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### **Deliverable D2.5: Sub-model Carbon Phytoplankton including user guide**

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## **D2.5 Sub-model Carbon Phytoplankton including user guide**

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## 1. INTRODUCTION

Increasing inorganic carbon concentrations have been shown to promote primary production and carbon assimilation in marine phytoplankton (Hein and Sand-Jensen, 1997; Riebesell, 2004; Engel et al., 2008; Tortell et al., 2008; Egge et al., 2009), an effect rarely represented in ecosystem models. Here we present a module allowing for such carbon enhancement. As an example, the module is developed for the European Regional Seas Ecosystem Model (ERSEM; Blackford et al. 2004), a MEECE model, and we provide the necessary technical information aiding the inclusion of this module in other ecosystem models as well.

*ERSEM* is a mature plankton functional type model related to, but more complex than, the NPZD type models. It represents the key processes of temperate shelf ecosystems; plankton community complexity, the microbial loop, variable nutrient stoichiometry, variable carbon: chlorophyll ratios, and a comprehensive description of benthic biochemical and ecological processes (<http://web.pml.ac.uk/meece/library/ersem.html>). Droop kinetics is employed in evaluating nutrient limitation (Droop 1974), and separate limitation factors are calculated for each phytoplankton group (Blackford et al. 2004). We have modified a version of *ERSEM* coupled to the 1D General Ocean Turbulence Model (GOTM; <http://www.gotm.net/>), providing information on Temperature (T), Salinity (S), and mixing.

### 1.1 Representation of phytoplankton carbon enhancement in models

We extend the relationship describing the rate of change of a planktonic functional type in *ERSEM* (Blackford et al. 2004), and related models (Vichi et al. 2007), to include increased organic carbon production with increasing CO<sub>2</sub>:

$$\frac{dP}{dt} = \text{photosynthesis} - \text{respiration} - \text{lysis} - \text{excretion} - \text{grazing} + \text{CO}_2 \text{ enhancement} \quad (1)$$

$$\text{photosynthesis} = r_{\text{ass}} \oplus t \oplus f_i \oplus P^C \oplus C^{\text{EN}} \quad (2)$$

where  $C^{\text{EN}}$ , the carbon enhancement factor, relative to the year 2005, is represented as:

$$C^{\text{EN}} = (p\text{CO}_2^{\text{yr}} - p\text{CO}_2^{2005}) * \alpha^{\text{EN}} + 1, \text{ where } \alpha^{\text{EN}} = 0.0005 \quad (3)$$

As an example of potential use, the parameterization of  $C^{\text{EN}}$  follows from the Pelagic Ecosystem CO<sub>2</sub> Enrichment Study III (PeECE III) mesocosm experiments (Riebesell et al., 2007; Bellerby et al., 2008) where  $C^{\text{EN}}$  is related to the initial atmospheric CO<sub>2</sub> concentration at the onset of the bloom. However, the module is prepared to easily accommodate other forcing mechanisms from the meta-analysis of the MEECE dataset.

## 2. IMPLEMENTATION AND USER GUIDE

We use diatoms as a showcase example of the carbon-enhancement process in ERSEM, but it can be straightforwardly adapted to any plankton functional group, and model. Requiring relatively moderate modifications in ERSEM, the inclusion of carbon enhancement is implemented directly into the model code itself, and activated from an input file through an integer runtime switch. This procedure is, in the same way, applicable to other model systems. In the case of FORTRAN90, this is achieved by:

```
select case (switch)
  case(1)
    lines of code1
  case(2)
    lines of code2
end select
```

If including larger amounts of code, it might be beneficial to utilize conditional compilation, as represented in FORTRAN90 as:

```
#ifdef flag1
  lines of code
#endif
```

In this way the code will only be added to the executable if the pre-compilation flag, *flag1*, is defined, resulting in a smaller executable.

We will in the following *provide information regarding the specific processes requiring modification* in ERSEM, and show the specific modifications performed.

*Affected processes* – As shown in (1), the primary production of the respective functional group with regards to carbon uptake must be modified. The process of nitrogen and phosphorus uptake should remain unchanged (Riebesell et al. 2007, Bellerby et al. 2008).

