

Ecology / Écologie

Relevance of various formulations of phytoplankton chlorophyll *a*:carbon ratio in a 3D marine ecosystem model

Vincent Faure^{a,b,*}, Christel Pinazo^a, Jean-Pascal Torrétou^{b,1}, Pascal Douillet^b

^a Station marine d'Endoume, centre d'océanologie de Marseille, LOB UMR 6535, université de la Méditerranée, 13007 Marseille, France

^b IRD, UR Camélia, BP A5, 98848 Nouméa cedex, New Caledonia

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Abstract

Numerous experimental studies showed that the phytoplankton Chl*a*-to-Carbon ratio (Chl*a*:C) is highly variable, whereas most of the marine ecosystem models use a constant ratio. In this work, we tested three different formulations for computing the modelled Chl*a* in a 3D coupled hydrodynamical–biogeochemical model of the Southwest lagoon of New Caledonia. The first formulation considers a constant Chl*a*:C ratio. In the second one, Chl*a* is a diagnostic variable related to the variable phytoplankton nitrogen-to-carbon ratio. In the last formulation, Chl*a* is a state variable of the model, which is dynamically simulated. Results showed important differences between the formulations, the first leading to overestimate the Chl*a* concentration in low nutrients conditions. Thus, this study strengthens the importance of the Chl*a* modelling in a coupled model in order to better estimate a crucial variable for validation of ecosystem models. **To cite this article:** V. Faure et al., *C. R. Biologies* 329 (2006).

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Résumé

Pertinence de diverses formulations du rapport Chlorophylle *a*:Carbon dans un modèle d'écosystème marin 3D. De nombreuses études expérimentales ont montré que le rapport entre la chlorophylle *a* et le carbone phytoplanctonique (Chl*a*:C) est fortement variable, alors que la plupart des modèles d'écosystème marin utilisent un rapport constant. Dans ce travail, nous avons testé trois formulations différentes pour calculer la valeur modélisée de Chl*a* dans un modèle 3D hydrodynamique–biogéochimique du lagon du Sud-Ouest de Nouvelle-Calédonie. La première formulation considère un rapport Chl*a*:C constant. Dans la seconde, la Chl*a* est une variable diagnostique reliée au rapport variable azote sur carbone phytoplanctonique. Dans la dernière formulation, la Chl*a* est une variable d'état du modèle, qui est simulée dynamiquement. Les résultats montrent des différences importantes entre les formulations, la première conduisant à surestimer la concentration en Chl*a* en situation de faibles ressources en nutriments. Cette étude renforce donc l'importance de la modélisation de la Chl*a* dans un modèle couplé, afin de mieux estimer une variable cruciale pour la validation des modèles d'écosystèmes. **Pour citer cet article :** V. Faure et al., *C. R. Biologies* 329 (2006).

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Keywords: 3D hydrodynamical–biogeochemical modelling; Chlorophyll:carbon ratio; Lagoon; New Caledonia

Mots-clés : Modélisation hydrodynamique–biogéochimique 3D; Rapport chlorophylle:carbone; Lagon; Nouvelle-Calédonie

* Corresponding author.

E-mail address: faure@com.univ-mrs.fr (V. Faure).

¹ Present address: ECOLAG, UMR 5119 CNRS–université Montpellier-2, case 093, 34095 Montpellier cedex 05, France.

1. Introduction

To validate a model is a tough issue because of the difficulty to link the modelled and the experimental variables. The most frequently met example is that of phytoplankton chlorophyll *a* (Chl*a*). As phytoplankton productivity is usually measured in carbon assimilation rate (^{14}C), modelled growth rate equations are often expressed in carbon. Thus, most biogeochemical models express phytoplankton in terms of carbon and several elements (nitrogen, phosphorus, silicon, etc.) that could control the growth rate [1]. However, the biomass is usually measured as Chl*a*. In order to compare model results and field data, the first approach is to use a constant ratio of Chl*a* to carbon (Chl*a*:C) for converting phytoplankton carbon (C) in Chl*a* (ERSEM II [2], MODECOGel [3]). However, this ratio appears to be highly variable. Measurements in microalgal cultures show that Chl*a*:C changes in response to ambient light, temperature and nutrients availability, ranging from 0.036 to 1.2 g Chl*a* (mol C) $^{-1}$ (i.e. 0.003 to 0.1 g Chl*a* (g C) $^{-1}$ [4]). Recent studies on oceanic communities confirm this high variability with values ranging from 0.15 to 0.36 g Chl*a* (mol C) $^{-1}$ (i.e. 0.0125 to 0.03 g Chl*a* (g C) $^{-1}$) in the surface waters of subtropical Atlantic Ocean, with a 3–7-fold variation with depth [5]. In the English Channel, measured ratios values ranged from < 0.12 to > 0.96 g Chl*a* (mol C) $^{-1}$ (i.e. 0.01 to 0.08 g Chl*a* (g C) $^{-1}$ [6]).

