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D2.9 Sub-model of coccolithophore (*E. huxleyi*) & user guide

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D2.9 Sub-model of coccolithophore (*E. huxleyi*) & user guide

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Summary

This document describes a computational method for calculating the ecological success of the abundant coccolithophore *Emiliania huxleyi*. This method is based on an up-to-date review of both older and more recent evidence as to the factors that favour or penalise *E. huxleyi* in ecological competition with other types of phytoplankton. Because ecological succession/competition is inherently about relative differences between different groups, which give any one particular group advantages under some environmental conditions but disadvantages under other conditions, this potentially presents a challenge for the plug-and-play modelling strategy. Here, however, we describe a plug-and-play module that has been developed to make the addition of *E. huxleyi* to a model a relatively easy and straightforward process. Previous algorithms for phytoplankton competition including *E. huxleyi* are reviewed, as is the experimental/observational literature on how *E. huxleyi* success is related to the state of the environment. Pseudo-code and FORTRAN versions of the module are presented, and an example of its use in a MEECE model (ERSEM) is described. ERSEM results are presented that show that this module operates correctly in ERSEM.

1. Introduction

1.1. Present understanding of factors controlling *E. huxleyi* competitive success

During the last 15 years, two main articles have reviewed and summarised the various evidence pertaining to the ecological niche of *E. huxleyi* (Tyrrell & Taylor, 1996; Tyrrell & Merico, 2004). These two articles considered the conditions that regulate the abundance of this organism, as did an earlier article by Holligan (1993b). Others have also reviewed the larger question of the ecology of coccolithophores as a whole (including most recently Balch (2004)). Paasche (2001) produced an extensive review of the physiology, morphology and reproduction of *E. huxleyi*. Here this subject of the ecological niche of *E. huxleyi* is revisited, and the subject is brought up to date by also including more recent evidence.

Over the last 20 years, our knowledge as to the environmental conditions favouring *Emiliania huxleyi* success has evolved, but it is still very far from complete. It was thought, in 1996, that a combination of high light and scarce phosphate (phosphate more limiting than nitrate) favoured *E. huxleyi* (Tyrrell & Taylor, 1996). The first of these two factors (the prediction that *E. huxleyi* outcompetes other phytoplankton at high light) comes partly out of a robust correlation between bloom occurrence and shallow mixed layer depth (MLD during *E. huxleyi* blooms is usually 10-20m, and is always ≤ 30m) (Nanninga & Tyrrell, 1996) and partly from PI curves. Later work has only further confirmed the strength of this association between shallow mixed layers and *E. huxleyi* blooms: (1) the eastern Bering Sea in 1997, the first year out of several in which massive blooms of *E. huxleyi* occurred there, experienced unusually strong stratification from June onwards, following a single strong storm in May (Stabeno et al. 2001; Hunt & Stabeno, 2002) and the interannual and seasonal variability of blooms in that area is successfully accounted for if a strong link to stratification is assumed (Iida et al., 2012); (2) A study of satellite images in the Black Sea found that *E. huxleyi* blooms did not occur randomly with respect to the circulation structure of the Black Sea, but rather that *E. huxleyi* bright waters were more frequently associated with cyclonic as opposed to anti-cyclonic eddies (Cokacar et al. 2001). The surface waters of cyclonic eddies tend to be more strongly stratified than those of anti-cyclonic eddies; (3) A study of *E.huxleyi* blooms in the subarctic N Atlantic south of Iceland used satellite and

in situ data sets to understand the environmental control over variability in coccolithophore abundance over a period of 7 years. Between 1997 and 2004, time-series analysis showed that high solar radiation, shallow mixed layer depth (< 20 m), and increased temperature explained >89% of the coccolithophore variation. One of the most extensive (> 995,000 km^2) blooms ever recorded in the ocean, which took place in this area in June 1998, was found to be associated with high light intensity, unusually high sea- surface temperature and a very shallow mixed layer (Raitsos et al., 2006).

The cause of this association between shallow mixed layer depth and blooms is not completely certain but probably occurs because *E. huxleyi* outcompetes other phytoplankton at high light intensities (Nanninga & Tyrrell, 1996). *E. huxleyi* bloom occurrence was compared on the global scale (as detected in SeaWiFS images by an automatic algorithm: [http://orbit-net.nesdis.noaa.gov/orad2/doc/ehux_www.html] with datasets of physical and nutrient parameters (Iglesias-Rodriguez et al. 2002). The study involved an objective analysis of parameters correlated with *E. huxleyi* blooms, although such correlations do not necessarily imply causation (for instance some association between *E. huxleyi* blooms and stratified waters is to be expected due to an effect of the blooms on the water state rather than vice-versa; Tyrrell et al., 1999). Their results suggested that *E. huxleyi* blooms are “confined primarily to nutrient-depleted, temperate, and high-latitude oceans with relatively high critical irradiances.” (Iglesias-Rodriguez et al. 2002).

