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Biogeochemical model of nitrogen cycling in Ahe (French Polynesia), a South Pacific coral atoll with pearl farming

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Abstract

A biogeochemical model (ECO3M-Atoll) was configured to simulate the lower food web in Ahe Atoll lagoon where phytoplankton is mostly nitrogen limited. Understanding the dynamics of phytoplankton – the main food source for oysters – is crucial for the management and the allocation of new pearl farming sites. After parametrizing the model with *in situ* observations, we tested different hypotheses about nitrogen cycling (benthic remineralization, atmospheric N fixation, etc.) and compared the results to a large observational dataset. Model results show that simulated (pico- and nano-) phytoplankton biomass and nitrogen concentrations are close to *in situ* data. The simulated biogeochemical processes (uptake and primary production) are also very similar to the observed values. In the model, primary production ranged from 1.00 to 2.00 mg C m⁻³ h⁻¹ for pico- and 0.40 to 1.00 mg C m⁻³ h⁻¹ for nanophytoplankton; mean N uptake was 2.02 μmol N m⁻³ h⁻¹ for pico- and 1.25 μmol N m⁻³ h⁻¹ for nanophytoplankton.

Keywords: Biogeochemical model; Ahe atoll; pearl farming; phytoplankton; nitrogen cycle

1. Introduction

After tourism, pearl farming represents the second largest source of income in French-Polynesia. The country dominated the market for black pearls during the 1980-90's. However, since the early 2000s, the sector is in crisis (Andréfouët et al., 2012), further exacerbated by the complexity of pearl farming. Pearl production depends on the life cycle of *Pinctada margaritifera* – the black-lip pearl oyster – and the success rate of farming is only about 30 % (about 300 sellable pearls per 1.000 grafted oysters) (Andréfouët et al., 2012).

In French Polynesia, pearl oysters are reared in fairly deep atoll lagoons. Atolls can be defined as productive micro-environments within an otherwise oligotrophic ocean. Indeed, atoll lagoons typically exhibit higher phytoplankton biomass and production compared to the

33 surrounding ocean (Charpy et al., 2012). Phytoplankton is the main food source for the
34 oysters. During its two life stages (larvae and adult), *Pinctada margaritifera* feed on two
35 different size classes of phytoplankton: while larvae consume mostly picophytoplankton (< 2
36 μm) adults prefer larger organisms such as nano- and microphytoplankton (> 2 and > 10 μm ,
37 respectively) (Pouvreau et al., 2000). Farmed oysters have to compete for phytoplankton with
38 zooplankton and several filter feeders such as mollusks (clams or wild oysters).

39 In atoll lagoons, the availability of nutrients is one of the main drivers of phytoplankton
40 growth. This bottom-up control depends on the atoll geomorphology (size, depth, and
41 exchange with the open ocean). In deep or well flushed lagoons, primary production is
42 typically more limited by nitrogen (N) than by phosphorus (P) (Dufour et al., 2001). The
43 exact sources of N in these ecosystems is still unclear. Several studies have shown that
44 remineralization sustains an important part of phytoplankton nitrogen uptake (Gaertner-
45 Mazouni et al., 2012; Lacoste and Gaertner-Mazouni, 2016; Pagano et al., 2017). The most
46 important sources of remineralized nitrogen are zooplankton, farmed oysters and associated
47 epibionts (Lacoste and Gaertner-Mazouni, 2016), bacterial output and viral lysis (Shelford et
48 al., 2012), coral and associated zooxanthella (Wild et al., 2004), and sediments (Gaertner-
49 Mazouni et al., 2012). There are also several exogenous nitrogen sources including
50 atmospheric N_2 fixation by diazotrophs (Charpy-Roubaud et al., 2001), geothermal endo-
51 upwelling bringing up nutrients from the deep (Rougerie et al., 1992), rainfall, and of course
52 anthropogenic inputs. Below, we will investigate some of these potential sources in more
53 detail in order to assess their relative importance for Ahe Atoll.

54 To further improve our understanding of nutrient cycles in atoll lagoons, biogeochemical
55 models (BGCMs) can provide a valuable framework. In tropical lagoons, BGCMs are often
56 used to understand how interactions between compartments change when the lagoon is open
57 or closed (Everett et al., 2007). Mongin and Baird (2014) used a BGCM to understand carbon
58 calcification and the impact of climate change (heat stress) on Great Barrier Reef. In New
59 Caledonia (Faure et al., 2010a,b; Fuchs et al., 2012, 2013; Hochard et al., 2010), modelling
60 has been used to understand seasonal changes in local lagoons and the effects of strong events
61 (El Niño and La Niña). However, only few studies have applied BGCMs to atolls. Niquil et
62 al. (1998) developed an inverse model to describe the planktonic food web in the Takapoto
63 Atoll (French Polynesia). Modelling was also used to understand the functioning of farmed
64 lagoons in temperate environments. For example, they were used to understand biodeposition

65 due to farming (Weise et al., 2009), to manage clam farms (Marinov et al., 2007), or to
66 investigate how farmed populations affect nutrient cycling (Cugier et al., 2010; Dowd, 2005).

67 In an effort to lend support to local pearl farmers and decision makers, this study adapted
68 an existing BGCM (see below) and applied it to Ahe Atoll (French Polynesia), a semi-
69 enclosed atoll environment with an extensive historical dataset useful for model validation
70 (Bouvy et al., 2012; Charpy et al., 2012; Fournier et al., 2012; Lefebvre et al., 2012; Pagano et
71 al., 2012; Thomas et al., 2010). A field campaign was conducted between November and
72 December 2017 with the specific purpose to collect *in situ* observations that would allow the
73 quantification (and thus parametrization) of the biogeochemical processes in the lagoon
74 (Rodier et al., 2021). The sampling strategy was designed to be able to describe the
75 biogeochemical state of the lagoon (*e.g.*, collecting phytoplankton biomass, dissolved organic
76 and inorganic matter concentration) and to provide the necessary information to correctly
77 parameterize the relevant dynamics in the BGCM (*e.g.*, primary production and nitrogen
78 uptake rates). The model presented here is a 0-dimensional (variables vary only over time),
79 deterministic BGCM that aims to capture the main biogeochemical processes taking place at
80 the lower trophic levels. The aim of this paper is to provide a first glimpse of the parameter
81 values that yield a satisfactory representation of the *in situ* ranges observed at Ahe Atoll.

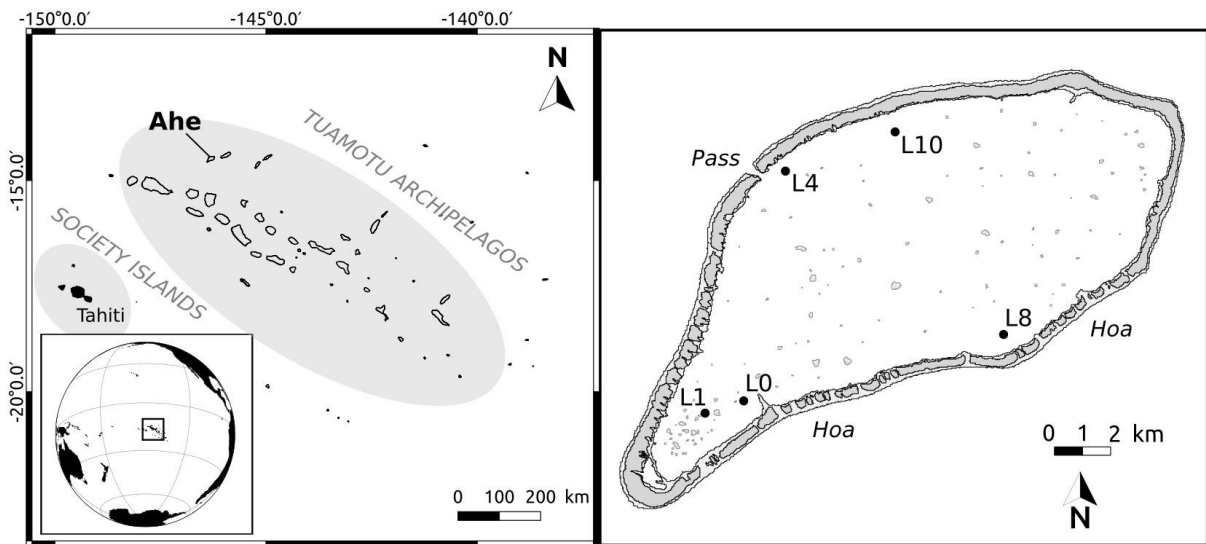
82 The model is based on the ECO3M-Lagoon configuration (Faure et al., 2010a,b) and has
83 been adapted for the Ahe Atoll. The simulation results provide a deeper understanding of the
84 nitrogen cycling in the lagoon and were used to test the impact of pearl farming on the
85 nitrogen cycle and phytoplankton biomass. Furthermore, the model was used to assess
86 whether nitrogen input primarily results from benthic or exogenous sources. In addition, we
87 tested the sensitivity of the new model configuration to different initial and light conditions
88 and whether it can successfully reproduce the different biogeochemical regimes found in
89 different parts of the lagoon. In the future, as part of the MANA (Management of Atolls)
90 project, the model will be coupled with MARS3D, a hydrodynamic model (Lazure and
91 Dumas, 2008), and with a dynamic energy budget (DEB) model developed by Thomas et al.
92 (2016) and Sangare et al. (2019) to understand the physiology and spatial distribution of *P.*
93 *margaritifera*. More precisely, the model will supply food inputs for studying the spawning of
94 mature oyster and food inputs for development of larvae.