Equation (1) can be written, in flux form (using the same notation as Vichi et al. 2007), as:

$$\left. \frac{\partial \mathcal{P}_c}{\partial t} \right|_b = \left[ \frac{\partial \mathcal{P}_c}{\partial t} \right]^{pp} - \left[ \frac{\partial \mathcal{P}_c}{\partial t} \right]^{rsp}_{o3} - \left[ \frac{\partial \mathcal{P}_c}{\partial t} \right]^{out}_{R1} - \left[ \frac{\partial \mathcal{P}_c}{\partial t} \right]^{out}_{R6} \pm \sum_{Zy} \left[ \frac{\partial \mathcal{P}_c}{\partial t} \right]^{prd}_{Zy} + \left[ \frac{\partial \mathcal{P}_c}{\partial t} \right]^{sink} \quad (4)$$

where the left side of the equation distinguishes the fluxes that contribute to the biological rate of change. The last term can be positive or negative depending on the vertical gradient. We have to alter the gross primary production (PPD), as this mediates transfer of inorganic CO<sub>2</sub> to the plankton. This is described by:

$$\left[ \frac{\partial P_c}{\partial t} \right]^{pp} = r_p P_c = (f_p^T f_p^I r_{0p}) P_c \quad (5)$$

When describing Diatoms, functional group 1 in ERSEM, Equation (5), thus takes the form:

$$\left[ \frac{\partial P1_c}{\partial t} \right]^{pp} = r_{p1} P1_c = (f_{p1}^T f_{p1}^I r_{0p1}) P1_c \quad (6)$$

The constant parameter  $r_{0p}$  represents the maximum potential specific growth rate at the reference temperature (10°C). The process of carbon enhancement on gross production is therefore represented by:

$$\left[ \frac{\partial P1_c}{\partial t} \right]^{pp} = r_{p1} P1_c = (f_{p1}^T f_{p1}^I r_{0p1}) P1_c \cdot C^{EN} \quad (7)$$

In ERSEM, respiration is divided into basal – and activity respiration, as described by:

$$\left[ \frac{\partial P_c}{\partial t} \right]_{-O3}^{rsp} = (a_{p1} + b_p f_p^T) P_c \quad (8)$$

The activity respiration ( $a_{p1}$ ) is a constant fraction of the assimilated carbon, which is in turn a function of the total rate of uptake minus the excretion loss. The basal respiration is dependent on the total growth rate, but modulated by the constant fraction of activity excretion, and the nutrient limitation. We thus need to enhance the activity respiration term in (8), as we have already altered the assimilation of carbon. This leads to the following expression:

$$\left[ \frac{\partial P_c}{\partial t} \right]_{-O3}^{rsp} = (a_{p1} \cdot C^{EN} + b_p f_p^T) P_c \quad (9)$$

### 3. MODEL CODE

An example showing the necessary modifications for including a *plug-and-play carbon enhancement module* in ERSEM follows below. The modifications were performed in the original subroutine describing Diatom dynamics; vphyt1 (located in pprod.F90), more specifically, in the parts of the code handling (i) total respiration flux, and (ii) gross production as a flux from inorganic CO<sub>2</sub> to Diatoms. The *integer runtime switch*, called Cenhance, needs to be set in the input file gotmersem.nml, a file necessary for running the coupled model system. Cenhance = 1 represents a run with carbon enhancement, while Cenhance = 0 represents a standard run. This ensures the *plug-and-play feature*, as there is no need for changing any parameters in the code itself.

**Statement of use:** We strongly encourage the User to contact the originators of this document (R. Bellerby: [Richard.bellerby@uni.no](mailto:Richard.bellerby@uni.no), G. Nondal: [gjslen@nersc.no](mailto:gjslen@nersc.no)), in order to receive supplementary information, prior to implementing the code.