Nanninga and Tyrrell (1996) suggested that the reason Ehux outcompetes other phytoplankton at high light intensities is that *E. huxleyi* is uniquely tolerant of high light intensities. At light intensities high enough to photoinhibit other species, *E. huxleyi* continues to thrive (Nanninga & Tyrrell, 1996). Laboratory and field PI-curves in which *E. huxleyi* has been acclimatised to and tested at high light intensities show a lack of photo-inhibition, even at the highest light intensities likely to be encountered in nature (Balch et al. 1992; Nanninga and Tyrrell 1996). While unusual tolerance of high light intensities may turn out to be important (but see Stolte et al. 2000), the evidence is not conclusive and there is as yet no widely accepted physiological reason (e.g. unique pigments) why *E. huxleyi* should outperform other phytoplankton at high light. There are, however, various partially supported and/or weakly rejected hypotheses. It is known that coccoliths do not act as “sunscreens” for visible light (Paasche and Klaveness 1970), although recent evidence suggests that they may act to block harmful UV radiation (Gao et al., 2009), which could potentially explain a high-light niche. However, calcification does not seem to facilitate energy dissipation under high irradiances (Trimborn et al., 2008), and so this is unlikely to be the reason for their success at high light. *E. huxleyi* is able to rapidly repair damage due to high photon flux densities, when it occurs (Ragni et al., 2008).

The second of these factors (low phosphate) that was considered to be important in 1996 was later rejected as an important control on *E. huxleyi* blooming. This followed a wide review of relevant evidence; most significantly, intense *E. huxleyi* blooms were observed to take place in an environment (the eastern Bering Sea shelf) where fixed nitrogen is clearly much more limiting than phosphate (Lessard et al., 2005).

By the time of a second review of factors crucial for *E. huxleyi* success, in 2004, it was concluded that blooms required some combination of (a) high light, (b) low silicate (to exclude diatoms) and possibly (c) high $CaCO_3$ saturation state (Ω) (Tyrrell & Merico, 2004).

The reason that concentrations of dissolved silicate (silicic acid) may be critical, despite *E. huxleyi* neither requiring nor taking up silicate, is the effect on diatom competitiveness. *E. huxleyi* is a fast-growing (*r*-selected) phytoplankton species, capable under favourable conditions of multiplying more rapidly than most other species. Most diatoms, however, can multiply even more rapidly than *E.*

huxleyi (Furnas 1990). Non-diatom fast-growers like *E. huxleyi* should do well in eutrophic or semi-eutrophic environments where diatoms are somehow excluded from the competition because dissolved silicate has been exhausted. When diatoms are not limited then they would be expected to outgrow *E. huxleyi*. In mesocosm experiments diatoms tend to dominate the phytoplankton community except when silicate is scarce (Egge and Aksnes 1992). Such a situation occurs towards the end of spring blooms in the northeast North Atlantic (Fasham et al. 2001, Fig. 12a), where *E. huxleyi* blooms also occur (e.g. Holligan et al. 1993a). The importance of silicate is supported by the temporal association between (a) the rise in *E. huxleyi* and decline in diatoms in the Black Sea since the 1960s (Mihnea 1997; Humborg et al. 1997) with (b) the fall in dissolved silicate levels, with wintertime concentrations decreasing from about 50 down to about 20 μMol kg^{-1} (Humborg et al. 1997). The large surplus of fixed nitrogen now left over following silicate depletion by winter/spring diatom blooms is now being removed by non-diatom species.

The importance of Ω to *E. huxleyi* shell-building (calcification) has been the subject of a large number of studies in recent years, due to concerns about harmful effects of ocean acidification (OA) on marine calcifiers. The evidence for an OA-related decline in calcification of coccolithophores in general, and also for *E. huxleyi* in particular, is equivocal (Ridgwell et al., 2009; Fabry, 2009). Some studies suggest reduced calcification at low Ω (e.g. Riebesell et al., 2001), other studies (e.g. Iglesias-Rodriguez et al.,2009) suggest the direct opposite. Overall there is no clear consensus even as to the sign of the effect.

