Modelling diatom and *Phaeocystis* blooms and nutrient cycles in the Southern Bight of the North Sea: the MIRO model

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Variable	Symbol
Biological state variables:	
Functional and structural motabolitos	DAE
Monomers	DAS
Reserves	DAR
Nanoflagellates: $NE - NEE + NES + NER$	Diffe
Functional and structural metabolites	NEE
Monomers	NES
Reserve products	NFR
Phaeocyctic colonies: $OP = OPE + OPS + OPR + OPM$	
Functional and structural	OPE
Monomers	OPS
Reserve products	OPR
Mucous matrix	OPM
Bacteria	BC
Microzooplankton	MZ
Copepods	CP
Organic matter:	
Monomeric: carbon nitrogen	BSC BSN
Dissolved polymers (high higherradability): carbon (C) nitrogen (N) phosphorus (P)	DC, DN, DP,
Dissolved polymers (low biodegradability): C. N. P	DC_1 , DN_1 , DP_1
Particulate organic matter (high biodegradability): C. N. P	PC_1, PN_1, PP_1
Particulate organic matter (low biodegradability): C. N. P	PC_2 , PN_2 , PP_2
Detrital biogenic silica: Si	BSi
Te encerie enteiente:	
Inorganic nutrients:	NO
Ammonium	NO ₃
Dhesphate	
Silicic acid	DSi
	1001

Appendix 1. MIRO model: the 32 state variables

Description	Symbol
Phytoplankton:	
Photosynthesis	φ_{i} ; i = DA, NF, OP
Growth	μ_i ; i = DA, NF, OP
Reserve/mucus synthesis	s_{ii} i = DAR, NFR, OPR, OPM
Reserve/mucus catabolism	c_{ii} i = DAR, NFR, OPR, OPM
Exudation	e_{ii} , i = DAS, NFS, OPS
Respiration	$resp_{i}$; i = DA, NF, OP
Autolysis	<i>lys</i> ; i = DA, NF, OP
Colony lysis	lyscol
Sedimentation	$sed_{i_{t}}$ i = DA, OP
Nutrient uptake	upt_{PHY}^{*} ; k = NO ₃ , NH ₄ , PO ₄ , SiO; PHY = DA + NF + OP
Zooplankton:	
Grazing	$g_{l/qi}$ l = MZ, CP
	for $l = MZ$, $q = BC$, NF
	l = CP, q = DA, MZ
Growth	μ_{ii} l = MZ, CP
Natural mortality	lys_l ; $l = MZ$, CP
Egestion	eg_{l} ; $l = MZ$, CP
Nutrient regeneration	reg_{1}^{k} ; 1 = MZ, CP; k = NH ₄ , PO ₄
Microbial loop:	
C and nutrient uptake	upt_{BC}^{k} ; k = BSC, BSN, NH ₄ , PO ₄
Growth	μ_{BC}
Natural mortality	lys_{BC}
Ammonification	$reg_{BC}^{NH_4}$
Nitrification	ni
Denitrification	dni
Ectoenzymatic hydrolysis of DOM	$elys_{Di}$; Di = DC _{1,2} = DN _{1,2} = DP _{1,2}
Hydrolysis of POM	$elys_{Di}$; Pi = PC _{1,2} = PN _{1,2} = PP _{1,2}
Dissolution of BSi	lys_{BSi}
Sedimentation of POM	sed_{Pi} ; Pi = PC _{1,2} = PN _{1,2} = PP _{1,2}
Benthos:	
Nitrification	ni ^B
PO ₄ /NH ₄ -adsorption/desorption	ads_{K}^{B} : k = NH ₄ , PO ₄
Nutrient exchanges at the sediment-water interface	J^k ; k = NO ₃ , NH ₄ , PO ₄ , SiO

