

# Effects of physical forcing on short-term plankton dynamics in a narrow coral reef lagoon (Ouano, New Caledonia): a two-week high-frequency study

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1	Effects of physical forcing on short-term plankton dynamics in a narrow coral reef
2	lagoon (Ouano, New Caledonia): a two-week high frequency study
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5	Luc Devenon <sup>1</sup> , Cristèle Chevalier <sup>1</sup>
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7 8 9 10 11	<sup>1</sup> Aix Marseille Université, Université de Toulon, CNRS, IRD, MIO UM 110, 13288, Marseille, France, Corresponding author: M. Rodier, Email: martine.rodier@ird.fr, Phone No:(33) 07 67 22 40 48.
12	ABSTRACT
13	The response of plankton communities to short-term climatic events was evidenced in a narrow
14	coral reef lagoon representative of the channel-type lagoons of the high islands of the tropical
15	Pacific. Phyto- and zooplankton data (abundance and taxonomic composition) were sampled at high
16	frequency for two weeks in April-May 2017 under various tidal conditions and combined with
17	environmental and physical measurements and modeling hydrodynamic products. The short-term
18	external events (wind, waves and rain) that occurred caused changes in the circulation patterns and
19	increased nutrient concentrations in the lagoon. The plankton reacted quickly to this enrichment,
20	with an increase in Chla and the rapid development of a microphytoplankton community dominated
21	by diatoms, and of opportunistic herbivorous zooplankton (tintinnids, appendicularians).
22	Zooplankton composition and distribution were strongly modulated by the circulation patterns
23	through advection and mixing. Our results show that the tidal and diel components of the temporal
24	variability of planktonic groups were blurred by sporadic event components (i.e., wind, wave and
25	rainfall events). Environmental and biological responses to these external physical forcings occurred
26	at lagoon scale in this channel-like lagoon, unlike what is observed in larger lagoons (such as the
27	southern lagoons of New Caledonia) where spatial variability is much higher.

Key Words: Coral-reef channel lagoon, Short-term variability, Plankton, Climatic events, Tide,
Wave, Cross-reef fluxes.

31

### 32 INTRODUCTION

33 Coral reef lagoons are subject to a wide range of physical forcings such as tides, wind, waves, coastal currents, evaporation, rainfall, river discharge and runoff (Andrews & Pickard, 1990; Hench 34 35 et al., 2008, Lowe et al., 2009; Dumas et al., 2012; Orpin and Ridd, 2012). In such ecosystems, the 36 relative importance of these forcings is determined not only by meteorological and oceanic 37 conditions, but also by the reef morphology and lagoon volume (Andréfouët et al., 2001). These 38 physical forcings control the nutrient availability as well as the exchanges, dispersal and transport of 39 living and non-living particles, which are key for the dynamics of plankton communities and for the ecological functioning of lagoon ecosystems (Kjerfve, 1994; Lowe & Falter, 2015). 40

The New Caledonia Lagoon (NCL; 23,400 km<sup>2</sup>), which extends over extensive oceanic gradients 41 42 with a wide variety of lagoon and reef barrier typologies (Millennium classification, Andréfouët et 43 al., 2006), is a good candidate for studying the effects of physical forcing on lagoon plankton 44 ecology. Historically, most of hydrodynamic/environmental studies on the NCL have been 45 conducted in the wide and semi-open southwestern and southern lagoons (SWL and SL) and have 46 included investigations of the physical and chemical factors, hydrodynamics and suspended particle 47 transport (Grenz et al., 2013 and references therein), biogeochemical processes and plankton 48 communities (Le Borgne et al., 2010; Fichez et al., 2010; Torréton et al., 2010; Neveux et al., 2009, 49 2010). The large size of these southern lagoons results in strong contrasts between nearshore waters 50 (bays) which are influenced by terrigenous and anthropogenic inputs and the near-reef waters which 51 are under the oligotrophic influence of the ocean, except during sporadic upwelling events (Hénin 52 and Cresswell, 2005) or uprising of the hydrographical structure near the reef which can impact the lagoon (Fichez et al., 2010; Neveux et al., 2010; Fuchs et al., 2013). The large size of the lagoon 53 54 also results in low temporal variability of environmental conditions and trophic status in most of the

inner lagoon and conversely greater amplitude of variability near the mainland shore (Le Borgne etal., 2010).

57 Comparatively, little work has been devoted to environmental, biogeochemical and plankton 58 studies in narrow lagoons (Tenório et al., 2005; Martias et al., 2018; Dupouy et al., 2020) although 59 they are numerous in New Caledonia and, in some cases, subject to strong anthropogenic pressure 60 (e.g. mining) or terrigenous influence (outflow and runoff from mid-sized rivers). In these narrow 61 lagoons the effects of physical forcing on the space and time scales of biological processes are 62 assumed to be different from those observed in the large southern lagoons (SWL, SL). 63 Against this background, a multidisciplinary study (OLZO project, 2016-2018) focusing on the 64 water circulation and plankton dynamics was conducted in a narrow lagoon (Ouano lagoon) located 65 on the west coast of New Caledonia. This site was selected as representative of a channel-type reef-

66 lagoon system as defined in Chevalier et al. (2015), i.e. a reef-parallel dimension (length) more than

67 2 times greater than the reef-normal dimension (width) and a well-defined reef barrier (typically

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69

outcropping during low spring tides) with passages toward the open ocean or adjacent lagoons. As

revealed by the first results of the OLZO project, the hydrodynamics of this channel-type lagoon is

70 complex and variable with exchanges between lagoon and open-ocean mainly driven by the cross-

71 reef flows induced by tides and wave-breaking processes over the reef barrier (Chevalier et al.,

2015; Sous et al., 2017). However, the effects of this complex hydrodynamics on short timescale
variations of nutrients and plankton have not yet been studied in these narrow lagoons.

In this paper, we analyze the short-term variability of plankton abundance and community structure using environmental and plankton data collected during an intensive 2-week field study in 2016 in Ouano lagoon. Hydrodynamic and phyto- and zooplankton properties were measured simultaneously which allowed the coupling of various physical processes and some key biological processes. Over the study period, the dataset includes different tide, wave, wind and rain conditions as well as hydrodynamic patterns allowing a study of short-term plankton dynamics under different environmental conditions. The main question addressed here is how plankton changes correlated

81 with rapid changes in hydrodynamic and environmental features driven by the different physical
82 forcing in this channel-type lagoon.

83

### 84 METHOD

### 85 Study site and sampling

This study was performed in Ouano lagoon during the OLZO cruise aboard the R/V Alis from 86 87 April 24 to May 8, 2016 (Sous, 2016). This weakly-anthropized channel-type lagoon located on the 88 south-west coast of New Caledonia is approximately 30 km long, 10 km wide and 10 m deep, with a total volume of about 2.1  $10^9$  m<sup>3</sup>. It is separated from the Coral Sea water by a coral reef barrier 89 90 which is fully submerged at high tide, and partly emerged at low tide depending on tide and wave 91 conditions. The lagoon is also directly open to the ocean through three reef passages (Ouaraï, Isié 92 and Saint-Vincent) and to the other lagoons through two other passages (N'Digoro and Ténia) (Fig. 93 1). The lagoon is under the influence of four main rivers, the Foa river flowing into Teremba bay in 94 the north, and the Ouenghi, the Bouloupari and the Tontouta rivers flowing into Saint Vincent Bay in the south, with a very extensive watershed (240 and 380 km<sup>2</sup>, respectively) and high flow rates 95 (up to  $2500 \text{ m}^3 \text{ s}^{-1}$  on average for the Tontouta river, Laroche et al., 2022). In this study, we focus on 96 97 the portion of the lagoon from the Ténia to the N'Digoro passages which has been well described in 98 terms of hydrodynamics with several ADCP and pressure sensor deployments between 2011 and 99 2016 (Chevalier et al., 2015; Sous et al., 2017).

During 15 days, a time-series at one station (L2, Fig. 1) was carried out with sampling every 3-4 hours. L2 (17m depth) was chosen as the most representative of the inner lagoon, far from the passages, the reef barrier and the coast. To place this time-series at L2 in a broader context, four additional stations were sampled in the lagoon, one to the north (L1, 14m depth), two to the south (L4, L5 13m) and one nearshore in a more confined area (L3, 12m), and two stations in the ocean off the passages (On and Os, ca 1000-2000m depth; Fig.1). Each additional station was sampled four times during four so-called spatial transects (Fig. 2A): twice under spring tide conditions (25-26

107	April and 5	5-6 May: tidal	range of	1.2 m and	1.8m, 1	respectively).	and twice	under neap tide
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108 conditions (28-29 April and 2-3 May; tidal range of 0.63 m and 0.71 m). All samplings were carried
109 out between 8 am and 1pm.