**Note:** Changes to the original FORTRAN90 code are highlighted in blue and italics.

```
!-----
SUBROUTINE vphyt1(I)
!
! !DESCRIPTION:
! Diatom dynamics
!
! IMPLICIT NONE
!
! INPUT VARIABLES:
integer,intent(in) :: i
! LOCAL VARIABLES:
real*8 :: sdoP1,sumP1,sugP1,seoP1,seaP1,sraP1,sunP1,runP1,rugP1,sP1R6,runP1c
real*8 :: runP1p,misP1p,rumP1p
real*8 :: runP1n,misP1n,rumP1n,rumP1n3,rumP1n4
real*8 :: etP1,SDP1,pe_R6P1
real*8 :: rho,Chl_inc,Chl_loss
real*8 :: phi,ChlCpp

#ifdef IRON
real*8 :: runP1f,rumP1f,misP1f
#endif
!..Regulation factors.....

!..Temperature response
  etP1 = q10P1X**((ETW(I)-10.0d0)/10.0d0) - q10P1X**((ETW(I)-32.0d0)/3.0d0)

!..Production.....
```

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

$$\text{ChlCpp} = \max(\min(\text{phimX}, \text{chl1(I)}/(\text{p1c(I)} - \text{chl1(I)} + \text{zeroX})), \text{ChlCmin})$$

!..Gross photosynthetic activity :

#ifndef IRON

$$\text{sumP1} = \text{sumP1X} * \text{etP1} * \text{iNP1s} * \text{iNP1f}$$

#else

$$\text{sumP1} = \text{sumP1X} * \text{etP1} * \text{iNP1s}$$

#endif

$$\text{phi} = \text{phiHX} + (\text{ChlCpp}/\text{phimX}) * (\text{phimX} - \text{phiHX})$$

$$\text{parEIR} = \text{pEIR\_eowX} * \text{EIR(I)}$$

IF (parEIR.gt.0.0) THEN

$$\text{sumP1} = \text{sumP1} * (1. - \exp(-\alpha\text{X} * \text{parEIR} * \text{ChlCpp}/\text{sumP1})) * \text{EXP}(-\beta\text{X} * \text{parEIR} * \text{ChlCpp}/\text{sumP1})$$

$$\text{rho} = \text{phi} * (\text{sumP1}/(\alpha\text{X} * \text{parEIR} * \text{ChlCpp}))$$

ELSE

$$\text{sumP1} = 0.0$$

$$\text{rho} = 0.0$$

END IF

!..Nutrient-stress lysis rate :

$$\text{sdoP1} = (1. \text{d0}/(\text{iNIP1} + 0.1 \text{d0})) * \text{sdoP1X}$$

!..Excretion rate, as regulated by nutrient-stress

$$\text{seoP1} = \text{sumP1} * (1. \text{d0} - \text{iNIP1}) * (1. \text{d0} - \text{pu\_eaP1X})$$

!..activity-dependent excretion :

$$\text{seaP1} = \text{sumP1} * \text{pu\_eaP1X}$$

$$\text{sugP1} = \text{sumP1} - \text{seoP1} - \text{seaP1}$$

!..Apportioning of LOC- and DET- fraction of excretion/lysis fluxes:

$$\text{pe\_R6P1} = \text{MIN}(\text{qplP1cX}/(\text{qpP1c(I)} + \text{ZeroX}), \text{qnlP1cX}/(\text{qnP1c(I)} + \text{ZeroX}))$$

$$\text{sP1R6} = \text{pe\_R6P1} * \text{sdoP1}$$

$$\text{fP1R6c(I)} = \text{sP1R6} * \text{P1cP(I)}$$

$$\text{fP1RDc(I)} = (1. \text{d0} - \text{pe\_R6P1}) * \text{sdoP1} * \text{P1cP(I)} + (\text{seoP1} + \text{seaP1}) * \text{P1c(I)}$$

!..Respiration.....

