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Sakina-Dorothee Ayata, Marina Lévy, Olivier Aumont, Antoine Sciandra, Jacques Sainte-Marie, et al.. Phytoplankton growth formulation in marine ecosystem models: should we take into account photo-acclimation and variable stoichiometry in oligotrophic areas?. *Journal of Marine Systems*, 2013, 125, pp.29-40. 10.1016/j.jmarsys.2012.12.010 . hal-00820981v2

HAL Id: hal-00820981

<https://hal.science/hal-00820981v2>

Submitted on 30 Aug 2013

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Accepted Manuscript

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PII: S0924-7963(13)00002-X
DOI: doi: [10.1016/j.jmarsys.2012.12.010](https://doi.org/10.1016/j.jmarsys.2012.12.010)
Reference: MARSYS 2315

To appear in: *Journal of Marine Systems*

Received date: 28 December 2011
Revised date: 11 December 2012
Accepted date: 28 December 2012

Please cite this article as: Ayata, S.-D., Lévy, M., Aumont, O., Sciandra, A., Sainte-Marie, J., Tagliabue, A., Bernard, O., Phytoplankton growth formulation in marine ecosystem models: Should we take into account photo-acclimation and variable stoichiometry in oligotrophic areas?, *Journal of Marine Systems* (2013), doi: [10.1016/j.jmarsys.2012.12.010](https://doi.org/10.1016/j.jmarsys.2012.12.010)

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Phytoplankton growth formulation in marine ecosystem models: should we take into account photo-acclimation and variable stoichiometry in oligotrophic areas?

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Abstract

The aim of this study is to evaluate the consequences of accounting for variable Chl:C (chlorophyll:carbon) and C:N (carbon:nitrogen) ratios in the formulation of phytoplankton growth in biogeochemical models. We compare the qualitative behaviour of a suite of phytoplankton growth formulations with increasing complexity: 1) a Redfield formulation (constant C:N ratio) without photo-acclimation (constant Chl:C ratio), 2) a Redfield formulation with diagnostic chlorophyll (variable and empirical Chl:C ratio), 3) a quota formulation (variable C:N ratio) with diagnostic chlorophyll, and 4) a quota formulation with prognostic chlorophyll (dynamic variable). These phytoplankton growth formulations are embedded in a simple marine ecosys-

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tem model in a 1D framework at the Bermuda Atlantic Time-series (BATS) station. The model parameters are tuned using a stochastic assimilation method (micro-genetic algorithm) and skill assessment techniques are used to compare results. The lowest misfits with observations are obtained when photo-acclimation is taken into account (variable Chl:C ratio) and with non-Redfield stoichiometry (variable C:N ratio), both under spring and summer conditions. This indicates that the most flexible models (i.e., with variable ratios) are necessary to reproduce observations. As seen previously, photo-acclimation is essential in reproducing the observed deep chlorophyll maximum and subsurface production present during summer. Although Redfield and quota formulations of C:N ratios can equally reproduce chlorophyll data the higher primary production that arises from the quota model is in better agreement with observations. Under the oligotrophic conditions that typify the BATS site no clear difference was detected between quota formulations with diagnostic or prognostic chlorophyll.

Keywords: Biogeochemical modelling, Phytoplankton, Photo-acclimation, Redfield ratio, Internal quota, BATS, Optimization, Micro-genetic algorithm.

1. Introduction

2 During the last twenty years, marine ecosystem (or biogeochemical) mod-
3 els have been widely used to study the response of primary production to
4 perturbation of the physical environment along a wide range of temporal
5 and spatial scales. Most of these models follow the same general structure:
6 they use nitrogen as the main currency, and account for a simplified food-web

7 which generally includes phytoplankton and zooplankton, and a regeneration
8 network with detritus, dissolved organic nitrogen, and various nutrients (i.e.,
9 Fasham et al., 1990). Whereas the complexity of marine biogeochemical mod-
10 els has increased in the last decade (reaching sometimes about eighty state
11 variables as in Follows et al., 2007), simple phytoplankton growth models are
12 still usually embedded within these ecosystem models, with strong simplifica-
13 tions on phytoplankton physiology, such as using constant C:N stoichiometry
14 or not accounting for photo-acclimation (using constant Chl:C ratio).

15 Phytoplankton growth formulations involving different complexities in
16 the representation of physiological processes (such as photosynthesis, nutri-
17 ent uptake, photo-acclimation, or energy storage) have been derived from
18 laboratory experiments (Zonneveld, 1998; Baklouti et al., 2006). However,
19 directly transposing the relationships derived from these laboratory exper-
20 iments, which generally involve a single phytoplankton species and explore
21 a limited set of forcing conditions (nutrient supply, temperature, light), to
22 global marine ecosystem models is not straightforward and is currently the
23 subject of some debates (Flynn, 2003a; Franks, 2009; Flynn, 2010; Anderson,
24 2010).

25 The simplest phytoplanktonic growth formulations use a classical Michaelis-
26 Menten representation of nutrient uptake (Monod, 1949, 1950) and assume
27 constant stoichiometry between carbon, nitrogen and phosphorus (Redfield
28 et al., 1963). In these models, phytoplankton are represented by a single state
29 variable, the phytoplankton biomass, expressed in nitrogen, phosphorus or
30 carbon currency. Because of their relative simplicity, these models are gen-
31 erally used for global scale studies (Aumont and Bopp, 2006; Follows et al.,

2007; Dutkiewicz et al., 2009). More sophisticated formulations, inspired from the original work of Droop (1968, 1983), explicitly account for the dynamics of internal quotas of phytoplanktonic cells (Flynn, 2008; Klausmeier et al., 2004; Bougaran et al., 2010; Mairet et al., 2011; Bernard, 2011). In these formulations, phytoplankton are represented by at least two variables, usually the phytoplankton biomass in both carbon and nitrogen currency. This allows to decouple the dynamics of nutrient uptake from carbon fixation, depending on the physiological state of phytoplankton. Various versions of such formulations have been successfully applied to 1D marine ecosystem models (Lancelot et al., 2000; Allen et al., 2002; Lefèvre et al., 2003; Mongin et al., 2003; Blackford et al., 2004; Salihoglu et al., 2008) and also attempted in 3D ecosystem models (Tagliabue and Arrigo, 2005; Vichi et al., 2007; Vichi and Masina, 2009; Vogt et al., 2010).

The dynamics of pigment contents, most frequently of chlorophyll *a* (Chl), can also be represented with different levels of complexity. The Chl:C ratios can either be constant (no photo-acclimation), diagnostic (from an empirical (Cloern et al., 1995; Bernard, 2011) or a mechanistic (Geider and Platt, 1986; Doney et al., 1996; Bissett et al., 1999) static relationship), or prognostic (i.e., with a dynamic evolution) (Flynn and Flynn, 1998; Geider et al., 1998; Baumert and Petzoldt, 2008; Ross and Geider, 2009). For instance, Geider et al. (1998) proposed a phytoplankton growth formulation calibrated for chemostat experiments, in which chlorophyll production is proportional to both nitrogen assimilation and carbon fixation.

The different behaviours associated to these different growth formulations have generally been examined in the context of laboratory experiments

57 (Vatcheva et al., 2006), i.e. for monospecific cultures under a limited set
58 of idealized forcing. Significant variations from Redfield stoichiometry ob-
59 served in experimental data of nutrient-limited phytoplankton cultures have
60 highlighted the limits of the Redfield-Monod-type models and the need for
61 non-Redfieldian formulations (quota formulations) (Sciandra, 1991; Dearman
62 et al., 2003; Flynn, 2003a, 2010). Besides, formulations that assume con-
63 stant Chl:C ratio fail to reproduce experimental data (Flynn et al., 2001)
64 or *in situ* observations (Doney et al., 1996; Lévy et al., 1998; Spitz et al.,
65 1998). However, it is not straightforward to find the right trade-off between a
66 model which is too simple to reproduce the observed dynamics and a complex
67 model with too many free parameters to tune against limited data (Flynn,
68 2003b). Based on comparisons with laboratory experiments, Flynn (2003a)
69 suggested that quota-type models with empirical Chl:C relationship "should
70 be adequate for most oceanographic modeling scenarios", although it must
71 be kept in mind that even if a model using simplified assumptions may fit to
72 observed data, it may not be acceptable (Mitra et al., 2007; Flynn, 2010).

73 A rigorous comparison of the qualitative and quantitative behaviours of
74 Redfield, quota-type, and mechanistic models in more realistic oceanic con-
75 ditions remains an open question. Based on model results at the Bermuda
76 Atlantic Time-series Study (BATS) site, Schartau et al. (2001) suggested
77 that an optimized model (i.e., after data assimilation procedure) with Red-
78 field stoichiometry may not be able to correctly simulate primary production
79 in oligotrophic subtropical regions, but, in an optimized marine ecosystem
80 model of the Northwestern Mediterranean Sea, Faugeras et al. (2003) could
81 not decipher significant differences between Redfield and quota growth for-

82 mulations.

83 In this context, the present work aims at comparing, in a rigorous frame-
84 work, the qualitative and quantitative behaviours of different formulations of
85 phytoplankton growth in an oceanographic context and to determine whether
86 increasing complexity leads to significant improvement of the seasonal dy-
87 namics of phytoplankton. This is examined with a 1D ecosystem model
88 which simulates a seasonal cycle at BATS station. This site was chosen
89 because strongly variable Chl:C and C:N ratios have been observed at this
90 station over the year (for the phytoplankton and the particulate organic mat-
91 ter, respectively; Sambrotto et al., 1993; Michaels and Knap, 1996; Steinberg
92 et al., 2001). A coherent suite of consistent phytoplankton growth formula-
93 tions is constructed by adding stepwise complexity. Constant, diagnostic,
94 and prognostic Chl:C ratios are considered with Redfield stoichiometry or
95 with variable C:N ratio. All formulations are then incorporated within the
96 same ecosystem model applied in a 1D framework at BATS. Data assimila-
97 tion through micro-genetic algorithm is used to calibrate the different models.
98 This enables to compare the different formulations on the basis of their best
99 performance relatively to standard observations.

100 After briefly presenting the study site, we describe the general structure of
101 the marine ecosystem model and the different phytoplankton growth formu-
102 lations. Then we present the micro-genetic algorithm used to tune the model
103 parameters. In the Results section, the outputs of the different formulations
104 are described and the skill of each formulation to reproduce observations
105 is assessed. Finally, the choice of the phytoplankton growth formulation in
106 marine biogeochemical models is discussed.