110

#### 111 Environmental variables

- 112 Meteorological data (wind speed and direction, rainfall) were available from the ship's weather
- station and the meteorological station of La Foa located further north on the same coast
- 114 (http://www.meteo.nc). Current speed and direction were measured every 20 minutes with ADCPs
- 115 moored for ~ 3 months (from April 22 to August 3, 2016), in the passages (at 17m depth), behind
- 116 the reef barrier (at 4m) and in the lagoon (at 8m) at L2 (Fig. 1).
- 117 During the campaign, a CTD profiler (SBE 19+, SeaBird) equipped with a Wet Labs

118 ECO NTU Turbidity Sensor was deployed at each station/sampling, from the sub-surface to the

119 bottom in the lagoon and to 200m depth in the ocean, recording vertical profiles of temperature,

120 salinity, fluorescence and turbidity. Water samples for nutrients and chlorophyll were collected

121 using a 5-litre Niskin bottle at 2 depths (5 and 10 m) in the lagoon and at 3 depths in the ocean,

122 including one in the Deep Chlorophyll Maximum, DCM (3, 50 and 70/80m).

123 Nitrate + nitrite (NOx), phosphate (PO<sub>4</sub>) and orthosilicic acid (Si(OH)<sub>4</sub>) samples were HgCl<sub>2</sub>-

124 poisoned and analyzed post-cruise by colorimetric methods using a SEAL Analytical Autoanalyzer

125 III as described in Aminot and Kérouel (2007). Note that silicates are available at all stations during

126 the transects but several data are lacking for the time-series at L2, due to technical issues. Total

- 127 chlorophyll a (Chla) concentrations were determined on 0.55 L water samples filtered on GF/F
- 128 Whatman filters and analyzed by fluorometry after methanol extraction (Le Bouteiller et al., 1992;

129 Raimbault et al., 2004) using a Turner Design fluorometer.

### 131 Plankton collection and analysis

132 Plankton samples were collected with a WP2 net (50cm aperture diameter) equipped with an 80 µm mesh size net at the same frequency as the environmental variables. The net was towed 133 134 vertically from the bottom (or 150 m depth at the ocean station) to the surface at a constant speed of 1 m s<sup>-1</sup>. All samples were immediately preserved in 4% borax-buffered formalin. The volume 135 filtered by the net (V, in  $m^3$ ) was calculated using the formula V = S. L combining the surface area 136 of the net mouth (S=0.196 m<sup>2</sup>), and the length of the towed cable (L, in m). V varied between 1 and 137 8 m<sup>3</sup> at the lagoon stations and was 29.5 m<sup>3</sup> at the oceanic station. No clogging was observed. 138 In the laboratory, the samples were processed by combining two analytical imaging techniques, after 139 140 separating each sample into three size-fractions by sieving. The smaller fractions (80-200µm and 141 200-1000 µm), also including the large microphytoplankton, were analyzed with a FlowCAM (Fluid Imaging Technologies Inc. Series VS-IV, Benchtop model) and the fraction > 1000 µm with a 142 143 ZooScan (Gorsky et al., 2010). For each FlowCAM analysis, the entire size-fraction was re-diluted 144 into a known water volume called initial volume (Vi), ranging from 45 to 400 ml, depending on the density of particles in the samples. Analyses were then immediately processed, stopping 145 146 automatically when the number of particles counted reached 3000. Thus, the analytical volume (Va) 147 varied from 0.5 to 12 ml for the 80-200µm fraction and from 1.6 to 31 ml for the 200-1000µm 148 fraction. The percentage of the total size-fraction analyzed with the FlowCAM (100.Va/Vi) varied 149 from 0.3 to 21% for the 80-200µm fraction and from 0.9 to 43% for the 200-1000µm fraction. For 150 the ZooScan, analysis was performed on the whole >1000µm size fraction or on a sub fraction (25 151 or 50%, obtained with a Motoda splitter) for the most concentrated samples, in order to obtain 152 around 1000-1500 zooplankton items on the scan (range recommended by the manufacturer for 153 optimum counting). The number of images analyzed ranged from 90 to 1600 for non-fractionated 154 samples and from 800 to 1900 for the fractionated samples.

After analyses with FlowCAM or ZooScan, each image was processed using ZooProcess (Gorsky et al., 2010), which is embedded in the ImageJ image analysis software. Finally, Plankton Identifier 157 (http://www.obs-vlfr.fr/~gaspari/Plankton Identifier/ index.php) was used for automatic classification of plankton taxa categories. The results of the automatic classification were then 158 manually validated by an expert. The abundance of each taxa (ind.m<sup>-3</sup>) was calculated for each size 159 160 fraction taking account the volume of the sample filtered by the net and the sub-sample analyzed, 161 and the final *in situ* plankton abundance was obtained by cumulating the abundances of the three size-fractions. Using these imaging techniques, we were able to identify 27 planktonic groups 162 163 (including 3 protozoplankton groups and 17 metazooplankton groups).

164 The relatively poor level of taxonomic determination by imaging is largely related to the fact that the samples were taken with an 80µm net, which favors the mixing of detritus and plankton. As a 165 result, the quality of images was not always sufficient to obtain a more precise taxonomic level. 166 167 Therefore, a more thorough taxonomic analysis of the zooplankton was performed by microscopy on 168 selected samples: all samples in the ocean, and fifty samples in the lagoon at L2 during five periods (26-27 and 28-29 April. 30 April-2 May, 4-5 and 6-8 May). The taxa were enumerated under a 169 170 dissecting microscope (Olympus SZX200, magnification 200 to 500) using sub-samples. At least 100 individuals of the main taxa were counted in each sub-sample, and the rarest taxa in the whole 171 sample. Zooplankton taxa were identified according to Tregouboff and Rose (1957), Razouls et al. 172 173 (2005, 2023) and Conway et al. (2003).

Total zooplankton abundance obtained with the two counting methods (imagery and microscopy) were well correlated (r=0.759; n=57) and a Bland Altman analysis shows that the sampling points were distributed in a relatively balanced way on either side of the mean difference between the two counting methods (imaging – microscopy; mean =  $48 \pm 1119$  ind m<sup>-3</sup>): 58% and 42% respectively. In addition, only 3 points are slightly outside the 95% confidence interval (-2168 to +2265): two in the lower part (-2364, -2550) and one in the upper part (+2457).

180

181 Numerical products from the hydrodynamics model

183 The numerical hydrodynamics model of Ouano lagoon used in this paper is from Chevalier et al. (2015), and is based on 3D Regional Ocean modelling system (ROMS) tools (Shchepetkin & 184 185 McWilliams, 2005). The bathymetry was obtained from the Service Hydrographique et 186 Oceanographique de la Marine (SHOM/MOP) maps. This model was constrained by the tide, the 187 residual current along the coast and by the waves breaking on the reef and inducing cross-reef 188 fluxes. The S2 and M2 tidal components were imposed at open boundaries using the ADvanced 189 CIRCulation model on the New Caledonia region (Luettich et al., 1992). The cross-reef fluxes were 190 parameterized by considering significant wave height data from the WaveWatch-III database. 191 To characterize the lagoon ecological functioning, we focused on the age and origin of the lagoon 192 water calculated according to the Constituent-oriented Age and Residence time Theory (De Brye et 193 al., 2013 and references therein). These relevant quantities integrate the dynamics and history of 194 lagoon waters (Delhez & Deleersnijder, 2002). For instance, as defined by De Brye et al. (2013), 195 "the age of a water parcel located at point x and time t is the time elapsed since the water parcel 196 entered the domain of interest", while the origin indicates where the parcel came from. More details 197 of the numerical modeling and calculation of age and origin of the lagoon water are given in 198 Chevalier et al. (2015).

199

### 200 Data analyses

201 The environmental (temperature, salinity, nutrients, turbidity) and plankton (Chla, total 202 abundance of microphyto-, proto- and metazooplankton, relative abundance of the main taxonomic 203 groups) variables were submitted to a normalized principal component analysis (PCA). Water age 204 and current speed were considered as additional variables. The variations of phyto- and zooplankton 205 assemblages were investigated using Nonmetric Multidimensional Scaling (NMDS). The abundance 206 of the taxa was square root transformed before estimation of resemblance using the Bray Curtis 207 metric. The resemblance matrix was then ordinated using NMDS. A SIMPER (percentage of 208 similarity) analysis was performed to identify the taxa contributing most to similarity within and

209 dissimilarity between the different clusters identified. All statistical analyses were performed using

- 210 Primer 7 software. In addition, relationships between physical, chemical and biological variables
- 211 were analyzed using cross-correlations, which allow estimation of the degree of covariation of two
- 212 variables as a function of the time lag between them.