As a consequence, adding a variable Chl*a* content in an ecosystem model appears to be an important challenge. One simple solution could be to impose a Chl*a*:C ratio dependent on the internal N:C ratio of phytoplankton [7]. Another way is to use an empirical model describing Chl*a*:C, as a function of temperature, daily irradiance and nutrient-limited growth rate [8]. Finally, several mechanistic approaches were developed to explicitly model the Chl*a* content [9–12].

This study aims at testing and comparing the inclusion of different formulations of Chl*a* in a 3D coupled model and at studying the impact on phytoplankton dynamics, and thus the ecosystem functioning. Three different formulations are considered: a constant Chl*a*:C ratio (CHL_CST), a Chl*a*:C ratio calculated from a stationary equation (CHL_ST), and, finally, a formulation using a dynamic equation to compute the concentration of Chl*a* (CHL_DYN). The model used in this work was first developed by Pinazo et al. [13] on the Southwest lagoon of New Caledonia. The choice of the site came from the contrasted status of its waters over the lagoon, associated with a high variability of the climatic conditions. Besides, this model expressed phytoplankton both

in carbon and nitrogen, with a variable N:C ratio, and thus permitted to use the formulations described above.

2. Materials and methods

2.1. Study site

New Caledonia is located in the Pacific Ocean at 22°S and 165°E and is subject to tropical or subtropical meteorological conditions. Winds are characterized by two main directions [14]. Trade winds blowing from 60° to 160° at speed higher than 4 m s $^{-1}$ represent 69% of yearly wind occurrence (~ 250 d yr $^{-1}$) around Nouméa. Westerly winds blowing from 220° to 300° at speeds higher than 2 m s $^{-1}$ represent less than 12% of yearly wind occurrence. The study area is the Southwest (SW) lagoon of New Caledonia, delimited by the land and the barrier reef between the Mato pass in the South, and the Uitoe pass in the North (Fig. 1). It receives freshwater runoffs from three main rivers (Pirogues, Coulée, and Dumbéa), but river flow rates are usually low, with 5 m 3 s $^{-1}$ (yearly average) for the largest one, the Dumbéa River [13]. The central part of the lagoon is characterized by oligotrophic to mesotrophic waters (yearly average 0.25 \pm 0.01 μg Chl*a* l $^{-1}$, [15]), whereas a local eutrophication is perceptible near the city of Nouméa (146 000 inhabitants). In addition to this local enrichment due to urban effluents, nickel industry delivers industrial effluents [16]. In this lagoon, phytoplankton biomass displays a weak seasonality, associated with marked short-term (week) variations [15] and interannual differences [17].

2.2. Hydrodynamic model

Hydrodynamic studies have been conducted in New Caledonia for over 25 years [18,19]. Recently, a model of the water circulation in the Southwest lagoon was developed and validated [20–23]. In these papers, model description, circulation analysis, vertical structure of the currents, and the initial and boundary conditions were presented in details. In this study, we use a $\Delta x = \Delta y = 500$ m grid spacing and 10 σ -levels.

2.3. Biogeochemical model

The first biogeochemical model was developed by Bujan et al. [24] and Pinazo et al. [13]. An improved version was implemented by Faure [25] by adding an explicit microbial loop. The structure of the whole model is described in Fig. 2. The structure is typical of

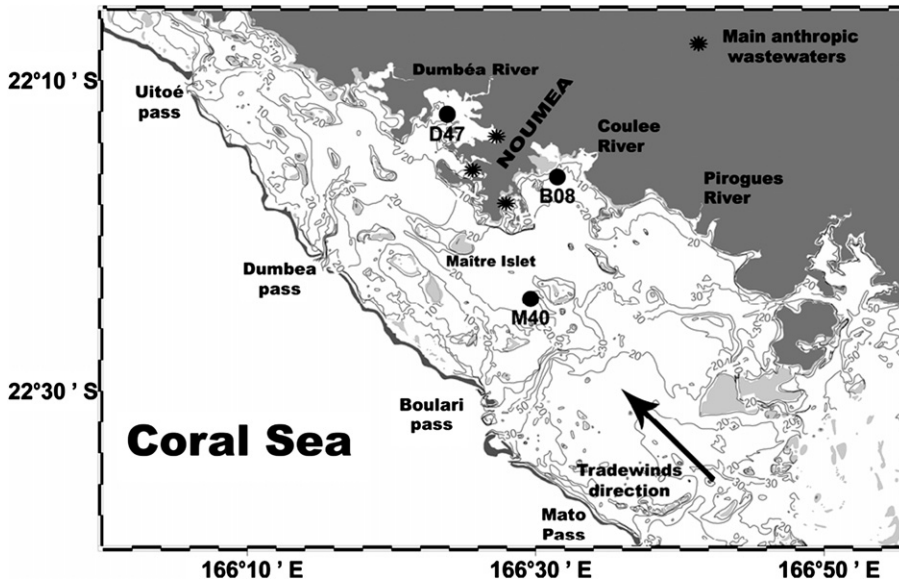


Fig. 1. Map of the Southwest lagoon of New Caledonia. Black dots represent the studied stations (M40, B08, D47).

