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Importance of light for the formation of algal blooms by *Emiliania huxleyi*

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ABSTRACT: A review of natural bloom and mesocosm data for *Emiliania huxleyi* suggests a connection between bloom formation, shallow mixed layers and high light intensities. But how does *E. huxleyi* differ from other algae in its response to light, and what is the cause of the competitive advantage at high light intensities? In this article, *P-I* curves for calcified, naked and de-calcified cultures of *E. huxleyi* are presented. The experimental results show that a lack of photoinhibition in *E. huxleyi* up to at least 1000 µEin m^{-2} s^{-1} may contribute to the dominance of this species at high light intensities, and that this lack of photoinhibition is *not* due to the presence of reflective coccoliths around the cell.

KEY WORDS: *Emiliania huxleyi* · Photosynthesis *P-I* curves · Photoinhibition · Stratification · Phytoplankton ecology

INTRODUCTION

Emiliania huxleyi is a unicellular marine algal species capable of generating vast blooms in the open ocean, with cell concentrations of up to 10000 cells ml^{-1} (Holligan et al. 1993a), and areal extents of more than 100000 km^2 (Brown & Yoder 1994). These blooms are climatically important due to the emission of dimethylsulphide (DMS) and to the production of organic and inorganic carbon, the latter in the form of large numbers of minute plates of calcium carbonate (coccoliths) (Westbroek et al. 1993). Coccoliths are attached to cells initially, but detach in low numbers during growth (Balch et al. 1993, Bleijswijk et al. 1994b) and in high numbers during the senescent phase of a bloom (Westbroek et al. 1993). Free coccoliths can occur in concentrations of up to 300000 coccoliths ml^{-1} in the open ocean (Holligan et al. 1993a).

For the purpose of predicting future environmental impacts of these blooms it is necessary to understand the factors causing them; i.e. which biological, chemical and/or physical properties of the water are influential in causing a bloom of *Emiliania huxleyi* to develop? A survey of literature on these blooms in the field (where a bloom is defined as a cell concentration exceeding 1000 cells ml^{-1}) reveals a common hydrographic feature associated with all known blooms of *E. huxleyi*: they all occur in highly stratified water where the mixed layer depth is usually ~10 to 20 m, and is almost always ≤30 m. This assertion holds true for blooms in the Gulf of Maine (Townsend et al. 1994), in the North Atlantic (Holligan et al. 1993a, Malin et al. 1993), in the North Sea (Holligan et al. 1993b, Wal et al. 1995), off the Scilly Isles (to the west of the English Channel) (Garcia-Soto et al. 1995), in the Southern Benguela Upwelling (Mitchell-Innes & Winter 1987), and in the Norwegian fjords (Braarud 1945, Birkenes & Braarud 1952, Berge 1962, Braarud et al. 1974, Paasche & Kristiansen 1982, Kristiansen et al. 1994). Stratification occurs together with *E. huxleyi* in the northern and central North Sea, whereas stratification does not usually occur in the southern North Sea and neither does *E. huxleyi* (Houghton 1991, Holligan et al. 1993b). However, an exception to the general pattern was encountered in the Celtic and Armorican shelf

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region (Holligan et al. 1983), where *E. huxleyi* was observed to be present in bloom proportions at depths up to 60 m, albeit with the greatest cell concentrations nearest to the surface. In the Skagerrak, a bloom of *E. huxleyi* (Pingree et al. 1982) was detected in a sub-surface thermocline layer, but the layer was fairly close to the surface (from 10 to 15 m depth). In another case (Kristiansen et al. 1994), cell concentrations of *E. huxleyi* were ≥1000 cells ml^{-1} from the surface down to nearly 20 m, but concentrations were significantly greater at a depth of about 10 m than at shallower depths. In contrast, similar concentrations of other phytoplankton species can occur in deeper mixed layers with a depth of 75 m or more (e.g. Braarud 1945; Williams 1974, Fig. 51; Williams & Hopkins 1976, Fig. 64).