213 To estimate the periodicity of the different variables during the time-series at L2, we used a

214 classical Discrete Fourier Transform. Due to the short duration and time-discretization of the

215 measurement, we selected four frequency windows: 1) high frequency variability with frequency >

216  $2/day (period < \frac{1}{2} day), 2)$  semi-diurnal variability with frequency ~  $2/day (period ~ \frac{1}{2} day), 3)$ 

217 diurnal variability with frequency ~ 1/day (period ~ 1 day), and 4) sporadic event with frequency <

- 218 1/day (period > 1 day).
- 219

### 220 **RESULTS**

### 221 Meteorological and hydrodynamic conditions

The study was performed over two sets of spring tides and one set of neap tides (Fig. S1) and under variable weather conditions. Initially the wind was weak (Fig. S1), but from 26 April a SE trade wind episode began with an intensity up to 20-25 m s<sup>-1</sup> and lasted until 2 May after which the wind became weak again. Precipitation was limited to only a short episode of rain on April 28, coinciding with a drop in wind speed.

227 Concomitant with the strengthening of winds, southwesterly significant wave height (SWH)

increased between April 25 and 27 (from 0.5 m to 2 m), then decreased until May 4 (to 0.5 m) and

increased towards the end of the study (to 1.2 m) (Fig. 2a). The water age varied with time at L2 and

230 was inversely correlated with the SWH, but also with the wind and cross reef currents, with a time

lag of ~ 1 days (Fig. 2b). Water age also varied spatially from rapid renewal (water age < 1 day)

near the reef barrier to slow water renewal (up to 10 days) near the coast and in the bays. For

- instance, the mean values over the study period ranged from 1.5 to 2 days at L2, L4, L5, from 2.8 to
- 234 3.5 at L1 and from 5.5 to 7 at the most coastal station L3.

235 The hydrodynamic model revealed four periods with different circulation patterns (Fig. 3), which can be related to the dominant patterns identified in Sous et al. (2017). At the start of the survey (23-236 237 25 April), cross-reef flow was low and the main ocean/lagoon exchanges were through passages: 238 water enters the lagoon from the north through the Isié and Ouaraï reef passages and exits from the 239 south through the Ténia Saint Vincent passage. The internal lagoon circulation was mainly southward and fits the "Southward circulation pattern" defined by Sous et al. (2017). Then, from 25 240 241 to 27 April, during the episode of strong winds and under the effect of the strong swell, cross-reef 242 flows increased, seeming to determine the global lagoon circulation which also increased. Water 243 exited the lagoon through all passages and circulation was mainly northward, which corresponds to 244 the "Classical pattern". From April 28 to May 4, the circulation pattern was the same but with lower 245 velocities, resulting in weaker exchanges with the open ocean and the neighboring lagoons. At the 246 end of the campaign, the flows strengthened slightly, the circulation remained mainly northward but 247 the flow through the Isié and Ouaraï reef passages was again directed inwards, which corresponds to 248 the "Isié reversal pattern". In all circulation patterns, the current over the reef was directed towards the lagoon varying with the tide from 0 to 0.25 m s<sup>-1</sup>, and was well correlated with the SWH (r =249 250 0.923, n = 1600).

251

### 252 Time-series of environmental variables and plankton abundance at station L2.

During the period of easterly trade winds and strong swell (27 April to 1 May), the temperature decreased and the salinity increased (except just after the rain) at L2, even though the range of variations remained relatively low (26.7- 26.1 °C and 35.60 - 35.86, respectively). At the same time, the turbidity sharply increased throughout the water column. When the winds abated after May 1, the temperature increased again and turbidity decreased overall, with no clear change in salinity (Fig. S2).

Apart from the high daily variability, NOx concentrations at L2 increased in two steps, first
between 25 and 28 April at the beginning of the strong wind and swell period (from 0.09 and 0.34)

 $\mu$ mol L<sup>-1</sup>) and then between 29 April and 1 May after the rain event (from 0.18 to 0.38  $\mu$ mol L<sup>-1</sup>) (Fig. 4a). Afterwards, mean daily concentrations remained relatively high between 0.25 and 0.40  $\mu$ mol L<sup>-1</sup>). Despite the lack of data at the beginning and the end of the survey, our results also showed a clear silicate increase after the rain event. In contrast, phosphates showed no clear temporal pattern over the study period (Fig. 4b).

Daily chlorophyll concentrations increased at the beginning of the study from 0.32 to 0.57  $\mu$ g L<sup>-1</sup>, 266 in parallel to the NO<sub>x</sub> increase, and then decreased between 30 April and 1 May down to 0.40  $\mu$ g L<sup>-1</sup> 267 268 before gradually increasing again (Fig. 4c). On the other hand, microphytoplankton (> 80µm) abundance was very low at the beginning, increased sharply on 1 May, mainly due to the 269 270 development of diatoms (> 90% abundance), and returned to initial values by the end (Fig. 4d). 271 The protozooplankton (mainly tintinnids and foraminifers) showed a very rapid increase in abundance between 30 April and 2 May, followed by a sharp decrease due to the collapse of 272 273 tintinnids (Fig. 5a). The total metazooplankon abundance showed an initial peak, and then a second 274 increase in parallel to that of protozooplankton (Fig. 5b). Copepods (nauplii and older stages) as well as gelatinous organisms (mainly appendicularians of the genus Oikopleura) and other 275 276 holoplankton organisms (pteropods, crustaceans, etc.) showed an initial peak (Fig. 5c, d, e) 277 concomitant with the metazooplankton peak. Afterwards, the abundance of other holoplankton and older stages of copepods remained fairly stable (around 50 in m<sup>-3</sup> and 2000 ind m<sup>-3</sup>, respectively). 278 while nauplii clearly increased from 29 April to 5 May. Appendicularians showed a peak in 279 abundance from 1 to 3 May (up to 3600 ind m<sup>-3</sup>, Fig. 5d), concomitant with the increase in 280 281 microphytoplankton and protozooplankton, and the decrease in chlorophyll. In contrast to the other 282 metazooplankton groups, meroplankton (echinoderms, cirripeds, gastropods and bivalve larvae) was scarce during the first three days, but then increased to a maximum on May 2 (up to 3200 ind  $m^{-3}$ ) 283 before decreasing again to around 500 ind  $m^{-3}$  until the end (Fig. 5f). Copepoda (nauplii and older 284 285 stages) dominated the metazooplankton throughout the survey, accounting for >70% of total

abundance, except on May 2 when meroplankton and gelatinous were predominant (70% of totalabundance).

288 Cross-correlation analyses showed no clear relationships (p >0.001) between nutrients (NOx and 289 PO<sub>4</sub>) and physical variables (wind speed, current speed, water height, wave height, water age, 290 temperature, salinity), whatever the lag time considered. Chlorophyll was correlated negatively to 291 water height (r=-0.34; p<0.001) and positively to wind (r=0.365; p<0.001) with no time-lag. 292 Microphytoplankton and protozooplankton showed no correlation with water height but were 293 positively correlated to wind speed (r= 0.39 and 0.420 respectively; p< 0.0001), current (r= 0.60 and 294 r=0.71; p<0.00001) and waves (r=0.70 and 0.72; p<0.00001) with a 5-day time lag. When 295 considering no time-lag, microphytoplankton was negatively correlated to the same variables (r=-0.33, p< 0.01; r=-0.55, p<0.00001; r=-0.52, p<0.00001). Total metazooplankton and main 296 297 taxonomic groups showed no significant correlation with physical variables with no time lag, except 298 for appendicularians and meroplankon, which were both negatively correlated to current speed (Fig. 299 6). With increasing time lag, metazooplankton showed (i) alternating positive and negative 300 correlation with water height roughly corresponding to ebb and flow sequence, and (ii) relatively 301 high positive correlations with waves and current with a time lag > 5 days. The relationship of 302 metazooplankton with water height seems to be mainly due to copepods which showed almost the 303 same pattern (even more accentuated, Fig. 6b). This pattern mainly reflects the alternation of higher 304 copepod abundances during high water and lower abundances during low water. Finally, 305 appendicularians showed high positive correlation with current after a 5-day time lag and 306 meroplankton with waves and current but after a time lag of 3.5 days (Fig. 6c and d). 307 In complement to the cross-correlation analysis, Fourier analysis (Fig. 7) showed that most of the 308 variability of temperature and salinity is explained by processes with a frequency < 1/day. The 309 variability of nutrients and Chla is more balanced between the different processes considered, 310 although the contribution of the day-night cycle is dominant for Chla. Day-night and tidal cycles 311 have only a small influence on the temporal variability of planktonic component abundance,

312 whereas sporadic events (< 1/day) strongly influence the variability of microphytoplankton,

313 protozooplankton, appendicularians and meroplankton.