High CO_2 may also have a favourable effect on coccolithophore photosynthesis, because of their comparatively low affinity for dissolved inorganic carbon (Rost & Riebesell, 2004), and this could potentially favour them in competition with other algae at high CO_2 and offset a potential disadvantage due to reduced calcification, if such actually occurs. Therefore the overall effect of high CO_2 / low pH on *E. huxleyi* competitive success (the subject of this deliverable) is uncertain.

Overall, our level of understanding is still rather low in some regards. It is difficult to make confident assertions about the factors controlling *E. huxleyi* competitiveness in the plankton. However, shallow mixed layers are clearly important. This is quite possibly because of a special affinity (or special tolerance) for high light.

1.2 Representation of *Emiliania huxleyi* in previous models

In a first study, Aksnes et al. (1994) gave *E. huxleyi* a high growth rate (in line with various data) and a competitive advantage when P is limiting but N more abundant. This allowed them to reproduce results from Norwegian mesocosms. Tyrrell & Taylor (1996) modelled *E. huxleyi* as part of the phytoplankton seasonal succession in the NE Atlantic, by attributing a combination of high light and scarce phosphate (phosphate more limiting than nitrate) as the conditions favouring *E. huxleyi* blooms. They were also represented with a high maximum potential growth rate. Following the publication of the paper by Lessard et al. (2005), however, N:P ratio has not been considered an important factor underpinning *E. huxleyi* success and has generally not been included in models as a factor driving *E. huxleyi* success (although see LeQuere et al., 2005).

Blooming activity of *E. huxleyi* in the eastern Bering Sea 1997-2003 was modelled by Merico et al. (2004). The best match between observed and modelled distribution of blooms was obtained by assuming that *E. huxleyi* has a particular advantage (1) at high light when photoinhibition limits the population of other flagellates, and (2) there is an extra microzooplankton grazing pressure on diatoms at low silicate and on coccolithophores at low $CaCO_3$ saturation state (Ω). The model included a switch such that this extra grazing was introduced for diatoms when silicate

concentrations fell below the threshold of 3 µM. The motivation for this extra grazing term in the diatom equation was to simulate the effect of microzooplankton selectively switching from *E. huxleyi* or other flagellates to diatoms under scarce silicate, due to diatom frustules becoming thinner. A similar model was used to simulate coccolithophore populations in the Norwegian Sea (Findlay et al., 2008).

Over the last decade or so there has been a trend towards global 'Phytoplankton Functional Type' (PFT) models (Gregg & Casey, 2007; LeQuere et al., 2005; Moore et al., 2002; etc) in which the phytoplankton are split up into several functional types such as nitrogen-fixing cyanobacteria, diatoms, coccolithophores, flagellates and dinoflagellates. Coccolithophores (typically based around *E. huxleyi*) are represented in some of these models. The representation is sometimes quite simplistic, for instance as a fixed % of non-diatom phytoplankton biomass (Moore et al., 2002). In others the model representation bears little resemblance to the suggestions outlined above: for instance, in one model (Gregg & Casey, 2007) coccolithophores were given a competitive advantage over diatoms and chlorophytes at low nutrients and low light values, but were at a disadvantage when nutrients and light were plentiful. In another model the coccolithophores are given a preference for waters with a low nitrate:phosphate ratios (LeQuere et al., 2005). In both cases the models produce coccolithophore blooms in some of the wrong places, for instance in the high latitude Southern Ocean where *in-situ* sampling shows coccolithophores (including *E. huxleyi*) to be absent or scarce (Gravelosa et al., 2008; Cubillos et al., 2007).

Another study (Joassin et al., 2009) has recently modelled the population dynamics of *E. huxleyi* in a mesocosm experiment. Because *E. huxleyi* dominated the phytoplankton biomass in the mesocosm bags, no other phytoplankton groups were modelled and there was therefore no competition. For this reason this model is not considered further here.

2. Implementation and user guide

2.1 Overview

Since there is no overall consensus as to the effect on calcification, it is not recommended at this time that *E. huxleyi* success be linked to carbonate chemistry in the MEECE models. For the same reason, the linkage between Ω and grazing pressure on *E. huxleyi* employed in Merico et al's model (2004) (because of variable calcification as a function of Ω, and suggested reduced grazing on heavily calcified cells) is also not recommended for use in MEECE. The strongest and most reliable evidence as to the most important factor which controls *E. huxleyi* blooms is that for a link with shallow mixed layers, most likely through a competitive advantage at high light intensities. Therefore it is this environmental factor which should be incorporated in the modelling.