The most likely reason for *Emiliania huxleyi* being able to out-compete other phytoplankton in stratified waters (surface waters in which the phytoplankton are continually kept very near to the surface) is a competitive advantage at higher light levels. If a non-motile phytoplankton cell is mixed evenly through the depth of the mixed layer, with an equal probability of being at any depth in the mixed layer at any moment in time, then the average light intensity (I_{av}) that it will experience is given by

$$I_{av} = \frac{1}{H}\int_0^H \{I_0 \cdot e^{-K_d \cdot z}\}dz = \left(\frac{I_0}{K_d \cdot H}\right)\{1.0 - e^{-K_d \cdot H}\} \quad (1)$$

where H is the depth of the mixed layer, I_0 is the irradiance intensity immediately below the water surface, z is depth and K_d is the vertical attenuation coefficient for the water. This assumes an exponential decay of light with depth which is only an approximation to the real case. A fairly typical oceanic value of K_d for photosynthetically active radiation (PAR) is 0.1 m^{-1} (Kirk 1994), and this value is a reasonable estimate of the mean K_d value for the North Atlantic and the seas around northern Europe (Simonot & Le Treut 1986), where *E. huxleyi* is most prevalent (Brown & Yoder 1994). This value of K_d relates to changes in the average light intensity with mixed layer depth as shown in Table 1.

Table 1. Example attenuation of average light in a surface mixed layer (I_{av}/I_0) against depth of the mixed layer (H), when the vertical attenuation coefficient (K_d) for the water is 0.1 m^{-1}

	H (m)							
	5	10	15	20	30	50	100	200
I_{av}/I_0 (%)	79	63	52	43	32	20	10	5

The average light intensity impinging on the circulated cells is therefore critically dependent on the mixed layer depth. Phytoplankton species which are evolutionarily adapted for high light levels will prosper when mixed layer depths are shallow. Such species would also be more likely to bloom in summer than winter months. Analysis of satellite images in the NE Atlantic south of Iceland shows that *Emiliania huxleyi* blooms in this region are most common in June and July (S. Groom pers. comm.; Brown & Yoder 1994, Fig. 5A), when mixed layer depths are shallow and surface irradiances are high. Blooms in the Norwegian fjords typically occur during May to August. While other factors (e.g. the nutrient status of the water) must also be important in determining the competitiveness of *E. huxleyi* [because *E. huxleyi* does not always bloom when the water is stratified and surface illumination is high (e.g. Joint & Pomroy 1986)], from the close correlation between blooms and stratification it seems as if high light is an essential, although not a sufficient, requirement for bloom formation.

Large concentrations of coccoliths increase the scattering of light in the water (Balch et al. 1991, 1996, Holligan et al. 1993a), and thereby cause an increase in the attenuation of light. At first sight it therefore seems as if the production of coccoliths by *Emiliania huxleyi* curtails its own success, if the species is indeed high light dependent. It could be suggested that this process is evidence against the 'high light hypothesis' for *E. huxleyi*. There are several counters to this argument though: (1) increased light attenuation also leads to increased stratification and more stable stratification, due to a decreased heating of deeper waters compared to surface waters (Kirk 1988, Sathyendrenath et al. 1991); (2) rapid attenuation of light will starve the thermocline of light, and may prevent the establishment of high concentrations of phytoplankton in the thermocline (P. M. Holligan pers. comm.), which could otherwise intercept the upwards flow of nutrients from below and starve the surface phytoplankton of nutrients (e.g. Taylor et al. 1986); and (3) destruction of its own niche, if indeed that occurs, may be compatible with kin selection (Hamilton 1964).

Alternative explanations of a preference for shallow mixed layers, in terms of temperature, salinity, and nutrient depletion are considered less convincing *Emiliania huxleyi* is known to be successful across a wide range of temperatures and salinities (Winter et al. 1994). Mesocosm experiments in the Norwegian fjords (Egge & Heimdal 1994) have shown that *E. huxleyi* blooms can occur at both low and high concentrations of phosphate and nitrate (see Fig. 1). In these experiments a natural assemblage of phytoplankton was introduced into mesocosm enclosures at the beginning of each experiment, and therefore many species were

