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Emiliania huxleyi population growth rate response to light and temperature: a synthesis

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ABSTRACT: The relationship between the maximum specific growth rate (μ, d^{-1}) of the coccolithophore *Emiliania huxleyi* and photon flux density (PFD, μmol photons m^{-2} s^{-1}) was quantified using a combination of quantile regression and culture experiment data from the literature (n = 1387). This relationship, used in ecosystem models incorporating *E. huxleyi* or coccolithophores as a functional group, is often assumed to follow a Monod function although values for the model parameters vary greatly. In this analysis, a Monod function was compared with other models to determine the model which best fit *E. huxleyi* growth rate data. Analysis showed that a Monod model of μ = 1.858 [PFD/(23.91 + PFD)] best described *E. huxleyi* maximum growth rate as a function of PFD. In addition, an expression combining the Monod function (this study) and the power function relating growth rate to temperature (Fielding 2013; *Limnol Oceanogr* 58:663–666) was calculated: when both temperature (*T*, °C) and PFD are known, the resulting expression μ = (0.199 × $T^{0.716}$) × [PFD/(14.2 + PFD)] predicts maximum *E. huxleyi* specific growth rate. Current literature models either overestimate or underestimate maximum growth rate by up to 3-fold over a wide range of PFDs. The use of the Monod function and the combined expression presented here is therefore recommended for future models incorporating the growth rate of *E. huxleyi* when either light or both temperature and light are known.

KEY WORDS: Coccolithophore · Photon flux density · PFD · Temperature · Monod function · Quantile regression · Calcium carbonate · Literature review

INTRODUCTION

Coccolithophore algae are the major calcium carbonate producers in the ocean and are therefore fundamental for driving the inorganic carbon pump from the ocean's surface waters to the deep sea (Rost & Riebesell 2004). Coccolithophore calcium carbonate production also influences alkalinity and dissolved inorganic carbon concentration in the upper ocean (Zeebe & Wolf-Gladrow 2001). Additionally, coccolithophores, as members of the haptophyte algae, produce higher levels of intracellular dimethylsulfoniopropionate than most other algal groups (Keller 1988). Therefore, modelling and predicting the growth of marine coccolithophore algae is key to understanding them as a component of biogeochemical cycles (e.g. organic carbon, calcium carbonate, dimethylsulfide) and aquatic food webs.

In the present-day ocean, *Emiliania huxleyi* is the most numerically important species of coccolithophore (Paasche 2001). *E. huxleyi* has a near ubiquitous distribution, being found in environments ranging from estuarine to open ocean, and from ~81°N (Hegseth & Sundfjord 2008, Sukhanova et al. 2009) to ~61°S (Findlay & Giraudeau 2000, Bollmann et al. 2009). Additionally, *E. huxleyi* forms large blooms at temperate latitudes (Tyrrell & Merico 2004).

Recent attempts to determine factors controlling patterns of *E. huxleyi* (and other coccolithophore) distribution and ecology in the present-day ocean calculate growth rate as a function of major external bottom-up limiting factors, such as temperature, light and nutrients. This approach first relies on determining the model variables describing the maximum growth rate response to individual limiting factors.

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These responses can then be combined to give an expression describing growth rate variation in complex environmental scenarios.

Previously, the effect of temperature on marine phytoplankton maximum growth rate (Eppley 1972) has been objectively defined using quantile regression (Koenker & Bassett 1978) on a large heterogeneous dataset derived from culture studies (Bissinger et al. 2008). The effect of temperature on maximum potential growth rate has also been quantified for *E. huxleyi* using the same method (Fielding 2013). The majority (>90%) of the *E. huxleyi* dataset used by Fielding (2013) was derived from nutrient-replete cultures, making it unsuitable for determining the effect of nutrient limitation on growth rate in a similar way. However, these culture data were measured under a wide range of light intensities, allowing the effect of light on maximum growth rate to be estimated using quantile regression.

Light intensity in the ocean varies significantly with depth below the sea-surface. Incident photosynthetically active radiation (λ = 400 to 700 nm) measured as photon flux density (PFD) at the sea-surface varies both spatially and temporally but can be at least 2000 µmol photons m^{-2} s^{-1} (Kirk 1994, Frouin & Murakami 2007). Light is then attenuated with depth depending on factors such as turbidity. *E. huxleyi* grows in ocean environments with highly variable light intensity, with PFDs ranging from <10 µmol photons m^{-2} s^{-1} (Egge & Heimdal 1994, Cortes et al. 2001) up to surface irradiance values.