!..Rest respiration rate :

$$\text{srsP1} = \text{etP1} * \text{srsP1X}$$

!..Activity respiration rate :

$$\text{sraP1} = \text{sugP1} * \text{pu\_raP1X}$$

*SELECT CASE (Cenhance)**CASE(1)*

*! Changing carbon uptake as a function of pCO2 according to Bellerby et al. (2008) and  
! Riebesell et al. (2007).*

*pco2a5 = 379.48 !! setting atmospheric pCO2 to the level after which carbon  
!!enhancement occurs, here taken as 2005*

*IF (PCO2A .GT. pco2a5) THEN  
cen=((PCO2A-pco2a5)\*0.0005)+1. ! Carbon enhancement factor  
ELSE  
cen=1 ! no carbon enhancement  
ENDIF*

*!..Total respiration flux:*

$$fP1O3c(I) = srsP1 * P1cP(I) + sraP1 * P1c(I) * cen$$

*!..Gross production as flux from inorganic CO2 to P1:*

$$fO3P1c(I) = sumP1 * P1c(I) * cen$$

$$rugP1 = fO3P1c(I)$$

*CASE(0)*

*! standard run without C enhancement*

*!..Total respiration flux:*

$$fP1O3c(I) = srsP1 * P1cP(I) + sraP1 * P1c(I)$$

*!..Gross production as flux from inorganic CO2 to P1:*

$$fO3P1c(I) = sumP1 * P1c(I)$$

$$rugP1 = fO3P1c(I)$$

*CASE(2:)*

*Write (6,\*) 'ERROR: Cenhancement switch out of range!!'*

*END SELECT*

*!..Production and productivity*

$$sunP1 = sumP1 - (seoP1 + seaP1 + sraP1) \quad ! \text{ net productivity}$$

$$runP1 = sunP1 * P1c(I) - srsP1 * P1cP(I) \quad ! \text{ net production}$$

*!..To save net production*

$$netP1(I) = runP1$$

*!..Carbon Source equations*

$$rho = DMIN1(rho, 0.1D0)$$

*! Chl changes (note that Chl is a component of PXc and not involved  
! in mass balance)*

$$Chl\_inc = rho * (sumP1 - sraP1) * P1c(I)$$

$$Chl\_loss = (sdoP1 + srsP1) * Chl1P(I) + (seoP1 + seaP1) * Chl1(I)$$

```

SP1c(I) = SP1c(I)+fO3P1c(I)-fP1O3c(I)-fP1R6c(I)-fP1RDc(I)
SR1c(I) = SR1c(I)+(fP1RDc(I) * R1R2X)
SR2c(I) = SR2c(I)+(fP1RDc(I) * (1.0d0-R1R2X))
SR6c(I) = SR6c(I)+fP1R6c(I)
Schl1(I) = Schl1(I) + Chl_inc - Chl_loss
    
```

!..Phosphorus flux through P1.....

!..Lysis loss of phosphorus

```

fP1R6p = sP1R6 * min(qplP1cX*P1cP(I),P1pP(I))
fP1RDp = sdoP1 * P1pP(I) - fP1R6p
    
```

!..Net phosphorus uptake

```

rumP1p = qurP1pX * N1pP(I) * P1c(I)
misP1p = xqpP1X * qpRPIcX*P1cP(I) - P1pP(I)
runP1p = runP1 * qpRPIcX*xqpP1X
fN1P1p(I) = MIN(rumP1p, runP1p+misP1p)
    
```

!..Source equations

```

SP1p(I) = SP1p(I)+fN1P1p(I)-fP1RDp-fP1R6p
SN1p(I) = SN1p(I)-fN1P1p(I)
SR6p(I) = SR6p(I)+fP1R6p
SR1p(I) = SR1p(I)+fP1RDp
    
```

!..Nitrogen flux through P1.....

!..Nitrogen loss by lysis

```

fP1R6n = sP1R6 * min(qnlP1cX*P1cP(I),P1nP(I))
fP1RDn = sdoP1 * P1nP(I) - fP1R6n
    
```

!..Net nitrogen uptake

```

rumP1n3 = quP1n3X * N3nP(I) * P1c(I)
rumP1n4 = quP1n4X * N4nP(I) * P1c(I)
rumP1n = rumP1n3 + rumP1n4

misP1n = xqnP1X * qnRPIcX*P1cP(I) - P1nP(I)
runP1n = runP1 * qnRPIcX*xqnP1X
fNIP1n = MIN(rumP1n, runP1n + misP1n)
    
```

