at 0.10 % SI (2, Fig. 3) a thallus specific carbon content of 4.4 mol C m<sup>-2</sup>, however, will provide an unacceptable low growth rate. The  $D$ -value yielding a gross growth rate of 2 mmol C mol<sup>-1</sup> C d<sup>-1</sup> is 0.69 mol C m<sup>-2</sup> at this % SI. At even lower light, e.g. 0.01 % SI (3, Fig. 3),  $D$  must be lower than 0.05 mol C m<sup>-2</sup> before gross growth rate exceeds 2 mmol C mol<sup>-1</sup> C d<sup>-1</sup>. The upper level of  $D$ -values in 1 and 2 (Fig. 3) corresponds to that for leathery and foliose algae found in this study. A  $D$ -value of 0.05 mol C m<sup>-2</sup> for crustose algae is higher than the value calculated from Littler et al. (1986), which, however, represents an exceptionally deep living species. At higher light levels crustose algae may be thicker, such as

*Peysoneilia* sp. (a fleshy crustose algae) found to have its depth limit above the deepest occurring calcified crustose red algae (Agegian & Abbott 1985, Littler et al. 1985). Other data for thallus specific carbon in crustose macroalgae are not available. The last curve (4, Fig. 3) is for an alga living at great depths with only 0.0005 % SI at a latitude receiving a mean light intensity of 550 μmol m<sup>-2</sup> s<sup>-1</sup> at the sea surface (24° N), the conditions for the deepest occurring crustose in Littler et al. (1985). This species should, for a  $D$ -value of 0.0087 mol C m<sup>-2</sup>, be able to attain a gross growth rate of 1.2 mmol C mol<sup>-1</sup> C d<sup>-1</sup> (absorption by photosynthetic active pigments assumed to be 0.45 and quantum yield to be 95 mmol C mol<sup>-1</sup> photons). Dark respiration of this species must, therefore, be very low. Assuming a dark respiration rate as for *C. crispus* in this experiment (0.5 mmol C mol<sup>-1</sup> C d<sup>-1</sup>) the net growth rate will be 0.7 mmol C mol<sup>-1</sup> C d<sup>-1</sup> corresponding to a generation time of 3 yr. Survival at such a low growth rate is only possible in a stable environment with practically no grazing achieved by thallus calcification or lack of grazers.

The examples in Fig. 3 are based on the different morphological types, their mean depth limits obtained from Table 4 and realistic values for absorption and quantum yield from