107 2. Models and methods

108 2.1. Study site

109 The Bermuda Atlantic Time-series Study (BATS) site is located in the
110 Sargasso Sea, in the western North Atlantic subtropical gyre (31°40' N,
111 64°10' W). This station has been monthly sampled since October 1988 as
112 part of the US Joint Global Ocean Flux Study (JGOFS) program and the
113 data are freely available at <http://bats.bios.edu/index.html>. The sea-
114 sonal dynamics of nitrate, chlorophyll and primary production at BATS have
115 been described by Steinberg et al. (2001). In winter, strong vertical mixing
116 supplies nutrients to the surface layers, allowing a moderate bloom to occur
117 between January and March. In summer, nutrient supply collapses because
118 of thermal stratification and primary production is low, with a subsurface
119 chlorophyll maximum (60-120 m). *In situ* measurements also indicate that
120 the stoichiometric ratios of particulate C, N and P deviate from the tradi-
121 tional Redfield ratios, especially during the oligotrophic summer (Michaels
122 and Knap, 1996; Cotner et al., 1997; Steinberg et al., 2001).

123 2.2. General model structure

124 The general structure of the model is a simple 'NPZD' type ecosystem,
125 used in a 1D-framework which simulates the seasonal cycle of phytoplankton
126 at BATS station. We used the LOBSTER marine ecosystem model, which
127 has been previously used and calibrated for the North Atlantic (Lévy et al.,
128 2005; Kremer et al., 2009; Lévy et al., 2012). Besides phytoplankton (P_N),
129 the ecosystem model has five additional prognostic variables expressed in ni-
130 trogen units (mmolN.m^{-3}): Nitrate (NO_3), Ammonium (NH_4), Zooplankton

131 (Z_N), Detritus (D_N), and Dissolved Organic Matter (DOM) (Fig. 1). The
 132 photosynthetic available radiation (PAR) is derived from a two-wavelengths
 133 light absorption model, with absorption coefficients depending on the lo-
 134 cal phytoplankton concentrations. The detailed equations of the LOBSTER
 135 model are presented in Table 1. The definition of the parameters and their
 136 default values are presented in Table 2.

137 2.3. Model implementation

138 The ecosystem model is embedded in a simple 1D physical model, which
 139 accounts for the observed seasonal evolution of the mixed layer depth (MLD)
 140 and temperature at BATS in 1998. The 1D-model has 30 vertical layers,
 141 with a vertical discretization of 10 m from 0-100 m and then increasing
 142 with depth. Only vertical diffusion is taken into account. Monthly values
 143 of observed MLD, temperature and salinity at BATS in 1998 are used and
 144 linearly interpolated in time at each model time-step. The vertical eddy
 145 diffusivities K_z are diagnosed from the MLD: they are set to $1 \text{ m}^2 \cdot \text{s}^{-1}$ within
 146 the mixed layer and to $10^{-5} \text{ m}^2 \cdot \text{s}^{-1}$ below the mixed layer. A specific reaction
 147 term sm_s (source minus sink) is added to the diffusion equation. For each of
 148 the state variables i , the prognostic equation reads as follows:

$$\frac{\partial C_i}{\partial t} = \frac{\partial}{\partial z} \left(K_z \frac{\partial C_i}{\partial z} \right) + sm_s(C_i) \quad (1)$$

149 where C_i is the tracer concentration. The initial nitrate conditions are set
 150 to *in situ* observations at BATS in January 1998, whereas they are set to
 151 $0.1 \text{ mmolN} \cdot \text{m}^{-3}$ for the dissolved organic matter, to $0.03 \text{ mmolN} \cdot \text{m}^{-3}$ for
 152 the ammonium (Lipschultz, 2001), and to extremely low values for the other

153 state variables (10^{-8} mmolN.m⁻³). The biophysical model is spun up for one
154 year and a time step of 1.2 hours is used.

155 2.4. Increasing the complexity in the representation of phytoplankton

156 The complexity of phytoplankton growth formulations is progressively
157 increased. Four levels of complexity are compared: 1) a Redfield formula-
158 tion with constant Chl:C ratio, 2) a Redfield formulation with a diagnostic
159 Chl:C ratio, 3) a quota formulation with a diagnostic Chl:C ratio, and 4) a
160 quota formulation with a prognostic Chl:C ratio. In these formulations, the
161 phytoplankton compartment is thus represented by 1, 2 or 3 state variables.
162 For convenience, these formulations have then been named P1.0, P1.5, P2.5,
163 and P3.0 respectively, with the arbitrary convention that a prognostic state
164 variable counts for one and a diagnostic variable (chlorophyll) counts for a
165 half.

166 2.4.1. Redfield stoichiometry and constant Chl:C ratio (P1.0 formulation)

167 In the simplest formulation, phytoplankton are represented by a unique
168 state variable (P1.0 formulation) (Fig. 2A, Tables 4 and 5). The phytoplank-
169 ton carbon biomass P_C and nitrogen biomass P_N are related by a constant
170 Redfield ratio $R_{C:N} = P_C/P_N = 6.56$ molC.molN⁻¹. The Chl:C ratio $R_{Chl:C}$
171 of the phytoplanktonic cells is also assumed to be constant and equal to
172 $1/60$ gChl.gC⁻¹ (Fasham et al., 1990). Nitrogen uptake accounts for light
173 and nutrient limitation. Light limitation L_I is defined according to Webb
174 et al. (1974). Note that in order to keep the models as simple as possi-
175 ble, this expression is shared by the four phytoplankton growth formulations
176 P1.0, P1.5, P2.5, and P3.0. Nutrient-limitation L_N is expressed as the sum

177 of nitrate and ammonium limitations following Wroblewski (1977) and as
178 used in Fasham et al. (1990). Primary production (in carbon currency) is
179 proportional to nutrient uptake (in nitrogen currency) by the factor $R_{C:N}$.

180 *2.4.2. Redfield stoichiometry and diagnostic Chl:C ratio (P1.5 formulation)*

181 The structure of the P1.5 formulation is similar to that of P1.0, except
182 that photo-acclimation is accounted for (Tables 4 and 5). In this model, the
183 phytoplanktonic chlorophyll:carbon ratio $R_{Chl:C}$ is thus a diagnostic variable
184 (Fig. 2B), calculated following Geider et al. (1996, 1998) as a function of
185 light and nutrient limitation.

186 *2.4.3. Cell quota and diagnostic Chl:C ratio (P2.5 formulation)*

187 In the P2.5 formulation, the phytoplanktonic nitrogen:carbon ratio $Q =$
188 P_N/P_C is variable (quota formulation) (Tables 4 and 5). The phytoplanktonic
189 compartment is thus represented by two state variables: the phytoplanktonic
190 nitrogen biomass P_N and the phytoplanktonic carbon biomass P_C (Fig. 2C).
191 As in P1.5, the phytoplanktonic chlorophyll:carbon ratio $R_{Chl:C}$ is a diag-
192 nostic variable calculated following Geider et al. (1998). The formulations of
193 nutrient uptake and primary production have also been chosen following Gei-
194 der et al. (1996, 1998). Nutrient uptake (in nitrogen currency) is expressed
195 as the product of quota and nutrient limitation terms. Primary production
196 (in carbon currency) is expressed as the product of quota and light limitation
197 terms.

198 *2.4.4. Cell quota and prognostic chlorophyll (P3.0 formulation)*

199 The P3.0 formulation corresponds to P2.5 with the addition of a fully
200 prognostic equation for chlorophyll (Tables 4 and 5). Phytoplankton are thus

201 represented by three state variables: phytoplanktonic nitrogen biomass P_N ,
 202 phytoplanktonic carbon biomass P_C , and chlorophyll biomass P_{Chl} (Fig. 2D).
 203 The dynamical equation of the phytoplanktonic chlorophyll P_{Chl} is defined
 204 following Geider et al. (1998): the chlorophyll production is a function of ni-
 205 trogen uptake, carbon fixation (production) and light and it does not respond
 206 rapidly to environmental changes when using the original set of parameters.

207 2.4.5. Geider model (GP3.0 formulation)

208 All previous formulations share the same expression of light limitation,
 209 which is independent of nutrient limitation and internal C:N quota, an as-
 210 sumption that can be discussed (Flynn, 2003b, 2008). To check the conse-
 211 quences of this assumption, a fifth model is constructed from P3.0 by using
 212 the following light limitation term, which now depends on the internal C:N
 213 quota Q :

$$L_I(Q) = \left[1 - EXP \left(- \frac{\alpha \cdot R_{Chl:C} \cdot PAR}{\mu_m \cdot \frac{Q - Q_0}{Q_{max} - Q_0}} \right) \right] \quad (2)$$

214 This new formulation, named GP3.0, corresponds to the original phytoplank-
 215 ton growth formulation proposed by Geider et al. (1996, 1998), and which
 216 has been previously incorporated in various marine ecosystem models (e.g.,
 217 Moore et al., 2002; Lefèvre et al., 2003).

218 2.5. Parameter tuning using micro-genetic algorithm

219 Model parameters are tuned using a micro-genetic algorithm to best fit
 220 the observed seasonal cycle at BATS. Genetic algorithms are stochastic meth-
 221 ods in which a population of parameters evolves with mutation/selection pro-
 222 cesses (evolutionary tuning approach). In the particular case of micro-genetic
 223 algorithms, the size of the population is small and no mutation is considered

224 (Carroll, 1996). A micro-genetic algorithm with binary coding, elitism, tour-
225 nament selection of the parents, and uniform cross-over was used (Carroll,
226 1996; Schartau and Oschlies, 2003). At the beginning, a set (or population)
227 of parameter vectors (individuals) is randomly generated within a predefined
228 range (Table 7). Each parameter vector is coded as a binary string (chro-
229 mosome). Then, at each generation, the misfit of each parameter vector
230 (fitness of each individual) is estimated as the misfit (cost function) between
231 the data and the model outputs for this parameter vector. The parameter
232 vector with the lowest misfit (best individual of its generation or 'elite') is
233 conserved to the next generation. Then, four vectors are randomly chosen
234 and associated in two pairs. The vectors with the lowest misfit (best fitness)
235 within each pair are selected (parents), and a new parameter vector (child)
236 is produced by randomly crossing each bit of the two selected vectors. This
237 process (reproduction) is repeated until the replenishment of the population.
238 New generations are produced (evolution), until the population of parameter
239 vectors has converged (all the vectors are identical to the elite). Then, a
240 new generation is randomly generated, with the elite conserved. This pro-
241 cess was repeated 500 times for a population whose size was chosen equal
242 to the number of parameters to identify (Schartau and Oschlies, 2003). For
243 each model, the parameter space was reduced to the parameters for which
244 the cost function was the most sensible, as learnt from preliminary sensibility
245 analyses (four to six parameters depending on the model, see Table 7).