Model calculations of *E. huxleyi* and coccolithophore maximum growth rate as a function of PFD usually use the rectangular hyperbolic function after Monod (1949), where the maximum attainable growth rate (µ) at each PFD is described by

$$\mu = \mu_{opt} \times \frac{PFD}{K + PFD} \quad (1)$$

where μ_{opt} is the maximum growth rate at ∞PFD and K is the light half-saturation constant.

Sometimes a function incorporating inhibition of growth rate at high light intensities after Steele (1962) is used, where µ is described by

$$\mu = k \times \mu_{opt} \times PFD \times e^{1-k \times PFD} \quad (2)$$

where μ_{opt} is the maximum growth rate at the PFD which is optimal for growth rate and k is the initial slope of the curve at low light. The parameter values of these models are largely based on data from individual strains or from cultures grown under differing conditions even though models attempt to predict responses of natural populations which comprise diverse strain assemblages (Medlin et al. 1996). However, there is considerable intraspecific variation of *E. huxleyi* growth rate in relation to light intensity (Paasche 1999). Therefore, the suitability of current models for describing the maximum potential growth rate of *E. huxleyi* as a function of PFD in the ocean is not certain.

To better estimate parameters for models describing growth rate as a function of PFD for *E. huxleyi*, I applied quantile regression (Koenker & Bassett 1978) to literature growth rate data comprising numerous individual *E. huxleyi* strains and experiments. In addition, I applied quantile regression to the data using the combined best-fit models for growth rate as a function of PFD and growth rate as a function of temperature (Fielding 2013).

MATERIALS AND METHODS

Data collection

Emiliania huxleyi growth rate data (n = 1387) were obtained from literature culture experiments where light intensity data were also recorded. Data that were only presented graphically were extracted using Engauge Digitizer v.4.1. All growth rates were converted to cell-specific growth rate (µ, d^{-1}). Non-PFD light measurements (e.g. lumen ft^{-1}, Langleys min^{-1}, W m^{-2}) were converted to lux (lumen m^{-2}) and then converted to PFD (µmol photons m^{-2} s^{-1}) using the conversion factors in Table 1.

Literature-based E. huxleyi culture growth rate data were derived from 95 publications, detailing 213 strains from 67 different locations (Fig. 1). Literature culture experiments reported PFDs ranging from 3 to 1160 µmol photons m^{-2} s^{-1}, day lengths from 10 to 24 h, temperatures from 2 to 30°C, and salinities from 12 to 45. Around 7% of the data were from nutrient-limited cultures.

Table 1. Light conversion factors used to convert literature light intensity data expressed in lux (lumen m^{-2}) to µmol photons m^{-2} s^{-1} for different light sources. Units were multiplied by their respective conversion factors to obtain values in µmol photons m^{-2} s^{-1}

Light source	Factor
Cool white fluorescent	0.013
Daylight fluorescent	0.014
Unspecified fluorescent	0.0135
Halogen	0.019

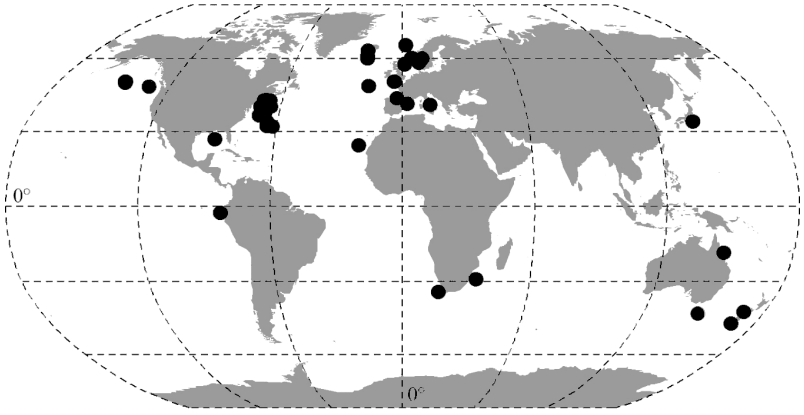

Fig. 1. Geographical locations of *Emiliania huxleyi* strains used in the literature compilation in this study (see Table S1 in the Supplement at www.int-res.com/articles/suppl/a073p163_supp.pdf for literature sources, strains used, and geographical location of strain origin)