314

# Space and time variations of environmental variables and plankton abundance during the four spatial transects

317 The temperature decreased in the whole lagoon and in the ocean between 25 and 28 April during 318 the wind and swell event, and increased again afterwards (Fig. S3a). In the ocean, the cooling (from 319 27.1°C to 25.4°C in surface) was associated with a general rise of the thermocline and DCM (Deep 320 Chlorophyll Maximum; Fig. S4). Compared to the initial values, NOx and silicate concentrations 321 increased at most stations, , while phosphate concentrations showed minor variations between 322 stations or dates (coefficient of variation, CV = 17% vs 30 and 36% for NOx and silicates) (Fig. 323 S3b). Chlorophyll showed a high variability (CV = 48%) between stations and dates (Fig. S3c). In 324 the lagoon, microphytoplankton was more abundant near the coast (L3) with a predominance of diatoms (mainly Chaetoceros spp.), while in the ocean abundance remained low and stable with a 325 326 predominance of filamentous cyanobacteria (mainly Trichodesmium spp.) (Fig.S3c). 327 Protozooplankton (mainly tintinnids) and metazooplankton (total and all groups) were much more 328 abundant in the lagoon than in the ocean (Fig. S5a and b). Protozooplankton showed maxima at 329 coastal station L3 and at L4 but crashed at the end of the survey. Metazooplankton, strongly 330 dominated by the copepods including nauplii, also showed maxima at L3. The meroplankton 331 abundance increased at all lagoon stations during the study, due to the increase of larvae of benthic 332 organisms (mainly gasteropods) and showed higher values at L3 and L2 (Fig. S5f). 333 The PCA on environmental and plankton variables (Fig. 8) explains 50 % of total variance on the 334 first factorial plane, including 35 % for the first axis. The first axis mainly illustrates spatial 335 variation with a clear opposition between the ocean (On and Os), positively correlated with the percentage abundance of cyanobacteria, dinoflagellates and copepods, and the most coastal lagoon 336 337 station (L3) mainly correlated with salinity, turbidity, Chla, phyto- and zooplankton abundance and

percentage abundance of diatoms and meroplankton. The second axis illustrates the time variation, mainly at the northern lagoon stations (L1 and L2) and in the ocean, with the initial sampling points (numbered 1) being more related to temperature and percentage abundance of copepods and tintinnids, and the final points (numbered 3 and 4) more related to Si(OH)<sub>4</sub>, NOx and percentage abundance of foraminifers and meroplankton. During the study, the northern lagoon stations (L1 and L2) varied from an oceanic to a more lagoon character while the southern stations (L3, L4, L5) appeared less variable.

345

### 346 Plankton communities: composition and spatio-temporal variations

347 Classification of microphytoplankton by FlowCAM identified seven groups for the whole set of 348 samples: 3 dinoflagellates (Ceratium, Ostreopsis, and other), 3 diatoms (Chaetoceros, Rhizosolenia, 349 and other), and 1 miscellaneous cyanobacteria (mainly, Trichodesmium). . NMDS analysis on 350 microphytoplankton along transects (data not shown; stress = 0.01) confirmed previous observations with i) cyanobacteria (and to a lesser extent dinoflagellates) correlated with ocean stations (On and 351 352 Os, at all periods) and northern lagoon stations (L1 and L2) at the beginning (25-26 April) 353 (similarity 90), and ii) diatoms correlated with the other lagoon sampling points (similarity 84). 354 Classification of metazooplankton by imagery (FlowCAM and ZooScan) enabled us to identify 355 seventeen taxonomic groups: 6 copepods (eggs + nauplii of copepods, *Oithona, Poecilostomatoida*, 356 Harpaticoida, others), 3 gelatinous (Appendicularia, Chaetognata and others), 3 other holoplankton (Ostracoda, other Crustacea, nematods) and 5 meroplankton (Polychaeta, Teleostei, Gasteropoda 357 358 and pluteus larvae, and other eggs). In addition to the imagery, microscopy (limited to the ocean and 359 L2) enabled the identification of seventy-seven metazooplankton taxa including 45 copepods, 6 360 gelatinous, 7 holoplankton and 9 meroplankton (Table 1). The majority of these taxa were present in 361 both ocean and lagoon samples. However, among the copepods, 4 were sampled only in the ocean (Candacia spp, Euchaeta, Lucicutia and Monstrillidae) and 10 only in the lagoon (Acartia tonsa, 362 363 Calanopia aurivii, Centropages furcatus, Cosmocalanus, Nannocalanus, Oithona aculeata and O.

*simplex, Clytemnestra, Macrosetella* and *Porcellidium*). On the other hand, medusa, amphipods and cladocerans were only found in the lagoon. Most of these taxa specific to the ocean or to the lagoon represent a very small percentage of the total abundance (< 0.5%), except for *Oithona simplex* (up to 8%). In the lagoon, the diversity index decreased after 26-27 April (Table 1).

368 The NMDS analysis performed on imagery data of the spatial transects (Fig. 9a) revealed that all

the initial sampling points (numbered 1) of the lagoon stations (except L3) form a homogenous

370 group (similarity 80.2) very close to the oceanic group, with both groups correlated with

371 *Poecilostomatoida (Oncaea and Corycaeus genera) and chaetognaths. In the following sampling* 

periods (numbered 2 to 4), the lagoon stations show a greater dispersion and dissimilarity with the

373 oceanic group (up to 39) than initially (30), mainly due to larvae of gastropods, *Oithona*, pluteus

374 larvae, appendicularians and polychaetes, (74% of the cumulative contribution to dissimilarity). For

375 the time-series at L2, NMDS analyses (including ocean sampling points for comparison) were

376 carried out on both imagery and microscopy data. Analysis on microscopy data clearly clustered the

377 zooplankton data into three groups (Fig. 9b). The first group (similarity 64) comprises the two ocean

378 stations defined mainly by *Clauso/Paracalanus, Oithona plumifera, Oncaea, Euchaeta,* 

379 Corycaeus/Farranula, and ostracods. The second group (similarity 53) represents station L2 on 26-

380 27 April and is defined by gasteropod larvae, indeterminate harpaticoids and cyclopids and Oithona

381 *simplex*. The third group (similarity 67) includes all other L2 sampling points and is defined by

382 *Oithona nana*, decapod larvae and appendicularians. The same trends were obtained with NMDS on

imagery data (Fig. 9c), reflecting in particular the changes over time of the zooplankton community

384 at L2.

385

#### 386 **DISCUSSION**

387 One of the main aims of this paper was to assess the short-term temporal dynamics of plankton

388 communities in relation to physical variations in a narrow coral-reef lagoon ('channel lagoon'),

through an integrated strategy coupling physical and biological approaches. The occurrence of two

climatic events (wind and rain) during our 15-days survey gave us the opportunity to observe the
 combined effects of different external and internal physical forcings on the trophic status and on the
 plankton communities, at a short-term scale.

393

# 394 Importance of short-term climatic events for hydrodynamic and enrichment processes in 395 shallow channel lagoons.

In coral reef lagoons, the tide is the permanent driver for circulation and ocean-lagoon exchanges and also to some extent for nutrient dynamics. Seasonal or occasional climatic conditions (wind, swell, rain and associated runoff) can combine with the tide to impact the lagoon status. In this paper, we show that short-term climatic events have a major influence on the trophic status of channel lagoons.

401 The first climatic event captured in the study was a short-term trade wind event accompanied by 402 nutrient and Chla enrichment in the lagoon and off the reef. In the ocean, local trade winds may 403 lead to enrichment of the upper layer due to sporadic upwelling as previously described off the 404 southwest coast of New Caledonia (Henin and Cresswell, 2005; Marchesiello and Estrade, 2010; 405 Ganachaud et al., 2010). Oceanic enrichment can also be explained by deeper mixing and 406 subsequent displacement of the underlying water induced by an increase in significant wave height 407 (as observed in this study, Fig. 2) and dominant wavelength (Pedlosky, 1998). Such sporadic events, 408 even if moderate, can have a significant impact on the nutrient dynamics of the near-reef barrier 409 ecosystem, especially in oligotrophic areas (Ganachaud et al., 2010), and also of the lagoon as 410 described in the southern New Caledonian lagoon (Neveux et al., 2010; Fuchs et al., 2013). In our 411 study, the direct contribution of ocean water to lagoon enrichment at the beginning of the study was 412 likely reinforced by the strong swell event occurring at the same time and during a spring tide, thus 413 increasing the renewal of the lagoon water by ocean surface water (Fig. 2). We estimate that the 414 ocean could contribute up to 35% of nutrient (NOx) enrichment at L2, by applying a dilution model

415 based on water age and lagoon/ocean nutrient concentrations (C. Chevalier, Marseille, personal416 communication).

417 Local winds also generate waves in the lagoon, which can promote the bottom shear stress, 418 leading to sediment erosion, highlighted here by the turbidity increase (Fig. S2), and thereby the 419 remobilization of pore water nutrients into the whole water column by vertical turbulent diffusion 420 driven by the wind. The water enrichment by this process could be high, if we refer to the 421 shallowness of the lagoon and to the high nutrient concentrations in the interstitial water as reported 422 for the southwestern lagoon of New Caledonia (Grenz et al., 2010). Significant wave height can 423 also contribute to the nutrient enrichment of the lagoon by promoting wave-breaking over the reef 424 barrier. This process leads to a strengthening of the inward cross-reef flow and of the turbulent passage of water above the reef, favoring the direct advection of nutrient-enriched cross-reef water 425 426 (Wyatt et al., 2012) and/or dissolved and particulate organic matter (mucus, algae filaments, etc.) 427 produced by the reef (e.g., Hata et al., 2002; Cuet et al., 2011).