246 2.6. Cost function and model comparison

247 *In situ* data measured at BATS in 1998, including monthly records of ni-
248 trate concentration, total particulate organic nitrogen concentration, chloro-

249 phyll concentration, and primary production, are used for optimization. In
 250 the model, total particulate organic nitrogen (PON) is taken as the sum
 251 of phytoplanktonic nitrogen, zooplanktonic nitrogen and detritus: $PON =$
 252 $P_N + Z_N + D_N$. These monthly profiles are re-gridded along the 1D ver-
 253 tical grid of the model. The cost function F is taken as the weighted
 254 sum of squared differences between monthly vertical profiles of observations
 255 $obs_n(k, l)$ and model outputs $mod_n(k, l)$ (Evans, 2003; Stow et al., 2009):

$$F = \frac{1}{KL} \sum_{n=1}^N \sum_{k=1}^K \sum_{l=1}^L W_n [obs_n(k, l) - mod_n(k, l)]^2 \quad (3)$$

256 Four data types are used ($N = 4$): nitrate concentration, chlorophyll concen-
 257 tration, total particulate organic nitrogen and primary production. The cost
 258 function is calculated from monthly data ($L=12$) and only the first vertical
 259 layers from 0 to 168 m are used ($K=15$). The weights W_n are chosen equal
 260 to the inverse of the standard deviation of the monthly observations ($1/\sigma_n$),
 261 with $\sigma_{NO_3} = 0.541 \text{ mmolN.m}^{-3}$, $\sigma_{Chl} = 0.080 \text{ mgChl.m}^{-3}$, $\sigma_{PON} = 0.106$
 262 mmolN.m^{-3} , $\sigma_{PP} = 0.177 \text{ mmolC.m}^{-3}.\text{d}^{-1}$.

263 Model outputs are also compared with *in situ* data and with each other
 264 using skill assessment technics, such as Taylor diagrams and target diagrams
 265 (Taylor, 2001; Stow et al., 2009; Jolliff et al., 2009). These diagrams can be
 266 seen as complementary indicators of the misfit between data and model out-
 267 puts, including correlation, root mean squared differences, relative standard
 268 deviations, and bias.

269 3. Results

270 3.1. Parameter tuning using micro-genetic algorithm

271 For each phytoplankton growth formulation, four to six parameters are
272 identified through an optimization algorithm, with the number of optimized
273 parameters increasing with the formulation complexity. The parameter val-
274 ues obtained after optimization are in the same range of magnitude among
275 the different models (Table 8). We can note that, after optimization and
276 compared to their initial default values, grazing parameters ($K_{g,g}$) and max-
277 imal Chl:N ratio ($R_{Chl:N}^{Max}$) are increased, whereas the other parameters remain
278 close to their default values. For each model, the best constrained parameter
279 is the initial PI slope α (as indicated by the evolution of the minimum mis-
280 fit obtained for each of the 64 possible values of this parameter during the
281 optimization procedure, not shown).

282 After optimization, cost functions are reduced for all models, by 23% for
283 P1.0 to 38% for P2.5 (Table 8). Model performances to reproduce all data
284 types are improved (Fig. 3). The optimizations increase the correlation be-
285 tween the model outputs and the observations (angular coordinates on the
286 Taylor diagram) and decrease the ratio of the standard deviations of model
287 outputs and observations (radial coordinates on the Taylor diagram). Op-
288 timizations also decrease the bias and the normalized unbiased root mean
289 squared differences between model outputs and observations (abscissae and
290 ordinates on the Target digram). Nitrate is the observation which is glob-
291 ally best reproduced by all models, contrary to particulate organic nitrogen
292 (PON).

293 *3.2. Seasonal dynamics*

294 The temporal evolution of the vertical profiles of nitrate, PON, chloro-
295 phyll and primary production confirms that all the models, after the param-
296 eter identification procedure, behave similarly. This may suggest a strong
297 impact of the initial conditions and physical forcing (Fig. 4). The evolutions
298 of nitrate and PON distributions are not significantly different between the
299 phytoplankton growth formulations. In response to the deepening of the
300 mixed layer in March, nitrate is entrained to the surface. It is then quickly
301 consumed in the euphotic layer during winter and spring, leaving very low ni-
302 trate concentrations in summer. Accordingly, PON and chlorophyll exhibit a
303 strong seasonal variability with a strong contrast between winter/spring and
304 summer. A strong phytoplankton bloom occurs between March and April,
305 characterized by high PON and chlorophyll concentrations in the surface
306 mixed layer, followed by a subsurface maxima in chlorophyll in summer.

307 Larger differences between phytoplankton growth formulations can be
308 seen in chlorophyll and production, with larger discrepancies between simu-
309 lations and observations than among simulations (Fig. 4). None of the model
310 correctly reproduces the exact dynamics of the observations. All models
311 are able to reproduce the subsurface chlorophyll maximum in summer, but
312 simulated chlorophyll concentrations are lower than observed whatever the
313 model, except during the bloom. None of the models is able to reproduce
314 the observed temporal evolution of production, which is characterized by a
315 maximum value in February and high values during the oligotrophic sea-
316 son. However, the high production period is longer for quota formulations.
317 As expected from previous studies (Doney et al., 1996; Spitz et al., 1998),

318 the Redfield formulation with constant Chl:C ratio (P1.0) is unable to si-
319 multaneously reproduce the deep chlorophyll maximum and the subsurface
320 production maximum during the oligotrophic season, because of its constant
321 Chl:C ratio (Fig. 5). Conversely, models with photo-acclimation (i.e., vari-
322 able Chl:C ratio) are all able to simulate the deep chlorophyll maximum and
323 the subsurface production maximum during the oligotrophic season. Taking
324 into account photo-acclimation allows to increase the C:Chl ratio in surface,
325 especially during oligotrophic conditions (Fig. 5).

326 The cell quota formulations with photo-acclimation (P2.5, P3.0 and GP3.0)
327 exhibit significant differences from the Redfield formulations in terms of
328 C:Chl ratio, phytoplankton biomass in carbon, and C:N ratio, particularly
329 during oligotrophic conditions (Fig. 5). During the bloom, lower C:Chl and
330 C:N ratios are simulated by the models that allow these ratios to vary. Dur-
331 ing the oligotrophic period, higher C:Chl and C:N ratios are simulated at the
332 surface by these models, with very close values for the three formulations.
333 The Redfield formulation with photo-acclimation (P1.5) simulates the lowest
334 variations of the C:Chl ratio, suggesting that this model could be less efficient
335 than the quota formulations to simulate photo-acclimation, likely because it
336 is less flexible.

337 *3.3. Annual and seasonal production in carbon and nitrogen*

338 In general, similar total and new productions in nitrogen are simulated
339 by the different models (relative differences about 5 %), except for the new
340 production between P1.0 and P2.5 (about 30 % higher for P2.5) (Table 9).
341 F-ratios vary from 0.43 to 0.49 during the bloom and from 0.20 to 0.27 dur-
342 ing the oligotrophic period. Total productions in carbon are much larger

343 for the formulations with a variable C:N quota than for the Redfield for-
344 mulations (about 50 % larger). This increase in carbon production is simu-
345 lated both during the bloom and during oligotrophic conditions, suggesting a
346 more efficient photosynthesis per chlorophyll content. Temporal evolution of
347 vertically-integrated daily production in nitrogen are close between models,
348 whereas strong differences are observed in vertically-integrated daily produc-
349 tion in carbon between Redfield and quota formulations, both during the
350 bloom and in summer (Fig. 6).

351 With cell quota formulations (P2.5, P3.0 and GP3.0), the C:N ratio of
352 total production is higher than the Redfield ratio and it increases at the
353 surface in summer, i.e. during oligotrophic conditions, with the highest C:N
354 values simulated by GP3.0 (about 15 at the surface at the end of the year)
355 (Fig. 7). Note that this feature is an emergent property of these cell quota
356 formulations, since the value of the C:N ratio was not constrained during
357 the optimization procedure. Besides, with the cell quota formulations the
358 C:N ratio of total production is always higher than the C:N ratio of phyto-
359 plankton, because of the cost of the nitrogen uptake (ζ parameter). With
360 the P2.5 formulation, for instance, the C:N ratios of total production and
361 of phytoplankton vary between 9 and 14 $molC.molN^{-1}$ and between 5 and
362 10 $molC.molN^{-1}$, respectively.

363 4. Discussion

364 The aim of the present work was to assess the consequences of taking into
365 account photo-acclimation and variable stoichiometry of the phytoplankton
366 growth in marine ecosystem models, by comparing the qualitative and quan-

367 titative behaviours of several growth formulations within a rigorous frame-
368 work. A parameter tuning based on optimization procedure was performed
369 before the comparison, using observed data of nitrate, particulate organic
370 nitrogen (PON), chlorophyll, and primary production at BATS. The opti-
371 mization increases the ability of all models to reproduce the observed data.
372 Globally, all models behave similarly after optimization and no difference
373 in the ability to reproduce nitrate or PON data is observed. However, as
374 expected from previous studies at BATS (Doney et al., 1996; Spitz et al.,
375 1998), photo-acclimation (i.e., a variable Chl:C ratio) is needed to simul-
376 taneously reproduce subsurface production and deep chlorophyll maximum
377 during oligotrophic conditions in summer. Moreover, Redfield formulations
378 underestimated production compared to quota formulations, which suggests
379 that the latter should be preferred. No clear difference is detected between
380 quota formulations with diagnostic or prognostic chlorophyll. Our main con-
381 clusion is that quota formulations with diagnostic or prognostic chlorophyll
382 enable to simulate more realistic values of chlorophyll and phytoplankton
383 production during oligotrophic conditions, compared with formulations with
384 constant Chl:C and C:N ratios. Indeed, these formulations are able to simu-
385 late a more 'flexible' phytoplankton physiology. They are then able to better
386 reproduce the phytoplankton dynamics under a wider range of environmental
387 conditions.