95 2. Materials and methods

96 2.1. Study site

97 Ahe Atoll is located in the north-western part of the Tuamotu Archipelago in French
98 Polynesia, about 500 km north-east of Tahiti (

99 **Fig. 1).** Ahe is a semi-enclosed atoll with a lagoon that is connected to the open ocean by
100 just one active pass on the north-western side of the atoll rim. Moreover, several *hoa* (shallow
101 reef flat spillways) exist on the southern and north-western sides of the rim. The lagoon
102 covers an area of 142 km² (main length = 23 km), has an average depth of 41 m (maximum 70
103 m), and a renewal time of about 250 days (Dumas et al., 2012). The climate is wet tropical
104 with one rainy season from November to April. Maximum precipitation occurs in December
105 and January. The air temperature varies only slightly over a year (25 – 29 °C). The wind
106 regime is dominated by moderate trade winds blowing from East-South-East (60° to 160°)
107 and with strong southerly winds in the austral winter (Dutheil et al., 2020). Our study period
108 (November/December 2017) corresponds to the hot season at the beginning of the rainy
109 period. Weather data indicated that while the rainy season had not yet started in November
110 2017, temperatures had already risen significantly since October 2017. During our field
111 campaign, we only had one rain event (December 2, 2017) and a constant trade wind regime
112 throughout.



113

114

115 **Fig. 1.** Left: Location map of French Polynesia and Ahe Atoll. Right: Locations of sampling
116 stations (black dots) and of the pass and hoa.

117

118 2.2. Dataset

1
2 119 For a multi-year model-data comparison, we used a large dataset consisting of data from
3
4 120 campaigns that took place in the Ahe lagoon in 2007 and 2008 (Thomas et al., 2010), in 2010
5
6 121 (Charpy et al., 2012), in 2012 and 2013 (Pagano et al., 2017), and in 2017 (Sangare et al., in
7
8 122 prep.). In order to implement and calibrate some of the key biogeochemical processes in the
9
10 123 model, we used data obtained at five stations in the lagoon (L0, L1, L4, L8, and L10 in **Fig. 1**)
11
12 124 during a single field campaign (AHE2017) that took place between November 27 and
13
14 125 December 07, 2017. More details about the sampling and analysis can be found in Rodier et
15
16 126 al. (2021).

17
18 127 At each station, vertical profiles of temperature, salinity, photosynthetically active
19
20 128 radiation (PAR), and dissolved oxygen concentration were recorded with a Seabird 19+ CTD
21
22 129 profiler of which we only used the values from 5 m. At L0, the CTD was also deployed in
23
24 130 mooring mode at a fixed depth of 5 m between Nov 29, 14:00h and Dec 01, 17:00h (total of
25
26 131 51 h) and between Dec 02, 16:00h and Dec 04, 08:00h (total of 40 h). This time series data
27
28 132 was used to parameterize the daily light availability.

29
30 133 Inorganic nutrients (NH_4^+ , $\text{NO}_2^- + \text{NO}_3^- = \text{NO}_x$, PO_4^-) and dissolved and particulate
31
32 134 organic matter (C, N, P) were sampled. $< 2 \mu\text{m}$, $> 2 \mu\text{m}$, and $> 10 \mu\text{m}$ Chla size classes
33
34 135 representing pico-, nano- and microphytoplankton biomass proxies, respectively, were also
35
36 136 collected. For reasons of simplicity, we grouped nano- and microphytoplankton together and
37
38 137 will refer to them collectively as nanophytoplankton throughout this manuscript.
39
40 138 Microphytoplankton are less common than nanophytoplankton in the Ahe lagoon, accounting
41
42 139 for less than 10 % of the total Chla (Charpy and Charpy-Roubaud, 1990).

43 140 To improve the model parameterization, we also measured several biogeochemical
44
45 141 pelagic and benthic fluxes that are not usually measured.

46
47 142 Carbon fixation (primary production) and nitrate and ammonium uptake rates of pico-
48
49 143 and nanophytoplankton were measured at each station ($^{13}\text{C}/^{15}\text{N}$ method). At L0, we also
50
51 144 obtained vertical profiles of primary production from the surface to a depth of 40m, at 5m
52
53 145 intervals. The resulting P/I curve was used to calibrate the relationship between solar
54
55 146 irradiance and photosynthesis in the model. Daily primary production was calculated from
56
57 147 carbon fixation and a photoperiod of 11.5h.

58
59 148 Finally, benthic flux chambers were deployed at each station to quantify nutrients (NH_4 ,

149 NO_x , Si(OH)_4 , PO_4) and oxygen fluxes at the sediment-water interface. Two different kinds of
150 chambers were used: one opaque chamber to simulate nighttime and a transparent chamber to
151 expose the sediments to the ambient light regime. More details can be found in Grenz et al.
152 (this issue).

153 **2.3. Biogeochemical model configuration: ECO3M-Atoll**

154 ECO3M-Atoll was adapted from the ECO3M-Lagoon configuration used by Faure et al.
155 (2010a, b) and by Fuchs et al. (2013, 2012) for the south-western lagoon of New Caledonia
156 (**Fig. 2**). They are based on the ECO3M platform developed by Baklouti et al. (2006a,b). One
157 of the main improvements over the ECO3M-Lagoon configuration, is that ECO3M-Atoll uses
158 two phytoplankton compartments for pico- and nanophytoplankton, respectively. While the
159 model has a typical NPZD (nutrients, phytoplankton, zooplankton, and detritus) structure,
160 zooplankton is parameterized as a “theoretical” population, i.e., it has no specific state
161 variable but all physiological functions and processes are described implicitly. Mass
162 conservation is achieved through a function that parameterizes predation by higher trophic
163 levels.

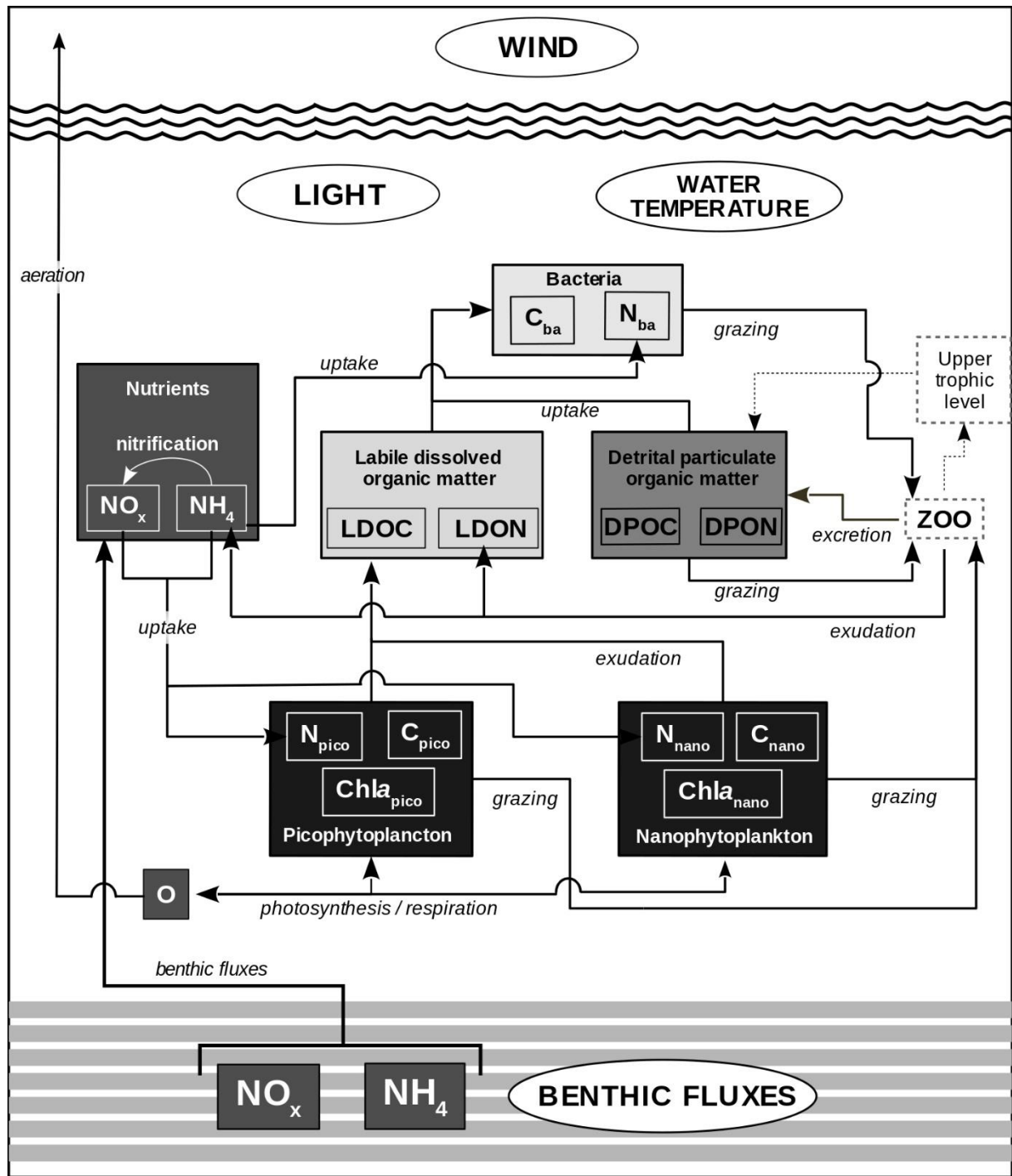


Fig. 2. Schematic diagram of the biogeochemical cycles represented in the ECO3M-Atoll model showing all state variables, processes, and forcings.