Appendix 3. The MIRO model: conservation equations

Phytoplankton <i>Diatoms:</i> $DA = DAF + DAS + DAR$; $z = depth$
$\frac{dDAF}{dt} = \mu_{DA} - \left[g_{CP/DA} + lys_{DA} + \frac{1}{z}sed_{DA}\right] \cdot \frac{DAF}{DA}$
$\frac{dDAS}{dt} = \varphi_{DA} - e_{DAS} - s_{DAR} + c_{DAR} - \mu_{DA} - resp_{DA} - \left[g_{CP/DA} + lys_{DA} + \frac{1}{z}sed_{DA}\right] \cdot \frac{DAS}{DA}$
$\frac{dDAR}{dt} = s_{DAR} - c_{DAR} - \left[g_{CP/DA} + lys_{DA} + \frac{1}{z}sed_{DA}\right] \cdot \frac{DAR}{DA}$
Nanophytoflagellates: NF = NFF + NFS + NFR
$\frac{dNFF}{dt} = \mu_{NF} - [g_{MZ/NF} + lys_{NF}] \cdot \frac{NFF}{NF} + [(1 - aggr) \cdot lyscol] \cdot \frac{OPF}{OP}$
$\frac{dNFS}{dt} = \varphi_{NF} - e_{NFS} - s_{NFR} + c_{NFR} - \mu_{NF} - resp_{NF} - [g_{MZ/NF} + lys_{NF}] \cdot \frac{NFS}{NF} + [(1 - aggr) \cdot lyscol] \cdot \frac{OPS}{OP}$
$\frac{dNFR}{dt} = s_{NFR} - c_{NFR} - [g_{MZ/NF} + lys_{NF}] \cdot \frac{NFR}{NF} + [(1 - aggr) \cdot lyscol] \cdot \frac{OPR}{OP}$
Phaeocystis colonies: OP = OPF + OPS + OPR + OPM
$\frac{dOPF}{dt} = \mu_{OP} - \left[lys_{OP} + \frac{1}{z}sed_{OP} + lyscol \right] \cdot \frac{OPF}{OP}$
$\frac{dOPS}{dt} = \varphi_{OP} - e_{OPS} - s_{OPR} + c_{OPR} - s_{OPM} + c_{OPM} - \mu_{OP} - resp_{OP} - \left[lys_{OP} + \frac{1}{z}sed_{OP} + lyscol \right] \cdot \frac{OPS}{OP}$
$\frac{dOPR}{dt} = s_{OPR} - c_{OPR} - \left[lys_{OP} + \frac{1}{z}sed_{OP} + lyscol \right] \cdot \frac{OPR}{OP}$
$\frac{dOPM}{dt} = s_{OPM} - c_{OPM} - \left[lys_{OP} + \frac{1}{z}sed_{OP} + lyscol \right] \cdot \frac{OPM}{OP}$

Zooplankton *Microzooplankton: MZ*

 $\frac{dMZ}{dt} = \mu_{MZ} - lys_{MZ} - g_{CP/MZ}$

dt Copepods: CP

 $\frac{dCP}{dt} = \mu_{CP} - lys_{CP}$

Microbial loop

Bacteria: BC

 $\frac{dBC}{dt} = \mu_{BC} - lys_{BC} - g_{MZ/BC}$ Organic matter: BSC, BSN, DC_i, DN_i, DP_i, PC_i, PN_i, PP_i (i = 1, 2)

Organic carbon

 $\begin{array}{l} \displaystyle \frac{dBSC}{dt} \ = \ elys_{DC1} + elys_{DC2} + lys_{DA} \frac{DAS}{DA} + lys_{NF} \frac{NFS}{NF} + lys_{OP} \frac{OPS}{OP} + e_{DA} + e_{NF} + e_{OP} - upt_{BC}^{BSC} \\ \displaystyle \frac{dDCi}{dt} \ = \ \varepsilon_{di} \ lys_{BIO} + \gamma_{di} eg_{ZOO} - elys_{DCi} + elys_{PCi} + \tau_{di} [1 - aggr] \cdot lyscol \frac{OPM}{OP} \\ \displaystyle \frac{dPCi}{dt} \ = \ \varepsilon_{pi} \ lys_{BIO} + \gamma_{pi} eg_{ZOO} - elys_{PCi} - \frac{1}{z} sed_{PCi} + \tau_{pi} [aggr] \cdot lyscol \\ \displaystyle \text{where} \end{array}$

$$\begin{aligned} lys_{BIO} &= lys_{DA} \frac{DAF + DAR}{DA} + lys_{NF} \frac{NFF + NFR}{NF} + lys_{OP} \frac{OPF + OPR}{OP} + lys_{BC} + lys_{MZ} \\ eg_{ZOO} &= eg_{CP} + eg_{MZ} + lys_{CP} \end{aligned}$$

Organic nitrogen

$$\begin{split} \frac{dBSN}{dt} &= elys_{DN1} + elys_{DN2} - upt_{BC}^{BSN} \\ \frac{dDNi}{dt} &= \varepsilon_{di} lysN_{BIO} + \gamma_{di} egN_{ZOO} - elys_{DNi} + elys_{PNi} \\ \frac{dPNi}{dt} &= \varepsilon_{pi} lysN_{BIO} + \gamma_{pi} egN_{ZOO} + \tau_{pi} [aggr] \cdot lyscol \cdot \frac{OPF}{CN_{PHY}} - elys_{PNi} - \frac{1}{z}sed_{PNi} \\ where \\ lysN_{BIO} &= \frac{1}{CN_{PHY}} \cdot \left[lys_{DA} \cdot \frac{DAF}{DA} + lys_{NF} \cdot \frac{NFF}{NF} + lys_{OP} \frac{OPF}{OP} \right] + \frac{lys_{BC}}{CN_{BC}} + \frac{lys_{MZ}}{CN_{ZOO}} \\ egN_{ZOO} &= fp_{CP} \cdot \left[\frac{1}{CN_{PHY}} \cdot \left[g_{MZ/NF} \cdot \frac{NFF}{NF} + g_{CP/DA} \cdot \frac{DAF}{DA} \right] + \frac{1}{CN_{CP}} \cdot \left[g_{CP/MZ} + g_{MZ/BC} + lys_{CP} \right] \right] \end{split}$$