Rivers and runoff are considered important sources of nutrient enrichment for coastal lagoons 428 429 (Fichez et al., 2010). Here, in the Ouano lagoon, such enrichment was detected at the lagoon scale even during a short rainfall event, and also affected the nearby ocean waters as observed in the south 430 431 (Os). This can be explained both by the small size and shallow depth of the lagoon and by the high 432 flow rates (Laroche et al., 2022) and nutrient content of the surrounding rivers (e.g., for the Tontouta river mean silicate value =  $310 \mu mol L^{-1}$  and nitrate value =  $6 \mu mol L^{-1}$ ; H. Lemonnier, Nouméa, 433 personal communication). The relative influence of oceanic and terrigenous inputs on the nutrient 434 435 dynamics of a narrow and shallow lagoon is strongly affected by the circulation patterns and 436 exchanges with the ocean, as demonstrated in this work. Thus, at the start of the survey, when there 437 was no wind, the ocean/lagoon exchange was mainly through the northern passages, and the lagoon 438 was mainly under the oligotrophic oceanic influence, particularly in the northern zone (L1 and L2). 439 With the wave intensification, the hydrodynamics changed drastically with an increase of cross-reef 440 current speed and a strengthening of lagoon circulation, favoring nutrient enrichment of the lagoon

by oceanic waters. Then, the lagoon came mostly under terrigenous influence, due to the rain event that occurred in a situation of weak ocean-lagoon exchanges and circulation linked to the decrease of wind, wave and tidal amplitude. This terrigenous influence came mainly from the south via St Vincent bay which receives the waters of three rivers (including La Tontouta). At the end of the survey, the circulation changed again with enhanced flow through the passages towards the lagoon, explaining a return to a more oligotrophic marine influence.

447 In summary, our study showed the high lagoon-scale temporal variability of the environmental 448 and trophic characteristics of a shallow channel lagoon, in response to external forcings (wind, 449 swell, rain) and associated hydrodynamic changes (circulation patterns). The typology of channel 450 lagoons such as Ouano (shallow depth and narrowness) maximizes the exchanges at the interfaces 451 (ocean/reef, land, bottom), which leads to this high variability and makes the disentangling of the 452 underlying processes controlling the trophic status more complex. Our results also highlighted the 453 importance of short-term climatic events in driving circulation patterns and nutrient dynamics in 454 these lagoons. This high temporal variability at lagoon scale contrasts with the greater stability of 455 larger lagoons such as the SWL in New Caledonia (Le Borgne et al., 2010), where oceanic and terrigenous influences are more restricted to the boundary zones, resulting in higher spatial 456 457 distributions of residence time, nutrients and planktonic variables (Pinazo et al., 2004; Jouon et al., 458 2006; Torréton et al., 2007; Fichez et al., 2010).

459

### 460 **Rapid responses of lagoon plankton communities to short-term environmental changes.**

The short-term changes in hydrodynamic and trophic conditions at the lagoon scale were accompanied by rapid changes in the plankton community composition. This may be explained by the response time of plankton to changes in trophic conditions which is typically much shorter in tropical than in temperate ecosystems (e.g. Hoover et al., 2006). In a channel lagoon, the rapid changes in local plankton communities may also be related to their mixing with allochtonous communities from neighbouring biotopes (reef, river, ocean and other lagoons), facilitated by the intense hydrodynamics and the proximity of border zones. Our results illustrate these two aspects of
the trophic and plankton community dynamics in response to rapid environmental changes in
tropical channel lagoons.

470

471 Trophic responses. The microphytoplankton quickly responded to the initial N-enrichment of the 472 lagoon associated with the trade wind and swell events, by an increase of its total biomass (Chla), 473 probably due to the proliferation of pico-nanoplankton, as described by Neveux et al (2010). In a 474 second step, the silicate and NOx inputs associated with the rain event promote the occurrence and 475 the relative abundance of diatoms (mostly *Chaetoceros* spp.). The link between diatoms and Si is 476 confirmed by a significant relationship between Si and diatom abundance (Log (diatoms) =  $6.13 \log$ ) 477 (Si) +1.038 with r=0.692; p<0.005) as observed in the SW lagoons (Jacquet et al., 2006). It is well 478 established that external nutrient inputs favor the development of nano- and microphytoplankton to 479 the detriment of picoplankton (Glibert et al., 2016).

480 The zooplankton responded rapidly to the initial increase of pico- and nanophytoplankton biomass with the proliferation of fast-growing opportunistic herbivorous species (tintinnids and 481 appendicularians) and a parallel decrease in taxonomic diversity (Frontier and Pichod-Viale, 1998). 482 483 The increasing abundance of nauplii, reflecting high egg production, is also a consistent zooplankton 484 response to increasing phytoplankton food resources (Mauchline, 1998). Likewise, the relative 485 importance of Oithona nana at the same time is an indication of phytoplankton enrichment in the 486 environment. As this species is considered as an indicator of eutrophication in mesotrophic coastal 487 environments (Serranito et al, 2016), it is interesting to find it associated here with enrichment in a 488 much more oligotrophic context.

In addition to the rapid bottom-up effect, a rapid grazing control on phytoplankton was
highlighted by the strong decrease of total Chl*a*, in parallel with the proliferation of opportunistic
herbivorous zooplankton (appendicularians and tintinnids) (Figs 4 and 5). This decrease was due to
the collapse of pico- and nanophytoplankton (representing on average 72% of Chl*a* in most lagoons

493 of New Caledonia; Torreton et al., 2010; Rodier and Arfi, 2021), which are the main prey for these 494 herbivorous zooplankton taxa (Kiorboe, 2011). Appendicularians are blooming organisms that have the capacity to filter large volumes of water (up to ~ 4 L ind<sup>-1</sup> d<sup>-1</sup>, Bochdansky et al., 1998) and to 495 496 graze efficiently on particles from a broad size-range, from pico- to nanophytoplankton (Fernández 497 et al., 2004). Tintinnids, known to be very efficient grazers of pico- and nanoparticles (Fenchel, 1980), could also have contributed to the depletion of the small phytoplankton. The top-down 498 499 control of pico- and nanophytoplankton by herbivorous zooplankton may also have favored the 500 proliferation of microphytoplankton by reducing competition for nutrients (Glibert et al., 2016). 501

502 Advection and community mixing. The abundance and structure of the plankton community can 503 also be modified by advection processes, especially for metazooplankton as shown here by close 504 relationships with some physical parameters (water height, current, wave). Cross-correlation 505 analyses revealed a clear tidal effect on copepod abundance (Fig. 6B), suggesting an alternation 506 between advection of oceanic zooplankton (less abundant) leading to a decrease in abundance 507 during the flood and advection of inner lagoon zooplankton (more abundant) leading to an increase 508 in abundance during the ebb. More generally, the mixing of oceanic plankton with lagoon plankton 509 appears to be more intense when the circulation pattern favours the advection of oceanic water into 510 the lagoon in a period of strong swell and increased exchanges (e.g., at the beginning of our survey). 511 This is shown by the multivariate analyses performed on phyto- and zooplankton taxonomic groups 512 identified by imagery (Fig. 8 and Figs 9A and C). Despite this mixing, the analysis carried out on 513 more detailed taxonomy using microscopy (Fig. 9B) shows that the lagoon zooplankton community 514 always remains clearly distinct from that of the ocean, whatever the forcing. In particular, O. 515 *simplex*, which is the only species that can be qualified as a lagoon-dwelling species because it is a 516 resistant euryhaline species (Grice, 1960; Chew & Chong, 2011), was always abundant in the 517 lagoon and undetectable in the ocean.

518 The abundance and structure of the zooplankton community can also be modified by the 519 advection of near-reef zooplankton driven by the increase of SWH leading to high and intense inward cross-reef flows (e.g., "Classical circulation pattern" in our study, Fig. 3). For instance, the 520 521 increased abundance of meroplankton in the lagoon (12-fold increase between 25 April and 2 May) 522 is likely the result of the advection of pelagic larvae from the reef macrofauna (Pagano et al., 2017; Santos et al., 2019 and references therein). The good correlation with a 3-day lag between 523 meroplankton and the SWH and the cross-reef current confirms this trend. The transport of 524 525 meroplankton from cross-reef to the inner lagoon leads to an enrichment and diversification of the lagoon zooplankton and therefore of the prey for zooplanktophagous organisms. This process favors 526 527 the connectivity between the reef barrier habitats and inner lagoon reefs (fringing and patch reefs), 528 increasing the dispersal potential for reef macrofauna larvae (Thomas et al., 2014) in these narrow 529 lagoons.