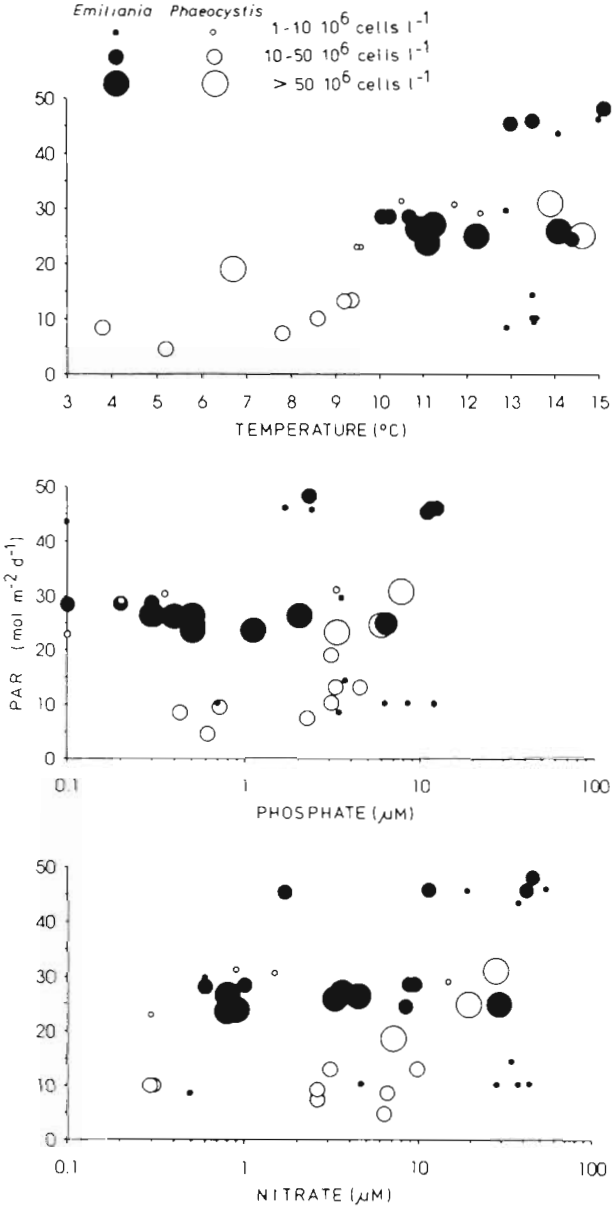

Fig. 1 Populations of *Emiliania huxleyi* and *Phaeocystis* sp. (other species not shown) in enclosure experiments during 1988–1992. Effects of surface irradiance (PAR, mol m^{-2} d^{-1}), temperature (°C), phosphate (µM kg^{-1}) and nitrate (µM kg^{-1}) on the dominance of the 2 species are illustrated. The light intensities (in mol m^{-2} d^{-1} = Ein m^{-2} d^{-1}) are 5 day averages, calculated by summing hourly averages of instantaneous light values throughout the day to obtain 24 h totals, and then averaging back over the 5 days before the bloom maximum to calculate a 5 day average (J. K. Egge pers. comm.). Assuming 12 h of daylight per day, 23 Ein m^{-2} d^{-1} is equivalent to ~530 µEin m^{-2} s^{-1}
Taken from (Egge & Heimdal 1994) with permission

present even though only the concentrations of *E. huxleyi* and *Phaeocystis* sp. are shown in the figure. The mesocosm experiments also give additional evidence to support a 'high light hypothesis' for *E. huxleyi*. This line of evidence is not tied to mixed layer depth: the mesocosms had a constant depth of 4 m, which was kept fully stirred throughout the duration of the experiments, and so there were no variations in mixed layer depth to cause variations in light intensity. Fig 1 shows the distribution of *E. huxleyi* population sizes against various environmental parameters (Egge & Heimdal 1994). In all 3 graphs the most striking correlation is between *E. huxleyi* cell concentration and light intensity, with *E. huxleyi* only blooming with surface light intensities of greater than ~23 Ein m^{-2} d^{-1} (~530 µEin m^{-2} s^{-1}). There is also a correlation with temperature in Fig. 1. However, light and temperature are not independent in the shallow mesocosms, and it is most likely that the apparent correlation between temperature and *E. huxleyi* success is a side effect of an actual correlation between light and *E. huxleyi* success.

If, as seems to be the case, *Emiliania huxleyi* has a competitive advantage at high light levels then it is interesting to investigate the underlying reason for this advantage. Two possible explanations are investigated in this paper: (1) that the light intensity at which the maximum photosynthetic rate is reached is increased due to the presence of coccoliths around the exterior of the cells; and (2) that there is an absence of photoinhibition in *E. huxleyi* at high light levels.