Modelling and statistical analysis

Quantile regression can be used to determine the relationship between environmental variables and growth rate for the upper edge of a scatterplot. This is especially useful for datasets where variables other than the one which has been measured are limiting to growth (Cade & Noon 2003) and has previously been used to solve similar problems (Bissinger et al. 2008, Fielding 2013). To reliably define the upper edge of the dataset a 99th quantile regression must be used, as calculating the 100th quantile does not generate parameter confidence intervals (Cade et al. 1999). In this paper, 99th quantile regression was used to infer the relationship between light intensity and maximum growth rate for a highly heterogeneous set of *E. huxleyi* strains and environmental conditions where growth was often limited by factors other than light. It should be noted that a 99th quantile regression is calculated using all data and not just from the points at the extreme upper edge of the dataset.

Quantile regression was used to estimate the upper edge of the dataset (99th quantile) using *R* v.2.15.3 with the quantreg v.4.96 package for a selection of models commonly used to relate algal growth or photosynthesis to light intensity (Table 2). Model deviance can be corrected to take into account the number of parameters in the model, with a higher number of parameters incurring a heavier penalty, using Akaike's information criterion (AIC; Akaike 1974), AIC = $2p - 2L_m$, where p is the number of parameters in the model and L_m is the maximised log likelihood ($-2L_m$ is equivalent to the deviance of the model fit). However, all the models used in this study use the same number of independently varied parameters ($p = 2$), making AIC redundant. Therefore, model fits are subsequently compared using only their deviances.

RESULTS

Maximum *Emiliania huxleyi* specific growth rate for individual measurements was 1.96 d^{-1} at approx. 600 µmol photons m^{-2} s^{-1} (Fig. 2). Maximum growth rates appear to fall sharply below ~100 µmol photons m^{-2} s^{-1}. Above 600 µmol photons m^{-2} s^{-1}, maximum growth rates also appeared to be suppressed although this is likely due to a lack of data (n = 13) in this PFD range.

Table 2. Model parameters with 95% confidence intervals and deviances for the models fit to the data in Fig. 2. Lower deviances indicate better relative model fits. PFD is photon flux density (µmol photons m^{-2} s^{-1}), μ_{opt} is the modelled maximum specific growth rate (d^{-1}) across the entire PFD range, K is the light half-saturation constant and k is the initial slope of the curve at low light

Model	Deviance	Equation	μ_{opt}	K or k
Monod (1949)	11.18	$\mu = \mu_{opt} \times \frac{PFD}{K + PFD}$	1.858 ± 0.032	23.91 ± 5.608
Smith (1936)	12.81	$\frac{\mu_{opt} \times k + PFD}{\sqrt{\mu_{opt}^2 + (k \times PFD)^2}}$	1.795 ± 0.021	0.058 ± 0.016
Webb et al. (1974)	12.86	$\mu_{opt} \times (1 - e^{-k \times PFD/\mu_{opt}})$	1.785 ± 0.022	0.069 ± 0.019
tanh (Jassby & Platt 1976)	13.28	$\mu_{opt} \times \tanh\left(\frac{k \times PFD}{\mu_{opt}}\right)$	1.780 ± 0.016	0.059 ± 0.020
Steele (1962)	24.34	$k \times \mu_{opt} \times PFD \times e^{1-k \times PFD}$	2.939 ± 0.207	0.004 ± 0.000

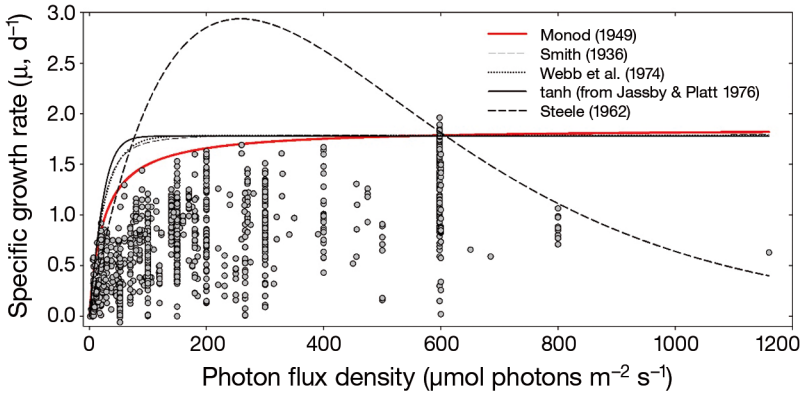

Fig. 2. *Emiliania huxleyi* specific growth rate versus photon flux density. Models (see Table 2) are fitted to the 99th quantile of the data