!..Partitioning over NH4 and NO3 uptake

```

IF (fNIP1n .gt. 0.0d0) THEN
  fN3P1n(I) = fNIP1n * rumP1n3 / rumP1n
  fN4P1n(I) = fNIP1n * rumP1n4 / rumP1n
ELSE
  fN3P1n(I) = 0.0d0
  fN4P1n(I) = fNIP1n
ENDIF
    
```

!..Source equations

$$\begin{aligned}
 SP1n(I) &= SP1n(I) + fN4P1n(I) + fN3P1n(I) - fP1RDn - fP1R6n \\
 SN3n(I) &= SN3n(I) - fN3P1n(I) \\
 SN4n(I) &= SN4n(I) - fN4P1n(I) \\
 SR6n(I) &= SR6n(I) + fP1R6n \\
 SR1n(I) &= SR1n(I) + fP1RDn
 \end{aligned}$$

!..Silicate flux through P1.....

!..Excretion loss of silicate  
 $fP1R6s = sdoP1 * P1s(I)$

!..Loss of excess silicate ( $qsP1c > qsP1cX$ )  
 $fP1N5s(I) = MAX ( 0.0d0, P1sP(I) - qsP1cX * P1cP(I) )$

!..Net silicate uptake  
 $fN5P1s = MAX ( 0.0d0, qsP1cX * runP1 ) - fP1N5s(I)$

!..Source equations  
 $SP1s(I) = SP1s(I) + fN5P1s - fP1R6s$   
 $SN5s(I) = SN5s(I) - fN5P1s$   
 $SR6s(I) = SR6s(I) + fP1R6s$

#ifdef IRON

!..Iron flux through P1.....

!..Iron loss by lysis  
 ! Because its high affinity with particles all the iron lost from phytoplankton by lysis is supposed to be associated to organic particulate detritus. (luca)

$$fP1R6f = sP1R6 * P1fP(I)$$

!..net iron uptake  
 $rumP1f = qurP1fX * N7fP(I) * P1c(I)$   
 $misP1f = qfRP1cX * P1cP(I) - P1fP(I)$   
 $runP1f = runP1 * qfRP1cX$   
 $fN7P1f(I) = MIN(rumP1f, runP1f + misP1f)$

!..Source equations  
 $SP1f(I) = SP1f(I) + fN7P1f(I) - fP1R6f$   
 $SN7f(I) = SN7f(I) - fN7P1f(I)$   
 $SR6f(I) = SR6f(I) + fP1R6f$

#endif

!..sedimentation and resting stages.....