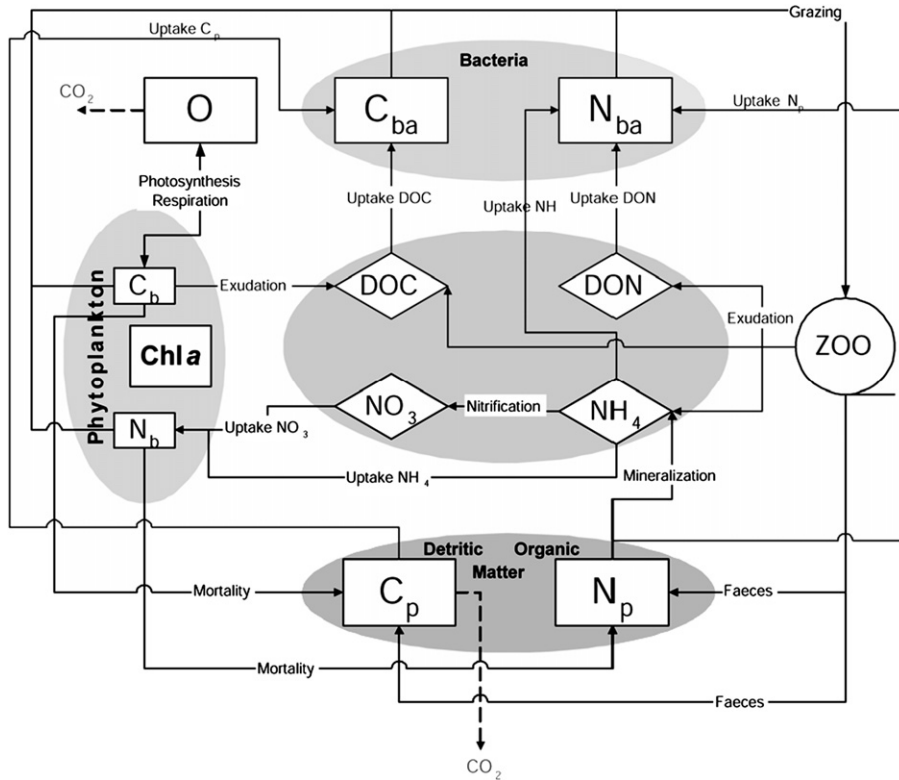


Fig. 2. The pelagic biogeochemical model.

NPZD models (nutrients–phytoplankton–zooplankton–detritus). However, the zooplankton is considered as a theoretical population, undifferentiated and static, and no state variable is associated to it. Thus, the model is

closed by a function of predation. Each compartment is expressed in carbon and nitrogen units, leading to 11 state variables (Table 1). One particularity of the model is the expression of the growth rate of phyto-

plankton based on the formulation of cell quota [26,27]. The variable stoichiometry allows taking into account the nutritional status of the cells, the nutrient limitation of phytoplankton growth, and the computation of nutrients uptake. Primary production is limited by temperature, light and nutrients (ammonium (NH₄) and nitrate (NO₃)). Bacterial production (BP) is also modelled with the cell quota concept [28]: BP is limited by the

Table 1
State variables in $\mu\text{mol l}^{-1}$, except Chla in $\mu\text{g l}^{-1}$

C_B	phytoplankton carbon
N_B	phytoplankton nitrogen
Chla	phytoplankton chlorophyll <i>a</i>
C_{BA}	bacterial carbon
N_{BA}	bacterial nitrogen
C_P	particulate detritic carbon
N_P	particulate detritic nitrogen
DOC	dissolved organic carbon
DON	dissolved organic nitrogen
NH₄	ammonium
NO₃	nitrate
O	oxygen

Table 2
List of equations linked with phytoplankton and Chlorophyll trends

Processes	Equation
C _B trend	$\frac{\partial C_B}{\partial t} = (1 - \text{exuDOC}) \cdot P^C \cdot C_B - \xi \cdot (V_{\text{NH}_4}^C + V_{\text{NO}_3}^C) \cdot C_B - g^B \cdot C_B - R^C \cdot C_B \quad (1)$
C _B growth rate	$P^C = P_m^C \cdot \left[1 - \exp\left(\frac{\alpha_{\text{Chla}} \cdot E \cdot Q_C^{\text{Chla}}}{P_m^C}\right) \right] \quad (2)$
Maximal C _B growth rate	$P_m^C = \mu_{\text{max}}(T) \cdot \left[\frac{Q_C^N - \min Q_C^N}{\max Q_C^N - \min Q_C^N} \right] \quad (3)$
Carbon specific nitrogen uptake	$V_N^C = \max V_N^C \cdot \left[\frac{\max Q_C^N - Q_C^N}{\max Q_C^N - \min Q_C^N} \right] \cdot \left(\frac{N}{N + K_N} \right), \quad N = \text{NH}_4, \text{NO}_3 \quad (4)$
Chla :C _B ratio [13]	$Q_C^{\text{Chla}} = \text{mean } Q_C^{\text{Chla}} \quad (5)$
Chla :C _B ratio [7]	$Q_C^{\text{Chla}} = Q_C^N \cdot \left(\min Q_N^{\text{Chla}} + (\max Q_N^{\text{Chla}} - \min Q_N^{\text{Chla}}) \cdot \frac{(Q_C^N - \min Q_C^N)}{\max Q_C^N - \min Q_C^N} \right) \quad (6)$
Chla trend [11,29]	$\frac{\partial \text{Chla}}{\partial t} = \rho_{\text{Chla}} \cdot (V_{\text{NH}_4}^C + V_{\text{NO}_3}^C) \cdot C_B - g^B \cdot \text{Chla} - R^{\text{Chla}} \cdot \text{Chla} \quad (7)$
Regulatory term	$\rho_{\text{Chla}} = \frac{\max Q_N^{\text{Chla}} \cdot P^C}{\alpha_{\text{Chla}} \cdot Q_C^{\text{Chla}} \cdot E} \quad (8)$