The rectangular hyperbolic Monod model (Eq. 1)

$$\mu = 1.858 \times \frac{\mathrm{PFD}}{23.91 + \mathrm{PFD}} \quad (3)$$

best described the 99th quantile of the specific growth rate response to PFD (Fig. 2, Table 2). In contrast, the Steele model (Eq. 2) had a relatively high deviance and visibly overestimated maximum growth rate by almost double at intermediate PFDs while marginally underestimating maximum growth rate at low PFDs. The other models (Smith 1936, Webb et al. 1974; and the tanh model from Jassby & Platt 1976) had intermediate deviances. While these models were nearly identical to the Monod model at PFDs above ~400 µmol photons m^{-2} s^{-1}, they visibly overestimated maximum growth rate at lower PFDs.

As the shapes of the responses of *E. huxleyi* maximum growth rate to both PFD (this study) and temperature (Fielding 2013) have been quantified, it is possible to formulate a combined expression by substituting μ_{opt} (from the Monod model) with the power function describing the maximum attainable growth rate as a function of temperature (Fielding 2013), as:

$$\mu = (a \times T^{b}) \times \left(\frac{\mathrm{PFD}}{K + \mathrm{PFD}}\right) \quad (4)$$

where K is the light half-saturation constant, T is the temperature (°C), and a and b are the slope and the power component of the growth rate versus temperature response, respectively. Quantile regression of this combined PFD plus temperature model through the 99th quantile of the data results in:

$$\mu = (0.199 \times T^{0.716}) \times \left(\frac{\mathrm{PFD}}{14.2 + \mathrm{PFD}}\right) \quad (5)$$

as shown in Fig. 3.

DISCUSSION

Growth rate response to light intensity

This study represents the first synthesis of literature-based *Emiliania huxleyi* growth rate data as a function of light intensity. Previous studies have quantified models describing growth rate response only from individual strains or from a small number of strains, despite there being considerable intraspecific variation of *E. huxleyi* growth rate in relation to light intensity (Paasche 2001). As a result, the use of these models incorporating coccolithophores such as *E. huxleyi* (e.g. Merico et al. 2004) may not be straightforward. However, this study provides an estimate of maximum growth rate as a function of light intensity from a multi-strain dataset which may be reasonably assumed to more accurately represent a natural, genetically diverse global *E. huxleyi* population.

Potential biases

The dataset used in this study is larger (n = 1387) than the minimum of n = 500 recommended by Rogers (1992) for calculating the 99th quantile. How-

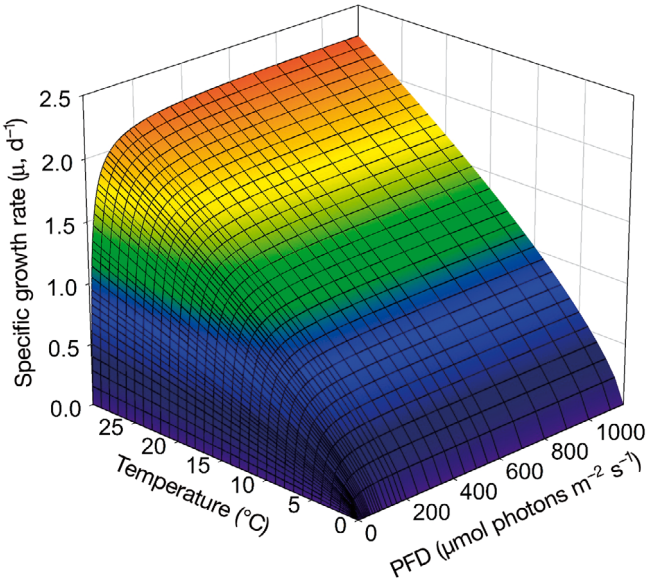

Fig. 3. 99th quantile regression of *Emiliania huxleyi* growth rate response to both photon flux density and temperature. Note reduced axes compared with Fig. 2. Colour scale: specific growth rates (blue–red: low–high)

ever, determining the best-fit model for the upper edge of the dataset may be complicated by sampling bias. Quantile regression is based on least absolute deviations and is therefore less sensitive to extreme values and outliers than ordinary least squares regression (Bissinger et al. 2008). Nevertheless, the lack of data (<1%) and lower measured maximum growth rates above 600 µmol photons m^{-2} s^{-1} may affect model parameter estimates.