Organic phosphorus

$$\begin{split} \frac{dDPi}{dt} &= \varepsilon_{di} lys P_{BIO} + \gamma_{di} eg_{ZOO} - elys_{DPi} + elys_{PPi} \\ \frac{dPPi}{dt} &= \varepsilon_{pi} lys P_{BIO} + \gamma_{pi} eg P_{ZOO} + \tau_{pi} [aggr] \cdot lyscol \cdot \frac{OPF}{CP_{PHY}} - elys_{PPi} - \frac{1}{z} sed_{PPi} \\ \text{where} \\ lys P_{BIO} &= \frac{1}{CP_{PHY}} \cdot \left[lys_{DA} \cdot \frac{DAF}{DA} + lys_{NF} \cdot \frac{NFF}{NF} + lys_{OP} \frac{OPF}{OP} \right] + \frac{lys_{BC}}{CP_{BC}} + \frac{lys_{MZ}}{CP_{ZOO}} \\ eg P_{ZOO} &= fp_{CP} \cdot \left[\frac{1}{CP_{PHY}} \cdot \left[g_{MZ/NF} \cdot \frac{NFF}{NF} + g_{CP/DA} \cdot \frac{DAF}{DA} \right] + \frac{1}{CP_{CP}} \cdot \left[g_{CP/MZ} + g_{MZ/BC} + lys_{CP} \right] \right] \end{split}$$

Nutrients

$$\begin{split} \frac{dNO_3}{dt} &= -upt_{PHY}^{NO3} + ni - \frac{1}{z}J^{NO3} \\ \frac{dNH_4}{dt} &= -upt_{PHY}^{NH4} - ni - \frac{1}{z}J^{NH4} + reg_{BC}^{NH4} + reg_{MZ}^{NH4} + reg_{CP}^{NH4} \\ \frac{dPO_4}{dt} &= -upt_{PHY}^{PO4} - upt_{BC}^{PO4} - \frac{1}{z}J^{PO4} + elys_{DPi} + elys_{PPi} + reg_{MZ}^{PO4} + reg_{CP}^{PO4} \\ \frac{dDSi}{dt} &= -upt_{DA}^{DSi} + lys_{BSi} \\ \frac{dBSi}{dt} &= -k_b^{Si}BSi + \frac{1}{CSi} \cdot \left[g_{CP/DA} + \frac{1}{z}sed_{DA}\right] \cdot \frac{DAF}{DA} \end{split}$$

Phytoplankton	
Photosynthesis	
$\varphi_i = k_{\max}^i \left[1 - e^{\frac{-\alpha^i I}{k_{\max}^i}} \right] \cdot i F$	(1)
where $\alpha^i = rac{k_{ ext{max}}^i}{I_k^i}$ and I_k^i = light adaptation	
$I = I_0[1 - a_{sea}] \cdot e^{-\eta z}$	
α_{sea} : sea surface albedo	
$\eta = \eta_m + \eta_{solt} \frac{1}{1 - 1} [DAF + NFF + OPF]$	
CChi	
Lysis and exudation $lys_i = k_{lys}^i \cdot i$	(2)
where $k_{lys}^i = k_{lys\min}^i [1+7.5 \cdot (1-\tilde{N}_i)]$	(3)
$e_i = \varepsilon \cdot iS$	(4)
Synthesis (s) and catabolism (c) of intracellular reserve products	
$S_i = \frac{iS}{iT} - k_s$ where $s_i = sr_{\max}^i \frac{S_i^2}{c^2 - t^2} \cdot iF$	(5)
$L^{i} \qquad S_{i}^{i} + K_{S}^{i}$ $c_{i} = k_{P}^{i} \cdot iR$	(6)
Synthesis (c) and catabolism (c) of <i>Phaeocystic</i> mucus	(-)
$S_{i} = S_{i}^{2} = OPF$	(7)
$S_{OP} = SIIId_{max} \frac{1}{S_i^2 + k_S^2} \cdot OTT$	(7)
$c_{OP} = k_{cR}^i \cdot [OPM - OPM_{\min}]$ where $\mu_i = \mu_{\max}^i \frac{S_i^2}{S_i^2 + k_S^2} \cdot \tilde{N}_i \cdot iF$	(8)
Growth and respiration $S^{2} = z$	
$\mu_i = \mu_{\max}^i \frac{S_i}{S_i^2 + k_S^2} \cdot N_i \cdot iF$	
where $DIN = NO_{+} + NH_{-}$	
$\tilde{N}_{-1} = \frac{DIN \cdot PO_4 \cdot DSi}{DIN \cdot PO_4 \cdot DSi}$	(9)
$k_{P}^{DA} \cdot DIN \cdot DSi + k_{N}^{DA} \cdot PO_{4} \cdot DSi + k_{Si}^{DA} \cdot DIN \cdot PO_{4} + DIN \cdot PO_{4} \cdot DSi$	
$\tilde{N}_{NF,OP} = \frac{DIN \cdot PO_4}{k_N^{NF,OP} \cdot PO_4 + k_P^{NF,OP} \cdot DIN + DIN \cdot PO_4}$	
$resp_i = k_f^i \cdot iF + \xi \mu_i$	(10)
where $\xi = ecs_{NH4} \left[1 - f_{NO3} \right] + ecs_{NO3} f_{NO3}$ (metabolic cost)	
Sedimentation (diatoms, biogenic silica)	
$sed_{DA} = k_{sed}^{DA} DA$	(11)
$sed_{BSi} = k_{sed}^{DA} BSi$	(12)
where $k_{sed}^{DA} = k_{sed\min}^{DA} [1 + 5 \cdot (1 - \tilde{N}_{DA})]$	
Nutrient uptake	
$upt \frac{NO3}{PEIV} = \frac{f_{NO3}}{f_{NO3}} \sum_{\mu_i} \mu_i$	(13)
$CN_{PHY} = CN_{PHY} $	
where $f_{NO3} = 1 - \frac{I_m NH_4}{NH_4 + k_i}$	
$upt_{PHY}^{NH4} = \frac{1 - f_{NO3}}{CN_{PHY}} \sum_{i} \mu_{i}$	(14)
$upt_{DA}^{Si} = \mu_{DA}SiC$	(15)
$upt_{PHY}^{POA} = \frac{1}{2\pi}\sum_{i}\mu_{i}$	(16)
$CP \frac{1}{T}$	