164

165 The model describes both the carbon and nitrogen cycles and consists of six
 166 compartments that use either carbon or nitrogen units: picophytoplankton (pico-),
 167 nanophytoplankton (nano-), bacteria, detritic particulate organic matter (DPOM), and labile
 168 dissolved organic matter (LDOM). At Ahe, phytoplankton are not limited by phosphorus
 169 (Charpy et al., 2012). The DOM compartment contains ammonium (NH_4), nitrate + nitrite
 170 (NO_x), and dissolved oxygen (O_2). In total there are 15 state variables (**Table 1**), and even
 171 chlorophyll *a*, which is a diagnostic variable, is also calculated from the phytoplankton's
 172 internal N/C ratio $Q_c^N phyto$ (Faure et al., 2006, 2010a; Smith and Tett, 2000) (see Appendix
 173 A). Moreover, this internal N/C ratio varies between prescribed phytoplankton-specific upper
 174 and lower bounds and is recalculated at each time step. This ratio contains information about
 175 the nutritional state of the cells when compared to the Redfield ratio (Redfield et al., 1963).
 176 This nutritional state is taken into account to calculate the growth and nutrient uptake rates
 177 (Tett, 1987). The same framework is used to express bacterial processes (Thingstad, 1987).

178 **Table 1.** State variables used in the ECO3M-Atoll model (except Chla which is a diagnostic
 179 variable).

Variables	Definitions	Units
C_{pico}	Picophytoplankton carbon	$\mu\text{mol L}^{-1}$
C_{nano}	Nanophytoplankton carbon	$\mu\text{mol L}^{-1}$
N_{pico}	Picophytoplankton nitrogen	$\mu\text{mol L}^{-1}$
N_{nano}	Nanophytoplankton nitrogen	$\mu\text{mol L}^{-1}$
$Chla_{pico}$	Picophytoplankton chlorophyll <i>a</i>	$\mu\text{g Chla L}^{-1}$
$Chla_{nano}$	Nanophytoplankton chlorophyll <i>a</i>	$\mu\text{g Chla L}^{-1}$
C_{ba}	Bacteria carbon	$\mu\text{mol L}^{-1}$
N_{ba}	Bacteria nitrogen	$\mu\text{mol L}^{-1}$
DPOC	Detrital particulate organic carbon	$\mu\text{mol L}^{-1}$
DPON	Detrital particulate organic nitrogen	$\mu\text{mol L}^{-1}$
LDOC	Labile dissolved organic carbon	$\mu\text{mol L}^{-1}$
LDON	Labile dissolved organic nitrogen	$\mu\text{mol L}^{-1}$
NH_4	Ammonium	$\mu\text{mol L}^{-1}$
NO_x	Nitrates	$\mu\text{mol L}^{-1}$

O

Oxygen

 $\mu\text{mol L}^{-1}$

181

182

As the phytoplankton variables were split into two different size classes (compartments), new equations were added and others from the original ECO3M-Lagoon configuration had to be updated. The parameter values were chosen based on the *in situ* data collected during the AHE2017 field campaign (Rodier et al., 2021) (Table 2).

The initial slope of the P/I curve (Fig. 3.A) was used to determine the Chl-specific light absorption coefficient ($\alpha_{chl a}$, Table 2). This coefficient is used to calculate pico- and nanophytoplankton growth (Eqs. 1-3). To simplify, we use the subscript “phyto” to denote both pico- and nanophytoplankton (see Appendix B).

$$P_{phyto}^C = \mu_{max}(T)_{phyto} \cdot \left[1 - \exp\left(\frac{-\alpha_{Chla} \cdot PAR \cdot Q_C^{Chla}}{\mu_{max}(T)_{phyto}}\right) \right] \quad (1)$$

$$\mu_{max}(T)_{phyto} = a_{phyto} \cdot \exp(b_{phyto} T) \cdot Q_{phyto} \quad (2)$$

$$Q_{phyto} = \frac{Q_C^N phyto - \min Q_C^N phyto}{\max Q_C^N phyto - \min Q_C^N phyto} \quad (3)$$

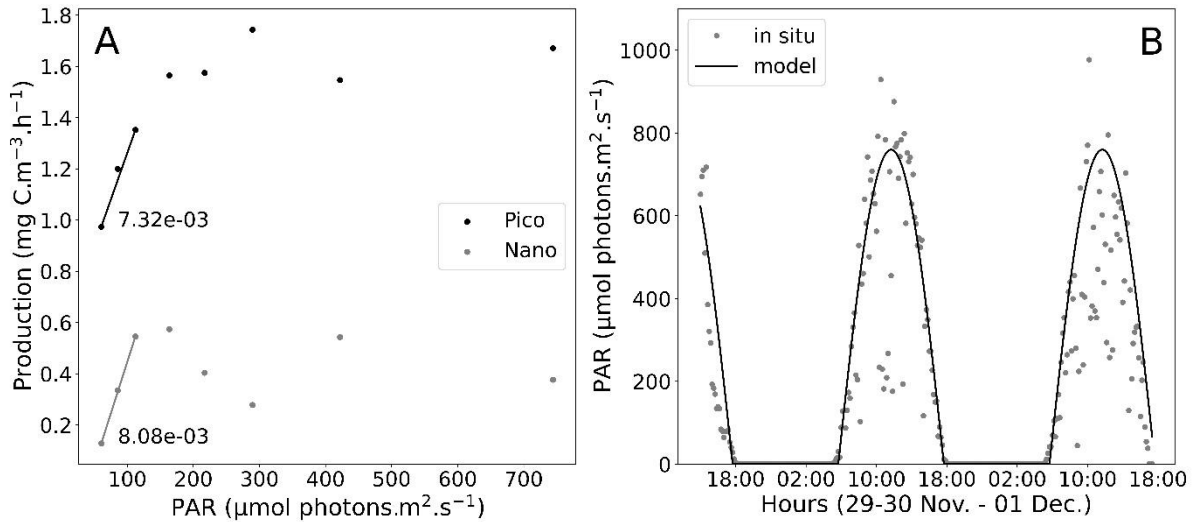


Fig. 3. A: Production/Irradiance curve of pico- (black) ad nano- (grey). B: PAR measurement (grey dots) and light function (black line).

195

Table 2. Parameters values for pico- and nanophytoplankton used during the calibration simulation at L0.

Parameters (units)	Pico-	Nano-	References
--------------------	-------	-------	------------

αChla (mg C. $\text{m}^{-1}.\text{h}^{-1}$. (μmol photons $.\text{s}^{-1}$) $^{-1}$)	7.32×10^{-3}	8.08×10^{-3}	Fig. 3.A
$\max V_{\text{NH}_4}$ ($\mu\text{mol N} . \text{m}^{-3} . \text{h}^{-1}$)	22	11	
$\max V_{\text{NO}_x}$ ($\mu\text{mol N} . \text{m}^{-3} . \text{h}^{-1}$)	6	4	Rodier pers. comm.
μ_{\max} (d^{-1})	0.70	0.34	
g (d^{-1})	1.89	1.47	Projet 9ème FED Professionnalisation et perennisation de la perliculture, 2010
K_{NH_4} ($\text{mmol N} . \text{m}^{-3}$)	0.05	0.30	
K_{NO_x} ($\text{mmol N} . \text{m}^{-3}$)	0.60	1.12	Assumed

198
199 All our simulations were made in 0D and over a period of 300 days to reach a steady
200 state, representative of a 5 m depth water cell. The temporal evolution of biogeochemical
201 processes or variable concentrations has the same shape (Supplementary Figure 1S). The
202 curve shows a spin-up period lasting 25 days. From the beginning of the simulation, the
203 modeled phytoplankton are nutrient limited. Then, after about 50 days, the model tends to
204 reach a steady state and is fully limited by nutrients. Results shown below correspond to
205 daytime values (as all *in situ* data was measured during daytime) after 200 days once the
206 simulation had become stable .

207 The model was forced using realistic average temperatures, wind velocities , and light
208 intensities in order to reproduce the ecosystem functioning at 3m depth. All stations used the
209 same constant temperature and wind speeds of 28.4 °C and 5.4 m s^{-1} , respectively,
210 corresponding to the mean *in situ* values during the AHE2017 campaign. Wind was used only
211 to drive oxygen aeration and light was prescribed based on a day/night cycle using actual
212 PAR measurements at L0 (**Fig. 3.B**):

$$PAR = \max\left(0, PAR_{\max} \times \sin\left(\pi \times \frac{t}{12}\right)\right) \quad (4)$$

213
214 where PAR_{\max} is the maximum value of PAR (in $\mu\text{mol photons s}^{-1}$) at noon and t is time (in
215 hours).