$$\begin{aligned}
 SDP1 &= resP1mX * MAX(0.d0, (esNIP1X - iNIP1) ) \\
 SDP1c(I) &= SDP1c(I) + SDP1 \\
 SDP1p(I) &= SDP1p(I) + SDP1 \\
 SDP1n(I) &= SDP1n(I) + SDP1
 \end{aligned}$$

```
SDP1s(I) = SDP1s(I) + SDP1
SDChl1(I) = SDChl1(I) + SDP1
#ifdef IRON
SDP1f(I) = SDP1f(I) + SDP1
#endif

!..add dia
! IF ((P1c(I) .LT. 0.2).AND. (parEIR .GT. 0.5)) THEN
!   SP1c(I) = SP1c(I) + (0.2 - P1c(I))
!   SP1n(I) = SP1n(I) + (0.2 - P1c(I))*16.0/106.0
!   SP1p(I) = SP1p(I) + (0.2 - P1c(I))/106.0
!   SP1s(I) = SP1s(I) + (0.2 - P1c(I))*16.0/106.0
!   SChl1(I) = SChl1(I) + (0.2 - P1c(I))*ChlCpp
!   END IF

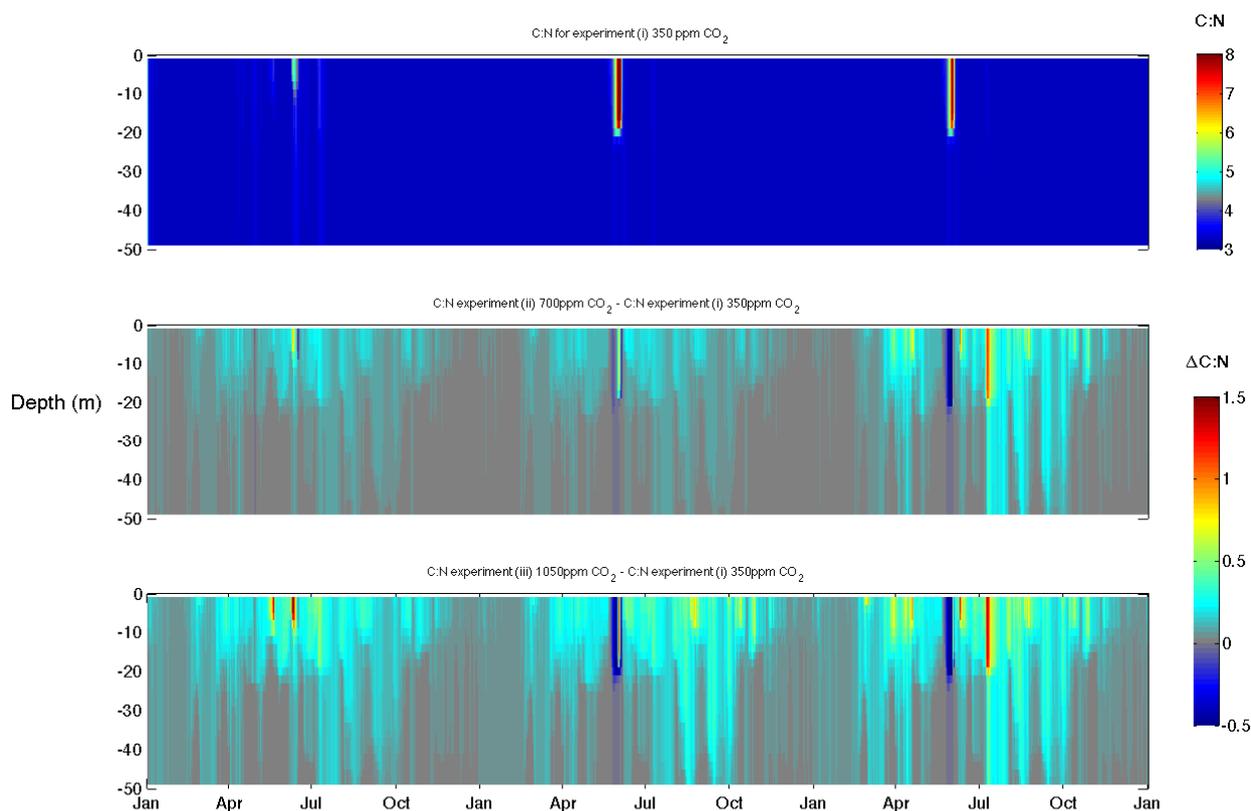
RETURN

END SUBROUTINE vphyt1
```

```
!-----
```