The competitive advantage of *Emiliania huxleyi* at high light could also be explained by enhanced rates of photoadaptation (Lewis et al. 1984), for instance if *E. huxleyi* is able to adjust its chlorophyll content more rapidly than other species, and fast enough to keep in step with the changing light intensity due to being circulated within the mixed layer. However, photoadaptive differences do not seem to be a plausible explanation of the high light success of *E. huxleyi* in the mesocosm experiments [the mesocosms were of a constant depth and were mixed at a constant rate using a pump (Egge & Heimdal 1994)], and for this reason photoadaptation will not be considered further here.

METHODS

Organism and cultivation conditions. An axenic calcifying culture of *Emiliania huxleyi* clone BOF92 was kindly provided by Prof. E. Paasche (University of Oslo, Norway), who started this clone by single-cell reisolation from isolate 5/90/25j. Isolate 5/90/25j was obtained by J. C. Green from the Atlantic at 48° N, 17° W in May 1990. From the clone BOF92 a non-calcifying culture was obtained after prolonged cultivation in Eppley medium (Eppley et al. 1967). The calcifying culture was maintained in F/25 medium. F/25 medium is identical to Eppley medium except for the added

amounts of KNO_3 and K_2HPO_4, which are 25 times less for both compounds.

For the photosynthesis experiments cells were used from batch cultures in the exponential phase of growth. The calcifying culture was grown in F/25 and in Eppley medium. The non-calcifying culture was grown in Eppley medium. The batch cultures had a volume of 200 ml, were incubated in conical flasks (500 ml), bubbled with humid sterile air (1.4 l h^{-1}), and were kept at pH 8.1 ± 0.3 and 18°C. The conical flasks were placed on a glass plate just above the light source (Philips TL tubes, cool-white, colour 33). The incident light intensity was 200 µEin m^{-2} s^{-1} for 24 hours per day. The cultures were illuminated continuously to prevent synchronous cell division as the latter may affect the results when photosynthesis rates are related to cell numbers. Prior to the estimation of the photosynthesis rates the 3 cultures were treated as follows. First the pH was measured. The pH of the non-calcifying culture (culture B) was 8.18 and not modified. The calcified culture in F/25 medium had a pH of 7.82 and was divided into 2 aliquots. In one aliquot (culture A) the pH was adjusted to 8.2. In the other aliquot (culture C) first the coccoliths were dissolved by lowering the pH with HCl to a value of 5.0 for a period of 3 min, followed by readjustment with NaOH to a pH of 8.2. The dissolution of all extracellular coccoliths was checked by microscopy and analyses of particulate calcium. The pH of the calcified culture in Eppley medium (culture D) was 7.98 and adjusted to 8.2. After pH measurement/modification cultures A, B, C and D were incubated on a gyratory shaker at 18°C and a low light intensity (10 to 20 µEin m^{-2} s^{-1}) during 2, 3.5, 5 and 7 h, respectively.

Analyses. Photosynthesis versus irradiance (*P-I*) curves were monitored using a Clark-type polarographic oxygen electrode according to Dubinsky et al. (1986). In these photosynthesis experiments algae were incubated into a stirred, thermostated PVC chamber and irradiated with a collimated light beam from a tungsten light source which was attenuated to the desired light intensities by a series of nickel screens. Thus the light beam passed successively a nickel screen, a lens of colourless glass, a thin layer of colourless glass, a layer of approximately 1 cm clear water (the thermostated compartment for cooling), and again a layer of thin colourless glass before entering the compartment with the algae. The intensity of light leaving the compartment with algae, through a thin colourless glass layer at the back side, was measured and used as the value for the light intensity in the algal compartment. To obtain the total oxygen production rates the oxygen consumption rate in the dark (due to algal respiration and oxygen uptake by the electrode) was determined and added to the detected oxygen production rate under light conditions.

Intensities of PAR were measured with a quantum radiometer photometer (Licor, Lincoln, NE, USA, model LI-189, equipped with a quantum sensor type LI-190 SB).