216 Different metrics are used for the statistical model-data comparison. The mean absolute
217 error (MAE), the root mean square error (RMSE), the percentage model bias (PB), and the
218 Willmott index (d1) (Willmott, 1982) are calculated using:

219 $MAE = \frac{\sum_{i=1}^n |M_i - D_i|}{n} \quad (5)$

220 $RMSE = \sqrt{\frac{\sum_{i=1}^n (M_i - D_i)^2}{n}} \quad (6)$

221 $PB(\%) = \frac{\sum_{i=1}^n (D_i - M_i)}{\sum_{i=1}^n D_i} \times 100 \quad (7)$

222 $d1 = 1 - \frac{\sum_{i=1}^n (M_i - D_i)^2}{\sum_{i=1}^n ((M_i - \bar{D}) + (D_i - \bar{D}))^2} \quad (8)$

223

224

2.4. Simulation strategy

2.4.1. Sensitivity to environmental forcing

227 Simulations to test model sensitivity to environmental forcing and parameters were
 228 performed at station L0 (**Table 3**) where the continuous PAR measurements were performed.
 229 To assess the model sensitivity to external forcing, the light and temperature ranges were
 230 chosen to be representative of the typical values encountered in Ahe atoll. The light range is
 231 based on PAR_{max} (see Section 2.2). The temperature range was chosen based on a one-year
 232 *in situ* dataset (Sangare, pers. comm.).

2.4.2. Sensitivity to model parameters

234 The sensitivity analysis was performed using the index described by Chapelle et al.,
 235 (2000):

236
$$IS\% = \left(\frac{100}{p}\right) \cdot \frac{1}{N} \sum_{i=1}^N \frac{|X_i - X_i^{raw}|}{X_i^{raw}} \quad (9)$$

237 where p is the percentage of parameter change ($\pm 10\%$ in this study), $N = 3600$ (only the last
 238 150 days are taken into account with hourly results), X_i is the variable value at time t after the
 239 parameter change, X_i^{raw} is the variable value at time t in the control simulation. IS% is used to
 240 identify the most sensitive parameters (*i.e.*, parameters whose variation causes the strongest
 241 deviation of state variables from the reference simulation).

242

243 **Table 3.** Initial conditions for the five Ahe stations.

	L0	L1	L4	L8	L10
C_{pico} ($\mu\text{mol.L}^{-1}$)	0.709	0.710	0.347	0.276	0.379
N_{pico} ($\mu\text{mol.L}^{-1}$)	0.029	0.108	0.053	0.042	0.058
Chl_a_{pico} ($\mu\text{g Chl.a.L}^{-1}$)	0.259	0.238	0.116	0.093	0.127
C_{nano} ($\mu\text{mol.L}^{-1}$)	0.187	0.196	0.066	0.049	0.066
N_{nano} ($\mu\text{mol.L}^{-1}$)	0.029	0.030	0.010	0.007	0.010
Chl_a_{nano} ($\mu\text{g Chl.a.L}^{-1}$)	0.069	0.081	0.027	0.020	0.027
C_{ba} ($\mu\text{mol.L}^{-1}$)	0.83	0.83	0.83	0.83	0.83
N_{ba} ($\mu\text{mol.L}^{-1}$)	0.14	0.14	0.14	0.14	0.14
DPOC ($\mu\text{mol.L}^{-1}$)	3.98	16.67	2.50	12.50	12.50
DPON ($\mu\text{mol.L}^{-1}$)	1.25	2.143	0.71	1.79	1.43
LDOC ($\mu\text{mol.L}^{-1}$)	7.50	10.80	9.57	8.76	8.76
LDON ($\mu\text{mol.L}^{-1}$)	2.40	2.65	2.18	1.95	2.16
NH₄ ($\mu\text{mol.L}^{-1}$)	0.012	0.013	0.028	0.012	0.025
NO_x ($\mu\text{mol.L}^{-1}$)	0.187	0.085	0.073	0.058	0.091
O ($\mu\text{mol.L}^{-1}$)	190	186.5	186.8	181.9	184.1

244

245 After this initial sensitivity analyses, two types of simulations were run: a reference
 246 simulation (control) – testing the sensitivity to initial conditions – and simulations to test
 247 various hypotheses about N inputs and grazing. The initial conditions of state variables were
 248 set according to *in situ* the values at each station (**Table 3**).

249 2.4.3. Sensitivity to initial conditions at the five stations

250 Reference simulations (named S0) were run at all stations (L0 to L10) with the same
 251 parametrization but different initial conditions. These simulations allowed us to compare
 252 modelled fluxes (nutrients uptake rates and primary production), final nutrient concentrations,

253 and phytoplankton biomass to *in situ* values at each station.

254 Four other simulations testing the process hypotheses were performed at all stations to
255 study the model response to changes in grazing, benthic fluxes, N fixation, and NO_x inputs.
256 The influence of two different kinds of nitrogen sources were tested.

257 2.4.4. Sensitivity to grazing mortality

258 Lacoste and Gaertner-Mazouni (2016) showed that nitrogen remineralization due to the
259 grazing by oysters (and associated epibiont filter-feeders) was stronger than nitrogen
260 remineralization in the sediment. Therefore, we ran several grazing simulations (S1.1, S1.2,
261 S1.3). Grazing rates were taken from the report of Projet 9ème FED Professionnalisation et
262 perennisation de la perliculture (2010). In S1.1, the grazing value for nanophytoplankton was
263 increased from 1.45 to 2.50 d⁻¹ to account for grazing by mesoplankton, oysters, and other
264 higher predators. In S1.2, picoplankton grazing was increased from 1.70 to 1.85 d⁻¹ to account
265 for grazing by nano- and mesoplankton. In S1.3, the grazing rate in both phytoplankton
266 compartments was increased.

267 2.4.5. Sensitivity to N-cycle components

268 Other N-cycle components were tested. In simulation S2, we added *in situ* benthic fluxes
269 obtained in 2017 using benthic chambers. Benthic nitrate and ammonium fluxes were
270 implemented as follows: the fluxes measured in dark chambers were used during night-time
271 and those measured in transparent chambers during the day were used during daytime (**Table**
272 **4**). Moreover, as demonstrated by Charpy-Roubaud et al. (2001) at Tikehau Atoll, benthic
273 nitrogen fixation may take place in the sediment. Therefore, in simulation S3 simulation we
274 applied a NH₄ influx of 0.18 μmol L⁻¹ h⁻¹. In simulation S4, an exogenous input of 0.36 μmol
275 L⁻¹ h⁻¹ of NO_x was used. We measured high NO_x values in rainwater (49 μmol L⁻¹) and in the
276 ground water below a *motu* (a coral sand island on the reef crown of an atoll) north of Ahe
277 Atoll (38 μmol L⁻¹).

278

279 **Table 4.** Benthic fluxes in the model in μmol m⁻² h⁻¹. Positive values represent fluxes from
280 the sediment to the water column and negative values represent fluxes from the water column
281 to the sediment.

NH ₄		NO _x	
Day	Night	Day	Night

L1	+8	+2	+63	-90
L4	+1	+0.3	+0.8	-12
L8	+7	+5	+85	-125
L10	+1.5	-3.4	+5.8	-25

282

283 3. Results

284 Three types of sensitivity analyses were performed on the control simulation: sensitivity
 285 to forcing conditions, to initial conditions, and to the choice of parameter values.

286 3.1. Sensitivity to environmental forcing

287 PAR_{max} and the water temperature were increased in 10 steps from 100 to 1300 μmol
 288 photons $\text{m}^{-2} \text{s}^{-1}$ and 23 to 31 $^{\circ}\text{C}$, respectively. We then compared the final pico- and nano-
 289 biomasses obtained for these different forcing levels (**Fig. 4**).

290 Pico- is more sensitive to changes in environmental forcing than nano-. Indeed, pico-
 291 varies between 0 and 0.2 $\mu\text{g Chla.L}^{-1}$, while nano- varies between 0 and 0.125 $\mu\text{g Chla L}^{-1}$.
 292 Moreover, below about 250 to 400 $\mu\text{mol photons m}^2 \text{s}^{-1}$, the impact of temperature changes
 293 are rather small on phytoplankton biomass, resulting in a pico- biomass of 0.0 and 0.10 and
 294 nano- biomass of 0 and 0.075 $\mu\text{g Chla L}^{-1}$ for temperatures of 31 $^{\circ}\text{C}$ and 25 $^{\circ}\text{C}$, respectively.
 295 For higher light intensities, primary production is no longer light-limited and becomes more
 296 sensitive to temperature. For example, at 700 $\mu\text{mol photons m}^2 \text{s}^{-1}$, the pico- biomass is 1.6
 297 times higher and the nano- biomass increased by a factor 2.

298 For the light and temperature ranges observed during the AHE2017 campaign, *i.e.*,
 299 temperatures between 28.3 and 29.5 $^{\circ}\text{C}$ and PAR between 550 and 1200 $\mu\text{mol photons m}^2 \text{s}^{-1}$,
 300 the model predicts only very small changes in phytoplankton biomass (white box in **Fig. 4**).