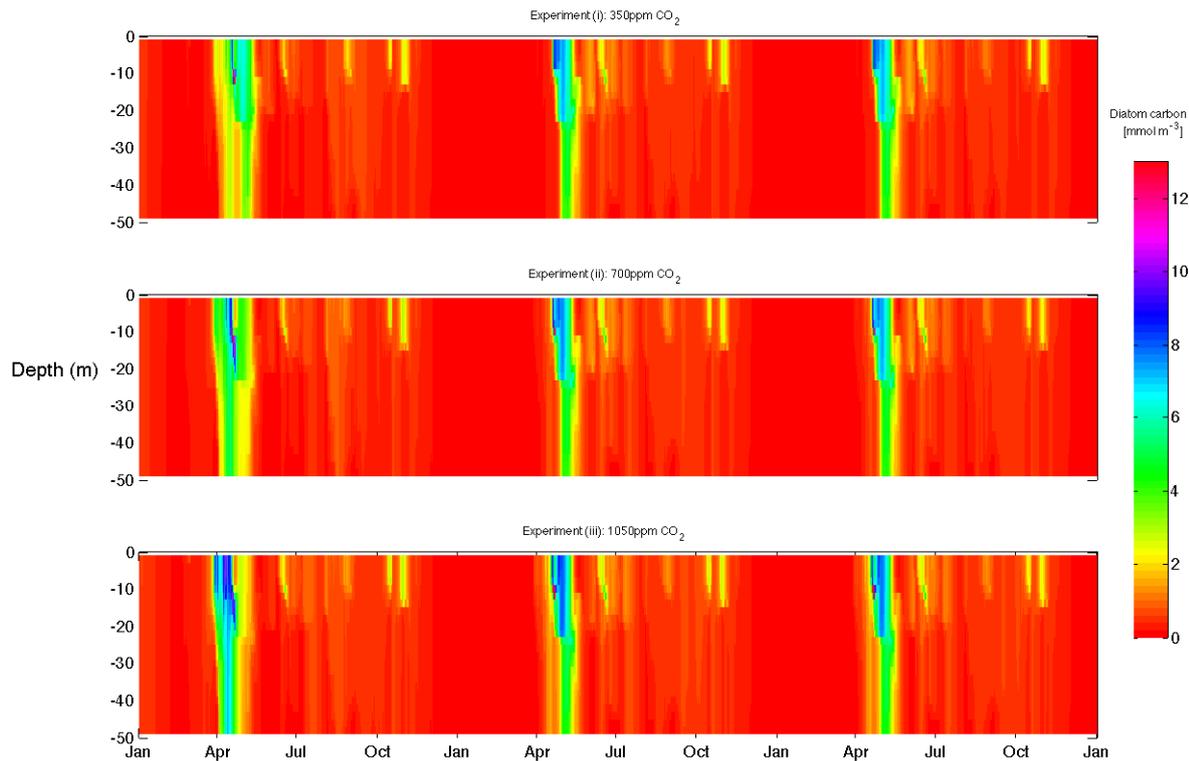
### 3.1 Model results and discussion

After implementing the changes, as described above, the ERSEM-GOTM model pairing was run for the L4 site (50°15'N, 04°13'W) outside of Plymouth, UK, for three different experiments, each run for 3 years: (i) with an atmospheric CO<sub>2</sub> concentration of 350ppm, (ii) 700ppm and (iii) 1050ppm. Daily mean model output for the total water column of L4 was used. A Hovmöller plot of the C:N ratio ( $R_{C:N}$ ) for the control run, together with the difference between  $R_{C:N}$  at carbon enhancement and control are shown in figure 1.