For analyses of particulate calcium, cells and coccoliths were collected on membrane filters (type HVLP, 0.45 µm pore size, Millipore Co, Bedford, MA, USA) and rinsed with 1 M $(NH_4)_2CO_3$. Subsequently, the filters were incubated in 20 ml 0.5 M HNO_3 to extract the calcium. The concentration of calcium in the HNO_3 solution was determined in an atomic absorption spectrophotometer (Paasche & Brubak 1994).

The pH of algal cultures was determined with a glass-electrode calibrated with (low ionic) buffer solutions from Merck (Darmstadt, Germany, art. no. 12052). The protein contents of cultures were assayed according to Lowry et al. (1951). Cell numbers were determined in a Bürker haemocytometer with a depth of 0.100 mm. To determine the presence of coccoliths at the surface of cells a light microscope with cross-polarised illumination was used.

RESULTS

Photosynthesis rates were determined for the following cell suspensions of *Emiliania huxleyi*:

A — untreated calcified cells grown in F/25 medium,

B — untreated non-calcified cells grown in Eppley medium,

C — acid-treated originally calcified cells grown in F/25 medium,

D — untreated calcified cells grown in Eppley medium.

From each of these cultures the cell number, % of non-calcified cells, protein content and particulate calcium were measured (Table 2). In cultures A and D the calcified cells were usually covered with 1 layer of coccoliths. Furthermore, culture A and especially culture D contained a large number of free coccoliths. The total amount of coccoliths can roughly be calculated from the average calcium content of a single coccolith which is 0.67 pg (Fagerbakke et al. 1994). Thus 1.4 and 2.6 mg particulate calcium l^{-1} is equal to 2.1×10^6 and 3.9×10^6 coccoliths ml^{-1}, respectively. Of the acid-treated cells 4% had 1 or 2 coccoliths. These coccoliths were formed during the 5 h incubation period between acid treatment and analysis of the photosynthesis rate. The protein content was measured to make it possible to relate the photosynthesis rates to the cellular protein content. From Table 2 it is also evident that the cellular protein content of the cells grown in Eppley medium (B and D) exceeded that of cells grown in F/25 medium. Therefore, the protein content is not a suitable parameter to relate photosynthesis rates to, when cells cul-

Table 2. *Emiliania huxleyi*. Data of the cultures used for photosynthesis measurements: (A) calcified culture on F/25; (B) non-calcified culture on Eppley; (C) decalcified culture on F/25; and (D) calcified culture on Eppley

Culture	Cells (ml^{-1})	Protein content ($mg\ l^{-1}$)	Cells with no liths (%)	Particulate calcium ($mg\ l^{-1}$)
A	3.9×10^5	1.7	15	1.4
B	7.5×10^5	5.2	98	<0.1
C	3.9×10^5	1.7	96	<0.1
D	3.8×10^5	2.4	26	2.6

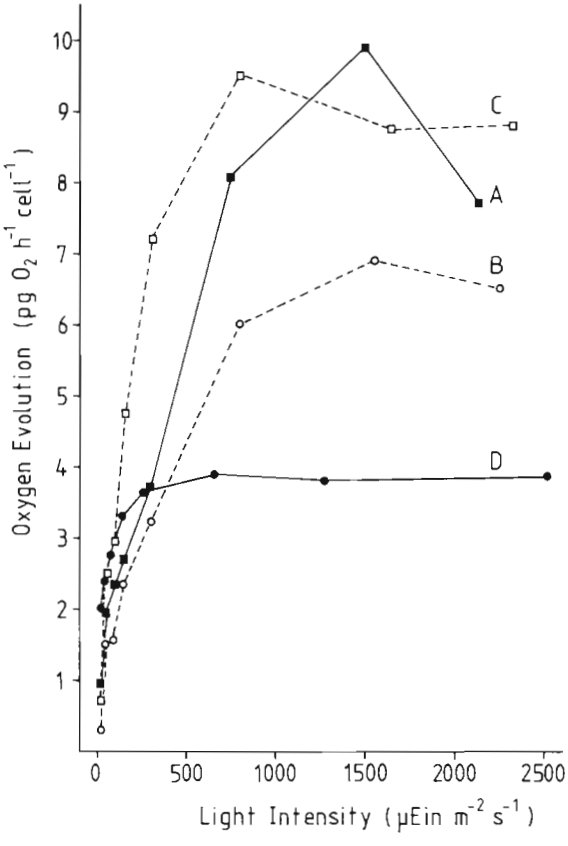

Fig. 2. Photosynthesis (oxygen evolution) versus light intensity for *Emiliania huxleyi*, with and without coccoliths, and cultivated in Eppley or F/25 medium. (■) A, untreated calcified cells (F/25); (○) B, untreated non-calcified cells (Eppley); (□) C, acid de-calcified cells (F/25); (●) D, untreated calcified cells (Eppley)

tivated in Eppley medium and in F/25 medium are to be compared.