The plug-and-play module described below allows calculation of the key parameters for *Emiliania huxleyi* as a phytoplankton state variable. *E. huxleyi* needs to be added as an extra phytoplankton group (by duplicating the code for a pre-existing group), and the outputs from the plug-and-play module then define how it should be parameterised. This module produces the coefficients needed for *E. huxleyi* to be modelled.

2.2 Interface variables

The module for *E. huxleyi* requires the following information to be passed to it:

1. the maximum growth rate (typical units of d^{-1}) for the closest group of phytoplankton already in

the model ('flagellates' or 'small phytoplankton' or 'non-diatom phytoplankton'). [MUMAX_ORIG]

2. the maximum growth rate (typical units of d^{-1}) for diatoms, if present as a separate group in the model. [MUMAX_DIA]
3. the Michaelis-Menten half-saturation constant with respect to irradiance (typical units of μEinstein m^{-2} s^{-1} or W m^{-2}), for the closest group of phytoplankton already in the model. [KH_I_ORIG]
4. the Michaelis-Menten half-saturation constant with respect to nitrate (typical units of μmol kg^{-1}), for the closest group of phytoplankton already in the model. [KH_NO3_ORIG]
5. the Michaelis-Menten half-saturation constant with respect to ammonium (typical units of μmol kg^{-1}), for the closest group of phytoplankton already in the model. [KH_NH4_ORIG]
6. the Michaelis-Menten half-saturation constant with respect to phosphate (typical units of μmol kg^{-1}), for the closest group of phytoplankton already in the model. [KH_PO4_ORIG]
7. the Q10 coefficient for the effect of temperature on growth (unitless), for the closest group of phytoplankton already in the model. [Q10_ORIG]
8. the vertical sinking rate of cells (typical units of m day^{-1}), for the closest group of phytoplankton already present in the model. [V_ORIG]
9. the zooplankton feeding preference (unitless) for the closest group of phytoplankton already present in the model. [ZPR_ORIG]
10. the Michaelis-Menten half-saturation constant for zooplankton grazing (typical units of) on the closest group of phytoplankton already in the model. [KH_Z_ORIG]
11. The sub-model produces the following outputs:
12. the maximum growth rate (typical units of d^{-1}) for *E. huxleyi* ('flagellates' or 'small phytoplankton' or 'non-diatom phytoplankton'). [MUMAX_EH]
13. the Michaelis-Menten half-saturation constant with respect to irradiance (typical units of μEinstein m^{-2} s^{-1} or W m^{-2}), for *E. huxleyi*. [KH_I_EH]
14. the Michaelis-Menten half-saturation constant with respect to nitrate (typical units of μmol kg^{-1}), for *E. huxleyi*. [KH_NO3_EH]
15. the Michaelis-Menten half-saturation constant with respect to ammonium (typical units of μmol kg^{-1}), for *E. huxleyi*. [KH_NH4_EH]
16. the Michaelis-Menten half-saturation constant with respect to phosphate (typical units of μmol kg^{-1}), for *E. huxleyi*. [KH_PO4_EH]
17. the Q10 coefficient for the effect of temperature on growth (unitless), for *E. huxleyi*. [Q10_EH]
18. the vertical sinking rate of cells (typical units of m day^{-1}), for *E. huxleyi*. [V_EH]
19. the zooplankton feeding preference (unitless) for *E. huxleyi*. [ZPR_EH]
20. the Michaelis-Menten half-saturation constant for zooplankton grazing (typical units of mmol m^{-3}) on *E. huxleyi*. [KH_Z_EH]

2.3. Specifics of implementation and user guide

Because of a restricted supply of nutrients, the availability of which normally controls the overall phytoplankton abundance, patterns of abundance of any one phytoplankton group in a model are dependent upon interactions and competition with the other phytoplankton groups (Gregg & Casey, 2007) and upon predation by zooplankton grazers. *E. huxleyi* parameters are therefore calculated with reference to the values used for other groups.

As discussed above, the most important aspect is that *E. huxleyi* outperforms other phytoplankton under high light conditions. In order to represent this in the model, *E. huxleyi* is given a higher half-saturation constant (I_H) than for other groups, where the effect of light on growth (ψ(I)) is calculated

according to the function:

$$\Psi(I) = \frac{I}{I+I_H} \quad (4)$$

where I is the ambient level of irradiance.

To compensate for reduced performance (lower ψ(I)) at all light values except higher ones, *E. huxleyi* needs to be given a slightly higher maximum growth rate to compensate.

For nutrient limitation of *E. huxleyi* it is suggested that it be given identical properties to other groups, because of a lack of clear evidence that *E. huxleyi* is better or worse than other groups at high or low concentrations of any one nutrient. Likewise for temperature.