Microzooplankton Grazing $g_{MZ} = g_{MZ/BC} + g_{MZ/NF}$ where: $g_{MZ/BC} = g_{\max}^{MZ/BC} \frac{BC^2}{\left[k_{\sigma}^{MZ/BC}\right]^2 + BC^2} MZ$ (17) $g_{MZ/NF} = g_{\max}^{MZ/NF} \frac{NF^2}{\left[k_{\alpha}^{MZ/BC}\right]^2 + NF^2} MZ$ (18)Growth (19) $\mu_{MZ} = y_{MZ/BC} \cdot g_{MZ/BC} + y_{MZ/NF} \cdot g_{MZ/NF}$ Natural mortality (lysis) $lys_{MZ} = k_d^{MZ} \cdot MZ$ (20)Egestion (21) $eg_{MZ} = fp_{MZ} \cdot g_{MZ}$ Excretion and nutrient regeneration $ex_{MZ} = [1 - fp] \cdot g_{MZ} - \mu_{MZ}$ (22) $reg_{MZ}^{NH4} = [1 - fp] \cdot \left[\frac{1}{CN_{BC}}g_{MZ/BC} + \frac{1}{CN_{PHY}}g_{MZ/NF}NFF / NF\right] - \frac{1}{CN_{MZ}}\mu_{MZ}$ (23) $reg_{MZ}^{POA} = [1 - fp] \cdot \left[\frac{1}{CP_{BC}}g_{MZ/BC} + \frac{1}{CP_{PHV}}g_{MZ/NF}NFF / NF\right] - \frac{1}{CP_{MZ}}\mu_{MZ}$ (24)Copepods Grazing $g_{CP} = g_{\max}^{CP} \frac{DA^2 + MZ^2}{\left[k_{\sigma}^{CP}\right]^2 + DA^2 + MZ^2} CP$ (25) $g_{CP/DA} = g_{CP} \frac{DA}{DA + MZ}$ $g_{CP/MZ} = g_{CP} \frac{MZ}{DA + MZ}$ Growth $\mu_{CP} = y_{CP} \cdot g_{CP}$ (26)Mortality $lys_{CP} = kd_{CP} \cdot CP^2$ (27) Egestion (28) $eg_{CP} = fp_{CP} \cdot g_{CP}$ Excretion and nutrient regeneration $ex_{CP} = [1 - fp]g_{CP} - \mu_{CP}$ (29) $reg_{CP}^{NH4} = [1 - fp] \cdot \left[\frac{1}{CN_{MZ}}g_{CP/MZ} + \frac{1}{CN_{PHY}}g_{CP/DA}DAF/DA\right] - \frac{1}{CN_{CP}}\mu_{CP}$ (30) $reg_{CP}^{PO4} = [1 - fp] \cdot \left[\frac{1}{CP_{MZ}}g_{CP/MZ} + \frac{1}{CP_{PHV}}g_{CP/DA}DAF / DA\right] - \frac{1}{CP_{CP}}\mu_{CP}$ (31)