The *P-I* curves of the 4 cultures are shown in Fig. 2. The rate of photosynthesis is measured as an oxygen production rate. For all cultures the maximal rate of photosynthesis is achieved at light intensities above 500 μEin m^{-2} s^{-1}. The value of the maximal rate of photosynthesis (P_{max}) varies considerably. The value of P_{max} will depend on several factors such as pigment content, velocity of photochemical electron transport and availability of nutrients (Darley 1982, Dubinsky et al. 1986, Post et al. 1989). Differences in the values of these parameters among the 4 batch cultures may be responsible for the differences in P_{max} and may also influence the light intensity at which the maximal photosynthetic rate is reached. The 2 cultures in F/25 medium exhibited higher P_{max} values than the 2 cultures in Eppley medium, but the difference may just have been due to experimental variation. A separate control experiment (results not included) showed that the acid treatment used to decalcify the cells in culture C had little or no effect on the *P-I* curve obtained. At high light intensities, up to at least 1000 μEin m^{-2} s^{-1}, there was no photoinhibition in any of the cultures.

DISCUSSION

Ecological implications

As mentioned earlier, one hypothesis to account for the success of *Emiliania huxleyi* in shallow mixed layers has been related to the light-scattering coccoliths surrounding the cell as this might provide protection from the harmful effect of high light intensities (Lohmann 1913, Braarud et al. 1952, Berge 1962). At high light intensities 2 possible effects of coccoliths can be distinguished. The first involves the light intensity at which P_{max} is reached (I_{sat}). If coccoliths acted as 'protective light screens' then calcified cells would possess a higher I_{sat}. The results just described indicate that this hypothesis is not correct, and confirm a conclusion reached in earlier work that '...coccoliths do not act as protective light screens...' (Paasche & Klaveness 1970).

The second effect concerns photoinhibition at light intensities beyond I_{sat}. Many species of phytoplankton start to experience light saturation at ~400 to 500 μEin m^{-2} s^{-1} (PAR), and then at higher light intensities the photosynthetic rate declines due to photoinhibition. This decline can be rather drastic, for example with the photosynthetic rate of natural assemblages decreasing to 80% of P_{max} at 1000 μEin m^{-2} s^{-1}, and then to 60% of P_{max} at 1500 μEin m^{-2} s^{-1} (Kirk 1994, Fig. 10.1; see also Platt et al. 1980). However, it is apparent from Fig. 2 that photoinhibition does not occur for *Emiliania huxleyi* until light intensities greater than 1000 to 1500 μEin m^{-2} s^{-1} are attained, and even at such high intensities the photoinhibition is not at all pronounced. The importance of photoinhibition in nature is fre-