It is recommended, given the lack of firm knowledge to the contrary (although see Frada et al., 2004), that *E. huxleyi* losses should be calculated in an identical fashion to those of other, equivalent, phytoplankton such as small flagellates.

The sub-module for *E. huxleyi* competitive success therefore consists of the following (in pseudo-code):

```
--

MUMAX_EH = 1.3 * MUMAX_ORIG

IF (MUMAX_EH >= MUMAX_DIA)
MUMAX_EH = 0.5 * (MUMAX_ORIG+MUMAX_DIA) ENDIF

KH_I_EH = 2.5 * KH_I_ORIG KH_NO3_EH = KH_NO3_ORIG
KH_NH4_EH = KH_NH4_ORIG
KH_PO4_EH = KH_PO4_ORIG Q10_EH = Q10_ORIG

V_EH = V_ORIG ZPR_EH = ZPR_ORIG KH_Z_EH = KH_Z_ORIG

--
```

Table 1 shows a comparison of the parameters (coefficients) used for different groups by Tyrrell & Taylor (1996), although a higher affinity (lower half-saturation constant) for phosphate is now no longer encouraged.

	Phytoplankton Groups				
Parameters	*E. huxleyi*	Diatoms	Flagellates	Dinoflagellates	Picophytoplankton
μ_{max}	1.8	1.9	1.4	0.3	1.4
I_H	100	40	40	40	40
N_H	0.3	0.3	0.3	0.3	0.3
A_H	0.05	0.05	0.05	0.05	0.05
Si_H	n.a.	1.0	n.a.	n.a.	n.a.
P_H	0.005*	0.05	0.05	0.05	0.05
V	0.0	1.5–12.0†	0.0	0.0	0.0
P_0	1.0	0.00001	1.0	1.0	1.0

Table 1: Parameter values for each phytoplankton group in the model: (1) μ_{max} is the maximum growth rate (day $^{-1}$); (2) I_H is the half-saturation constant for light (μEin m $^{-2}$ s $^{-1}$); (3) N_H is the half-saturation constant for nitrate (μmol kg $^{-1}$); (4) A_H is the half-saturation constant for ammonia (μmol kg $^{-1}$); (5) Si_H is the half-saturation constant for silicate (μmol kg $^{-1}$), for diatoms only; (6) P_H is the half-saturation constant for inorganic phosphate (μmol kg $^{-1}$); (7) V is the sinking rate (m day $^{-1}$); (8) and P_0 is the both the initial concentration and the threshold concentration below which each type of phytoplankton is not allowed to fall (mg C m $^{-3}$).
*, the limitation of *E. huxleyi* by phosphate is not a straightforward Michaelis-Menten function (see text for details). †, the diatom sinking rate increases at low silicate concentrations.

Table 1. Example of comparative parameter values used for Emiliania huxleyi and other phytoplankton functional groups, taken from (Tyrrell & Taylor, 1996).

3. Code

3.1. Example sub-module code in FORTRAN

This code is written assuming that the values of the competitor group have already been defined and made available to this point in the code (for instance passed as arguments if this code is placed within a subroutine or function).

```
DOUBLE PRECISION mumax_eh, kh_i_eh, kh_no3_eh
DOUBLE PRECISION kh_nh4_eh, kh_po4_eh, q10_eh mumax_eh = 1.3 *

mumax_orig

IF  (mumax_eh .GE. mumax_dia) THEN
mumax_eh = 0.5 * (mumax_orig+mumax_dia)
ENDIF

kh_i_eh = 2.5 * kh_i_orig kh_no3_eh = kh_no3_orig
kh_nh4_eh = kh_nh4_orig kh_po4_eh = kh_po4_orig q10_eh = q10_orig

v_eh = v_orig zpr_eh = zpr_orig kh_z_eh = kh_z_orig
```

3.2. Example use of the sub-module (incorporation in ERSEM)

The code below has been added to the standard ERSEM model and run coupled to the 1D General Ocean Turbulence model (GOTM Burchard et al., 1999) for a station located in the North Sea (56N, 3E). Atmospheric forcing and initial condition were as in the hindcast of the 3D model for the North Western European Shelf domain of MEECE (D3.4). Here, the results for flagellates and coccolithophores are shown, in order to evidence how the new parameterisation gives coccolithophores a competitive success at high irradiance.