To test the effect of data above 600 µmol photons m^{-2} s^{-1} on the model, these data were removed and the models were re-run. Removal of these data did not alter the order of model goodness of fit but did slightly alter parameters for some of the models by <0.7%, although these differences were not noticeable when plotted. Nevertheless, the use of the Monod model to describe *E. huxleyi* growth rate response to light intensity above 600 µmol photons m^{-2} s^{-1} should be made with this caveat until further data from these high PFDs can be included in the dataset. However, *E. huxleyi* photosynthesis is notable for not displaying inhibition at high light intensities of up to 2500 µmol photons m^{-2} s^{-1} (Paasche 2001). Therefore, it is possible that maximum growth rates at high light intensities are similarly uninhibited.

As was highlighted by Fielding (2013), only a small proportion of the data are from strains isolated from the Southern Hemisphere and far from continental land masses (Fig. 1). Although it is not anticipated that strains from different regions will have different light-dependent growth rate responses, the application of the recommended growth rate–PFD model should be made with this caveat in mind.

Ideally, the growth rate response to both light and temperature would be modelled for each individual geographic or climatic region. This would serve both to elicit any differences between regional-level populations of *E. huxleyi* and to test whether the global growth rate response models for light and temperature were universally applicable. However, dividing the current dataset into regional subsets would detract from the power of the combined global growth rate response curve. A regional subset of the current dataset would not be derived from as large a range of culture variables due to the smaller number of experiments carried out on that subset — for example, only temperatures between 15 and 20°C or only PFDs below 50 µmol photons m^{-2} s^{-1}.

A further problem with dividing the current dataset into regional subsets is that many regions (e.g. South Africa, N Pacific) only have data derived from a small number of strains or in some cases from a single strain. There appears to be almost as much intraspecific diversity within discrete geographic populations of *E. huxleyi* than there is between populations from different regions (Iglesias-Rodríguez et al. 2006). Therefore, any differences observed in growth rate response curves between subsets may not reflect a true regional difference but may simply be a result of under-sampling of the genetic diversity in each specific region.

The division of the current dataset into regional subsets at the present stage may therefore be a little premature, and more comprehensive data coverage of individual regions is likely necessary before any such analysis is made. The responses presented here and in Fielding (2013) are, as such, still only relatively blunt tools with which to parameterise *E. huxleyi* growth rate models.

Further bias may be introduced into the dataset by the use of varying light sources in different literature studies. Photosynthetically active radiation as measured by PFD includes all wavelengths between 400 and 700 nm. However, although 2 data points with the same PFD would have the same quantity of photons passing through this broad spectral band every second, the spectral quality of the 2 data may be different. For the collated literature studies presented here, the light source was specified for 78% (n = 1082) of the data. Around 75% of the entire dataset are from cultures grown using fluorescent tubes, of which 52% were cool white, 26% were daylight and 22% were unspecified. Around 3% of the dataset were from cultures grown using halogen lamps, of which one datum was from a study published in 1992 (Balch et al. 1992) and the remainder were from a study published in 1967 (Paasche 1967). These data all fell well below the upper edge of the scatterplot and any resultant differences in spectral quality are not likely to influence the results of this study. The 22% of the dataset where the light source was unspecified were all from studies published in 1995 or after, of which 82% were published in 2000 or after. As the last recorded usage of halogen lamps in this dataset was from 1992, it is likely that data from cultures with unspecified light sources were also grown using fluorescent tubes.

Combined growth rate response to light and temperature

In addition to determining its response to PFD, this study represents the first attempt at simultaneously quantifying the response of *E. huxleyi* maximum specific growth rate to both light and temperature. This combined model (see Results) can now be compared

to other models used to estimate maximum specific growth rate for *E. huxleyi* and for coccolithophores as a functional group from temperature and light intensity.

Four of the literature models for *E. huxleyi* use a rectangular hyperbola (Monod 1949), while one uses a hyperbolic tangent (tanh; Jassby & Platt 1976) function to describe growth rate versus PFD. In addition, 2 of the models use an exponential function after Eppley (1972) to describe growth rate response to temperature, while 3 use an exponential Q_{10} function (van't Hoff 1884). The combined expressions used in these studies to calculate specific growth rate from both temperature and PFD are detailed in Table 3.