quently ignored, but 'The inhibition of photosynthesis at high light intensities must be taken into account in ecological studies, since the intensities typically experienced in the surface layer of natural waters in sunny weather are in the range that can produce photoinhibition' (Kirk 1994, p. 284). In oceanic water a large part of photoinhibition may be attributed to UV light (Kirk 1994, p. 286). Yellow pigments in particular provide protection against UV light and yellow pigments have indeed been detected in *E. huxleyi* (Kraay et al. 1992). In addition, *in situ* phytoplankton assemblages have been shown to be more susceptible to photoinhibition at higher latitudes such as 60° N (Harrison & Platt 1986), where blooms of *E. huxleyi* are most usually found (Brown & Yoder 1994). The theoretical maximum downwelling light intensity that can be encountered in the field (immediately below the sea-surface from an overhead sun unobscured by cloud and coming through a dry, clean atmosphere) is ~2000 µEin m^{-2} s^{-1} (PAR), although in practice values of greater than 1500 µEin m^{-2} s^{-1} are only rarely encountered (Kirk 1994). Using Eq. (1), if I_0 is 1500 µEin m^{-2} s^{-1} then the average light intensity in a mixed layer of 15 m depth (K_d = 0.1 m^{-1}) is ~780 µEin m^{-2} s^{-1}. This is compatible with the observation that *E. huxleyi* frequently occurs in mixed layers of ~15 m depth, and that other phytoplankton start to experience photoinhibition at ~400 to 500 µEin m^{-2} s^{-1}. A cruise in 1994 measured in-water scalar light intensities of up to 950 µEin m^{-2} s^{-1} in a bloom of *E. huxleyi* in a Norwegian fjord (depth = 2.5 m, *E. huxleyi* present at >11000 cells ml^{-1}), and of up to 1140 µEin m^{-2} s^{-1} in a bloom of *E. huxleyi* in the North Sea (depth = 2.25 m, *E. huxleyi* present at >5000 cells ml^{-1}) (Runar Dalløkken unpubl. data). The

Table 3. *Emiliania huxleyi*. Summary of experimentally derived *P-I* curves. The columns in the table are (from left to right): (1) reference: used as source of information; (2) I_{sat}: the light intensity at which the maximum *y*-axis value in the *P-I* curve is first obtained (µEin m^{-2} s^{-1}); (3) photoinhibition: whether it was encountered at the light intensities used, and if so then the light intensity at which photoinhibition started to take effect (µEin m^{-2} s^{-1}); (4) *y*-axis: the entity represented by the *y*-axis of the *P-I* curve (growth as no. of doublings d^{-1}, photosynthetic carbon uptake or photosynthetic oxygen evolution); (5) temperature (°C) at which the experiment was carried out; (6) medium, the nutrient medium used (non-std: non-standard); (7) I_{accl}: the light intensity to which the cultures were acclimatised before the experiment (µEin m^{-2} s^{-1}) (na signifies not applicable for *in situ* and growth experiments); and (8) strain and place of origin

Source	I_{sat}	Photoinhibition?	*y*-axis	Temp.	Nutrient	I_{accl}	Strain, place of origin
Mjaaland (1956)	150[a]	Yes (400[a])	Growth	18.0	'Soil extract'	na	PML P3
Paasche (1963)	85[a]	No (up to 144[a])	C uptake	18.5	Non-std	62[a]	Oslo fjord
Paasche (1964) (2 curves)	110[a] or 150[a]	No (up to 360[a])	C uptake	18.5	Non-std	36[a]	F402 Oslo fjord
Paasche (1967) (4 curves)	240–300[b]	Some (300[b])	Growth	21	Non-std	na	Oslo fjord
Paasche & Klaveness (1970) (3 curves)	150[a]	No (up to 170[a])	C uptake	21	Eppley	230[a]	*F*
Brand & Guillard (1981) (2 curves)	320–740[b]	No (up to 740[b])	Growth	21	F/2	na	A47 (Brand), Sargasso Sea
Balch et al. (1992) (2 curves)	700 or ≥1600	No (up to 1600)	C uptake	15	F/50 + 2 µM NO_3	1160	Bigelow 88E, Gulf of Maine
Balch et al. (1992)[c]	900	No (up to 1600)	C uptake	*In situ*	*In situ*	na	*In situ*, 2 m depth, Gulf of Maine
Fernandez et al. (1993)[c] (4 curves)	600	Some (900)	C uptake	?	*In situ*	na	*In situ*, NE Atlantic
(Holligan et al. (1993a)[c]	250	Yes (600)	C uptake	?	*In situ*	na	*In situ*, NE Atlantic
Nimer & Merrett (1993)	400	No (up to 500)	C uptake	15	Non-std	50	Bigelow 88E
Nimer & Merrett (1993)	400	No (up to 500)	O_2 evol.	15	Non-std	50	Bigelow 88E
Bleijswijk et al. (1994a) (2 curves)	70	No (up to 150)	Growth	10	Non-std	na	Ch24-90, Ch25-90 North Sea
Nielsen (1995) (6 curves)	300	No (up to 300)	O_2 evol.	15	Non-std	80	Plymouth B 92/317
This study (4 curves)	500–1000	No (up to 1000)	O_2 evol.	18	Eppley or F/25	200	BOF92, NE Atlantic