Q_X^Y represents the ratio $Y:X$.

cell internal quota in carbon and nitrogen. All state variables equations could be found in Pinazo et al. [13] and Faure [25]. Here, we present only the pertinent equations (Table 2).

Three different formulations were tested in order to model the Chla concentration (CHL_CST, CHL_ST, CHL_DYN). In Table 2, Eqs. (1) to (4) were the same for each formulation, describing the trend of phytoplankton carbon and the carbon specific nitrogen uptake (on NH₄ and NO₃).

In CHL_CST, modelled Chla concentration was computed using a constant Chla:C ratio equal to 0.24 g Chla (mol C)⁻¹ (Table 2, Eq. (5)).

As the model simulated a variable phytoplankton N:C ratio, the second formulation chosen (CHL_ST) was a stationary equation from Smith et al. [7] (Table 2, Eq. (6)). This equation calculated the Chla:C ratio of phytoplankton depending on their internal N:C ratio. The Chla:C ratio is positively correlated with the N:C ratio. In CHL_ST, Chla is not a state variable, but a diagnostic variable, and permitted to diminish computation time.

In CHL_DYN, Chla is an explicit state variable in the ecosystem model. The Chla synthesis is modelled with a dynamic equation from Geider et al. [11] and Lefèvre et al. [29] (Table 2, Eqs. (7)–(8)). Carbon-specific Chla synthesis is determined by the rate of nitrogen assimilation (Table 2, Eq. (4)), and a regulatory term (Table 2, Eq. (8)).

2.4. Coupled model

Eq. (1) gives the standard three-dimensional equation for each of the biogeochemical concentration (*Conc*). *BIO_TEND* represents the gain and losses of the considered variable:

$$\begin{aligned} \frac{\partial \text{Conc}}{\partial t} + U \frac{\partial \text{Conc}}{\partial X} + V \frac{\partial \text{Conc}}{\partial Y} + (W - W_B) \frac{\partial \text{Conc}}{\partial Z} \\ = \text{BIO_TEND} + \frac{\partial}{\partial X} \left(K_X \frac{\partial \text{Conc}}{\partial X} \right) \\ + \frac{\partial}{\partial Y} \left(K_Y \frac{\partial \text{Conc}}{\partial Y} \right) + \frac{\partial}{\partial Z} \left(K_Z \frac{\partial \text{Conc}}{\partial Z} \right) \end{aligned}$$

The standard structure of three-dimensional biogeochemical equations is presented in Eq. (1). The left-hand side of the equation accounts for temporal variability, vertical and horizontal advection, and settling velocity of particles. The right-hand side of the equation accounts for biogeochemical gain and loss (*BIO_TEND*), and turbulent diffusivities. The current velocities (*U*, *V*, *W*) and the diffusivity coefficients (*K_X*, *K_Y*, *K_Z*) calculated by the hydrodynamic model were used as forcing variables for the biogeochemical model.

The hydrodynamic model was forced by tide and by realistic wind with a time step of 10 min. It was dynamically coupled with the biogeochemical model [25]: the scheme of advection–diffusion calculated the evolution of biogeochemical variables in parallel to the execution of the physical code, with the same time step of 50 s. The biogeochemical model was forced by irradiance measured each hour, and calculated the trends of biogeochemical variables, with a time step of 20 min.

2.5. Simulation strategy

Initialization conditions were established thanks to a campaign during which 90 stations were sampled over the lagoon (Camecal 5, 19–27 June 2003). Boundary conditions were adjusted to field measurements and published data (Table 5). Freshwater inputs from the three main rivers were introduced in the model. The strong trophic gradient between the bays around Nouméa and the central part of the lagoon led us to

consider the inputs in nitrogen from human sewages in three bays of Nouméa (Sainte-Marie, Koutio and Grande Rade, see Fig. 1). Moreover, coupling between pelagic processes and benthic mineralization could represent a source of nitrogen in coastal areas of the lagoon (C. Grenz, unpublished data). We added a constant positive flux of ammonium and nitrate into the pelagic water column along the coastline (NH₄: 15 μmol m⁻² h⁻¹; NO₃: 5 μmol m⁻² h⁻¹; Grenz, unpublished data).