 $\begin{aligned} & \text{Microbial loop} \\ & Bacteria \\ & \text{Growth} \\ & \mu_{BC} = y_{BC} \cdot upt_{BC} \end{aligned} \tag{32} \\ & \text{Carbon and nutrient uptake} \\ & upt_{BC}^{BSC} = b_{\max} \frac{S^{ut}}{S^{ut} + k_{BSC}} BC \end{aligned} \tag{33}$

where
$$S^{ut} = BSC - 0.1 \cdot k_{BSC}$$

Carbon and nutrient uptake (continued) N uptake	
$upt_{BC}^{N} = upt_{BC}^{BSC} \cdot \frac{BSN}{BSC}$	(34)
P uptake	
$upt_{BC}^{PO4} = \frac{1}{CP_{BC}}\mu_{BC}$	(35)
N regeneration (ammonification)	
$reg_{BC}^{NH4} = upt_{BC}^N - \frac{1}{CN_{BC}}\mu_{BC}$	(36)
Nitrification	
$mi = mi_{\max} \frac{NH_4}{NH_4 + k_{ni}^{NH4}}$	(37)
Lysis	
$lys_{BC} = k_d^{BC} BC$	(38)
<i>Organic matter</i> <i>i</i> : (1) labile polymers; (2) semi-labile polymers Ecto-hydrolysis of dissolved polymers	
$elys_{DC_i} = ei_{\max} \frac{DCi}{DCi + ki_b} BC$	(39)
$elys_{DNi} = elys_{DCi} \frac{DNi}{DCi}$	(40)
$elys_{DPi} = elys_{DCi} \frac{DPi}{DCi}$	(41)
Hydrolysis of particulate organic matter	
$I_{YSPCi} = k_i b \cdot PCi$ $I_{YSPNi} = k_i b \cdot PNi$	(42) (43)
$i_{y_{SPPi}} = k_i b \cdot PPi$ $i_{y_{SP2i}} = k_i b \cdot BSi$	(44)
	(43)
Sedimentation of particulate organic matter $sed_{PCi} = k_{sed} \cdot PCi$	(46)
$sed_{PNi} = k_{sed} \cdot PNi$ $sed_{PNi} = k_{sed} \cdot PPi$	(47) (48)
Benthic processes (other than organic matter degradation)	()
Nitrification	
$ni^p = ni_{max}^p NH_4$	(49)
Ammonium adsorption/desorption	
$ads^B_{NH4} = k_{am}NH_4$	(50)
Phosphate adsorption/desorption	
Oxic layer	
$ads^B_{PO4} = k_{pa}PO_4$	(51)
Anoxic layer	
Anoxic layer $ads_{PO4}^B = k_{pe}PO_4$	(52)
Anoxic layer $ads_{PO4}^{B} = k_{pe}PO_{4}$ Temperature dependence of physiological parameters	(52)

Appendix 5. The MIRO model: parameters. *Temperature-dependent; **nutrient stress-dependent. State variables: F (functional and structural metabolites), R (reserve products), S (monomers)