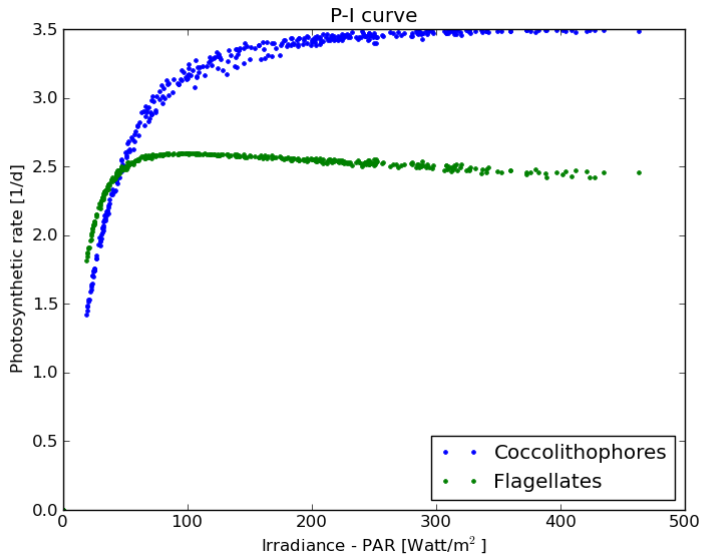

Figure 1: *P-I curve for coccolithophore and flagellates: coccolithophores are more competitive in assimilating inorganic carbon at irradiances higher than 50W/m^2. Furthermore, no photoinhibition is observed in this PFT.*

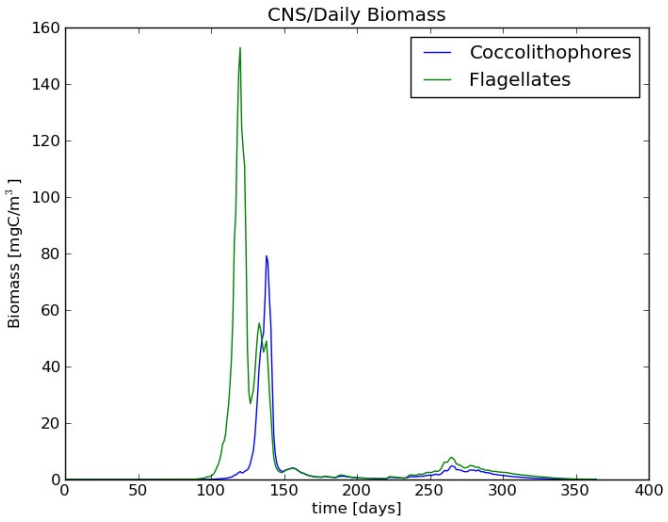

Figure 2: *Biomass concentration of the two groups. Flagellates bloom at the end of April (~day 120) while coccolithophores three weeks later in the second half of May (~day 140).*

These results were obtained by incorporating the method recommended above. Coccolithophores and flagellates were made identical except with regards to the relationship between photosynthetic rate and irradiance. Affinities for nutrients, for example, are identical.

The equation for the dependency of photosynthesis on irradiance in ERSEM (modified from Geider 1997) is:

$$P = P_{max} \cdot \left(1 - e^{\left(\frac{-\alpha I Chl C}{P_{max}}\right)}\right) \cdot \left(e^{\left(\frac{-\beta I Chl C}{P_{max}}\right)}\right)$$

where:
P = photosynthetic rate
Pmax = maximum photosynthetic rate
α = initial slope
I = Irradiance
ChlC = Chl:C ratio
β = photoinibition parameter

As suggested above $P_{max,coccol.} = 1.3 \cdot P_{max,flagellates}$

Figure 1 shows that photosynthesis in flagellates reaches saturation at about 80W/m^2 while in coccolithophores at about 220W/m^2, corresponding to the factor 2.5 suggested above. Setting the coefficient β to zero for coccolithophores removes photoinhibition in their case.

The code below shows the subroutine to simulate coccolithophores in the ERSEM model. All coccolithophore code is shown except that relating to calcification, which does not affect coccolithophores competitive success and was covered separately in deliverable D2.2. This subroutine is a copy of the subroutine simulating the flagellates (the ERSEM PFT most similar to coccolithophores). Table 2 show the values of these parameters in the two PFTs.