In comparison with the combined model presented in this study, all 5 literature models (Fig. 4A–E) overestimate *E. huxleyi* maximum growth rate by >300% across a wide range of PFDs at low temperatures, while all 5 models overestimate *E. huxleyi* maximum growth rate to a lesser extent across a wide range of PFDs and temperatures, with the exception of Findlay et al. (2008), where growth rate is underestimated over the majority of the PFD and temperature range (Fig. 4A). The model used by Joassin et al. (2011) overestimated maximum growth rate across the entire PFD and temperature range (Fig. 4B).

The widespread overestimation of maximum *E. huxleyi* growth rate by literature models is largely due to the use of overly high values for μ_{opt} (i.e. the maximum growth rate across all temperatures and light intensities). For example, Merico et al. (2006) give a maximum specific growth rate of 1.15 d^{-1} at 0°C. However, extrapolation using the specified temperature–growth rate function results in high maximum specific growth rates of 4.05 d^{-1} at 20°C and an even higher 7.61 d^{-1} at 30°C, much higher than that observed in *E. huxleyi* culture experiments.

In addition to overly high μ_{opt} in literature models, the literature values for the initial slope of the growth rate response to PFD, with the exception of those used by Oguz & Merico (2006) and Joassin et al. (2011), are also higher than that presented in this study. This results in generally shallower PFD–growth rate slopes up to the growth optima in literature models, and therefore in the underestimation of growth rate at low PFD values across all or the majority of the temperature range for these studies (Fig. 4A,C,E). Hence, previously used parameters for both PFD and temperature components of growth rate models appear to be inappropriate for *E. huxleyi* and it is recommended that the combined model parameters presented in this study should be used in future.

In addition to modelling the coccolithophore *E. huxleyi* as a discrete ecosystem component, there are some studies which model all coccolithophore spe-

Table 3. Models used in literature studies to predict maximum specific growth rate (μ) from temperature (*T*, °C) and photon flux density (PFD, μmol photons m^{-2} s^{-1}). The differences between these models and the combined temperature–photon flux density model calculated in this study are shown in Fig. 4

Literature model	*T* model	PFD model	Equation
E. huxleyi			
Findlay et al. (2008)	Eppley	Monod	$(0.5\times e^{0.063\times T})\times\left(\frac{PFD}{205+PFD}\right)$
Joassin et al. (2011)	Q_{10}	Monod	$(2.64 / 1.5^{(20-T)/10})\times\left(\frac{PFD}{20+PFD}\right)$
Merico et al. (2004, 2006)[a]	Eppley	Monod	$(1.5\times e^{0.063\times T})\times\left(\frac{PFD}{205+PFD}\right)$
Oguz & Merico (2006)	Q_{10}	tanh	$(2.2 / 1.5^{(20-T)/10})\times\tanh\left(\frac{0.026\times PFD}{2.2 / 1.5^{(20-T)/10}}\right)$
Tyrrell & Taylor (1996)	Q_{10}	Monod	$(1.8 / 2^{(16-T)/10})\times\left(\frac{PFD}{100+PFD}\right)$
Coccolithophores			
Gregg et al. (2003)	Eppley	Monod	$(0.228\times e^{0.063\times T})\times\left(\frac{PFD}{71.2+PFD}\right)$
Gregg & Casey (2007)	Eppley	Monod	$(0.321\times e^{0.063\times T})\times\left(\frac{PFD}{71.2+PFD}\right)$