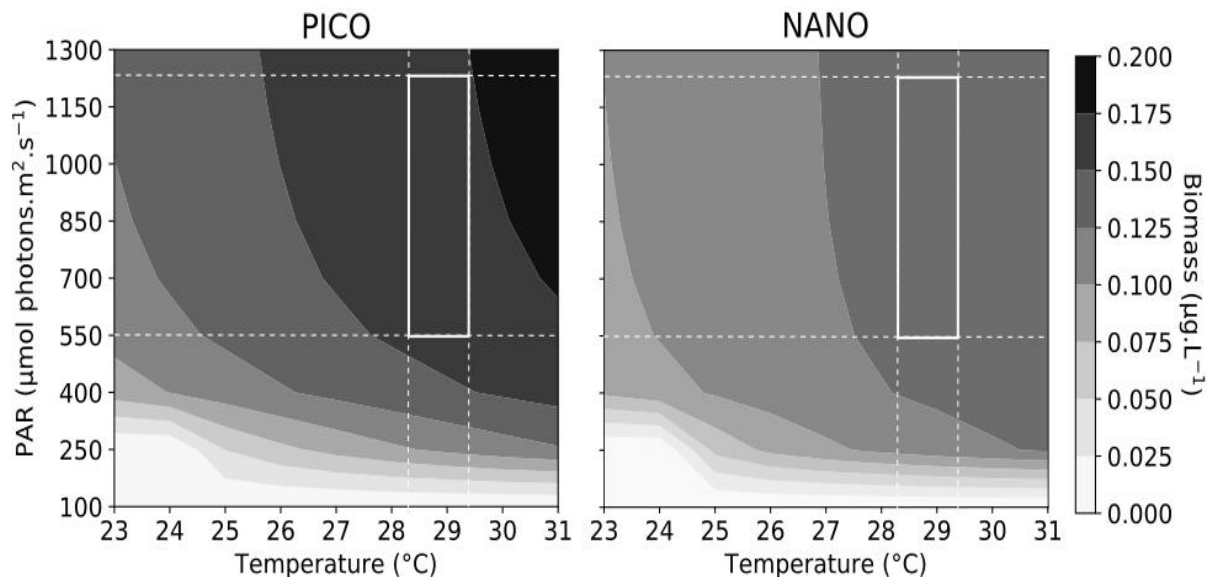


Fig. 4. Influence of temperature and maximum daily PAR on pico- (left) and nano- (right) biomass ($\mu\text{g Chla L}^{-1}$). The white box represents the *in situ* light and temperature ranges encountered during the AHE2017 campaign.

3.2. Sensitivity to model parameters

Indices of sensitivity (IS) for phytoplankton chlorophyll a, nutrients, and dissolved and particulate organic nitrogen are presented for a $\pm 10\%$ variation in parameter values (**Fig. 5**). The fractions of dissolved organic carbon (d_C) and nitrogen (d_N) assimilated by zooplankton were found to be the most sensitive parameters and influence all the state variables shown in **Fig. 5**. These parameters represent the ratio of the dissolved over the particulate pool, once assimilated by zooplankton and upper trophic levels. Increasing d_C by 10% led to an IS of 31% for NO_x and 17% for LDON. A 10% decrease in d_N yielded an IS of 37% for NO_x and 19% for LDON. Grazing parameters (g_{pico} , g_{nano}) are also sensitive and mainly impact the phytoplankton and nutrients. IS for pico- is about 1.36 and 1.10% for -10 and +10% changes in g_{pico} , respectively. The same variations in g_{nano} produce IS values for nano- of 1.28 and 1.07%, respectively. The same variations in grazing rates yield a maximum IS for NH_4 of 2.02%. Also, μ_{max} mainly impacts nutrients and phytoplankton as it controls phytoplankton biomass production and, in turn, the nutrient concentrations through the microbial loop. Unsurprisingly, maxV , *i.e.*, the maximum nutrient uptake rate (NH_4 and NO_x) by phytoplankton, affects nutrient concentrations.