Parameter	Units	Flagellates		Coccolithophores	
		ERSEM name		ERSEM name	
P_{max}	1/d	sumP2X	2.7	sumP5X	3.5
$ChlC_{max}$	mgChl/mgC	phimP2X	0.035	phimP5X	0.028
	mgCm^2/mgChl/W/d	alfaP2X	2.98	alfaP5X	2.5
	mgCm^2/mgChl/W/d	betaP2X	0.02	betaP5X	0

Table 1: *Parameters used in the photosynthetic model for Flagellates and Coccolithophores*

This subroutine below, similar to the one presented in D2.5, follows the structure and the

naming convention of the ERSEM model (Blackford et al., 2004), hence readers are invited to read the paper for details. Specific conventions adopted in this subroutine are that P5 refers to the Coccolithophores PFT. Except for calcification, the code used is identical to that for flagellates. The two PFTs differ only in the parameter values used.

```
!-----------------------------------------------------------------------
subroutine Coccolithophores (I)
!
! !DESCRIPTION:
!.......................................................................

! Coccolithophore dynamics
! this subroutine simulates a group of calcifying autotrophic Plankton
! it follows ERSEM structures and naming convention for variables (as MEECE
D2.5 and 2.13)
! P5 refers to the coccolithophores PFT; L1 to attached coccoliths; L2 to
free-floating coccoliths
! It requires the compiling flag –DCOCCO to be compiled
! Calcification parameterisation can be selected at runtime by the switch
variable iswcal
!.......................................................................
!
!
! !USES:

      IMPLICIT NONE

   integer :: i

#ifdef COCCO
! !LOCAL VARIABLES:
real*8 :: sdoP5, sumP5, sugP5, seoP5, seaP5, sraP5, sunP5, runP5, rugP5
real*8 :: runP5p, misP5p, rumP5p
real*8 :: runP5n, misP5n, rumP5n, rumP5n3, rumP5n4
real*8 :: etP5,SDP5, pe_R6P5, sp5r6
real*8 :: Chl_inc, Chl_loss, rho, phi, chlcpp,fI
real*8 :: fcalc, fnut, fIcal, fdiss
real*8 :: Crate, iNP5p

!..Regulation
factors.....................................................

!..temperature response

      etP5 = q10P5X**((ETW(I)-10.0d0)/10.0d0) - q10P5X**((ETW(I)-
32.0d0)/3.0d0)

!..calculate chl to C ratio.............................................

!     chlcpp = min(phimP5X,chl5(I)/(p5c(I)-chl5(I)+zeroX))
```

```
      ChlCpp = chl5(I)/p5c(I)
      IF (chlcpp .LT. 0.0067) chlcpp = 0.0067

!..Gross photosynthetic activity :
      sumP5 = sumP5X*etP5

      phi = phiP5HX+ (chlcpp/phimP5X)*(phimP5X-phiP5HX)
      parEIR = pEIR_eowX*EIR(I)


      fI = (1.-exp(-alphaP5X*parEIR*chlcpp/sumP5)) * EXP(-
betaP5X*parEIR*chlcpp/sumP5)

      IF (pareir.gt.0.0) THEN
        sumP5 = sumP5 * fI
        rho = phi * (sumP5/(alphaP5X*parEIR*chlcpp))
      ELSE
        sump5 = 0.0
        rho = 0.0
      END IF

!..Nutrient-stress lysis rate :
!     fnut = 10.0*CL_EH*P5c(I)/L1c(I)

      sdoP5 = (1.d0/(iNIP5+0.1d0))*sdoP5X!+sdoP5X/10.0d0*P5cP(I) ! * fnut

!..Excretion rate, as regulated by nutrient-stress
      seoP5 = sumP5*(1.d0-iNIP5)*(1.d0-pu_eaP5X)

!..activity-dependent excretion :
      seaP5 = sumP5*pu_eaP5X
      sugP5 = sumP5-seoP5-seaP5

!..Apportioning of LOC- and DET- fraction of excretion/lysis fluxes:
      pe_R6P5 = MIN(qplP5cX/(qpP5c(I)+ZeroX),qnlP5cX/(qnP5c(I)+ZeroX))
      sp5r6 = pe_R6P5*sdoP5
      fP5R6c(I) = sp5r6*P5cP(I)
      fP5RDc(I) = (1.0d0-pe_R6P5) *sdoP5*P5cP(I) + (seoP5 + seaP5)*P5c(I)