530

*In summary*, the short-term temporal variability of planktonic communities observed in this type of 531 532 narrow lagoon is closely related to sporadic phenomena (i.e., winds, waves, and precipitation) that can blur the tidal and diel components, that are generally dominant in wider lagoon environments 533 534 such as in the southwestern lagoon (Le Borgne et al., 2010; Torreton et al., 2010) and in open coastal ecosystems (Goswami et al., 2000, Vineetha et al, 2015; Yelton et al, 2022). This short-term 535 536 temporal variability also tends to mask the spatial variability, which here is mainly expressed by higher plankton abundances in the most confined coastal zone (L3), as previously observed in two 537 538 bays north of Ouano lagoon (Ouarai and Chambeyron bays) by Carassou et al. (2010) and which can 539 be related to a longer water residence time (Delesalle and Sournia, 1992; Andréfouët et al., 2001). 540 These zones, characterized by lower water renewal and high plankton stocks, can therefore be 541 considered as hotspots of productivity and a nurseries for fish larvae (Carassou et al., 2010).

### 543 CONCLUSIONS

This study highlights the tight coupling between physical processes and nutrient dynamics, and 544 the rapid (on the order of a day), lagoon-scale responses of plankton to these forcings in shallow and 545 546 narrow coral-reef lagoons. The typology of these lagoons maximizes exchange at the interfaces 547 (ocean/reef, land, bottom) and connectivity between neighbouring habitats. This contrasts with the situation observed in large coral-reef lagoons (e.g., SL and SWL in New Caledonia) which are 548 549 characterized by more pronounced spatial gradients and overall lower temporal variability at the 550 lagoon-wide scale. Furthermore, our study confirms that episodic external forcing events (e.g., wind, 551 wave, rain, etc.), combined with the tide, determine circulation patterns and enrichment processes, 552 that regulate or structure plankton communities in coral reef systems, but we also suggest that these 553 processes are amplified in channel-type lagoons. The potential importance of external oceanic forcing on the nutrient and plankton dynamics in these lagoons is reinforced in New Caledonia by 554 555 the occurrence of coastal upwelling events along the western reef barrier (Hénin & Creswell, 2005) and by the predominance of the effect of waves over that of tides in this region of the South Pacific 556 557 Ocean (ratio tidal amplitude/wave height <1; Lowe & Falter, 2015).

558 Our observations and the whole dynamic story can most likely be generalized to the other 559 channel-type lagoons in New Caledonia or in other oceanic regions of the world such as the lagoons 560 of Toliara (Madagascar) and Mayotte in the Indian Ocean (Chevalier et al., 2017; Moustapha et al., 561 2021), taking into account local specificities in terms of hydrodynamic forcing (i.e., tides, swell, 562 dominant winds) and reef features.

The relative importance of oceanic *versus* terrigenous impacts on the lagoons depends on the climatic context and may vary in response to global change. How the high sensitivity of plankton communities to these external forcings contributes to the vulnerability and resilience capacity of these channel lagoon ecosystems, particularly in the case of extreme anthropogenic or natural perturbations (tropical storms and cyclones), deserves further investigation. It is therefore important to better analyze the plankton responses to such short-term events. In this regard, the coupling between high-frequency physical forcing and the short duration of plankton life cycles should be

570 better taken into account, especially in the case of narrow and shallow lagoons.

571

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- 583

## 584 DATA AVAILIBILITY

585 Data are available upon request to the corresponding author

### 586 **REFERENCES**

- 587 Aminot, A. and Kérouel, R. (2007) Dosage automatique des nutriments dans les eaux marines:
  588 méthodes en flux continu. Vol., Editions Quae.
- 589 Andréfouët, S., Muller-Karger, F. E., Robinson, J. A., Kranenburg, C. J., Torres-Pulliza, D.,
- 590 Spraggins, S. A. and Murch, B. (2006) Global assessment of modern coral reef extent and
- 591 diversity for regional science and management applications: a view from spaceProceedings of
- *the 10th international coral reef symposium.* Vol. 2. Japanese Coral Reef Society Okinawa, pp.
  1732-1745.
- Andréfouët, S., Pagès, J. and Tartinville, B. (2001) Water renewal time for classification of atoll
  lagoons in the Tuamotu Archipelago (French Polynesia). *Coral Reefs*, **20**, 399-408.
- Andrews, J. and Pickard, G. (1990) The physical oceanography of coral reef systems. 11-45.
   *Ecosystems of the world: Coral reefs. Elsevier, Amsterdam.*
- Bochdansky, A. B., Deibel, D. and Hatfield, E. A. (1998) Chlorophyll a conversion and gut passage
  time for the pelagic tunicate Oikopleura vanhoeffeni (Appendicularia). *J. Plankton Res.*, 20,
  2179-2197.
- Carassou, L., Le Borgne, R., Rolland, E. and Ponton, D. (2010) Spatial and temporal distribution of
  zooplankton related to the environmental conditions in the coral reef lagoon of New Caledonia,
  Southwest Pacific. *Mar. Pollut. Bull.*, 61, 367-374.
- 604 Chevalier, C., Devenon, J., Pagano, M., Rougier, G., Blanchot, J. and Arfi, R. (2017) The atypical
  605 hydrodynamics of the Mayotte Lagoon (Indian Ocean): Effects on water age and potential
  606 impact on plankton productivity. *Estuar. Coast. Shelf Sci.*, **196**, 182-197.
- 607 Chevalier, C., Sous, D., Devenon, J. L., Pagano, M., Rougier, G. and Blanchot, J. (2015) Impact of
  608 cross-reef water fluxes on lagoon dynamics: a simple parameterization for coral lagoon
  609 circulation model, with application to the Ouano Lagoon, New Caledonia. *Ocean Dynamics*, 65,
  610 1509-1534.

- 611 Chew, L. L. and Chong, V. C. (2011) Copepod community structure and abundance in a tropical 612 mangrove estuary, with comparisons to coastal waters. *Hydrobiologia*, **666**, 127-143.
- Conway, D. V. P., White, R. G., Hugues-Dit-Ciles, J., Gallienne, C. P. and Robins, D. B. (2003)
  Guide to the coastal and surface zooplankton of the South-Western Indian Ocean. DEFRA
  Darwin Initiative Zooplankton Programme, Version 1 . Vol. 15, Marine Biological Association
  of the United Kingdom Occasional Publications, Plymouth.
- 617 Cuet, P., Atkinson, M. J., Blanchot, J., Casareto, B. E., Cordier, E., Falter, J., Frouin, P., Fujimura,
- 618 H., Pierret, C., Susuki, Y. and Tourrand, C. (2011) CNP budgets of a coral-dominated fringing
- reef at La Reunion, France: coupling of oceanic phosphate and groundwater nitrate. *Coral Reefs*, 30, 45-55.
- De Brye, B., De Brauwere, A., Gourgue, O., Delhez, E. J. and Deleersnijder, E. (2013) Reprint of
  water renewal timescales in the Scheldt Estuary. *J. Mar. Syst.*, **128**, 3-16.
- Delesalle, B. and Sournia, A. (1992) Residence time of water and phytoplankton biomass in coral
  reef lagoons. *Cont. Shelf Res.*, 12, 939-949.
- Delhez, É. J. and Deleersnijder, É. (2002) The concept of age in marine modelling: II. Concentration
  distribution function in the English Channel and the North Sea. *J. Mar. Syst.*, **31**, 279-297.
- Dumas, F., Le Gendre, R., Thomas, Y. and Andrefouet, S. (2012) Tidal flushing and wind driven
  circulation of Ahe atoll lagoon (Tuamotu Archipelago, French Polynesia) from in situ
  observations and numerical modelling. *Mar. Pollut. Bull.*, 65, 425-440.
- 630 Dupouy, C., Röttgers, R., Tedetti, M., Frouin, R., Lantoine, F., Rodier, M., Martias, C. and Goutx,
- M. (2020) Impact of contrasted weather conditions on CDOM absorption/fluorescence and
  biogeochemistry in the eastern lagoon of New Caledonia. *Frontiers in Earth Science*, 8, 54.
- Fenchel, T. (1980) Suspension feeding in ciliated protozoa: feeding rates and their ecological
  significance. *Microb. Ecol.*, 6, 13-25.