[a]Sensitivity analysis run

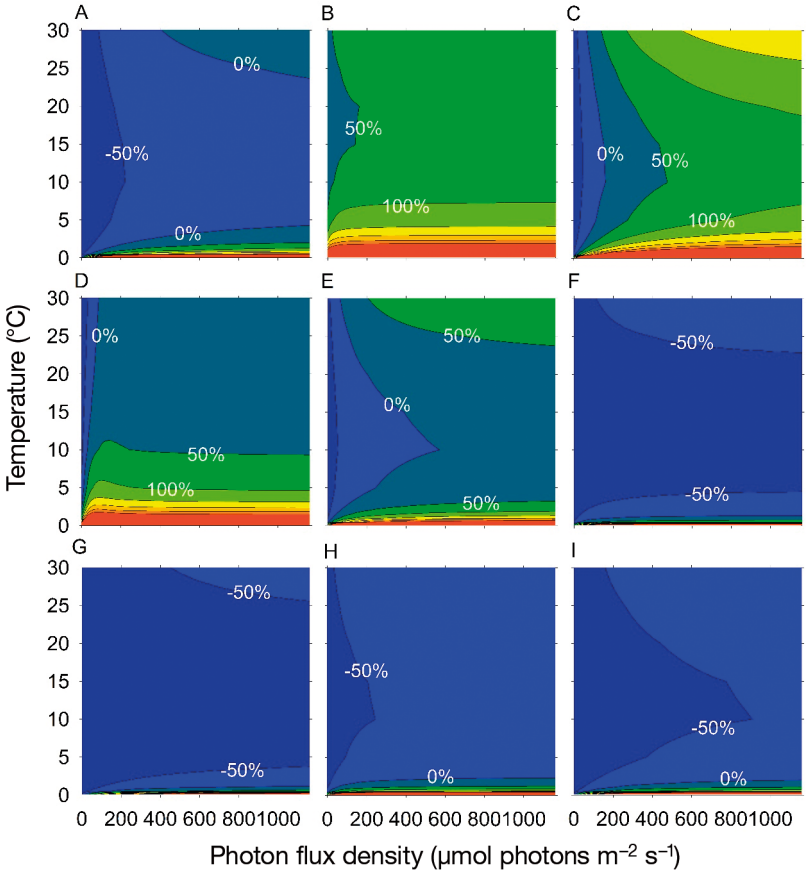

Fig. 4. The percentage which literature models (Table 3) underestimate (negative values) or overestimate (positive values) maximum specific growth rate compared to the combined temperature–photon flux density model presented in this study (Fig. 3). 0% equals no difference between the literature model and the model presented in this study. Contours are at 50% intervals although no data are shown above 300%. Colour scale: specific growth rates (blue–red: low–high). Models for *Emiliania huxleyi*: (A) Findlay et al. (2008), (B) Joassin et al. (2011), (C) Merico et al. (2004, 2006) (D) Oguz & Merico (2006) and (E) Tyrrell & Taylor (1996); and for coccolithophores as a functional group: (F) Gregg et al. (2003) low light model, (G) Gregg et al. (2003) high light model, (H) Gregg & Casey (2007) low light model and (I) Gregg & Casey (2007) high light model

cies as a combined functional group (Gregg et al. 2003, Le Quere et al. 2005, Gregg & Casey 2007). When compared to the combined PFD and temperature model presented in this study (Fig. 4F–I), coccolithophore functional group models described by Gregg et al. (2003) and Gregg & Casey (2007) have a lower maximum growth rate over almost the entire PFD range due to lower μ_{opt} values.

A multi-species coccolithophore population is indeed likely to have a lower combined maximum growth rate than a monospecific *E. huxleyi* population due to the inclusion of larger, slower growing species such as *Coccolithus* spp. and *Calcidiscus* spp. Existing functional group models likely somewhat reflect this lower multi-species coccolithophore community growth rate. However, *E. huxleyi* is one of the smallest (if not the smallest) species of coccolithophore (Buitenhuis et al. 2008) and is therefore likely to be the fastest growing as predicted by the metabolic theory of ecology (Brown et al. 2004). As such the 99th quantile *E. huxleyi* growth rate envelope presented in this study likely represents the maximum potential growth rate for all coccolithophore species as a functional group, and will become increasingly more appropriate as *E. huxleyi* starts to dominate the coccolithophore assemblage, for example in an *E. huxleyi* bloom scenario.

CONCLUSION

The Monod model presented in this study represents a first step towards quantifying the maximum specific growth rate response of *E. huxleyi* to light. It is recommended that the function $\mu = 1.858[PFD/(23.91 + PFD)]$, and not a Steele equation, be used in future models incorporating *E. huxleyi* growth rate. However, data from PFDs above 600 µmol photons m^{-2} s^{-1} and from a more geographically diverse set of culture strains than make up the current dataset will allow for a future reappraisal of this relationship. Where both temperature and PFD are known, maximum *E. huxleyi* growth rate should be calculated from the combined expression $\mu = (0.199 \times T^{0.716}) \times [PFD/(14.2 + PFD)]$.

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