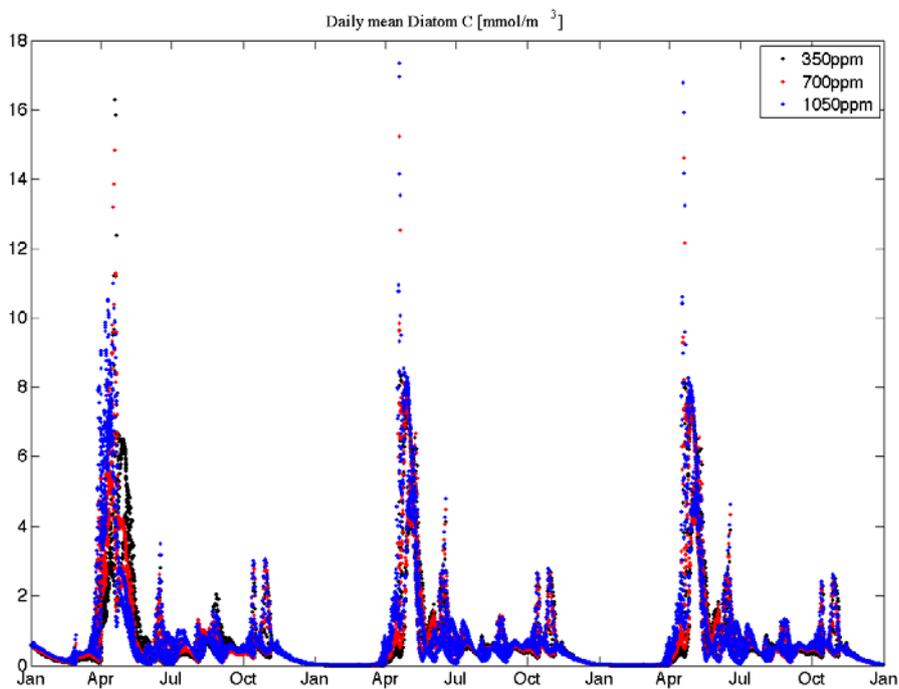


**Fig. 1** Hovmöller plot showing Diatom C ( $\text{mmol m}^{-3}$ ) vs. N ( $\text{mmol m}^{-3}$ ) at the L4 site for experiment (i: top plot), the difference in  $R_{C:N}$  between experiments (ii) and (i) is shown in the middle plot and the difference between experiments (iii) and (i) is shown in the bottom plot.

It is evident from figure 1 that there has been a significant increase in  $R_{C:N}$  from the control run to the carbon enhancement runs. It is further evident from figure 2 that the diatoms are assimilating more carbon at higher CO<sub>2</sub>, as also seen in figure 3. Figure 3 also suggests that the Diatom bloom starts sooner in the high CO<sub>2</sub> runs, as can be explained by the higher availability of carbon.



**Fig. 2** Hovmöller plot showing Diatom C ( $\text{mmol m}^{-3}$ ) at the L4 site for experiment (i; top plot), (ii; middle plot) and (iii; bottom plot).



**Fig. 3** Plot showing the daily mean carbon concentrations in diatoms ( $\text{mmol m}^{-3}$ ) for the three experiments: (i) 350ppm  $\text{CO}_2$  (black), (ii) 700ppm  $\text{CO}_2$  (red) and 1050ppm  $\text{CO}_2$  (blue).

## Conclusions

We have shown that the *carbon enhancement module works for ERSEM*. The model specific feedbacks to enhanced carbon assimilation will be further investigated through WP3, together with further assessment of the proposed parameterisation.

## 4. References

Bellerby R. G. J. , Schulz K. G. , Riebesell U. , Neill C. , Nondal G. , Heegaard E. , Johannessen T. and Brown K. R., 2008. Marine ecosystem community carbon and nutrient uptake stoichiometry under varying ocean acidification during the PeECE III experiment *Biogeosciences*, 5, 1517-1527.

Blackford, J. C., Allen, J. I. and Gilbert, F. J. (2004) Ecosystem dynamics at size contrasting sites: a generic modelling study. *J. Mar. Syst.*, 52, 191–215.

Droop, M.R., (1974). The nutrient status of algal cells in continuous culture. *Journal of the Marine Biological Association of the UK* 54, pp. 825–855.

Egge J. K., Thingstad T. F., Engel A., Bellerby R.G.J, and Riebesell U. (2009). Primary production during nutrient-induced blooms at elevated CO<sub>2</sub> concentrations. *Biogeosciences*, 6, 877-885.

Engel, A., Schulz, K.G., Riebesell, U., Bellerby R.G.J., Delille, B., Schartau, M. (2008). Effects of CO<sub>2</sub> on particle size distribution and phytoplankton abundance during a mesocosm bloom experiment (PeECE II). *Biogeosciences*, 5, 509–521.

Hein M. and Sand-Jensen K. (1997). CO<sub>2</sub> Increases Oceanic Primary Production. *Nature*, 388(6642), 526-527,.

Riebesell U., Schulz K. G., Bellerby R. G. J., Botros M., Fritsche P., Meyerhöfer M. Neill C., Nondal G., Oschlies A. and Wohlers J. (2007). Enhanced biological carbon consumption in a high CO<sub>2</sub> ocean. *Nature*, 450:545-549.

Vichi, M., Pinardi, N. and Masina, S. (2007). A generalized model of pelagic biogeochemistry for the global ocean ecosystem. Part I: Theory. *JMS* 64(2007) 89-109.