A 34-day realistic simulation of the model was run in order to examine the biogeochemical response of the Southwest lagoon to the transient meteorological conditions measured during June and July 2003 (Fig. 3). The simulation began on 19 June and ended on 23 July; it permitted to illustrate the model behaviour under different meteorological events. Firstly, a low irradiance (lower than 600 J cm⁻² d⁻¹) occurred around 27 June and 16 July, whereas the mean irradiance for this period is 1257 J cm⁻² d⁻¹; strong rains came with the second decrease of irradiance, leading to river flows in each river, up to 300 m³ s⁻¹ for the Dumbéa River. Secondly, a shift from a low northwest to a strong southeast wind took place around the 7 July. The duration of the simulation was chosen in order to compare model outputs with field data.

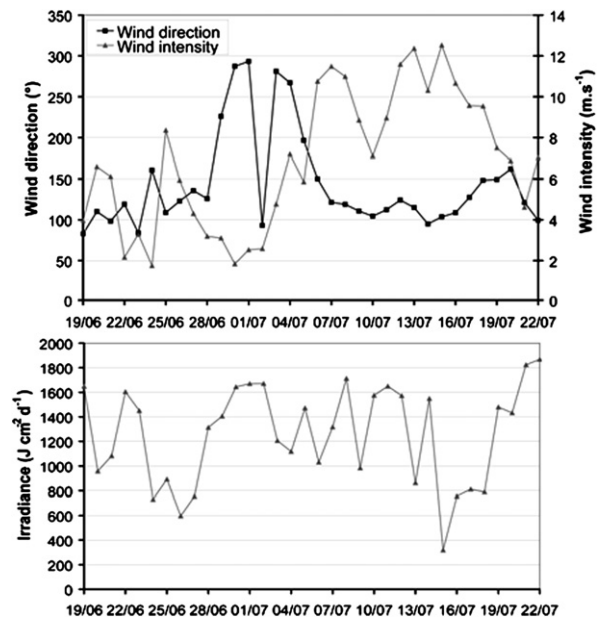


Fig. 3. Upper panel: wind intensity (m s⁻¹) and direction (○). Lower panel: irradiance (J cm⁻² d⁻¹). Data measured on Maître Islet from 19 June 2003 to 22 July 2003. Wind: mean values over 24 h of data measured every 10 min. Irradiance: daily sum of data measured every hour.

2.6. Measured data

Several lagoon surveys demonstrated that, on average, the water column is nearly homogeneous and that 3-m-depth samples are well representative of the whole water column [13,15]. For an easier presentation, results will be discussed after distinguishing three stations with increasing trophic status (Fig. 1): M40 represents the central part of the lagoon, B08 an open bay and D47 a semi-closed bay around Nouméa.

Experimental data were collected on 8 and 22 July at 3-m-depth on M40, B08 and on 10 and 23 July on D47. Chlorophyll *a* (Chl*a*) concentration was fluorometrically determined on 7-ml methanol extracts of 300-ml samples collected onto Whatman GF/F filters according to Holm-Hansen [30]. Ammonium concentration was fluorometrically determined on three 40-ml replicates on a Turner TD-700, using the *o*-phtaldialdehyde method [31].

3. Results

Like experimental studies, the model outputs showed the same homogeneity for the vertical distribution

of state variables and we chose therefore to present 3-m-depth model outputs, corresponding to the sampling depth. Fig. 4 presents for each station and each model formulation (CHL_CST, CHL_ST, CHL_DYN) the Chl*a* concentration, the Chl*a*:C ratio, the N:C ratio, the ammonium concentration (NH₄) and the gross primary production (PP).

The impact of physical forcings was evident and explained the main variations of the biogeochemical variables. The two low-irradiance events led to a decrease of PP, and river inputs in the bay (B08 and D47) caused an increase of NH₄ from 16 July. The wind shift of 7 July produced a decrease of Chl*a* in each zone. Oligotrophic waters coming from the southeastern end of the lagoon flushed the central part of the lagoon (M40), while the bays (B08 and D47) received the waters driven away from the central part of the lagoon. However, NH₄ increased in M40 because of low consumption of nutrients (low PP and low Chl*a* concentration) and active regeneration by bacteria.