388 *4.1. Parameter tuning*

389 In order to compare the different phytoplankton growth formulations, we
390 have followed the methodology which consists in calibrating parameters prior
391 to comparison using advanced parameter estimation approaches (Faugeras

392 et al., 2004; Friedrichs et al., 2006; Smith and Yamanaka, 2007; Ward et al.,
393 2010; Bagniewski et al., 2011). This ensures that all models performed the
394 best they could. Sensitivity analyses have been needed to properly choose
395 the cost function and the parameters to calibrate with the optimization pro-
396 cedure: the sensitivity of several cost functions have been tested *a priori*
397 and only the most constrained parameters have been selected as candidates
398 for the minimization algorithm. Optimization procedure also provides *a pos-*
399 *teriori* estimates of the parameter uncertainty (Matear, 1995; Fennel et al.,
400 2001; Faugeras et al., 2003; Schartau and Oschlies, 2003). For instance, using
401 dissolved inorganic nitrogen, PON, chlorophyll, silicate, and oxygen data to
402 optimize the parameters of a simple marine ecosystem model through varia-
403 tional optimization, Bagniewski et al. (2011) concluded that phytoplankton
404 parameters (such as μ , α , and m_P) were better constrained than zooplankton
405 parameters (such as g). In the present study, the strength of the minimiza-
406 tion algorithm has been qualitatively estimated from the shape of the misfit
407 function for each of the selected parameters. The best constrained parameter
408 is the initial PI slope α , which is not surprising since this parameter appears
409 in the equations of nitrate, PON, chlorophyll, and primary production, i.e.,
410 the data used during the optimization procedure.

411 4.2. Model framework

412 For the purpose of our study, we used a relatively simple biogeochemi-
413 cal model and the annual primary production in carbon was underestimated
414 with all the phytoplankton growth formulations (assuming the production
415 data are correct). This shortcoming is a problem faced by most biogeochem-
416 ical models in the North Atlantic subtropical gyre (see for instance Oschlies,

417 2002). Several reasons can be advanced to explain it. One reason is the
418 use of a simple 1D physical framework, since lateral transport, which could
419 provide an additional source of DOM that would then be remineralized *in*
420 *situ* (Williams and Follows, 1998), and nutrient supply by mesoscale and sub-
421 mesoscale processes (Oschlies, 2002; McGillicuddy et al., 2003; Lévy et al.,
422 2012) may significantly increase the production in the North Atlantic. A
423 second hypothesis is the lack of nitrogen-fixers in our model. Finally, a third
424 hypothesis would be that the structure of the model is not complex enough,
425 in particular because of the lack of explicit bacteria. Indeed, this compart-
426 ment may play an important role during summer, especially for regenerated
427 production (Steinberg et al., 2001). However, the presence of a DOM pool in
428 our model implicitly assumes remineralization through bacterial activity and
429 allows local remineralization of the organic matter being produced. Besides,
430 the LOBSTER model have been complexified with an explicit representa-
431 tion of bacteria and the versions of LOBSTER with and without bacteria
432 have been compared in the Mediterranean sea and showed little differences
433 in terms of primary production, even during the summer oligotrophic period
434 (Lévy et al., 1998). Moreover, sensitivities to the DOM remineralization rate,
435 which mimics the action of bacteria, did not enable to significantly change
436 the simulated primary production, further highlighting that the reason for
437 this might more probably be the lack of nitrogen sources in the model rather
438 than to the simplified microbial network. This model could also have been
439 improved by the representation of additional phytoplankton types, since the
440 composition of the phytoplankton community changes along the year, or
441 by the use of additional nutrients such as phosphate (Cotner et al., 1997;

442 Steinberg et al., 2001), but then it would have required to take into account
443 multi-nutrient growth limitation of phytoplankton. Although a better agree-
444 ment between model and observation might then be obtained using a more
445 complex biogeochemical model and/or a more realistic physical forcing, the
446 model framework can be used to compare the different phytoplankton growth
447 formulations in a robust manner.

448 *4.3. Photo-acclimation in marine biogeochemical models*

449 Our comparative modelling study at BATS suggests that taking into ac-
450 count photo-acclimation (i.e., a variable Chl:C ratio) is mandatory to si-
451 multaneously reproduce deep chlorophyll maximum and subsurface primary
452 production during oligotrophic conditions. Indeed, a model without photo-
453 acclimation (P1.0) is able to predict the spring bloom and the depth of the
454 chlorophyll maximum, but has difficulties to reproduce the high production
455 observed in summer in subsurface, compared to the formulations with photo-
456 acclimation that are more flexible. Since in the latter formulations the Chl:C
457 ratio can vary depending on environmental conditions (namely light and nu-
458 trient availability), they can better perform along a wider range of conditions
459 (surface and subsurface, spring and summer).

460 These results are in agreement with previous modelling studies at BATS
461 indicating that the phytoplankton dynamic could not be reproduced when
462 using a constant Chl:C ratio (Doney et al., 1996; Hurtt and Armstrong, 1996,
463 1999; Spitz et al., 1998, 2001; Fennel et al., 2001). Doney et al. (1996) hy-
464 pothesized that this may be "because not enough nutrient were available
465 to sustain [the production in summer]". Our comparative study highlights
466 that difficulties to simulate the high production in summer may partly be

467 due to the fixed Chl:C ratio, since models with variable Chl:C were able to
468 reproduce the observations better. Similarly, Fennel et al. (2001) and Spitz
469 et al. (1998) could not correctly reproduce observation data at BATS with
470 simple NPZD models with constant Redfield and Chl:N ratios, even after
471 parameter optimization. Fennel et al. (2001) suggested that this was due
472 to the physical forcing and/or to the too simple hypotheses of the ecosys-
473 tem model, whereas Spitz et al. (1998) proposed three possible explanations
474 for this failure: the use of a Redfield stoichiometry, the absence of photo-
475 acclimation, and approximations about vertical processes. In the present
476 study, the same physical forcing is used for all models and our results indi-
477 cate that the failure to reproduce the nitrate and chlorophyll data may be
478 due to the absence of photo-acclimation (constant Chl:N ratio). Our results
479 are in agreement with the improvements of the Fasham model proposed by
480 Hurtt and Armstrong (1996, 1999) using a variable Chl:N ratio as a function
481 of the irradiance, or by Spitz et al. (2001) using a prognostic Chl:N ratio:
482 photo-acclimation of phytoplankton should be taken into account to simulate
483 the subsurface chlorophyll maximum under summer oligotrophic conditions.
484 In summer this chlorophyll maximum is observed in subsurface, with max-
485 imum production rates at the surface. This means that the phytoplankton
486 decrease its pigment content at the surface and increase it to collect more
487 light in subsurface. Our results suggest that such flexibility in phytoplankton
488 physiology can only be simulated in marine ecosystem models if the ratio of
489 pigment content over biomass can vary depending on environmental condi-
490 tions (photo-acclimation).

491 Our suite of numerical experiments also allows to compare several formu-

492 lations of photo-acclimation. The P2.5 formulation, with diagnostic chloro-
493 phyll, and the P3.0 formulation, with fully dynamical chlorophyll, produced
494 relatively similar results. Slight differences were observed between the P3.0
495 and the GP3.0 formulations, both with dynamical chlorophyll but with differ-
496 ent light limitation formulations. In the latter, light limitation is a function
497 of the cell quota, as recommended by Flynn (2003b) to assure that, at steady
498 state, the growth-irradiance curve has the correct initial slope. However, phy-
499 toplankton growth in the ocean is often not at steady state. Additional data
500 on phytoplanktonic carbon concentration and C:N ratio would be needed
501 to constrain these cell quota formulations with photo-acclimation and com-
502 pare their ability to reproduce phytoplanktonic dynamics. In the meantime,
503 and as suggested by Flynn (2003a) from growth formulation comparison for
504 laboratory experiments, phytoplankton models with diagnostic chlorophyll
505 should be preferred when coupled with marine ecosystem models.

506 *4.4. Stoichiometry of phytoplanktonic production*

507 Our results indicate that compared to Redfield growth formulations, quota
508 growth formulations better reproduce the primary production during oligo-
509 trophic conditions. Several problems arose from previous modelling studies
510 at BATS using constant C:N ratios with photo-acclimation because of the
511 assumed Redfield stoichiometry. Schartau et al. (2001) concluded that pro-
512 duction data could not be reproduced after optimization when a constant
513 C:N ratio was assumed. Schartau and Oschlies (2003) also indicated that the
514 parameter optimization of a Redfield NPZD model with photo-acclimation
515 leads to high value of the parameter α (initial PI slope) "likely [to] com-
516 pensat[e] for a deficiency in the parameterization of light-limited growth."

517 Finally, Oschlies and Schartau (2005) concluded that their model was unable
518 to reproduce the observed data after optimization due "both to errors in
519 the physical model component and to errors in the structure of the ecosys-
520 tem model, which an objective estimation of ecosystem model parameters by
521 data assimilation alone cannot resolve." Besides, the stoichiometry of total
522 particulate organic matter is known to be non-Redfield at BATS (Michaels
523 and Knap, 1996; Cotner et al., 1997), as already reported in other parts of
524 the North Atlantic (Sambrotto et al., 1993; Kortzinger et al., 2001). Sur-
525 face and mixed layer values of the C:N ratio of particulate organic matter
526 recorded at BATS in 1998 vary from 6.19 to 10.26 $molC.molN^{-1}$, with val-
527 ues larger than 8 $molC.molN^{-1}$ from June to August (Fig. 7). However,
528 the comparison of these observed values with simulated C:N ratios of pro-
529 duction and phytoplankton are not straightforward, since the proportions
530 of phytoplanktonic nitrogen and carbon relative to total particulate organic
531 nitrogen and carbon are unknown. Nevertheless, the increase of C:N ratios
532 during oligotrophic conditions is well reproduced by the cell quota formula-
533 tions, because of low nutrient availability during the summer. For cell-quota
534 formulations, it is then the ability of the C:N ratio to vary under changing
535 environmental conditions (flexibility) that is responsible to a more realistic
536 simulated production.