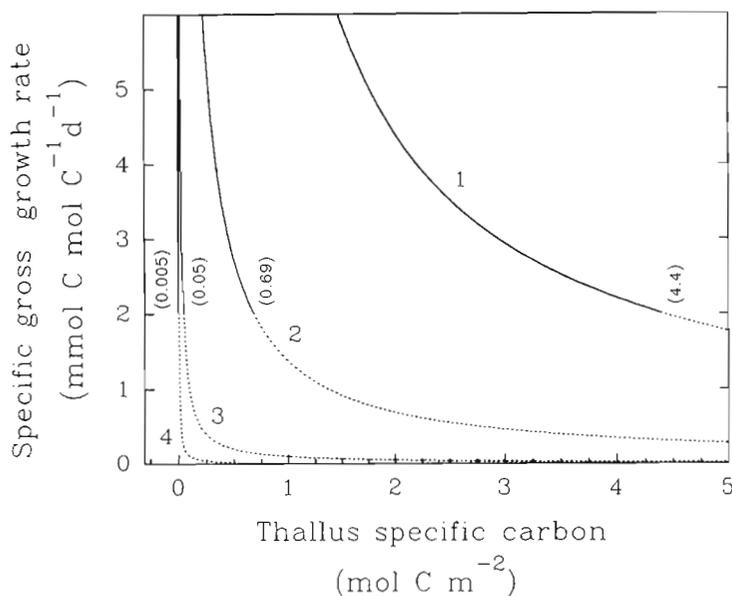


Fig. 3. Relationship between thallus specific carbon and specific gross growth rate at 4 combinations of light intensity and absorption. (1) A leathery alga living at 0.5 % SI, light absorption = 0.9; (2) A foliose alga living at 0.10 % SI, light absorption = 0.7; (3) A crustose algae living at 0.01 % SI, light absorption = 0.5; (4) A crustose alga living at 0.0005 % SI, light absorption = 0.45. Mean surface light (SI) was 238 μmol m<sup>-2</sup> s<sup>-1</sup> in examples 1 to 3 corresponding to Danish conditions (56° N) and 550 μmol m<sup>-2</sup> s<sup>-1</sup> in example 4 corresponding to conditions at Bahamas Islands (24° N). Quantum yield was in all cases assumed to be 95 mmol C mol<sup>-1</sup> absorbed photons. The thallus specific carbon where gross growth rate drops below 2 mmol C mol<sup>-1</sup> cell C d<sup>-1</sup> is indicated

Table 1. Values for  $D$ , where gross growth rates drop below  $2 \text{ mmol C mol}^{-1} \text{ C d}^{-1}$  are indicated. This level of gross growth rate allows a low positive net growth for species with a dark loss rate corresponding to the lowest experimentally derived dark respiration rates in Table 1. The indicated  $D$ -values are the maximum possible in each case, but for leathery and foliose algae, they correspond to measured values of  $D$  for these groups. We therefore conclude that Fig. 3 provides a realistic picture of possible combinations of depth limits, respiratory losses and net growth rates of marine macroalgae at low light.

The curves in Fig. 3 predict that thin thalli (i.e. low thallus specific carbon) ensure higher specific growth rates at light limitation than thick thalli. The crustose life form represents the most extreme adaptation and the most suitable multicellular thallus with low thallus specific carbon. Thick thalli, on the other hand, provide several advantages at high light such as greater mechanical strength, ability to form a canopy and shade-out competitors, better possibility for differentiation of cells and storage of carbohydrates and nutrients as exemplified by *Laminaria* species (Lüning 1971, Chapman & Lindley 1980). Thallus specific carbon, therefore, becomes an important part of the physiological features regulating vertical zonation and growth strategies of subtidal marine macroalgae. Low growth rate at low light also means that deep-living algae need long time to form the biomass. Accordingly, the proportion of perennial species increases with depth (Mathieson 1979).

In Danish coastal regions *Porphyra purpurea* and the erect form of *Petalonia fascia* only grow in shallow water (0 to 1.5 m) whereas the other 3 species occur in most of the subtidal zone with erect macroalgal vegetation except for the deepest parts where vegetation is dominated by *Phycodrys rubens* and *Delesseria sanguinea*. Because the 5 species had approximately the same light requirements for survival in our laboratory experiments the differences in depth-zonation must be related to their growth form/strategy. *Porphyra purpurea* and *Petalonia fascia* are probably restricted to very shallow water due to their annual lifecycle and *Fucus serratus* and *Chondrus crispus* are probably excluded from the deepest parts due to their thick thallus. However, additional experiments are needed on the physiology of particularly deep-living species and on actual loss rates in the field for different species, to further evaluate the parameters that determine macroalgal depth zonation.

We conclude that macroalgal growth and survival in low light require high photosynthetic efficiency at low light, low dark respiration rate, low thallus specific carbon, resistance against grazing, and possibly a perennial life cycle. High quantum yield and high

photosynthetic efficiency seem to be common among most species. Dark respiration rates, on the other hand, can vary over 2 orders of magnitude ( $0.5$  to  $30 \text{ mmol C mol}^{-1} \text{ C d}^{-1}$ , half-life of the carbon content at 1386 and 23 d respectively) but even at the lowest respiration rates, low thallus specific carbon (i.e. a thin thallus) is essential for growth at low light.

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