[a]Assumes a conversion factor of 1000 lux = 12.0 µEin m^{-2} s^{-1} (LI-COR calibrations)
[b]Assumes a conversion factor of 1.0 cal. cm^{-2} min^{-1} = 1.0 langley min^{-1} = 3210 µEin m^{-2} s^{-1} (LI-COR calibrations)
[c]Ship-board experiments with *in situ* phytoplankton samples

Charles Darwin cruise no. 60 in 1991 measured in-water downwelling light intensities of up to 935 µEin m^{-2} s^{-1} in a bloom of *E. huxleyi* at 63° N in the NE Atlantic (depth = 1 m, *E. huxleyi* present at ~10000 cells ml^{-1}) [Biogeochemical Ocean Flux Study (BOFS) North Atlantic Dataset CD-ROM].

The results in this paper suggest that *Emiliania huxleyi*'s lack of photoinhibition may be a critical aspect in which it is different from other algae. Coccoliths do not appear to prevent photoinhibition. Nevertheless, the light-scattering properties of coccoliths may be important for the success of *E. huxleyi*. In fact, coccoliths with a diameter of 1 to 2 µm, as is the case for *E. huxleyi*, appear to provide more scattering per unit weight than smaller or larger coccoliths (Balch et al. 1996), and their size may therefore be the result of an evolutionary selection pressure towards greater scattering. This highly efficient scattering causes a decrease in the penetration of light and heat into the depths of the water (Holligan et al. 1993a), concentrating the heat near the surface of the water (Holligan & Balch 1991), where it contributes to establishing and maintaining shallow stratification (Simonot et al. 1988). In addition, the rapid attenuation of light could be important for the upwards flow of nutrients as explained in the introduction. Thus, the production of coccoliths may be important in establishing and maintaining the niche of *Emiliania huxleyi*. This can be compared with e.g. the formation of H_2S by sulphate-reducing bacteria in marine sediments. The production of H_2S contributes to the maintenance and extension of an anoxic area with a redox potential optimal for growth of sulphate-reducing bacteria (Postgate 1984). Another example concerns lactic acid bacteria which can lower the pH of their environment by the production of lactic acid. As lactic acid bacteria possess a high tolerance for acid, the production of lactic acid enables them to eliminate competition from most other bacteria in environments that are rich in nutrients (Stanier et al. 1976).

Comparisons with previous work

The high light intensities for photosynthetic saturation in *Emiliania huxleyi*, as measured in this study, are higher than those obtained in many previous experiments (Table 3, column 2), but this may in part be due to differences in methodology. One important factor may be the light intensity at which the cultures are grown. In this study this light intensity was 200 µEin m^{-2} s^{-1}, but in other studies lower light intensities were often applied (column 7). Another factor may be whether growth (cell doublings) or carbon uptake/oxygen evolution were measured (column 4), since the two may not always be coupled (Zevenboom & Mur 1984, Banse 1994). The temperature at which the experiments are carried out is also crucial (column 5), as is the nutrient media used (column 6).

The high I_{sat} values and lack of photoinhibition obtained here are compatible with some of the previous experiments, especially the more recent ones (Table 3, columns 2 and 3). The highest growth rates ever measured for *Emiliania huxleyi* (2.6 and 2.8 doublings d^{-1}) were obtained at high light intensities of 760 and 740 µEin m^{-2} s^{-1} (Brand & Guillard 1981, Brand 1982), higher than the light intensities used in previous growth experiments. The high saturating light intensity indicated by the experiments in this paper is relevant for future laboratory studies of this species. In the past it has been assumed that light values of as little as 100 µEin m^{-2} s^{-1} are saturating for *E. huxleyi*, but this may well not be the case.

CONCLUSIONS

P-I curves have been derived for calcified, non-calcified and decalcified cultures of *Emiliania huxleyi*. Comparing these *P-I* curves revealed that the lack of photoinhibition in *E. huxleyi* at light intensities up to 1000 or 1500 µEin m^{-2} s^{-1} is *not* due to reflection of light away from the cells by coccoliths. This absence of photoinhibition may contribute to the dominance of *E. huxleyi* in surface waters of the ocean when mixed layer depths are shallow.

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