537 Similarly, an *in situ* study of the evolution of the C:N ratios of particu-
538 late organic matter and production in the mixed layer in the North-East At-
539 lantic indicated that these C:N ratios were higher during summer than during
540 spring, with values of C:N ratio of production of 10-16 and 5-6 $molC.molN^{-1}$,
541 respectively (Kortzinger et al., 2001). These results suggest that our conclu-

542 sions at BATS may extend to other areas in the ocean. Besides, it would be
543 interesting to adapt this study to a station where data of phytoplanktonic
544 nitrogen and carbon would be available in order to discriminate between the
545 different quota formulations (P2.5, P3.0, and GP3.0).

546 *4.5. Implications for marine ecosystem modelling*

547 Several recent studies, that have compared different biogeochemical mod-
548 els, have focused on the structure of the model rather than on the formu-
549 lation of phytoplankton growth (Friedrichs et al., 2006, 2007; Ward et al.,
550 2010; Kriest et al., 2010; Bagniewski et al., 2011). Friedrichs et al. (2006)
551 found that a change in the physical model had a more important impact than
552 a change in the ecosystem model complexity. Similarly, Kriest et al. (2010)
553 demonstrated that increasing complexity of a simple biogeochemical model at
554 global scale did not necessarily improve the model's performance. Neverthe-
555 less, the choice of model complexity (food web structure, description of key
556 physiological processes, parameter estimations, plankton functional types) is
557 one of the challenges of future marine ecosystem modelling (Flynn, 2003a;
558 Le Quéré et al., 2005; Flynn, 2010; Anderson, 2010; Allen and Fulton, 2010;
559 Allen and Polimene, 2011). Besides, the use of complex models is still under
560 debate because of our lack of specific knowledge in parameterizing plankton
561 physiology and its variability (Anderson, 2005; Allen et al., 2010; Allen and
562 Polimene, 2011).

563 Our study allows to quantify the error made when a constant Redfield
564 stoichiometry is considered (instead of a variable C:N ratio) in phytoplank-
565 ton growth formulation, as it is still the case in most biogeochemical mod-
566 els, especially when they are used at global scale. Indeed, only a few global

567 ecosystem models decouple nitrogen and carbon dynamics (Vichi et al., 2007;
568 Vichi and Masina, 2009). A recent study using a marine ecosystem model at
569 global scale decoupled nitrogen and phosphorus dynamics relative to carbon,
570 but still used a Monod-type version of nutrient limitation (Tagliabue et al.,
571 2011). This model was thus "in between" Monod-Redfield and cell quota for-
572 mulations. Global scale models that decouple carbon and nitrogen uptakes
573 are particularly needed to study the impact of increased CO₂ in the ocean.
574 Indeed, carbon dioxide enhances carbon fixation but not dissolved inorganic
575 nitrogen uptake, thus potentially increasing C:N ratios. Such processes have
576 already been observed in mesocosm experiments (Riebesell et al., 2007), and
577 should now be incorporated in global marine ecosystem models. Besides, cli-
578 mate change will likely modify to some degree the stoichiometry of inorganic
579 and organic C:N:P in the oceans (Hutchins et al., 2009). For these reasons,
580 models without enough 'flexibility' in their formulation will not be able to
581 represent the non-linearities between carbon and nitrogen assimilation. In
582 parallel with model improvements, field and *in situ* experiments should con-
583 tinue in collaboration with modelers to increase our knowledge in plankton
584 physiology and dynamics under varying environment and provide data to
585 calibrate and validate models.

586 **5. Conclusion**

587 The aim of the present work was to assess the advantages of taking into
588 account photo-acclimation and variable stoichiometry of the phytoplankton
589 growth in marine ecosystem models. After parameter calibration through
590 an optimization procedure, lower misfits with observed data at BATS were

591 simulated when photo-acclimation and non-Redfield stoichiometry were con-
592 sidered (i.e., variable Chl:C and C:N ratios). The main differences in qual-
593 itative and quantitative behaviours of phytoplankton growth models were
594 observed under oligotrophic conditions, because of the lack of model flexibil-
595 ity. In agreement with previous studies, photo-acclimation was mandatory
596 to simultaneously reproduce the observed deep chlorophyll maximum and
597 subsurface production during oligotrophic conditions. Moreover, quota for-
598 mulations enabled a better agreement with production data in subsurface and
599 during oligotrophic conditions than Redfield formulations. No clear differ-
600 ence was detected between quota formulations with diagnostic or prognostic
601 chlorophyll, and more data would be needed to discriminate between these
602 quota formulations with photo-acclimation. Future work would embed these
603 different phytoplankton growth formulations within a 3D physical model to
604 test whether our results can be generalized under contrasted oceanic regime
605 and at basin scale (Ayata et al., *in prep.*).

606 **6. Acknowledgements**

607 This work was supported by the *Action Collaborative de Recherche NAU-*
608 *TILUS* funded by the french *Institut National de la Recherche en Informa-*
609 *tique et en Automatismes* (INRIA) and is part of the TANGGO initiative
610 supported by the CNRS-INSU-LEFE program. SDA was supported by a
611 post-doctoral fellowship from INRIA. The authors would like to thank Kevin
612 Flynn and an anonymous reviewer for their constructive comments on a first
613 version of this manuscript.

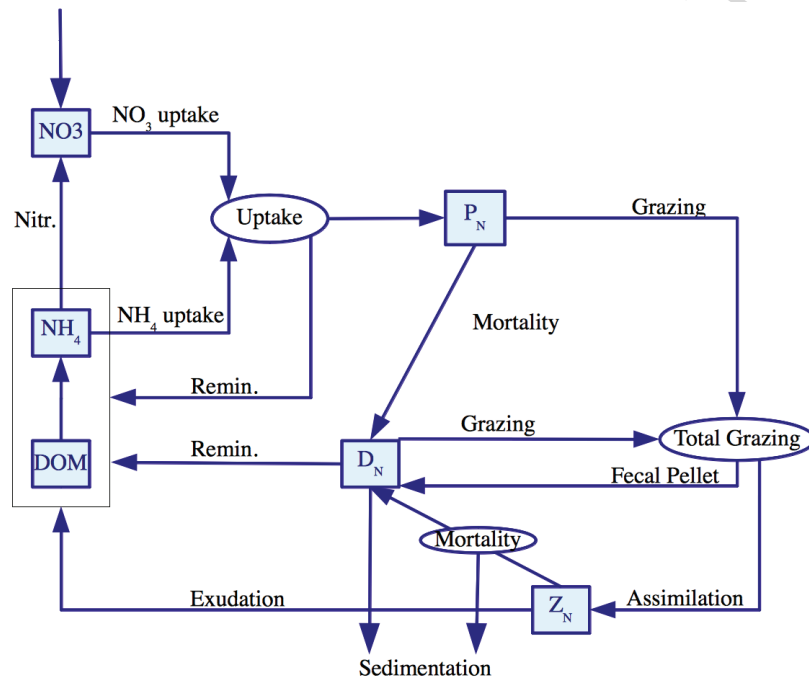
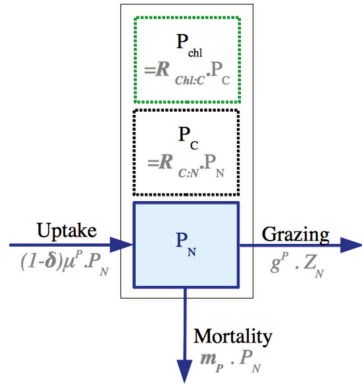
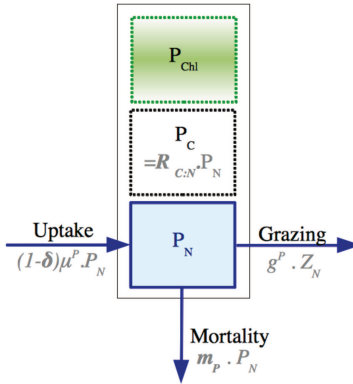


Figure 1: Structure of the LOBSTER marine ecosystem model. The six state variables are in nitrogen currency (blue color). The detailed equations of the model are given in Table 1. Nitr.: Nitrification; Remin.: Remineralization.

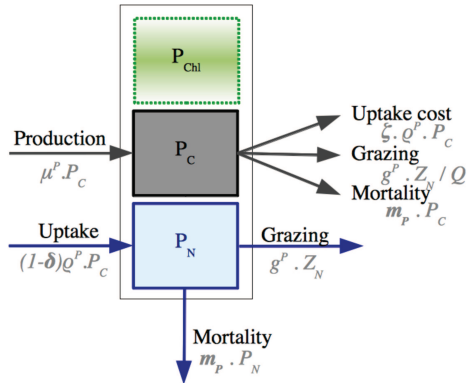
A) P1.0



B) P1.5



C) P2.5



D) P3.0

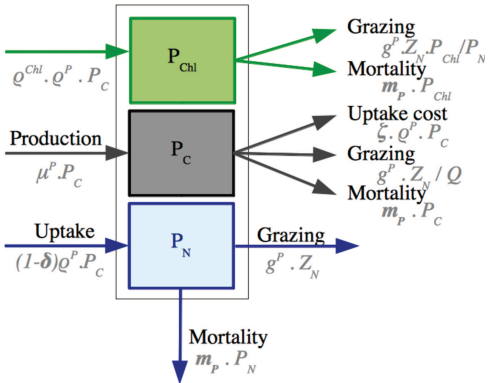


Figure 2: Structure of the phytoplankton growth formulations: A) Redfield formulation with constant chlorophyll:carbon ratio (P1.0), B) Redfield formulation with diagnostic chlorophyll (P1.5), C) quota formulation with diagnostic chlorophyll (P2.5), and D) quota formulation with prognostic chlorophyll (P3.0). Note that the Geider formulation (GP3.0) shares the same structure as P3.0. State variables are in plain color and diagnostic variables in shaded color. The colors of the variables indicate their currency: blue for nitrogen, grey for carbon, and green for chlorophyll.

Figure 3: Taylor and target diagrams of the monthly vertical profiles of nitrate concentration (diamonds), PON concentration (triangles), chlorophyll concentration (circle) and primary production (square) calculated for each formulation with default parameters (empty symbol) and after optimization (full symbol). The Taylor diagram represents in polar coordinates the normalized standard deviation and the correlation between observation and model output. On this diagram, the distance with the point of coordinates (1,0) measures the normalized root mean squared differences between observation and model output.