Symbol	Description	Unit	Value	Origin and source
Phytoplankto Carbon metal	n polism losses			
k_{\max}^{DA} *	Max. photosynthetic capacity rate of DA at optimal temperature	h^{-1}	0.12	Estimated from photosynthesis–light relationship data (C. Lancelot & V. Rousseau unpubl.)
$k_{ m max}^{N\!F}$ *	Max. photosynthetic capacity rate of NF at optimal temperature	h^{-1}	0.10	Estimated from photosynthesis–light relationship data (C. Lancelot & V. Rousseau unpubl.)
$k_{ m max}^{OP}$ *	Max. photosynthetic capacity rate of OP at optimal temperature	h^{-1}	0.30	Estimated from photosynthesis–light relationship data (Lancelot & Mathot 1987)
I_k	Light adaptation parameter	$\mu mol \; m^{-2} \; s^{-1}$	20 to 65	Photo-adaptation to ambient light (Lancelot et al. 1991)
smu_{max} *	Max. rate of OP mucus synthesis	h^{-1}	0.20	Estimated from photosynthesis–light relationship data (Lancelot & Mathot 1987)
μ_{max}^{DA} *	Max. F synthesis rate of DA at optimal temperature	h^{-1}	0.05	Estimated from temperature dependence (protein synthesis) experiments (Lancelot et al. 1998)
μ_{max}^{NF} *	Max. F synthesis rate of NF at optimal temperature	h^{-1}	0.09	Estimated from temperature dependence (protein synthesis) experiments (Lancelot et al. 1998)
μ_{max}^{OP} *	Max. F synthesis rate of OP at optimal temperature	h^{-1}	0.09	Estimated from temperature dependence (protein synthesis) experiments (Lancelot et al. 1998, Schoemann et al. 2004)
sr ^{DA} _{max} *	Max. R synthesis rate of DA at optimal temperature	h^{-1}	0.10	Estimated from best fitting of ¹⁴ C time-course exp. (e.g. Lancelot & Mathot 1985a, Mathot et al. 1992) using AQUAPHY equations
sr ^{NF} *	Max. R synthesis rate of NF at optimal temperature	h^{-1}	0.10	Estimated from best fitting of ¹⁴ C time-course exp. (e.g. Mathot et al. 1992) using AQUAPHY's equations
<i>ST</i> ^{<i>OP</i>} * [*]	Max. R synthesis rate of OP at optimal temperature	h^{-1}	0.10	Estimated from best fitting of ¹⁴ C time-course exp. (e.g. Lancelot & Mathot 1985b, Mathot et al. 1992) using AQUAPHY equations
k_s	Half saturation constant of S assimilation	mgC:mgC	0.06	Adjusted from ¹⁴ C experiments (Mathot et al. 1992)
k_{cR}^{DA}	Specific rate of DAR catabolism	h^{-1}	0.06	Estimated from best fitting of ¹⁴ C time-course experiment using AQUAPHY equations (e.g. Lancelot & Mathot 1985a, Mathot et al. 1992)
k_{cR}^{NF}	Specific rate of NFR catabolism	h^{-1}	0.06	Estimated from best fitting of ¹⁴ C time-course exp. (e.g. Mathot et al. 1992) using AQUAPHY equations
k_{cR}^{OP}	Specific rate of OPR catabolism	h^{-1}	0.06	Estimated from best fitting of ¹⁴ C time-course exp. (e.g. Lancelot & Mathot 1985b, Mathot et al. 1992) using AQUAPHY equations
k_F^{DA}	Constant of DA cell maintenance	h^{-1}	0.0004	Diatoms cultures in the dark (Verity 1982)
k_F^{NF}	Constant of NF cell maintenance	h^{-1}	0.0008	Estimated
k_F^{OP}	Constant of OP cell maintenance	h^{-1}	0.0008	Estimated
ecs _{NO3}	Energy cost of F synthesis (NO ₃ source)	mol C:mol C	0.8	Penning-De Vries et al. (1974)
ecs_{NO4}	Energy cost of F synthesis (NH ₄ source)	mol C:mol C	0.4	Penning-De Vries et al. (1974)
3	Excretion constant	h^{-1}	0.001	Average from photosynthesis/excretion light curves (Lancelot 1979, 1983)
k_{lys}^{DA**} min	Minimum specific rate of DA cellular autolysis	h^{-1}	0.0016	Adjusted based on Brussaard et al. (1995)
k_{lys}^{NF**} min	Minimum specific rate of NF cellular autolysis	h^{-1}	0.0025	Adjusted based on Brussaard et al. (1995)
k_{lys}^{OPC**} min	Minimum specific rate of 0P cellular autolysis	h^{-1}	0.003	Adjusted based on Brussaard et al. (1995)
$k_{lyscol_{\min}}$	Minimum specific rate of colony lysis	h^{-1}	0.002	Adjusted
$k_{lyscol_{\max}}$	Max. specific rate of colony lysis for $\frac{OPF}{OPM} > 1.7$	h^{-1}	0.02	
aggr	Fraction of colony lysis products that aggregates	Dimensionless	0.25	Adjusted
k_{sed}^{DA} ** $_{ m min}^{ m min}$ k_{sed}^{OP} ** $_{ m min}$	Minimum diatom (DA) sinking rate Minimum <i>Phaecystis</i> colony (OP) sinking rate	${ m m}~{ m h}^{-1} { m m}~{ m h}^{-1}$	0.0085 0.0085	SetCol experiments (Lancelot et al. 2004) SetCol experiments (Lancelot et al. 2004)

Appendix 5 (continued)