Simulated Chl*a* and PP highlighted the trophic status of each station. The PP and Chl*a*, averaged on the 34-day simulation, were 12.6 mg C m⁻³ d⁻¹ and 0.23

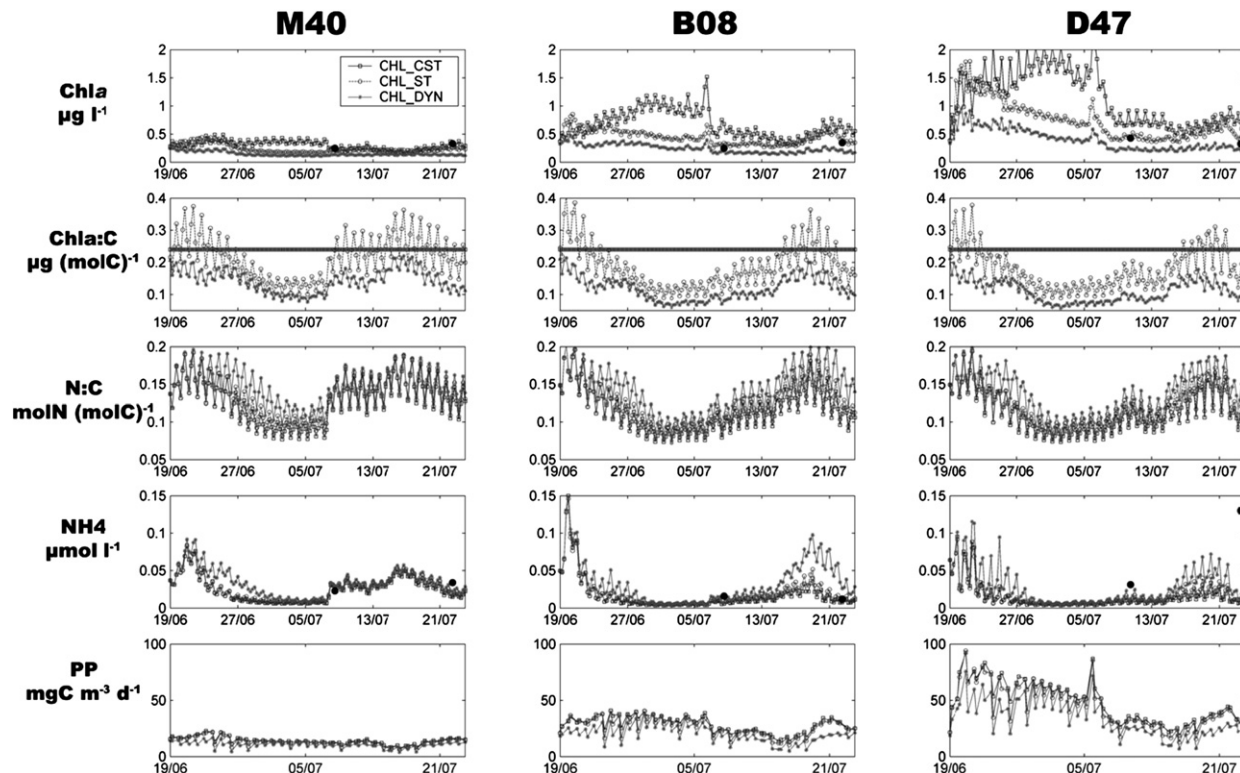


Fig. 4. Time evolution of simulated Chl*a* ($\mu\text{g l}^{-1}$), Chl*a*:C ratio ($\mu\text{g (mol C)}^{-1}$), N:C ratio ($\text{mol N (mol C)}^{-1}$), NH₄ ($\mu\text{mol l}^{-1}$) and primary production ($\text{mg C m}^{-3} \text{d}^{-1}$), at stations M40, B08 and D47. Different curves represent results from each model formulation. Square: CHL_CST; circle: CHL_ST; star: CHL_DYN. Filled circles represent the measured values for Chl*a* and NH₄. Remark: the line for Chl*a*:C ratio curves represents the constant ratio value in CHL_CST.

$\mu\text{g l}^{-1}$ at M40, $24.9 \text{ mg C m}^{-3} \text{ d}^{-1}$ and $0.45 \mu\text{g l}^{-1}$ at B08, whereas maximum values were $42.1 \text{ mg C m}^{-3} \text{ d}^{-1}$ and $0.75 \mu\text{g Chla l}^{-1}$ at D47. Comparisons between model formulations showed that CHL_CST predicted the highest values of PP and Chla, whereas CHL_DYN resulted in the lowest values, with CHL_ST displaying intermediate values (Table 4).

Values of Chla:C ratio for CHL_ST and CHL_DYN varied around the constant value of CHL_CST (Table 4). CHL_DYN predicted lower values than CHL_ST, and never reached the constant value of $0.24 \text{ g Chla (mol C)}^{-1}$. Moreover, the diel variations of the Chla:C in CHL_ST were higher than in CHL_DYN and reached up to $0.15 \text{ g Chla (mol C)}^{-1}$. Variations of Chla:C for each model formulation were well correlated with the change of the N:C ratio and hence with changes in NH_4 concentration. At each station, the maximum of the Chla:C coincided with the maximum of NH_4 concentration. Values of N:C ratio were higher for CHL_DYN due to a low carbon primary production, whereas this ratio was quite equivalent between CHL_CST and CHL_DYN. High values of N:C, leading to low nutrient uptake, explained the higher concentration in NH_4 for CHL_DYN during the low irradiance events.