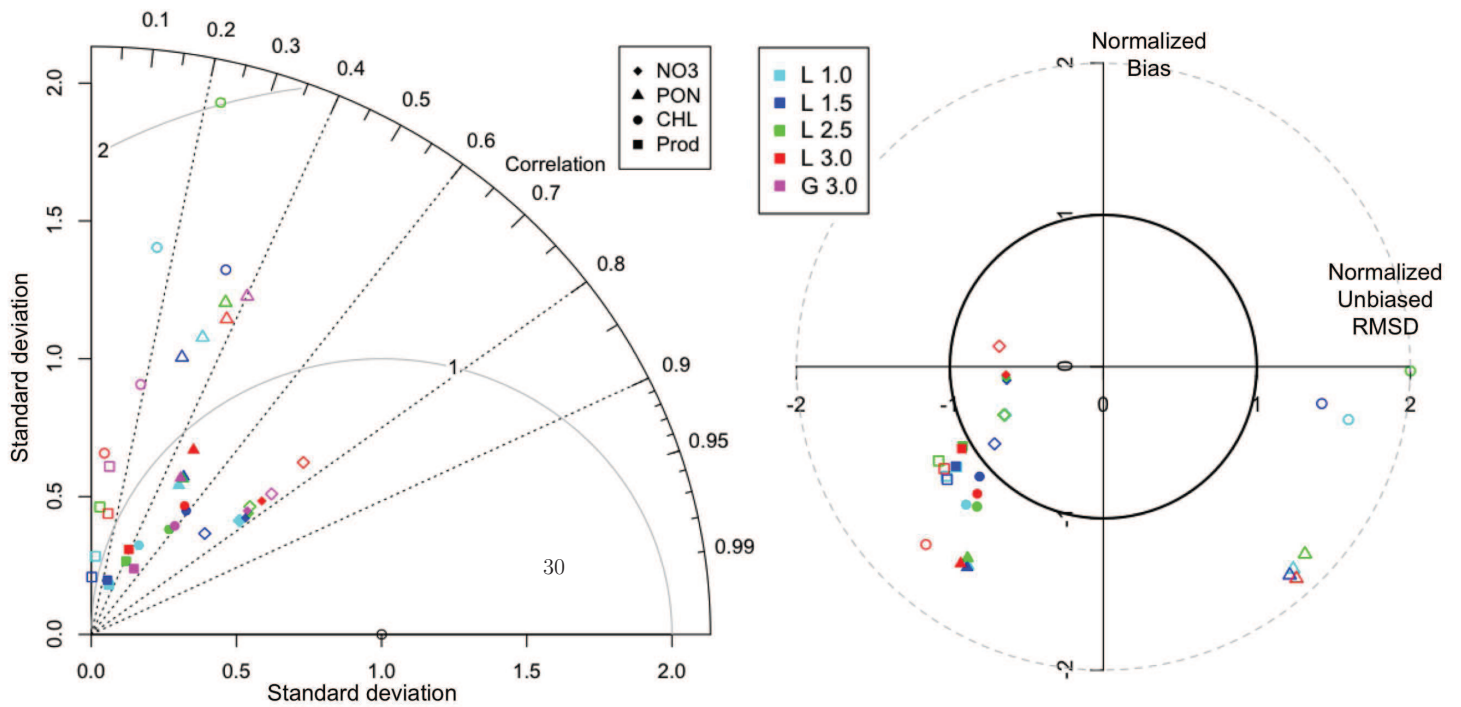


Figure 4: Seasonal cycles of nitrate, particulate organic nitrogen (PON), chlorophyll, and primary production at BATS in 1998, simulated with the different models after optimization and observed at BATS in 1998. The observed mixed layer depth is superimposed in white over the observed nitrate profiles.

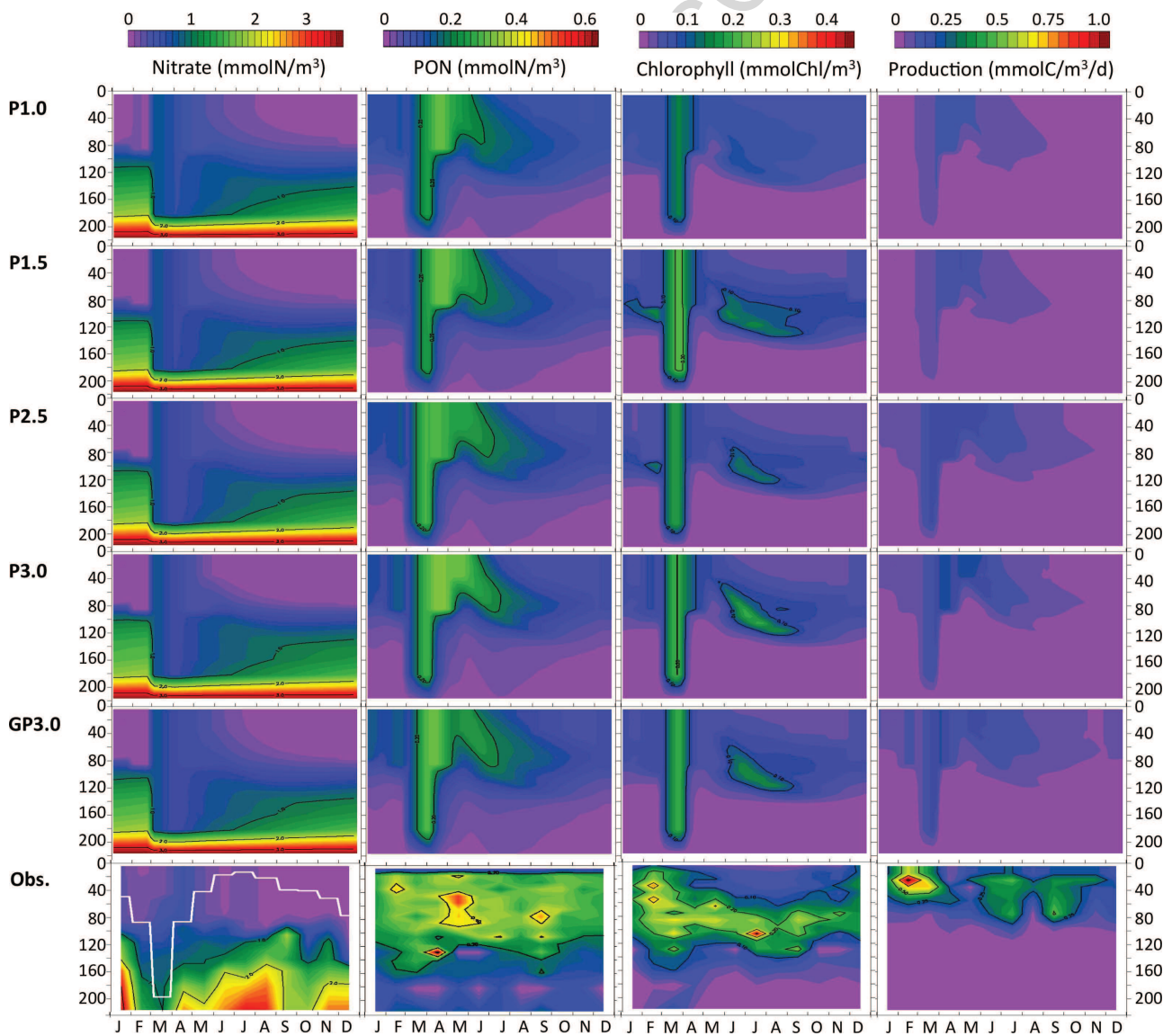


Figure 5: Average vertical profiles during boom (Mar-Apr) and during oligotrophic conditions (Jul-Aug) of the concentrations of phytoplanktonic nitrogen, phytoplanktonic carbon, C/ N ratio and C:Chl ratio, simulated with P1.0 (dark blue), P1.5 (light blue), P2.5 (green), P3.0 (red), and GP3.0 (magenta) after optimization.

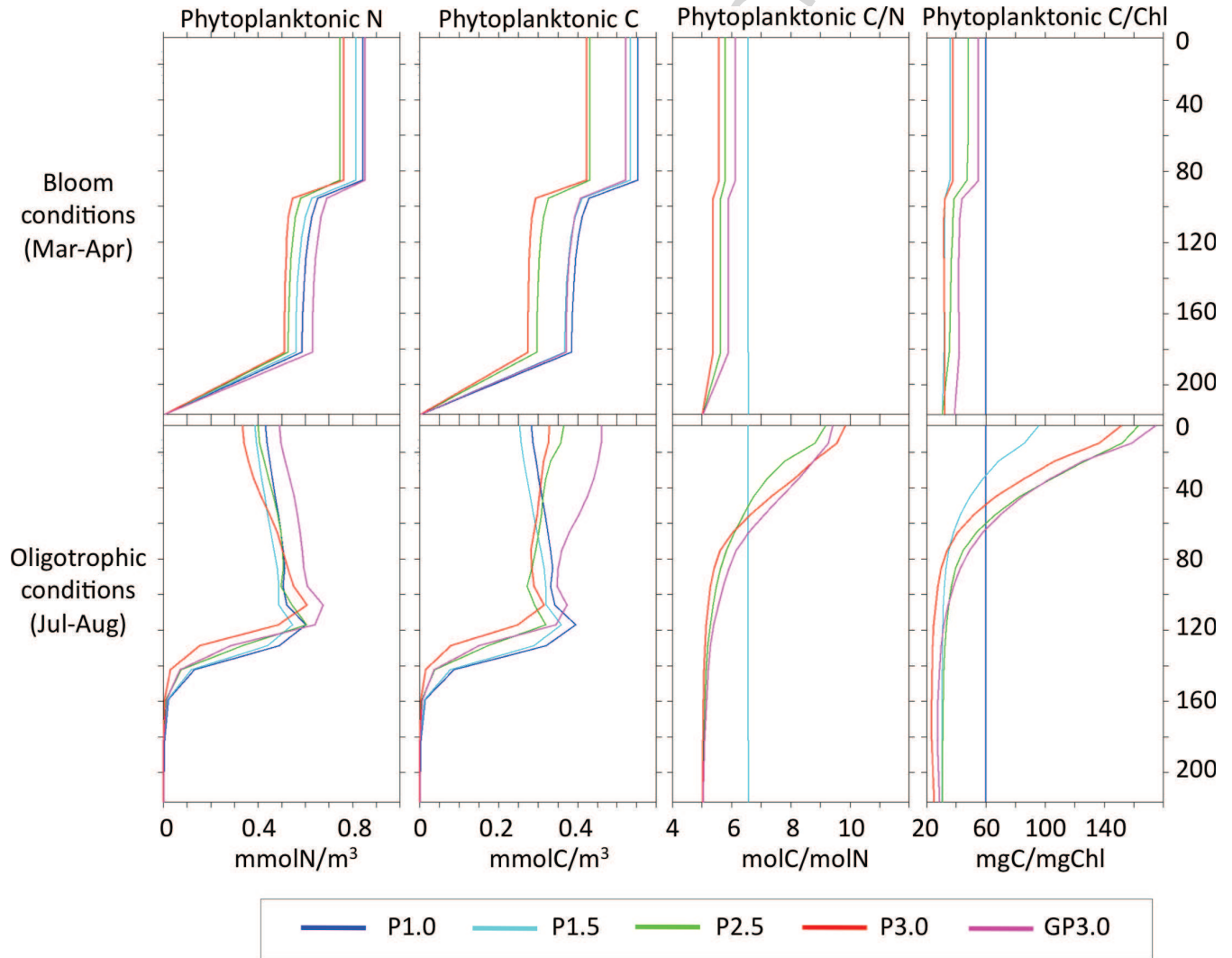


Figure 6: Temporal evolution of integrated daily production in carbon and in nitrogen from 0 to 234 m, simulated by the Redfield formulations P1.0 (blue) and P1.5 (light blue), and by the quota formulations P2.5 (green), P3.0 (red), and GP3.0 (magenta) after optimization. The observed values of the integrated daily production in carbon at BATS are indicated (black crosses).