Symbol	Description	Unit	Value	Origin and source
Nutrient up	take			
k_N^{DA}	Half saturation constant for DIN uptake (DA)	mmol N m $^{-3}$	0.80	Size-adjusted from literature (Stolte 1996)
$k_N^{N\!F}$	Half saturation constant for DIN uptake (NF)	mmol N m $^{-3}$	0.50	Size-adjusted from literature (Stolte 1996)
k_N^{OP}	Half saturation constant for DIN uptake (OP)	mmol N m $^{-3}$	2	Size-adjusted from literature (Lancelot et al. 1986, Stolte 1996)
i_m	Max. rate of NO_3 uptake inhibition by NH_4	mmol N:mmol N	0.8	Elskens et al. (1997)
k_i	Half saturation constant of NO_3 uptake inhibition by NH_4	mmol N m-3	0.57	Tungeraza (2000)
k_P^{DA}	Half saturation constant for PO4 uptake (DA)	mmol P m ⁻³	0.3	Size-adjusted from literature
k_P^{NF}	Half saturation constant for PO ₄ uptake (NF)	mmol P m ⁻³	0.1	Size-adjusted from literature
k ^{OP}	Half saturation constant for PO_4 uptake (OP)	mmol P m $^{-3}$	0.001	Chosen very low to consider ability to use organic P (Veldhuis et al. 1991)
k_{DSi}^{DA}	Half saturation constant for Si uptake (DA)	mmol Si m $^{-3}$	0.40	Adjusted to average minimum ambient concentration at 330
Cellular stoi	chiometry			
CChl	Chl <i>a</i> :C ratio for F metabolites	mg chl:mg C	0.04	Estimated from biochemical composition of field phytoplankton (growing phase) (Lancelot-Van Beveren 1980)
CN_{PHY}	C:N ratio for F metabolites	mmol C:mmol N	4.10	Estimated from protein and chl <i>a</i> content of field phytoplankton (growing phase) (Lancelot-Van Beveren 1980)
CP_{PHY}	C:P ratio for F metabolites	mmol C:mmol P	65	Biochemical composition (Lancelot- Van Beveren 1980, Redfield et al. 1963)
SiC	Si:C ratio for DAF metabolites	mmol Si:mmol C		Rousseau et al. (2002)
	Days 1 to 150 early spring diatom Days 151 to 365: spring-summer diatoms		0.36 0.11	
Temperatur T ^{DA}	e adaptation	°C	5 5	Lancolot et al. (1008), Rousseau (2000)
1 opt	Days 1 to 150 early spring diatom Days 151 to 365: spring-summer diatoms	C	15	Lancelot et al. (1330), Rousseau (2000)
T_{opt}^{NF}	NF optimal growth temperature	°C	15	Lancelot et al. (1998), Schoemann et al. (2004)
I opt	DA temperature interval	-C	15	Lancelot et al. (1998), Schoemann et al. (2004)
UI _{DA}	DA temperature interval Days 1 to 150 Days 151 to 365	°C	1.6 12	Lancelot et al. (1998), Rousseau (2000)
dT_{NF}	NF temperature interval	°C	12	Lancelot et al. (1998), Schoemann et al. (2004)
dT_{OP}	<i>OP</i> temperature interval	°C	12	Lancelot et al. 1998; Schoemann et al. (2004)
Microzoopl	ankton MZ			
Carbon met	abolism and losses			
$g_{\max}^{MZ/BC*}$	Max. specific grazing rate on bacteria BC (optimal temperature)	h ⁻¹	0.05	Adjusted from grazing experiments (Becquevort 1999)
$g_{\max}^{MZ\!/\!NF*}$	Max. grazing rate on nanoflagellates NF (optimal temperature)	h^{-1}	0.04	Adjusted from grazing experiments (Weisse & Scheffel-Möser 1990, Becquevort 1999)
$k_{ m g}^{MZ/BC}$	Half saturation constant for grazing on BC	mg C m ⁻³	40	Adjusted from grazing experiments (Becquevort 1999)
$k_{ m g}^{MZ/NF}$	Half saturation constant for grazing on NF	mg C m^{-3}	5	Adjusted from grazing experiments (Weisse & Scheffel-Möser 1990, Becquevort 1999)
Y _{MZ/NF}	Growth efficiency (prey = NF)	Dimensionless	0.35	Estimated from Hansen (1992)
Y _{MZ/BC}	Growth efficiency (prey = BC)	Dimensionless	0.1	Estimated (= 0.3×0.3)
fp_{MZ}	Egested fraction of ingestion	Dimensionless	0.25	Arbitrary
k_d^{MZ*}	Mortality rate	h^{-1}	0.002	Estimated from Billen et al (1990)
Cellular stoichiometry				
CN_{MZ}	C:N ratio	mg C:mmol N	63	Redfield et al. (1963)
NP_{MZ}	N:P ratio	mol N:mol P	16	Redfield et al. (1963)
CP_{MZ}	C:P ratio	mg C:mmol P	1008	Redfield et al. (1963)
Temperature adaptation				
T_{opt}^{MZ}	Optimal temperature	°C	15	Adjusted to prey temperature dependence
dT_{MZ}	Temperature interval	°C	12	Adjusted to prey temperature dependence

Appendix 5 (continued)