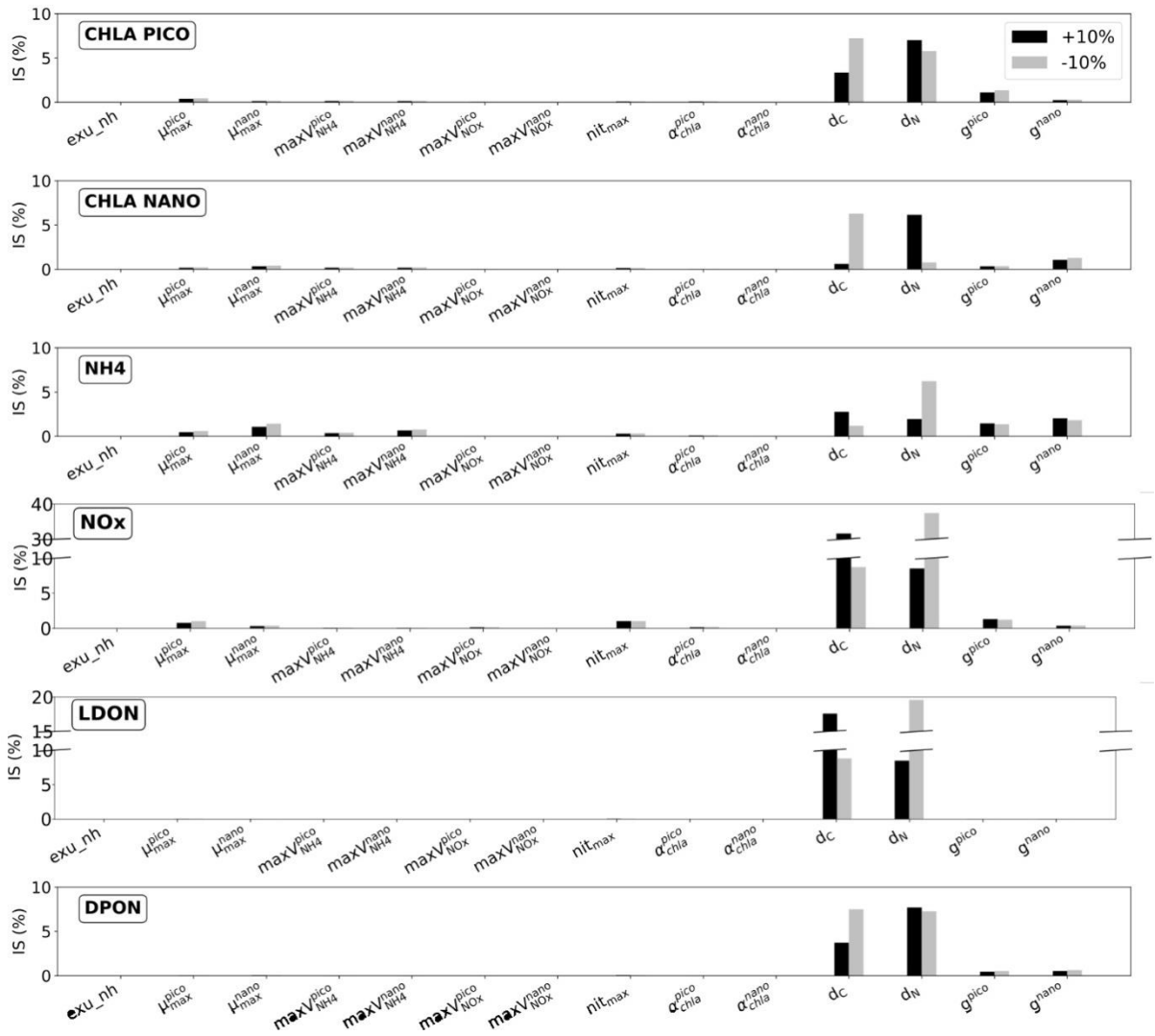


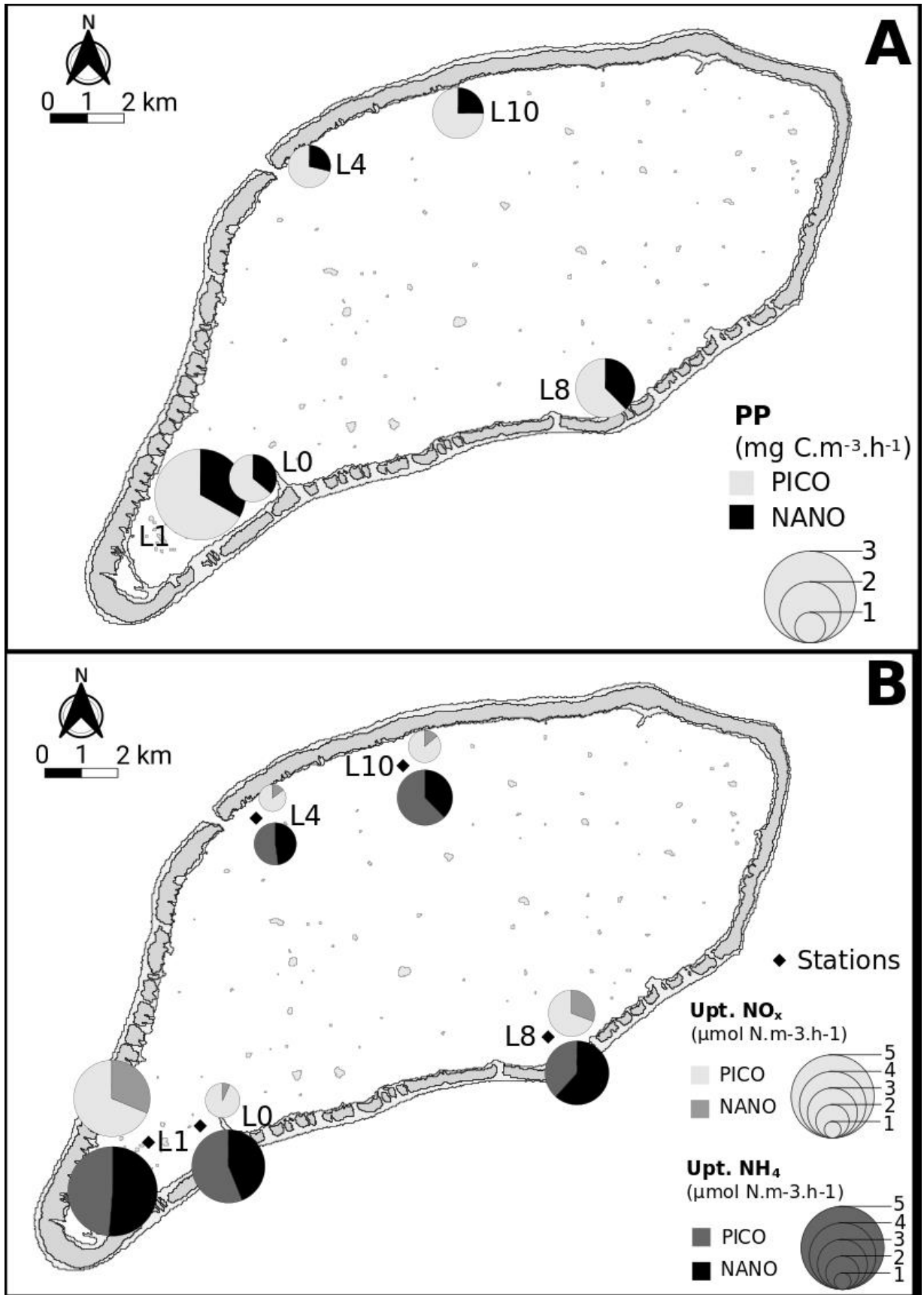
Fig. 5. Mean IS% index calculated for Chlorophyll a (pico- and nano-), nutrients (NH₄ and NO_x), and dissolved and particulate organic nitrogen (LDON and DPON) concentration.

3.3. Sensitivity to initial conditions at all five stations

The reference simulation (S0) was performed to compare modelled to *in situ* data. More specifically, we focused on the maximum NH₄ and NO_x uptake rates and primary production (occurring during the model spin-up). While phytoplankton did not seem to be nutrient limited during the field experiments (Rodier et al., 2021), the model was set up with nutrient limitation. Moreover, while uptake rates in the field were measured for NO₃, the model uses uptake rates for NO_x which seemed justified since NO_x is essentially represented by NO₃ in Ahe lagoon (Charpy et al., 2012). Results of primary production (**Fig. 6.A**) show a clear spatial pattern with maxima of about 2 mg C m⁻³ h⁻¹ for pico- and 1 mg C m⁻³ h⁻¹ for nano- at Station L1, which seems to be about 2 to 3 times more productive than other stations. At all

333 stations, nano- contributed between 25 and 40% to the total primary production, with a
334 lagoon-wide average of 32%. Moreover, the three southern stations (L0, L1 and L8) seem to
335 show a higher proportion of PP by nano- compared to the two northern stations.

336 NH_4 and NO_x uptake rates from the model and *in situ* observations cannot be compared
337 quantitatively because of the difference between nutrient limitation during the experiments
338 and in the model. . However, we can compare the ratios between pico- and nano- and between
339 NH_4 and NO_x uptake rates at different stations. Everywhere, uptake of NH_4 was greater than
340 of NO_x (**Fig. 6.B.**). Moreover, uptake rates were greater at L1 and lower at L4. The NH_4
341 uptake by pico- represented more than 50% of the total NH_4 uptake, except at L1 and L8. At
342 all stations except L1, NO_x uptake appears lower than NH_4 uptake. The NO_x uptake by pico-
343 at L1 and L8 represent 70% of the total and more than 80% at L0, L4, and L10.



344

345 **Fig. 6.** Maps of modeled biogeochemical fluxes at all 5 stations. **A:** Primary production (PP)
 346 by pico- and nano-. **B:** Uptake rates of NH₄ and NO_x by pico- and nano-.

347 From among the different statistical metrics used, MAE and RMSE show best results for
 348 pico-, NH₄, and NO_x (**Table 5**). Bias can be considered poor when its value is above 40 %
 349 (Maréchal, 2004). Pico- and NOD have the lowest bias. Uptake rates of NH₄ and NO_x show a
 350 good result for d1 with significant values for PP, pico-, nano-, NH₄ and NO_x.

351 **Table 5.** Statistical analyses comparing observations with model results of the S0 simulation.
 352 MAE = Mean Absolute Error, RMSE = Root-Mean-Square Error, d1 = Willmott index
 353 (1982). Note that the row "Uptake NH₄ and NO₃" represents the ratio between the pico- and
 354 nano- uptake. * Significant values of d1 (> 0.70).

	MAE	RMSE	Bias (%)	d1
PP	0.40	0.94	61.70	0.77*
Uptake NH ₄ NO ₃	0.27	0.12	43.02	0.10
Pico-	0.028	0.004	12.22	0.66
Nano-	0.972	0.258	317.82	0.14
NH ₄	0.036	0.070	74.05	0.48
NO _x	0.091	0.171	49.26	0.21
NOD	2.715	0.920	22.52	0.26

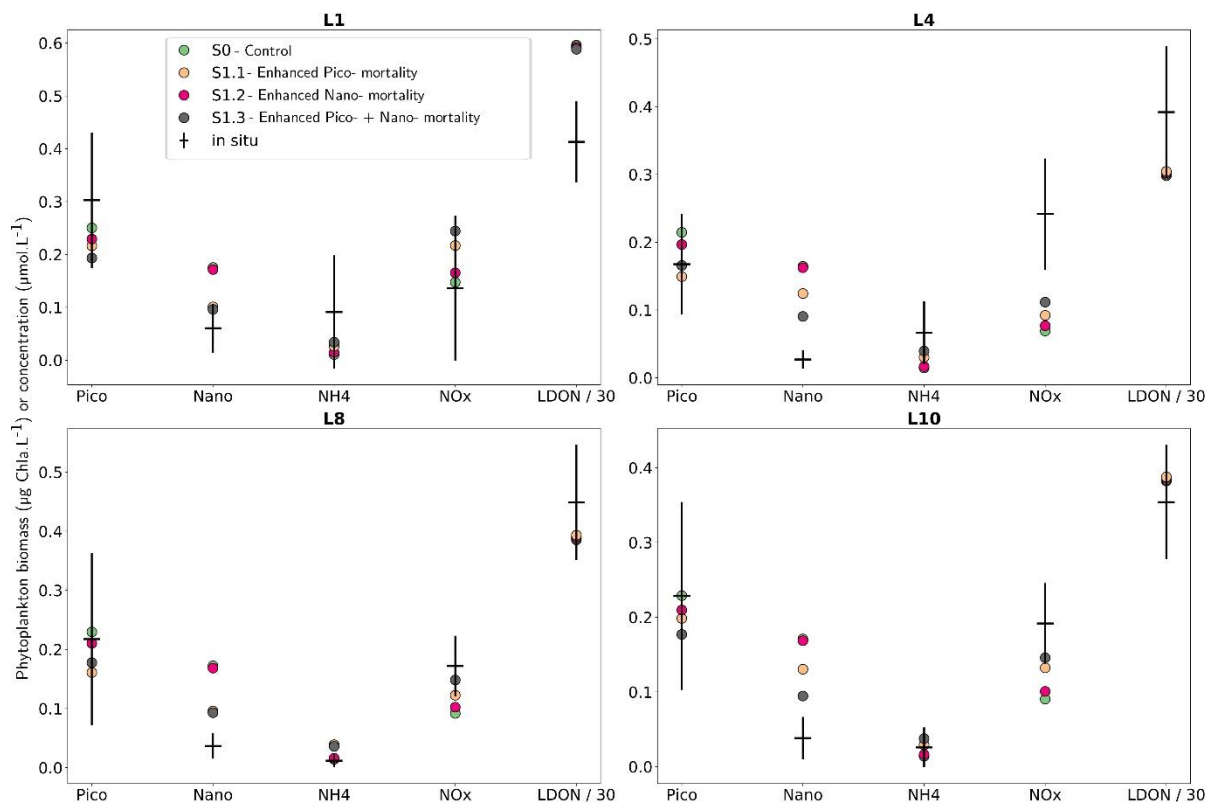
355

356 A graphical comparison is shown in **Fig. 7** and **Fig. 8**.

357 3.4. Sensitivity to grazing

358 At each station and for each grazing scenario, the pico- biomass was lower than in S0
 359 even if the nano- grazing rate was increased (**Fig. 7**). In contrast, the nano- biomass was lower
 360 when the nano- or both the pico- and nano- grazing rates were increased (S1.3). At all
 361 stations, the S1 and S0 nano- biomasses are nearly identical. At L1 and L4, the S1.1 and S1.3
 362 nano- biomasses we are very similar. Overall, the simulated pico- biomass appears to be
 363 closer to *in situ* values at L4 and L8. Comparing between different simulations, the nano-
 364 biomass appears closer to *in situ* values in S1.1 and S1.3. In all grazing simulations, NH₄ and
 365 NO_x concentrations were higher than in S0, increasing from about 0.012 to 0.035 μmol L⁻¹ for
 366 NH₄ and 0.10 to 0.18 μmol L⁻¹ for NO_x, when the grazing rates are increased. This increase is
 367 more pronounced when just the nano- or both the pico- + nano- grazing rates are increased. In
 368 these three simulations, the nutrient concentrations were closer to *in situ* values at L1, L4, and

369 L8 for NH_4 and at L4, L8, and L10 for NO_x . Finally, LDON concentrations did not affect
 370 these grazing simulations.