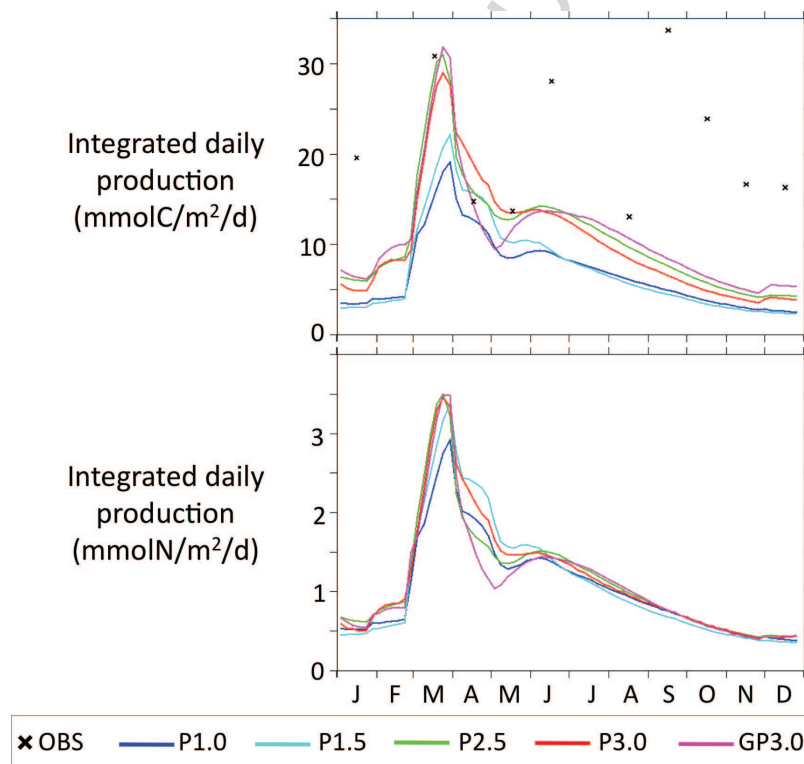


Figure 7: Temporal evolution of the C:N ratio of the production and of the phytoplankton at 0-10 m, 40-50 m and 90-100 m after optimization, simulated by the Redfield formulations P1.0 and P1.5 (light blue), and by the quota formulations P2.5 (green), P3.0 (red), and GP3.0 (magenta). The C:N ratio of the production is calculated as the ratio between the total production in carbon and the total production in nitrogen. The observed surface values of the C:N ratio of the total particulate organic matter measured at BATS in 1998 are superimposed on the simulated C:N ratio of the phytoplankton (black crosses).

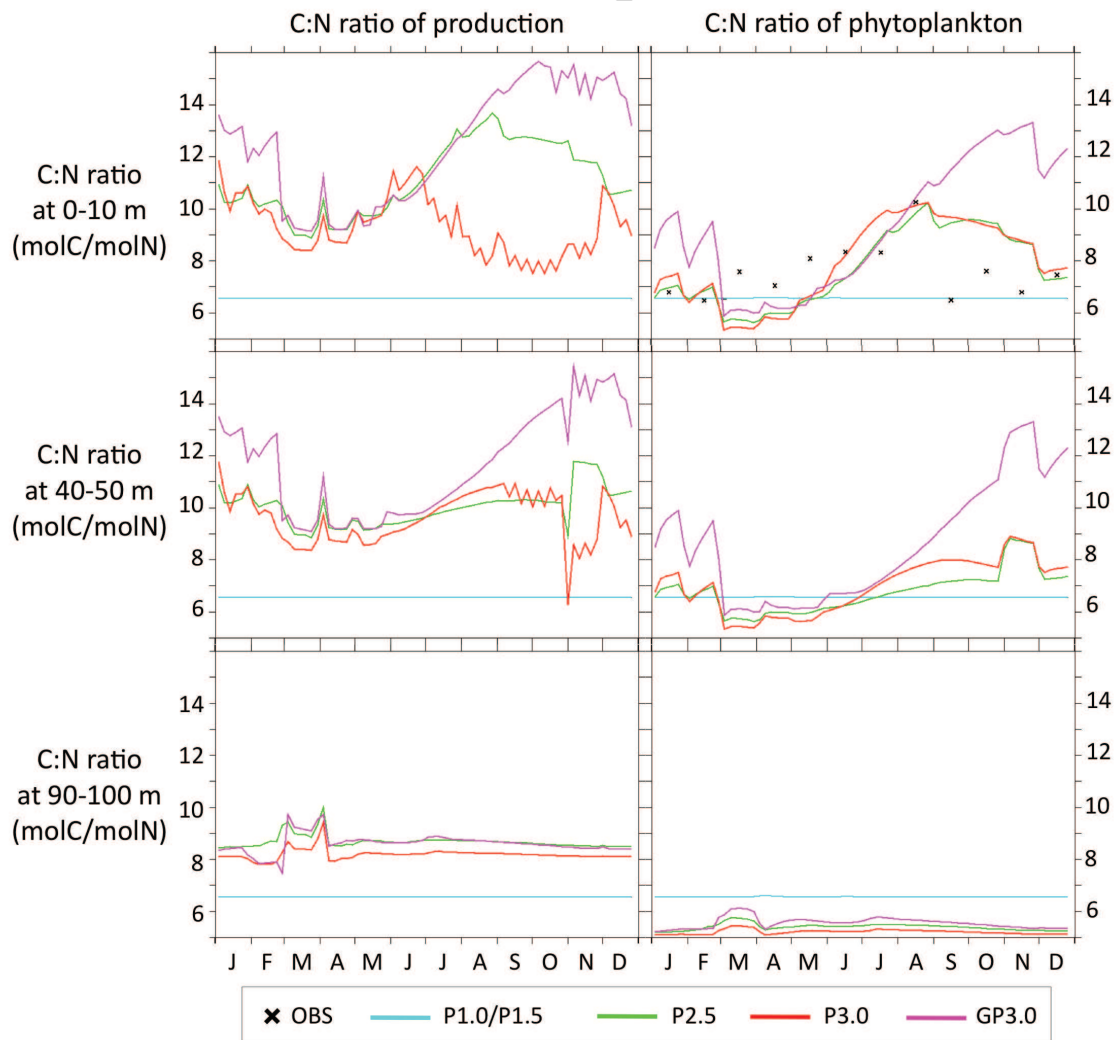


Table 1: Equations of the LOBSTER marine ecosystem model. The source minus sink (*sms*) terms of the equations are given for each of the six state variables of the model (in nitrogen currency): nitrate (NO_3), ammonium (NH_4), phytoplankton (P_N), zooplankton (Z_N), detritus (D_N), and dissolved organic matter (DOM). The phytoplankton growth formulation is a Redfield formulation with constant Chl:C ratio (P1.0 formulation). The definition of the parameters and their default values are presented in Table 2.

Definition	Equation
Nitrate source minus sink	$sms(\text{NO}_3) = \lambda_{\text{NH}_4} \cdot \text{NH}_4 - \frac{L_{\text{NO}_3}}{L_N} \cdot \text{uptake}$
Ammonium source minus sink	$sms(\text{NH}_4) = -\lambda_{\text{NH}_4} \cdot \text{NH}_4 - \frac{L_{\text{NH}_4}}{L_N} \cdot \text{uptake} + \lambda_{\text{DOM}} \cdot \text{DOM} + f_n \cdot (\delta \cdot \text{uptake} + \lambda_Z \cdot Z_N + \lambda_D \cdot D_N)$
Phytoplankton source minus sink	$sms(P_N) = (1 - \delta) \cdot \text{uptake} - G_P - m_P \cdot P_N$
Zooplankton source minus sink	$sms(Z_N) = a_Z \cdot (G_P + G_D) - m_Z \cdot Z_N^2 - \lambda_Z \cdot Z_N$
Detritus source minus sink	$sms(D_N) = m_P \cdot P_N + f_Z \cdot m_Z \cdot Z_N^2 + (1 - a_Z) \cdot (G_P + G_D) - G_D - \lambda_D \cdot D_N - w_D$
DOM source minus sink	$sms(\text{DOM}) = (1 - f_n) \cdot (\delta \cdot \text{uptake} + \lambda_Z \cdot Z_N + \lambda_D \cdot D_N) - \lambda_{\text{DOM}} \cdot \text{DOM}$
Nitrogen uptake	$\text{uptake} = \mu_m \cdot L_N \cdot L_I \cdot P_N$
Light limitation	$L_I = \left[1 - e^{\left(-\frac{\alpha \cdot R_{\text{Chl:C}} \cdot P_{\text{AR}}}{\mu_m} \right)} \right]$
Nutrient limitation	$L_N = L_{\text{NO}_3} + L_{\text{NH}_4}$
Nitrate limitation	$L_{\text{NO}_3} = \frac{\text{NO}_3}{K_{\text{NO}_3} + \text{NO}_3} \cdot e^{-\psi \cdot \text{NH}_4}$
Ammonium limitation	$L_{\text{NH}_4} = \frac{\text{NH}_4}{K_{\text{NH}_4} + \text{NH}_4}$
Grazing on phytoplankton	$G_P = g \cdot \frac{p \cdot P_N}{K_g + p \cdot P_N + (1-p) \cdot D_N} \cdot Z_N$
Grazing on detritus	$G_D = g \cdot \frac{(1-p) \cdot D_N}{K_g + p \cdot P_N + (1-p) \cdot D_N} \cdot Z_N$
Grazing preference for phytoplankton	$p = \frac{\bar{p} \cdot P_N}{\bar{p} \cdot P_N + (1-\bar{p}) \cdot D_N}$

Table 2: Parameters of the LOBSTER model, with default values from previous studies (Lévy et al., 2005; Kremer et al., 2009).