Model outputs for Chla fitted well with field data (closed circles on Fig. 4), especially for CHL_ST. Simulated NH_4 concentrations were also consistent with field data, except on 22 of July in D47. This surprising high value could be explained by an unpredicted advective transport of allochthonous ammonium coming from Nouméa City or might be the result of analytical contamination.

4. Discussion

4.1. Validity of simulated variables

The simulated variables appeared to be consistent with usual observations in the Southwest lagoon of New Caledonia [15–17,19]. The gradient of primary production between the central part of the lagoon and the bays was well reproduced. The average simulated values (Table 4) appeared to be coherent with the measured data, with a yearly averaged PP of 8.1 and $45.3 \text{ mg C m}^{-3} \text{ d}^{-1}$ at M33 (close to M40) and N12 (in a semi-closed bay of Nouméa), respectively [15]. The measured value of Chla and NH_4 concentrations were well reproduced by the model, especially when using the CHL_ST model (Fig. 4). The simulated Chla:C ratios ranged from a minimum value of $0.07 \text{ g Chla (mol C)}^{-1}$ to a maximum of $0.375 \text{ g Chla (mol C)}^{-1}$. These values fall

within the range reported in experimental studies on microalgal culture (0.036 to $1.2 \text{ g Chla (mol C)}^{-1}$) [4], in subtropical Atlantic Ocean waters (0.15 to $0.36 \text{ g Chla (mol C)}^{-1}$) [5] and in English Channel waters (0.12 to $0.96 \text{ g Chla (mol C)}^{-1}$) [6]. The simulated phytoplankton N:C ratio ranged from 0.076 to $0.19 \text{ mol N (mol C)}^{-1}$. These values are consistent with the 0.08 – 0.164 range reported in the North Pacific Central Gyre [32], or with the 0.07 – 0.14 range observed in the Atlantic Ocean (BATS) [29].

4.2. Behaviour of each model

As shown by a previous modelling study [13,23], the lagoon channel is deeply influenced by hydrodynamics resulting from trade winds. Oceanic waters enter the lagoon by the southern sector end, and very short flushing times of water are computed in the central part of the lagoon [23]. In our simulation, the different model formulations did not show large differences in M40, therefore under strong hydrodynamical forcings (strong trade winds), the complexity of a biogeochemical model does not significantly change the outputs [33].

However, flushing times of waters in areas like bays around Nouméa are longer [23], and therefore these zones are more controlled by biogeochemical processes. In B08 and D47, each model formulation clearly produced different outputs. During the first part of the simulation (19 June to 7 July), using CHL_CST, Chla remained very high in B08 and D47, thanks to a high carbon production. At the opposite, using CHL_ST or CHL_DYN, Chla started to decrease on 27 June, when the NH_4 concentration was too low to maintain the N:C ratio. Using these two model formulations, during the rain event and nitrogen inputs on 16 July, the N:C and Chla:C ratios increased, leading to an increase of Chla (slight for CHL_DYN). It appeared that a constant Chla:C ratio could lead to overestimate the Chla concentration in low nutrient conditions, since Chla could also be dependent upon the N:C ratio and thus on the nutrient resources. As a consequence, even if the carbon primary production could be well described and modelled, the conversion of phytoplankton carbon into Chla using a constant ratio would produce significant inaccuracy on the value of the Chla concentration.

Using the CHL_DYN simulation, the Chla:C ratio was low, leading to unrealistically low values of Chla in comparison with measured data (Fig. 4). Lefèvre et al. [29] showed that some parameters as $\mu_{\text{max}}(T)$ or α_{Chla} (Tables 2 and 3) could have a pronounced effect on the simulated value of Chla and perhaps a better estimation of our parameters could improve the outputs of

Table 3
List of parameters

Parameter	Definition	Value	Refs.
g^B	Grazing rate	0.4 d^{-1}	assumed
R^C, R^{Chla}	Respiration	0.1 d^{-1}	[29]
α_{Chla}	Chlorophyll-specific light-absorption coefficient	$8.5 \times 10^{-6} \text{ m}^2 \text{ mol C (g Chla J)}^{-1}$	assumed
ζ	Cost of nitrogen assimilation	$2.3 \text{ mol C (mol N)}^{-1}$	[29]
$\mu_{\max}(T) = a e^{bT}$	Maximum growth rate	$a = 9.8511 \times 10^{-6} \text{ s}^{-1}$ $b = 0.063321$	[13]
$\max V_{\text{NH}_4}^C$	Maximum uptake rate for NH_4	$2.1 \times 10^{-5} \text{ mol N (mol C)}^{-1} \text{ s}^{-1}$	[13]
$\max V_{\text{NO}_3}^C$	Maximum uptake rate for NO_3	$8.5 \times 10^{-6} \text{ mol N (mol C)}^{-1} \text{ s}^{-1}$	[13]
K_{NH_4}	Half saturation constant for NH_4 uptake	0.2 mol N	[13]
K_{NO_3}	Half saturation constant for NO_3 uptake	0.3 mol N	[13]
$\min Q_C^N$	Minimum phytoplankton N:C ratio	$0.05 \text{ mol N (mol C)}^{-1}$	[11]
$\max Q_N^{\text{Chla}}$	Maximum Chla:N ratio	$3.8 \text{ g Chla (mol N)}^{-1}$	assumed
$\min Q_N^{\text{Chla}}$	Minimum Chla:N ratio	$1 \text{ g Chla (mol N)}^{-1}$	[7]
$\max Q_C^N$	Maximum phytoplankton N:C ratio	$0.2 \text{ mol N (mol C)}^{-1}$	[13]
$\text{mean } Q_C^{\text{Chla}}$	Constant phytoplankton Chla:C ratio	$0.24 \text{ g Chla (mol C)}^{-1}$	[13]