371
 372 **Fig. 7.** Comparison between *in situ* data and the S0 and S1.1-3 model outputs at four stations.
 373 Reminder: S0 – control, S1.1 – higher pico- grazing, S1.2 – higher nano- grazing, and S1.3 –
 374 higher pico- + nano- grazing. Black vertical bars represent one standard deviation and black
 375 horizontal bars represent *in situ* means. Note that LDON values have been divided by 30 to fit
 376 onto the scale of this figure.

378 3.5. Sensitivity to N-cycle components

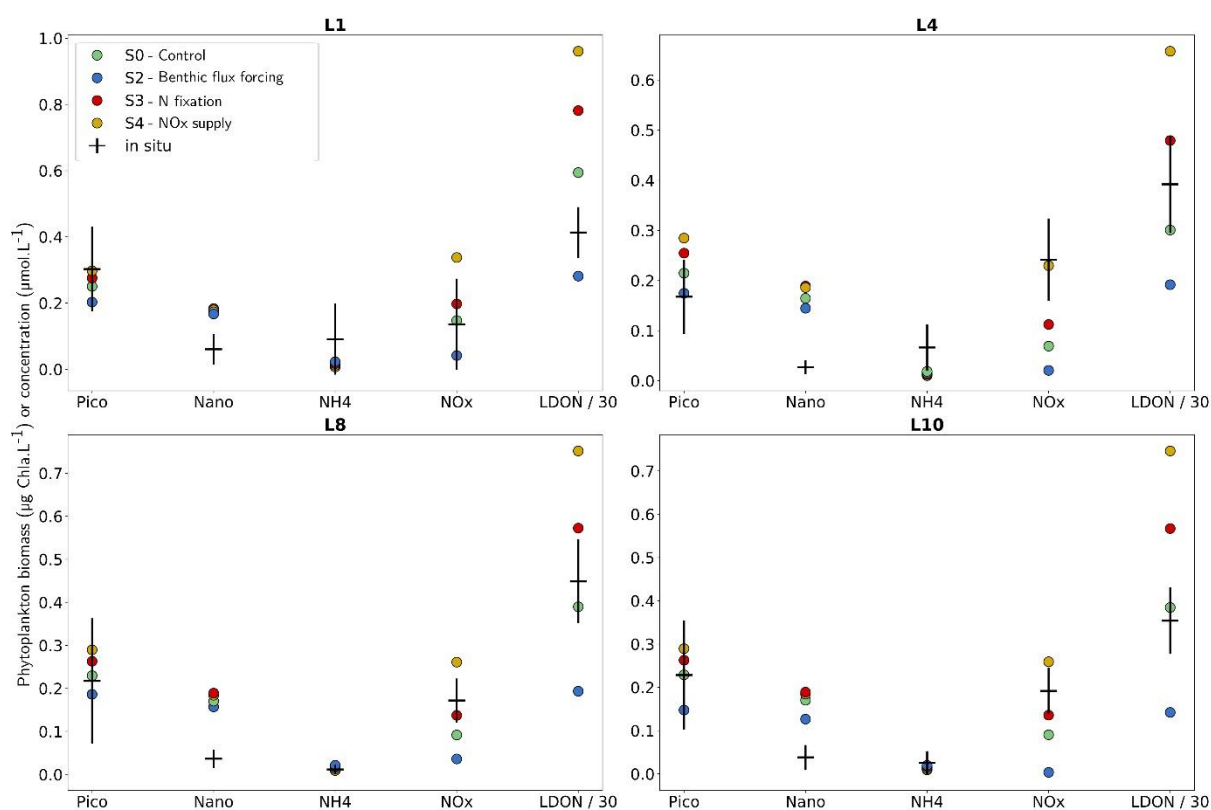
379 Benthic fluxes measured at the sediment - water interface show some differences between
 380 NH_4 and NO_x fluxes (Grenz et al., this issue). NH_4 fluxes were always positive (*i.e.*, from
 381 sediment to water column) except at L10 where they were negative during the day. In
 382 contrast, NO_x fluxes were always positive during nighttime and always negative during
 383 daytime. Moreover, NH_4 fluxes were lower than NO_x fluxes (**Table 4**). These benthic fluxes
 384 varied between stations with higher values observed at L1 and L8 (Grenz et al., this issue). In
 385 the S2 simulation (benthic fluxes simulation), NO_x concentrations at L1 and L10 decreased
 386 significantly (by about $0.1 \mu\text{mol L}^{-1}$), while at other stations this decrease was less
 387 pronounced (about $0.05 \mu\text{mol L}^{-1}$). Modeled LDON was also lower at all stations. Concerning

388 NH_4 , no variation of concentrations is observed. Benthic fluxes reduced ambient NO_x
 389 concentrations. These NO_x concentrations are lower than *in situ* data at all stations, except at
 390 L1 where they are within the standard deviation. Overall, the modeled phytoplankton biomass
 391 was lower at each station, with the simulated nano- biomass closer to *in situ* values at all
 392 stations except L4.

393 In the nitrogen fixation simulation (S3), all variables were higher than *in situ* values. N
 394 fixation had no effect on NH_4 concentration but led to high NO_x concentrations at L4, L8, and
 395 L10. Moreover, the simulation results were improved with regard to the pico- biomass at L1.

396 Compared to S3, the S4 simulation, which considers anthropogenic inputs of NO_x , led to an
 397 even higher increase in concentrations at all stations, except for nano-. Moreover, the S4 pico-
 398 biomass was closer to *in situ* data at L1 and NO_x at L4.

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Fig. 8. Comparison between *in situ* data and model outputs. Reminder: S0 – Control, S2 – benthic flux forcing, S3 – N fixation, and S4 – NO_x supply. Black vertical bars represent one standard deviation and black horizontal bars represent *in situ* means. Note that LDON values have been divided by 30 to fit the scale of this figure.

400

401 **4. Discussion and conclusion**

402 **4.1. Sensitivity analysis**

403 The sensitivity analysis on forcing conditions suggested us to set the same light and
404 temperature on all stations. We observed no significant changes in the pico- or nano-
405 biomasses when varying the forcing conditions within the ranges observed during the
406 AHE2017 field campaign. We therefore applied the same constant environmental forcing
407 (water temperature of 28.5°C and PAR_{max} of 800 μmol photons m⁻² s⁻¹) across the model
408 domain. Moreover, this analysis confirms that the model conveys the lack of photo-inhibition
409 measured in the Ahe lagoon (Lefebvre et al., 2012). This is partly due to the shape of the
410 primary production equation and, more specifically, how it accounts for light limitation (see
411 Appendix A.1.2). The lagoon typically exhibits higher temperatures in its south-western part
412 (Dumas et al., 2012; Rodier et al., 2021). While this higher temperature may affect
413 phytoplankton communities and the overall biogeochemistry, it is not taken into account by
414 our present model. In the future, by implementing different PAR and temperature values at
415 different locations, the model may be able to account better for these spatial heterogeneities.

416 The sensitivity analysis allowed us to understand the behavior of the new model
417 configuration and identify differences compared to the Caledonian configuration. Compared
418 to the sensitivity analysis of the ECO3M Lagoon configuration in Faure et al. (2010a), the
419 ECO3M-Atoll configuration appears less sensitive. The model appeared most sensitive to
420 changes in the fraction of dissolved organic matter (carbon and nitrogen) assimilated by
421 zooplankton (parameters d_C and d_N , respectively), the grazing rate (g), and the maximum
422 phytoplankton growth rate (μ_{max}). d_C affects carbon assimilation, but also nitrogen (NH₄,
423 NO_x, LDON and DPON). This can be explained by the fact that the model allows a variable
424 stoichiometry. Nutrient uptake is controlled by the external nutrient concentrations and an
425 internal quota function based on the N/C ratio. Therefore, when d_C changes, the
426 phytoplankton carbon varies and N/C is modified because of respiration which is not
427 controlled by the quota function but set to a constant value (R_{phyto}). This modulates the uptake
428 rate and impacts NH₄ concentration. While this phenomenon may also exist in the ECO3M-
429 Lagoon configuration, it may be amplified in the present configuration which has two
430 phytoplankton compartments instead of only one. Moreover, as in the ECO3M-Lagoon
431 configuration, nutrients were more sensitive to parameter changes than phytoplankton
432 biomass. In summary, our analysis confirmed that that changes in grazing mostly affect
433 phytoplankton and ammonium as grazing not only has a direct impact on the amount of

434 phytoplankton grazed but also indirectly affects NH_4 via the remineralization through the
435 microbial loop.