Symbol	Definition	Value	Unit
Nutrient-related parameters			
K_{NO_3}	NO ₃ half saturation constant	0.7 e-6	mmolN.m ⁻³
K_{NH_4}	NH ₄ half saturation constant	0.001 e-6	mmolN.m ⁻³
ψ	Inhibition of NO ₃ uptake by NH ₄	3	unitless
λ_{NH_4}	NH ₄ nitrification rate	0.05	d ⁻¹
Phytoplankton growth and death			
α	Photosynthesis-irradiance (PI) initial slope	1.82	d ⁻¹ .W ⁻¹ .m ² .gC.gChl ⁻¹
μ_m	Maximal growth rate of phytoplankton	1	d ⁻¹
δ	Excretion ratio of phytoplankton	0.05	unitless
m_P	Phytoplankton mortality rate	0.05	d ⁻¹
Zooplankton grazing and mortality			
K_g	Grazing half saturation constant	1 e-6	mmolN.m ⁻³
g	Maximal zooplankton grazing rate	0.8	d ⁻¹
a_Z	Assimilated food fraction	0.7	unitless
λ_Z	Exsudation rate of zooplankton	0.07	d ⁻¹
m_Z	Zooplankton mortality rate	0.12 e+6	d ⁻¹ .mmolN ⁻¹ .m ³
\tilde{p}	Zooplankton preference for detritus	0.8	unitless
f_Z	Fraction of slow sinking mortality	0.5	unitless
Remineralization			
λ_{DOM}	Remineralization rate of DOM	0.006	d ⁻¹
f_n	NH ₄ /DOM redistribution ratio	0.75	unitless
w_D	Detritus sedimentation speed	3	m.d ⁻¹
λ_D	Remineralization rate of detritus	0.05	d ⁻¹

Table 4: Equations of the different phytoplankton growth formulations. P1.0: Redfield formulation with constant Chl:C ratio. P1.5: Redfield formulation with diagnostic Chl:C ratio. P2.5: Cell-quota formulation with diagnostic Chl:C ratio. P3.0/GP3.0: Cell-quota formulation with prognostic Chl:C ratio. The definition of the parameters and their default values are presented in Tables 2 and 5. Source minus sink functions (*sms*) are only for prognostic variables (in bold).

Model(s)	Definition	Equation
P1.0	Phytoplanktonic nitrogen	$sms(P_N) = (1 - \delta).uptake - G_P - m_P.P_N$
	Phytoplanktonic carbon	$P_C = R_{C:N}.P_N$
	Chlorophyll	$P_{Chl} = R_{Chl:C}.P_C$
	Nitrogen uptake	$uptake = \mu_m.L_N.L_I.P_N$
	Primary production	$prod = R_{C:N}.uptake$
P1.5	Phytoplanktonic nitrogen	$sms(P_N) = (1 - \delta).uptake - G_P - m_P.P_N$
	Phytoplanktonic carbon	$P_C = R_{C:N}.P_N$
	Chlorophyll	$P_{Chl} = \left(R_{Chl:C}^{Min} + \frac{(R_{Chl:C}^{Max} - R_{Chl:C}^{Min}).2.\mu_m.L_N}{2.\mu_m.L_N + (R_{Chl:C}^{Max} - R_{Chl:C}^{Min}).\alpha.PAR} \right) .P_C$
	Nitrogen uptake	$uptake = \mu_m.L_N.L_I.P_N$
	Primary production	$prod = R_{C:N}.uptake$
P2.5	Phytoplanktonic nitrogen	$sms(P_N) = (1 - \delta).uptake - G_P - m_P.P_N$
	Phytoplanktonic carbon	$sms(P_C) = prod - \zeta.uptake - G_P.\frac{P_C}{P_N} - m_P.P_C$
	Chlorophyll	$P_{Chl} = \left(R_{Chl:C}^{Min} + \frac{(R_{Chl:C}^{Max} - R_{Chl:C}^{Min}).2.\mu_m.L_N}{2.\mu_m.L_N + (R_{Chl:C}^{Max} - R_{Chl:C}^{Min}).\alpha.PAR} \right) .P_C$
	Nitrogen uptake	$uptake = \rho_m.L_Q^N.L_N.P_C$
	Primary production	$prod = \mu_m.L_Q^I.L_I.P_C$
	Quota-limitation of uptake	$L_Q^N = \left(\frac{Q_{max} - Q}{Q_{max} - Q_0} \right)^n$
	Quota-limitation of prod.	$L_Q^I = \frac{Q - Q_0}{Q_{max} - Q_0}$
P3.0	Phytoplanktonic nitrogen	$sms(P_N) = (1 - \delta).uptake - G_P - m_P.P_N$
GP3.0	Phytoplanktonic carbon	$sms(P_C) = prod - \zeta.uptake - G_P.\frac{P_C}{P_N} - m_P.P_C$
	Chlorophyll sms	$sms(P_{Chl}) = prod_{Chl} - G_P.\frac{P_{Chl}}{P_N} - m_P.P_{Chl}$
	Nitrogen uptake	$uptake = \rho_m.L_Q^N.L_N.P_C$
	Primary production	$prod = \mu_m.L_Q^I.L_I.P_C$
	Chlorophyll production	$prod_{Chl} = \frac{R_{Chl:N}.14}{\alpha.PAR.P_{Chl}}.prod.uptake$
	Quota-limitation of uptake	$L_Q^N = \left(\frac{Q_{max} - Q}{Q_{max} - Q_0} \right)^n$
	Quota-limitation of prod.	$L_Q^I = \frac{Q - Q_0}{Q_{max} - Q_0}$

Table 5: Parameters of the different phytoplankton growth formulations and associated default values from Geider et al. (1998).

Symbol	Definition	Default	Unit	Models
Constant ratios				
$R_{Chl:C}$	Chlorophyll:Carbon ratio	1/60	gChl.gC ⁻¹	P1.0
$R_{C:N}$	Phytoplankton C:N Redfield ratio	6.56	molC.molN ⁻¹	P1.0 P1.5
Diagnostic chlorophyll				
$R_{Chl:C}^{Min}$	Minimum Chl:C ratio	1/200	mgChl.mmolC ⁻¹	P1.5 P2.5
$R_{Chl:C}^{Max}$	Maximum Chl:C ratio	1/30	mgChl.mmolC ⁻¹	P1.5 P2.5
Nutrient uptake				
ρ_m	Maximum uptake rate (defined by $\rho_m = \mu_m \cdot Q_{max}$)	0.2	molN.molC ⁻¹ .d ⁻¹	P2.5 P3.0
ζ	Cost of nitrogen assimilation	3	mol C.mol N ⁻¹	P2.5 P3.0
Phytoplanktonic cell quotas				
Q_0	Minimum value of Q	1/20	mol N.mol C ⁻¹	P2.5 P3.0
Q_{max}	Maximum value of Q	1/5	mol N.mol C ⁻¹	P2.5 P3.0
n	Shape factor	1	-	P2.5 P3.0
Chlorophyll synthesis				
$R_{Chl:N}^{Max}$	Maximum Chl:N ratio	2	gChl.gN ⁻¹	P3.0

Table 7: Parameter range allowed for optimization. Each parameter was binary coded on 6 bits (and had then 64 possible values).

Parameter	Lower bound	Upper bound	Increment
α	0.3	12.9	0.2
μ_m	0.1	6.4	0.1
K_g	1.0e-7	32.5e-7	0.5e-7
g	0.1	6.4	0.1
ζ	1.00	4.15	0.05
$R_{Chl:N}^{Max}$	0.1	6.4	0.1

Table 8: Optimized parameters and associated cost functions (F).

Parameter	Default values	Optimized values				
		P1.0	P1.5	P2.5	P3.0	GP3.0
α	1.82	1.7	1.1	2.3	1.7	2.1
μ_m	1	0.3	0.6	1.0	1.7	0.6
K_g	10.0e-7	23.0e-7	18.0e-7	22.5e-7	23.0e-7	26.0e-7
g	0.8	5.0	4.2	5.1	5.3	5.1
ζ	3.00	-	-	3.52	3.24	3.36
$R_{Chl:N}^{Max}$	3	-	-	-	6.4	5.6
F after optimization		0.855	0.823	0.790	0.802	0.773
F with default value		1.118	1.217	1.1217	1.120	1.052

Table 9: Total productions, new production, and f-ratio (new production/total production in nitrogen) simulated at BATS in 1998 after optimization.

Annual values				
Model	Total Production ($molC/m^2$)	Total Production ($molN/m^2$)	New Production ($molN/m^2$)	f-ratio
P1.0	2.495	0.380	0.126	0.33
P1.5	2.647	0.403	0.133	0.33
P2.5	3.903	0.415	0.163	0.39
P3.0	3.728	0.421	0.134	0.32
GP3.0	3.970	0.399	0.135	0.34

Bloom period (Mars to April)				
Model	Total Production ($molC/m^2$)	Total Production ($molN/m^2$)	New Production ($molN/m^2$)	f-ratio
P1.0	0.855	0.130	0.064	0.49
P1.5	1.014	0.154	0.076	0.49
P2.5	1.292	0.143	0.062	0.43
P3.0	1.309	0.153	0.073	0.48
GP3.0	1.240	0.136	0.066	0.48

Oligotrophic period (July to August)				
Model	Total Production ($molC/m^2$)	Total Production ($molN/m^2$)	New Production ($molN/m^2$)	f-ratio
P1.0	0.424	0.064	0.016	0.25
P1.5	0.403	0.061	0.012	0.20
P2.5	0.678	0.069	0.017	0.25
P3.0	0.605	0.066	0.013	0.20
GP3.0	0.725	0.071	0.019	0.27

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