Table 4

Primary Production (PP, in $\text{mg C m}^{-3} \text{ s}^{-1}$), Chla:C ratio (g (mol C)^{-1}) and Chla ($\mu\text{g l}^{-1}$), in M40, B08 and D47, averaged on the 34-day simulation. Values are presented for each model formulation: CHL_CST, CHL_STA, and CHL_DYN

	M40			B08			D47		
	CHL_CST	CHL_ST	CHL_DYN	CHL_CST	CHL_ST	CHL_DYN	CHL_CST	CHL_ST	CHL_DYN
Average PP	14.09	13.26	10.43	28.35	26.43	20.17	47.88	44.33	34.09
Average Chla:C	0.24	0.21	0.14	0.24	0.18	0.19	0.24	0.18	0.1
Average Chla	0.29	0.24	0.15	0.67	0.45	0.25	1.1	0.74	0.4

Table 5

Boundary conditions of state variables

	Chla ($\mu\text{g l}^{-1}$)	C _{BA} ($\mu\text{mol l}^{-1}$)	N _{BA} ($\mu\text{mol l}^{-1}$)	C _P ($\mu\text{mol l}^{-1}$)	N _P ($\mu\text{mol l}^{-1}$)	DOC ($\mu\text{mol l}^{-1}$)	DON ($\mu\text{mol l}^{-1}$)	NH ₄ ($\mu\text{mol l}^{-1}$)	NO ₃ ($\mu\text{mol l}^{-1}$)	O ($\mu\text{mol l}^{-1}$)
Boundary conditions	0.2	0.7	0.11	2.1	0.5	3	0.62	0.02	0.001	180

the dynamic model. The difficulty could be to establish a set of parameters able to describe contrasted trophic status such as those encountered in the Southwest lagoon of New Caledonia.

5. Conclusion – perspectives

Few model studies focused on including a dynamic model of phytoplankton Chla into a coupled physical–biogeochemical model [29,34]. Indeed, most of the models before 1995 [8] and 1997–1998 [4], and still nowadays, use a constant Chla:C ratio, producing biased results on the value of Chla concentration. The paradox is that these Chla values were generally used to validate these models. As Chla is one of the essential variables in modelling and field data, a modelled

variable Chla:C ratio seems an important step in the development and validation of an ecosystem model.

A comparison between a Redfieldian and a dynamic model [34] showed that fluxes and stocks can be equally well predicted by both models. Both Lefèvre et al. [29] and Faugeras et al. [34] found a good agreement between dynamic model outputs and field data, suggesting that such model was relevant. And indeed, this first attempt of comparing different formulations in the SW lagoon of New Caledonia showed that the three different formulations displayed overall the same pattern.

In Faugeras et al.'s study [34], the variability of the simulated variables was much higher in the mechanistic model thanks to a faster response of this model to its environment. Our results in the Southwest lagoon of New Caledonia showed equivalent conclusions, with strong variations occurring during transient events such

as modifications of the nutrients status or of the hydrodynamical forcings. For example, using CHL_DYN and CHL_ST simulations, the impact of nutrients availability on the Chla:C ratio, and thus on Chla, is clearly faster than using the CHL_CST model. Thus, in providing a thinner time resolution of the processes involved in phytoplankton dynamics, a variable Chla:C ratio allows a better description of the impact of short-term forcing, which is especially important in the ecosystem studied.

In parallel, this work underlines the importance of short-term sampling and the obvious difficulty to interpret field data in such a highly variable environment. Moreover, such modelling approaches could allow investigating the implication of high variability fluxes and variables on the carbon and nitrogen cycles of marine ecosystems.

In this comparative study of the SW lagoon of New Caledonia, the CHL_ST simulation appeared the most appropriate, since it provided outputs that were the closest to measured values, with a minimum parameterization and computation time. We can expect in the future that a dynamic model of the Chla (CHL_DYN) with a better parameterization will possibly give satisfactory and better results. Before applying such a model, an evaluation of parameters specific to our ecosystem will be required. Nevertheless, the cost in computation time will be particularly higher. Besides, others formulations, like the empirical one from Cloern et al. [8], could also be considered and tested in order to proceed with the study of Chla:C ratio in 3D ecosystem models.

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