Symbol	Description	Unit	Value	Origin and source
Copepods: CP	nlism and losses			
$g_{\rm max}^{CP}$ $k_{\rm g}^{CP}$ y_{CP}	Max. specific grazing rate (optimal temperature) Half-saturation constant for grazing on DA+ MZ Growth efficiency	h ⁻¹ mg C m ⁻³ Dimensionless	0.04 50 0.25	Estimated from grazing data (Daro 1985) Estimated from grazing data (Daro 1985) Hecq (1981)
$fp_{CP}\ kd_{CP}^{*}$	Egested fraction of ingestion Mortality rate	$\begin{array}{c} \text{Dimensionless} \\ h^{-1} \end{array}$	0.25 0.0003	Average from literature Adjusted (quadratic closure term)
Cellular stoichi	iometry C.N., I	C IN	60	
CN _{CP}	C:N ratio	mg C:mmol N	63 16	Redfield et al. (1963)
CP	C.P. ratio	ma Commol P	1008	Redfield et al. (1963) Redfield et al. (1963)
С1 СР		ing C.ininoi i	1000	Reulield et al. (1903)
T_{opt}^{CP}	Optimal growth temperature	°C	16	Adjusted from observed seasonal cycle (Hecq 1981)
dT_{CP}	Temperature interval	°C	12	Adjusted from observed seasonal cycle (Hecq 1981)
Microbial loop)			
Organic matter	c			
ϵ_{D1}	Labile DOM (D1) share of lysis products	Dimensionless	0.3	Adjusted
ϵ_{D2}	Semi-labile DOM (D2) share of lysis products	Dimensionless	0.2	Adjusted
ϵ_{P1}	Labile POM (P1) share of lysis products	Dimensionless	0.1	Adjusted
ϵ_{P2}	Semi-labile POM (P2) share of lysis products	Dimensionless	0.4	Adjusted
τ_{d1}	Labile DOM share of OPM lysis products	Dimensionless	0.5	Adjusted
τ_{p1}	Labile POM share of OP aggregates	Dimensionless	0.5	Adjusted
$\gamma_{D1}^{CP,MZ}$	Labile DOM share of fecal pellets	Dimensionless	0.1	Adjusted
$\gamma_{D2}^{CP,MZ}$	Semi-labile DOM share of fecal pellets	Dimensionless	0.2	Adjusted
γ_{P1}^{P1}	Labile POM share of fecal pellets	Dimensionless	0.3	Adjusted
γ _{P2} , Bacterioplankt	on	Dimensioniess	0.4	Adjusted
el _{max}	Max. specific rate of D1 ecto-enzymatic hydrolysis at optimal temperature	n -	0.75	Microbial bio-assay (Billen & Servais 1989)
e2 _{max} *	Max. specific rate of D2 ecto-enzymatic hydrolysis at optimal temperature	h ⁻¹	0.25	Microbial bio-assay (Billen & Servais 1989)
k1 _h	Half saturation constant for D1 ecto- enzymatic hydrolysis	mg C m ⁻³	250	Microbial bio-assay (Billen & Servais 1989)
$k2_h$	Half saturation constant for D2 ecto- enzymatic hydrolysis	mg C m⁻³	2500	Microbial bio-assay (Billen & Servais 1989)
b_{\max} *	Max. specific rate of BS uptake at optimal temperature	h^{-1}	0.6	Microbial bio-assay (Billen & Servais 1989)
k _{BSC} YBC	Half saturation constant for BSC uptake Growth efficiency	mg C m ⁻³ Dimensionless	25 0.2	Microbial bio-assay (Billen & Servais 1989) Mean estimate from North Sea data (Billen et al. 1991)
k_d^{BSC*}	Autolysis specific rate at optimal temperatue	h^{-1}	0.01	Adjusted
ni _{max}	Max. rate of nitrification	mmol N m ⁻³ h ⁻¹	0.03	Unknown & Adjusted for BCZ
k_{ni}^{NH4}	Half saturation constant for nitrification	mmol N m ⁻³	5	Unknown & Adjusted for BCZ
Cellular stoichi	iometry			
CN_{BC}	C:N ratio	mg C:mmol N	56	Compilation (Kirchman 2000)
NP_{BC}	N:P ratio	mol N:mol P	16	Redfield et al. (1963)
CP_{BC}	C:P ratio	mg C:mmol P	896	Redfield et al. (1963), Kirchman (2000)
Temperature a T ^{BC} _{opt}	daptation Optimal temperature	°C	30	Compilation for temperate systems (Billen et al. 1991)
dT_{BC}	Temperature interval	°C	18	Compilation for temperate systems (Billen et al. 1991)
POM degradation and benthic diagenesis				
D_i	Apparent diffusion coefficient (interstitial phase)	$\mathrm{m}^2 \mathrm{h}^{-1}$	$1.8 imes 10^{-5}$	Fick's law
D_s	Mixing coefficient (solid phase)	$m^2 h^{-1}$	1.8×10^{-6}	Fick's law
k_{1b}^{*}	Hydrolysis rate of PC_1 at T_{opt}	h^{-1}	0.005	Billen et al. (1989)
k_{2b}	Hydrolysis rate of PC ₂	h^{-1}	0.00025	Billen et al. (1989)
k_{1p}^{*}	Hydrolysis rate of PP_1 at T_{opt}	h^{-1}	0.05	Billen et al. (1989)
k_{2p}	Hydrolysis rate of PP ₂	h^{-1}	0.0025	Billen et al. (1989)
k_{BSi}	Biogenic silica dissolution rate	h^{-1}	0.0002	Adjusted
ni_{\max}^B	Benthic nitrification constant	Dimensionless	1	Billen et al. (1989)
k _{am}	NH ₄ adsorption constant	Dimensionless	6	Adjusted from Krom & Berner (1980a)
k _{pa}	PO ₄ adsorption constant (oxic layer)	Dimensionless	1	Adjusted
K_{pe} T^{BC}	PO_4 adsorption constant (anoxic layer)	Dimensionless	0.5	Adjusted from Krom & Berner (1980a,b)
1 opt	Optimal temperature	°C	3U 10	Identical to planktonic bacteria
$u I_{BC}$	remperature interval	-C	10	identical to planktonic bacteria

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