436

437 **4.2. Biogeochemical fluxes in the water column**

438 The model parameters were based on specific *in situ* measurements of nutrients and
439 phytoplankton concentrations as well as biogeochemical processes (Rodier et al., 2021). Some
440 of the model results presented in Section 3.3 were close to *in situ* data. The model predicted
441 the share of nano- in the total primary production in the lagoon to be 32 % while *in situ* data
442 suggests a contribution of 25 ± 12 %. There was a clear difference between the northern and
443 southern parts of the lagoon: while nano- contributes only about 25 % of total primary
444 production at the northern L4 and L10 stations, in the south at L0, L1, and L8 it is of the order
445 of 40 % (**Fig. 6A**). In the *in situ* data, there appears to be more of an east-west rather than
446 north-south divide (Rodier et al., 2021).

447 Modelled uptake rates of both NH_4 and NO_x were highest at L1 and lowest at L4 (**Fig.**
448 **6B**). This may be due to different residence times across the lagoon which are highest near L1
449 (Dumas et al., 2012). In addition, L1 is in a particularly shallow part of the lagoon, in close
450 proximity to a local village (which may add anthropogenic inputs) and to high-density pearl
451 farms (Andréfouët et al., 2012). In contrast, L4 has the lowest residence time as it is near the
452 pass and thus exposed to more oligotrophic oceanic water (Dumas et al., 2012). These spatial
453 differences are also visible in the *in situ* data (Rodier et al., 2021). Nevertheless, since the
454 model is 0D, the inflow of oceanic water through the pass is not accounted for and the above
455 explanations cannot be used to explain the differences observed in the model results which
456 must therefore be due to differences in the initial conditions.

457 Moreover, in the reference simulation, NH_4 uptake by nano- represented less than 50 % of
458 the total, except at L1 and L8. The same results were found *in situ* by Rodier et al. (2021) for
459 L1, where nano- uptake reached 57% of the total, but not at L8. This may be again due to the
460 fact that L1 is located near high-density pearl farms (Andréfouët et al., 2012), hence nano-,
461 which is more grazed by oysters, may have adapted to the higher grazing pressure by
462 increasing their NH_4 uptake rates. L8 is not well represented by the model which may also be
463 due to its particular location at the confluence of the two main circulation cells (Dumas et al.,
464 2012). This station is thus influenced by both, oceanic water entering through the pass and
465 nutrient rich water coming from the SW part of the lagoon. As the model does not account for
466 any horizontal transport, it cannot represent this phenomenon correctly. The present results

467 thus merely reflect of our choice of initial conditions. At all stations, NO_x uptake was lower
468 than NH₄ uptake, in both *in situ* data and the model results. In the model, L1 showed the
469 highest NO_x uptake while *in situ* the uptake was highest at L0. Our choice of the initial
470 phytoplankton biomass at L0 may have been too low compared to *in situ* data. Concerning the
471 ratio of NO_x uptake between pico- and nano-, measurements showed clear spatial differences
472 across the lagoon, with 37 % of total NO_x uptake by nano- at L1 and > 50 % in the other
473 parts of the lagoon. In the model, on the contrary, the NO_x uptake due to picophytoplankton is
474 elsewhere greater than those due to nanophytoplankton at all the stations.

4.3. Determining the sources of N input

477 Grazing on phytoplankton may vary depending on the type of predator. As expected, in
478 the model, a higher grazing rate led to a decrease in phytoplankton biomass and an increase of
479 nutrient concentrations. However, pico- was sensitive to changes in grazing on nano-, while
480 nano- was not sensitive to changes in grazing on pico-. In addition, while NH₄ seemed rather
481 sensitive to changes in grazing it was relatively unaffected by other parameter changes
482 (simulations S2-4). In contrast, NO_x was less affected by changes in grazing pressure and
483 more sensitive to changes in the other parameters. In the grazing simulations (S1.x), the nano-
484 biomass values were closer to the *in situ* ranges which confirms that nano- would be
485 preferentially grazed by oysters and other higher predators. Moreover, modeled NH₄
486 concentrations in the grazing and benthic fluxes simulations (S2) were closer to *in situ*
487 values. The model thus seems to confirm that part of the remineralization described in Ahe by
488 Lacoste and Gaertner-Mazouni (2016). Gaertner-Mazouni et al. (2012) concluded that benthic
489 fluxes may contribute to meet phytoplankton nitrogen requirements near oyster farms. Grenz
490 et al. (this issue) also observed noticeable exchanges between the sediment and water column
491 near farms. The S2 simulation seems to confirm that remineralization occurs in sediments and
492 represents about 4 % of the phytoplankton NH₄ uptake, which is consistent with the
493 percentage measured by Rodier et al. (2021).

494 Except at L1 station where initial NO_x concentrations were high, the modeled NO_x
495 concentrations in S0 were lower than *in situ* data in. To increase these low concentrations, we
496 tested different hypotheses. First, Charpy-Roubaud et al. (2001) showed that atmospheric N₂
497 fixation was a potential source of nitrogen input to lagoons. By adding this source, we could
498 increase the NO_x concentration in the model. N₂ fixation may enrich the water column with
499 NH₄ after remineralization. Subsequent nitrification can then transform ammonium to nitrates.
500 This nitrification was boosted in the model, which is why, by implementing N₂ fixation, the

501 model showed an increase in NO_x . While data on N_2 fixation was available for Tikehau Atoll
502 there were no data for Ahe. The high values of NO_x measured in the rain water and ground
503 water lens could be due to human activities on the *motu* or to the local avifauna (Otero et al.,
504 2018). The improvement representation of NO_x concentration in simulations S3 and S4
505 confirms that additional NO_x inputs are indeed quite likely. Other hypotheses can also explain
506 this high NO_x concentrations, namely upwelling generated by an overturning circulation cell
507 in the north-eastern part of the lagoon (Dumas et al., 2012).

509 4.4. Conclusions and future work

510 While many hypotheses have been made to explain the nitrogen cycle and specifically the
511 origin of nitrogen in Polynesian atolls, it is still not completely understood. Modelling
512 provides a useful tool to quickly test these hypotheses. In this study, we used the new
513 ECO3M-Atoll model to run a set of simulations to test some of these hypotheses in the Ahe
514 lagoon. Overall, the model results were is similar ranges than the *in situ* data. The
515 simulations improved our understanding of the biogeochemical functioning of Ahe Atoll.
516 More specifically, we could confirm that nano- are grazed by oysters and higher predators
517 (Dupuy et al., 2009). Simulations to test the impacts of grazing and benthic fluxes showed the
518 ability of the model to represent the impact of remineralization by the grazing in water
519 column and the sediment. Finally, nitrogen fixation and NO_x inputs allowed to increase the
520 low NO_x concentrations.

521 One of the limitations in our approach was that we set the same light and temperature
522 conditions at all five stations. We did this because the sensitivity analysis did not show any
523 significant variability in phytoplankton biomass for the range of PAR and temperature values
524 observed during the AHE2017 field campaign. Nevertheless, *in situ* data showed small spatial
525 variabilities in temperature and phytoplankton community composition between the SW and
526 the other areas of Ahe lagoon. This could not be reproduced by our model. However, the
527 observed variation in phytoplankton communities may be caused by various factors such as
528 the presence of other organisms, nutrient conditions, pearl farms, anthropic inputs, etc.
529 Moreover, the d_C and d_N parameters were much more sensitive than in the ECO3M-Lagoon
530 configuration on which our ECO3M-Atoll model is based. This may be due to respiration
531 being constant and the fact that we used two instead of one phytoplankton compartment. In
532 the future, respiration could be controlled via a similar quota-based function that already
533 controls nutrient uptake and growth.

534 The model was run in 0D, which means that the forcing was constant and the
535 hydrodynamics (circulation, stratification, vertical mixing, etc.) were not represented. In the
536 future, ECO3M-Atoll will be coupled with a hydrodynamic model (MARS3D) will introduce
537 some more realism and variability to the modelled processes to facilitate a more in-depth
538 understanding of how the hydrodynamics and different temperatures and irradiances may
539 influence the biogeochemistry at Ahe Atoll. Moreover, by upgrading the model to 3D, the
540 forcing (grazing by oysters, benthic fluxes, anthropogenic inputs, N fixation) can vary
541 spatially and as a function of depth. Finally, the coupled model should be able to provide
542 information regarding the trophic forcing to the oyster dynamic energy budget (DEB) model
543 by Thomas et al. (2012) (see also Sangare et al., 2019). This set of coupled models will help
544 to investigate the influence of biogeochemistry on the life cycle of pearl oysters and on the
545 farming activity.

546
547 To conclude, this study presented the ECO3M-Atoll model, a new biogeochemical model
548 specifically configured for Ahe Atoll to study the nitrogen cycle and biogeochemical
549 ecosystem functional in a pearl farming atoll. A better understanding of the local nitrogen
550 cycle is pivotal to understand local phytoplankton dynamics, the principal food item of pearl
551 oysters in deep and semi-closed atolls. Future implementations of the physical-
552 biogeochemical-DEB coupled model will contribute to the improved management of pearl
553 farms, not only at Ahe but also at other pearl farming atolls of the Tuamotu Archipelago that
554 show a similar geomorphology to Ahe Atoll.

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