- Fernandez, D., Lopez Urrutia, A., Fernandez, A., Acuna, J. L. and Harris, R. (2004) Retention
  efficiency of 0.2 to 6 mu m particles by the appendicularians Oikopleura dioica and Fritillaria
  borealis. *Mar. Ecol. Prog. Ser.*, 266, 89-101.
- Fichez, R., Chifflet, S., Douillet, P., Gérard, P., Gutierrez, F., Jouon, A., Ouillon, S. and Grenz, C.
  (2010) Biogeochemical typology and temporal variability of lagoon waters in a coral reef
  ecosystem subject to terrigeneous and anthropogenic inputs (New Caledonia). *Mar. Pollut. Bull.*, **61**, 309-322.
- Frontier, S. and Pichod-Viale, D. (1998) *Ecosystèmes:structure fonctionnement évolution 2ème édition*. Vol., Dunod, Paris.
- Fuchs, R., Pinazo, C., Douillet, P., Fraysse, M., Grenz, C., Mangin, A. and Dupouy, C. (2013)
  Modelling ocean–lagoon interaction during upwelling processes in the South West of New
  Caledonia. *Estuar. Coast. Shelf Sci.*, 135, 5-17.
- Ganachaud, A., Vega, A., Rodier, M., Dupouy, C., Maes, C., Marchesiello, P., Eldin, G., Ridgway,
  K. and Le Borgne, R. (2010) Observed impact of upwelling events on water properties and
  biological activity off the southwest coast of New Caledonia. *Mar. Pollut. Bull.*, 61, 449-464.
- 650 Glibert, P. M., Wilkerson, F. P., Dugdale, R. C., Raven, J. A., Dupont, C. L., Leavitt, P. R., Parker,
- A. E., Burkholder, J. M. and Kana, T. M. (2016) Pluses and minuses of ammonium and nitrate uptake and assimilation by phytoplankton and implications for productivity and community composition, with emphasis on nitrogen-enriched conditions. *Limnol. Oceanogr.*, **61**, 165-197.
- 654 Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J. B., Cawood,
- A., Pesant, S., Garcia-Comas, C. and Prejger, F. (2010) Digital zooplankton image analysis
  using the ZooScan integrated system. *J. Plankton Res.*, **32**, 285-303.
- Goswami, S. C., Kumari, L. K. and Shrivastava, Y. (2000) Diel variations in zooplankton and their
  biochemical composition from Vengurla to Ratnagiri, west coast of India. *Indian J. Mar. Sci.*,
- **659 29,** 277-280.

- 660 Grenz, C., Denis, L., Pringault, O. and Fichez, R. (2010) Spatial and seasonal variability of sediment
- oxygen consumption and nutrient fluxes at the sediment water interface in a sub-tropical lagoon
  (New Caledonia). *Mar. Pollut. Bull.*, **61**, 399-412.
- Grenz, C., Le Borgne, R., Torréton, J.-P. and Fichez, R. (2013) New Caledonia lagoon: a threatened
  paradise under anthropogenic pressure. *Lagoons: Habitats and Species, Human Impacts and Ecological Effects'. (Ed. M. Mwinyihija.) pp*, 31-56.
- Grice, G. D. (1960) Calanoid and cyclopoid copepods collected from the Florida Gulf Coast and
  Florida Keys in 1954 and 1955. *Bull. Mar. Sci.*, 10, 217-226.
- Hata, H., Kudo, S., Yamano, H., Kurano, N. and Kayanne, H. (2002) Organic carbon flux in Shiraho
  coral reef (Ishigaki Island, Japan). *Mar. Ecol. Prog. Ser.*, 232, 129-140.
- Hench, J. L., Leichter, J. J. and Monismith, S. G. (2008) Episodic circulation and exchange in a
  wave-driven coral reef and lagoon system. *Limnol. Oceanogr.*, 53, 2681-2694.
- Hénin, C. and Cresswell, G. (2005) Upwelling along the western barrier reef of New Caledonia. *Mar. Freshwat. Res.*, 56, 1005-1010.
- Hoover, R. S., Hoover, D., Miller, M., Landry, M. R., Decarlo, E. H. and Mackenzie, F. T. (2006)
- Zooplankton response to storm runoff in a tropical estuary: bottom-up and top-down controls.
  Marine Ecology Progress Series, 318, 187-201.con
- Jacquet, S., Delesalle, B., Torréton, J.-P. and Blanchot, J. (2006) Response of phytoplankton
   communities to increased anthropogenic influences (southwestern lagoon, New Caledonia).
   *Mar. Ecol. Prog. Ser.*, **320**, 65-78.
- Jouon, A., Douillet, P., Ouillon, S. and Fraunié, P. (2006) Calculations of hydrodynamic time
  parameters in a semi-opened coastal zone using a 3D hydrodynamic model. *Cont. Shelf Res.*,
  26, 1395-1415.

- Kiørboe, T. (2011) How zooplankton feed: Mechanisms, traits and trade-offs. Biological Reviews,
  86, 311-339.
- Kjerfive, B. (1994) Coastal Lagoons In: B. Kjerfive (ed) *Coastal lagoon Processes*. Elsevier
  Oceanography Series 60, Amsterdam, pp. 1-8.
- Laroche, C., Chauveau, M., N'guyen, P., Wotling, G., Mir, J.-M. and Bernast, N. (2022) Plus de 60
  ans d'hydrométrie en Nouvelle-Calédonie bilan, pratiques, évolutions et perspectives. LHB,
  2050429.
- Le Borgne, R., Douillet, P., Fichez, R. and Torreton, J.-P. (2010) Hydrography and plankton
  temporal variabilities at different time scales in the southwest lagoon of New Caledonia: A
  review. *Mar. Pollut. Bull.*, 61, 297-308.
- Le Bouteiller, A., Blanchot, J. and Rodier, M. (1992) Size distribution patterns of phytoplankton in
  the western Pacific: towards a generalization for the tropical open ocean. *Deep Sea Res. (I Oceanogr. Res. Pap.)*, **39**, 805-823.
- 696 Lowe, R. J. and Falter, J. L. (2015) Oceanic forcing of coral reefs. Annu. rev. mar. sci., 7, 43-66.
- Lowe, R. J., Falter, J. L., Monismith, S. G. and Atkinson, M. J. (2009) Wave-driven circulation of a
  coastal reef–lagoon system. *J. Phys. Oceanogr.*, **39**, 873-893.
- Luettich Jr, R., Westerink, J. J. and Scheffner, N. W. (1992) ADCIRC: An advanced threedimensional circulation model for shelves, coasts, and estuaries. report 1. theory and
  methodology of adcirc-2ddi and adcirc-3dl., Tech. rep., DTIC Document. Army engineer
  waterways experiment station vicksburg MS.
- Marchesiello, P. and Estrade, P. (2010) Upwelling limitation by onshore geostrophic flow. *J. Mar. Res.*, 68, 37-62.

- Martias, C., Tedetti, M., Lantoine, F., Jamet, L. and Dupouy, C. (2018) Characterization and sources
  of colored dissolved organic matter in a coral reef ecosystem subject to ultramafic erosion
  pressure (New Caledonia, Southwest Pacific). *Sci. Total Environ.*, 616, 438-452.
- Mauchline, J. (1998) The biology of Calanoid copepods. In: J. H. S. Blaxter, A. J. Southward and P.
  A. Tyler (eds) *Adv. Mar. Biol.* Vol. 33. Academic Press, London, pp. 710.
- Moustapha, S., Chevalier, C., Sow, B., Pagano, M. and Devenon, J.-L. (2021) Coupled effects of
  tide and swell on water renewal in a meso-tidal channel lagoon: Case of the Toliara Lagoon
  (Madagascar). *Estuar. Coast. Shelf Sci.*, 259, 107463.
- Neveux, J., Lefebvre, J.-P., Le Gendre, R., Dupouy, C., Gallois, F., Courties, C., Gérard, P.,
  Fernandez, J.-M. and Ouillon, S. (2010) Phytoplankton dynamics in the southern New
  Caledonian lagoon during a southeast trade winds event. *J. Mar. Syst.*, 82, 230-244.
- Neveux, J., Tenório, M., Jacquet, S., Torréton, J.-P., Douillet, P., Ouillon, S. and Dupouy, C. (2009)
  Chlorophylls and phycoerythrins as markers of environmental forcings including cyclone Erica
  effect (March 2003) on phytoplankton in the southwest lagoon of New Caledonia and oceanic
  adjacent area. *Int. J. oceanogr.*, 2009.
- Orpin, A. R. and Ridd, P. V. (2012) Exposure of inshore corals to suspended sediments due to waveresuspension and river plumes in the central Great Barrier Reef: a reappraisal. *Cont. Shelf Res.*,
  47, 55-67.
- Pagano, M., Rodier, M., Guillaumot, C., Thomas, Y., Henry, K. and Andrefouet, S. (2017) Oceanlagoon water and plankton exchanges in a semi-closed pearl farming atoll lagoon (Ahe,
  Tuamotu archipelago, French Polynesia). *Estuar. Coast. Shelf Sci.*, **191**, 60-73.
- 726 Pedlosky, J. (1998) Ocean Circulation Theory. Springer, 453pp.
- Pinazo, C., Bujan, S., Douillet, P., Fichez, R., Grenz, C. and Maurin, A. (2004) Impact of wind and
  freshwater inputs on phytoplankton biomass in the coral reef lagoon of New Caledonia during