!     fch5r7c = pe_R6P5 * sdoP5 * chl5(I)
!     fch5R1c = ((1.0-pe_R6P5) * sdoP5 + seoP5 + seaP5) * chl5(I)

!..Respiration..........................................................

!..Rest respiration rate :
      srsP5 = etP5*srsP5X

!..Activity respiration rate :
      sraP5 = sugP5*pu_raP5X
!       IF (resP5mX .GT. 10.0) sraP5 = sraP5 + (P5resX*sugP5*pu_raP5X)

!..Total respiration flux :
      fP5O3c(I) = srsP5*P5cp(I)+sraP5*P5c(I)

!..Gross production as flux from inorganic CO2 to P5 :
      fO3P5c(I) = sumP5*P5c(I)
      rugP5 = fO3P5c(I)
```

```
!..Production and productivity
      sunP5 = sumP5-(seoP5+seaP5+sraP5) ! net productivity
      runP5 = sunP5*P5c(I) - srsP5*P5cP(I) ! net production

 !..To save net production
      netP5(I) = fO3P5c(I)-fP5O3c(I)-fP5R6c(I)-fP5RDc(I)

!..Chl changes (note Chl is a component of P*c and not involved is mass
balance)
      Chl_inc = DMIN1(rho,0.1D0) * (sumP5-sraP5)*P5c(I)
      Chl_loss = (sdoP5+srsP5)*Chl5P(I) + (seoP5+seaP5)*Chl5(I)

!..Carbon Source equations
      SP5c(I) = SP5c(I)+fO3P5c(I)-fP5O3c(I)-fP5R6c(I)-fP5RDc(I)
      SR1c(I) = SR1c(I)+(fP5RDc(I) * R1R2X)
      SR2c(I) = SR2c(I)+(fP5RDc(I) * (1.0d0-R1R2X))
      SR6c(I) = SR6c(I)+fP5R6c(I)
!       SR7c(I) = SR7c(I) + fCh5R1c + fch5R7c
      SChl5(I) = Schl5(I) + Chl_inc - Chl_loss

!..Phosphorus flux through P5.......................................

!..lysis loss of phosphorus
      fP5R6p = sp5r6 * min(qplP5cX*P5cP(I),P5pP(I))
      fP5RDp = sdoP5 * P5pP(I) - fP5R6p

!..Net phosphorus uptake
      rumP5p = qurP5pX * N1p(I) * P5c(I)
      misP5p = xqpP5X * qpRPIcX*P5cP(I) - P5pP(I)
      runP5p = runP5 * qpRPIcX*xqpP5X
      fN1P5p(I) = MIN(rumP5p, runP5p+misP5p)

!..Source equations
      SP5p(I) = SP5p(I)+fN1P5p(I)-fP5RDp-fP5R6p
      SN1p(I) = SN1p(I)-fN1P5p(I)
      SR1p(I) = SR1p(I)+fP5RDp
      SR6p(I) = SR6p(I)+fP5R6p
!       SR1p(I) = SR1p(I)+fP5RDp(I)

!..Nitrogen flux through P5.......................................

!..Nitrogen loss by excretion
      fP5R6n = sp5r6 * min(qplP5cX*P5nP(I),P5nP(I))
      fP5RDn = sdoP5 * P5nP(I) - fP5R6n

!..Net nitrogen uptake
      rumP5n3 = quP5n3X * N3n(I) * P5c(I)
      rumP5n4 = quP5n4X * N4n(I) * P5c(I)
      rumP5n = rumP5n3 + rumP5n4
      misP5n = xqnP5X * qnRPIcX*P5cP(I) - P5nP(I)
      runP5n = runP5 * qnRPIcX*xqnP5X
      fNIP5n = MIN(rumP5n, runP5n + misP5n)

!..Partitioning over NH4 and NO3 uptake
      IF (fNIP5n .gt. 0.0d0) THEN
         fN3P5n(I) = fNIP5n * rumP5n3 / rumP5n
```

```
         fN4P5n(I) = fNIP5n * rumP5n4 / rumP5n
      ELSE
         fN3P5n(I) = 0.0d0
         fN4P5n(I) = fNIP5n
      ENDIF

 !..Source equations
      SP5n(I) = SP5n(I)+fN4P5n(I)+fN3P5n(I)-fP5RDn-fP5R6n
      SN3n(I) = SN3n(I)-fN3P5n(I)
      SN4n(I) = SN4n(I)-fN4P5n(I)
      SR1n(I) = SR1n(I)+fP5RDn
      SR6n(I) = SR6n(I)+fP5R6n
 !      SR1n(I) = SR1n(I)+fP5RDn(I)

 !..sedimentation or vertical
 migration.....................................
      SDP5 = resP5mX * MAX(0.d0, (esNIP5X - iNIP5) )
      SDP5c(I) = SDP5c(I) + SDP5
      SDP5p(I) = SDP5p(I) + SDP5
      SDP5n(I) = SDP5n(I) + SDP5
      SDChl5(I) = SDChl5(I) + SDP5
 #endif
      RETURN
      END SUBROUTINE vphyt5
```

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