- the summer cyclonic period: a coupled three-dimensional biogeochemical modeling approach. *Coral Reefs*, 23, 281-296.
- Raimbault, P., Lantoine, F. and Neveux, J. (2004) Dosage rapide de la chlorophylle a et des
  phéopigments a par fluorimétrie après extraction au méthanol. *Comparaison avec la méthode classique d'extraction à l'acétone. Océanis*, **30**, 189-205.
- Razouls, C., De Bovée, F., Kouwenberg, J. and Desreumaux, N. (2005-2023) Diversité et répartition
  géographique chez les Copépodes planctoniques marins. http://copepodes.obs-banyuls.fr.
  http://copepodes.obs-banyuls.fr.
- Rodier, M. and Arfi, R. (2020) CLAPPP New Caledonian lagoons: Physics and Phytoplankton
  processes [Data set]. MIO UMR 7294 CNRS. doi.org/10.34930/2B52DEFE-E5F3-4FE2-9F2F739 741D90E624EA (données hydrologiques et planctoniques de 5 campagnes de mesures et 7
- 740 lagons échantillonnés autour de la Nouvelle-Calédonie).
- Santos, G. S., Stemmann, L., Lombard, F. and Schwamborn, R. (2019) Are tropical coastal reefs
  sinks or sources of mesozooplankton? A case study in a Brazilian marine protected area. *Coral Reefs*, 38, 1107-1120.
- 744 Serranito, B., Aubert, A., Stemmann, L., Rossi, N. and Jamet, J.-L. (2016) Proposition of indicators
- of anthropogenic pressure in the Bay of Toulon (Mediterranean Sea) based on zooplankton
  time-series. *Cont. Shelf Res.*, **121**, 3-12.
- 747 Shchepetkin, A. F. and Mcwilliams, J. C. (2005) The regional oceanic modeling system (ROMS): a
- split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model*. *Online*, 9, 347-404.
- 750 Sous, D. (2016) OLZO cruise, RV Alis, https://doi.org/10.17600/16003700
- 751 Sous, D., Chevalier, C., Devenon, J.-L., Blanchot, J. and Pagano, M. (2017) Circulation patterns in a
- channel reef-lagoon system, Ouano lagoon, New Caledonia. Estuar. Coast. Shelf Sci., 196, 315-
- 753 330.

- Tenório, M., Le Borgne, R., Rodier, M. and Neveux, J. (2005) The impact of terrigeneous inputs on
  the Bay of Ouinné (New Caledonia) phytoplankton communities: a spectrofluorometric and
  microscopic approach. *Estuar. Coast. Shelf Sci.*, 64, 531-545.
- Thomas, C. J., Lambrechts, J., Wolanski, E., Traag, V. A., Blondel, V. D., Deleersnijder, E. and
  Hanert, E. (2014) Numerical modelling and graph theory tools to study ecological connectivity
  in the Great Barrier Reef. *Ecol. Model.*, 272, 160-174.
- Torréton, J.-P., Rochelle-Newall, E., Jouon, A., Faure, V., Jacquet, S. and Douillet, P. (2007)
  Correspondence between the distribution of hydrodynamic time parameters and the distribution
  of biological and chemical variables in a semi-enclosed coral reef lagoon. *Estuar. Coast. Shelf Sci.*, **74**, 766-776.
- Torréton, J.-P., Rochelle-Newall, E., Pringault, O., Jacquet, S., Faure, V. and Briand, E. (2010)
  Variability of primary and bacterial production in a coral reef lagoon (New Caledonia). *Mar. Pollut. Bull.*, **61**, 335-348.
- 767 Tregouboff, G. and Rose, M. (eds) (1957) Manuel de planctonologie méditerranéenne, Vol. 1, Paris.
- Vineetha, G., Jyothibabu, R., Madhu, N. V., Kusum, K. K., Sooria, P. M., Shivaprasad, A., Reny, P.
  D. and Deepak, M. P. (2015) Tidal Influence on the Diel Vertical Migration Pattern of
  Zooplankton in a Tropical Monsoonal Estuary. *Wetlands*, 35, 597-610.
- Wyatt, A. S., Falter, J. L., Lowe, R. J., Humphries, S. and Waite, A. M. (2012) Oceanographic
  forcing of nutrient uptake and release over a fringing coral reef. *Limnol. Oceanogr.*, 57, 401419.
- Yelton, R., Slaughter, A. M. and Kimmerer, W. J. (2022) Diel behaviors of zooplankton interact
  with tidal patterns to drive spatial subsidies in the northern San Francisco Estuary. *Estuaries and Coasts*, 45, 1728-1748.
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- 780 Figure legends
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Fig. 1. Sampling stations (stars) during the OLZO cruise aboard the R/V ALIS (from 24 April to 8
May, 2016). The black dots refer to the position of ADCP moorings.

Fig. 2. (a) Time series of significant wave height (from model), cross-reef current speed (measured)

and water age at station L2; horizontal grey rectangles indicate the strong SE wind period and the

yellow lighting the rainy event. (b) Cross-correlograms between water age, current speed, wind

velocity and wave height. Significant values for p: p=0.05 (grey dotted lines), p=0.001 (grey dashed
lines), p=0.00001 (grey solid lines).

Fig. 3. Circulation patterns calculated from ADCP data, with corresponding patterns defined in Sous
et al. (2017). The direction and thickness of the blue arrows illustrate the direction and speed of the
vertically averaged current during each period.

Fig. 4. Time series at station L2 of (a) nitrogen oxidized nutrients (NOx) and silicate, (b) phosphate,
(c) chlorophyll concentrations and (d) 80µm net phytoplankton total abundances. Nutrient and
chlorophyll data were averaged over the water-column. Solid black lines represent the daily mean
values. The silicate series is incomplete (see methods). The horizontal grey rectangles indicate the
strong SE wind period and the yellow lighting the rainy event.

Fig. 5. Time series at station L2 of abundances of (a) total protozooplankton, (b) total

metazooplankton, (c) copepods, (d) appendicularians, (e) other holoplankton groups and (f)

meroplankton. Solid black lines represent the daily mean values. The horizontal grey rectangles

800 indicate the strong SE wind period and the yellow lighting the rainy event. Cop=copepodites,

801 Ad=adults)

802 Fig. 6. Cross-correlograms between metazooplankton abundance (total and main taxonomic groups)

and water height, current speed, and wave height. Significant values for correlation: p=0.05 (grey

dotted line), p=0.001 (grey dashed line), p=0.00001 (grey solid line).

Fig. 7. Fourier analyses of environmental and planktonic variables during the L2 time series.

806 Cumulative percentages of variability due to tidal (frequency = 2/day), day-night cycle (frequency =
807 1/day) and processes of higher (>2/day) or lower frequency (<1/day) associated with punctual</li>
808 events.

Fig. 8. PCA on environmental and plankton variables for ocean and lagoon stations during the four
spatial surveys: plots of the sampling points (a) and the variables (b) on the first factorial plane. The
numbers (1 to 4) next to the station symbols indicate the different sampling periods (25-26 April,

812 28-29 April, 2-3 May and 5-6 May, respectively).

813 Fig. 9. NMDS analyses on metazooplankton taxa abundance performed on (a) samples collected

814 during the four sampling transects and analyzed by imagery and on (b, c) samples collected along

815 the time series at L2 and analyzed either with (b) microscopy at selected dates or (c) with imagery at

816 every date (mean daily values), respectively. Symbols for taxa determined by microscopy (panel B)

are shown in Table 1. In panel a, the numbers (1 to 4) next to the station symbols indicate the

818 different sampling periods (see Fig. 8).

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### 820 Table legend

821 Table 1. Mean values (± standard deviation) of zooplankton abundance, taxa numbers and

822 percentage contribution of each taxon in the two oceanic stations (all samples) and at L2 (at different

823 periods). The taxa symbols used for the multivariate analyses are indicated in the second column.

824 Data derived from microscopic observations.

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### 826 Supplementary Material

Fig. S1. Time series of (a) water height and (b) wind speed. The horizontal grey rectangle indicatesthe rainy event.

Fig. S2. Vertical distribution of (a) temperature, (b) salinity and (c) turbidity during the time seriesat station L2.

Fig. S3. Mean values, at each station sampled during the four spatial transects, of: (a) temperature
and salinity, (b) nutrients, (c) chlorophyll and 80µm net phytoplankton. Mean values of temperature,
salinity, nutrient and chlorophyll were computed for the upper 0-20m layer in the ocean and for the
whole water column in the lagoon.

Fig. S4. Temperature, density and fluorescence profiles at the northern and southern oceanic station(On and Os) on four different dates corresponding to the first day of each spatial transect.

Fig. S5. Mean abundance values, at each station sampled during the four spatial transects, of: (a)
protozooplankton, (b) total metazooplankton, (c) copepods, (d) appendicularians, (e) other
holoplankton groups and (f) meroplankton. Data from vertical hauls of 80µm net. Cop=copepodites,
Ad=adultes.

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