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

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ABSTRACT

The response of plankton communities to short-term climatic events was evidenced in a narrow coral reef lagoon representative of the channel-type lagoons of the high islands of the tropical Pacific. Phyto- and zooplankton data (abundance and taxonomic composition) were sampled at high frequency for two weeks in April-May 2017 under various tidal conditions and combined with environmental and physical measurements and modeling hydrodynamic products. The short-term external events (wind, waves and rain) that occurred caused changes in the circulation patterns and increased nutrient concentrations in the lagoon. The plankton reacted quickly to this enrichment, with an increase in Chl_a and the rapid development of a microphytoplankton community dominated by diatoms, and of opportunistic herbivorous zooplankton (tintinnids, appendicularians). Zooplankton composition and distribution were strongly modulated by the circulation patterns through advection and mixing. Our results show that the tidal and diel components of the temporal variability of planktonic groups were blurred by sporadic event components (i.e., wind, wave and rainfall events). Environmental and biological responses to these external physical forcings occurred at lagoon scale in this channel-like lagoon, unlike what is observed in larger lagoons (such as the 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.

INTRODUCTION

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 et al., 2008, Lowe et al., 2009; Dumas et al., 2012; Orpin and Ridd, 2012). In such ecosystems, the relative importance of these forcings is determined not only by meteorological and oceanic conditions, but also by the reef morphology and lagoon volume (Andréfouët et al., 2001). These physical forcings control the nutrient availability as well as the exchanges, dispersal and transport of 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).

The New Caledonia Lagoon (NCL; 23,400 km²), which extends over extensive oceanic gradients with a wide variety of lagoon and reef barrier typologies (Millennium classification, Andréfouët et al., 2006), is a good candidate for studying the effects of physical forcing on lagoon plankton ecology. Historically, most of hydrodynamic/environmental studies on the NCL have been conducted in the wide and semi-open southwestern and southern lagoons (SWL and SL) and have included investigations of the physical and chemical factors, hydrodynamics and suspended particle transport (Grenz et al., 2013 and references therein), biogeochemical processes and plankton communities (Le Borgne et al., 2010; Fichez et al., 2010; Torréton et al., 2010; Neveux et al., 2009, 2010). The large size of these southern lagoons results in strong contrasts between nearshore waters (bays) which are influenced by terrigenous and anthropogenic inputs and the near-reef waters which are under the oligotrophic influence of the ocean, except during sporadic upwelling events (Hénin 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 also results in low temporal variability of environmental conditions and trophic status in most of the

55 inner lagoon and conversely greater amplitude of variability near the mainland shore (Le Borgne et
56 al., 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
68 outcropping during low spring tides) with passages toward the open ocean or adjacent lagoons. As
69 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.,
72 2015; Sous et al., 2017). However, the effects of this complex hydrodynamics on short timescale
73 variations of nutrients and plankton have not yet been studied in these narrow lagoons.

74 In this paper, we analyze the short-term variability of plankton abundance and community
75 structure using environmental and plankton data collected during an intensive 2-week field study in
76 2016 in Ouano lagoon. Hydrodynamic and phyto- and zooplankton properties were measured
77 simultaneously which allowed the coupling of various physical processes and some key biological
78 processes. Over the study period, the dataset includes different tide, wave, wind and rain conditions
79 as well as hydrodynamic patterns allowing a study of short-term plankton dynamics under different
80 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**

86 This study was performed in Ouano lagoon during the OLZO cruise aboard the R/V Alis from
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
89 total volume of about $2.1 \cdot 10^9 \text{ m}^3$. It is separated from the Coral Sea water by a coral reef barrier
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 (Ouarai, 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
95 in the south, with a very extensive watershed (240 and 380 km², respectively) and high flow rates
96 (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
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).

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

107 April and 5-6 May; tidal range of 1.2 m and 1.8m, respectively), and twice under neap tide
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
113 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 (NO_x), phosphate (PO_4^-) and orthosilicic acid ($\text{Si}(\text{OH})_4$) samples were HgCl_2 -
124 poisoned and analyzed post-cruise by colorimetric methods using a SEAL Analytical Autoanalyzer
125 III as described in Aminot and K  rouel (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 (Chl a) 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.

130

131 **Plankton collection and analysis**

132 Plankton samples were collected with a WP2 net (50cm aperture diameter) equipped with an 80
133 μm mesh size net at the same frequency as the environmental variables. The net was towed
134 vertically from the bottom (or 150 m depth at the ocean station) to the surface at a constant speed of
135 1 m s^{-1} . All samples were immediately preserved in 4% borax-buffered formalin. The volume
136 filtered by the net (V , in m^3) was calculated using the formula $V = S \cdot L$ combining the surface area
137 of the net mouth ($S=0.196 \text{ m}^2$), and the length of the towed cable (L , in m). V varied between 1 and
138 8 m^3 at the lagoon stations and was 29.5 m^3 at the oceanic station. No clogging was observed.
139 In the laboratory, the samples were processed by combining two analytical imaging techniques, after
140 separating each sample into three size-fractions by sieving. The smaller fractions (80-200 μm and
141 200-1000 μm), also including the large microphytoplankton, were analyzed with a FlowCAM (Fluid
142 Imaging Technologies Inc. Series VS-IV, Benchtop model) and the fraction $> 1000 \mu\text{m}$ with a
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 (V_i), ranging from 45 to 400 ml, depending on the
145 density of particles in the samples. Analyses were then immediately processed, stopping
146 automatically when the number of particles counted reached 3000. Thus, the analytical volume (V_a)
147 varied from 0.5 to 12 ml for the 80-200 μm fraction and from 1.6 to 31 ml for the 200-1000 μm
148 fraction. The percentage of the total size-fraction analyzed with the FlowCAM ($100 \cdot V_a/V_i$) varied
149 from 0.3 to 21% for the 80-200 μm fraction and from 0.9 to 43% for the 200-1000 μm fraction. For
150 the ZooScan, analysis was performed on the whole $>1000\mu\text{m}$ 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.

155 After analyses with FlowCAM or ZooScan, each image was processed using ZooProcess (Gorsky
156 et al., 2010), which is embedded in the ImageJ image analysis software. Finally, Plankton Identifier

157 ([http://www.obs-vlfr.fr/~gaspari/Plankton_Identifier/](http://www.obs-vlfr.fr/~gaspari/Plankton_Identifier/index.php) index.php) was used for automatic
158 classification of plankton taxa categories. The results of the automatic classification were then
159 manually validated by an expert. The abundance of each taxa (ind.m^{-3}) was calculated for each size
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
162 size-fractions. Using these imaging techniques, we were able to identify 27 planktonic groups
163 (including 3 protozooplankton groups and 17 metazooplankton groups).

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

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

180

181 **Numerical products from the hydrodynamics model**

182

183 The numerical hydrodynamics model of Ouano lagoon used in this paper is from Chevalier et al.
184 (2015), and is based on 3D Regional Ocean modelling system (ROMS) tools (Shchepetkin &
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 (Chl*a*, 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 $2/\text{day}$ (period $< \frac{1}{2}$ day), 2) semi-diurnal variability with frequency $\sim 2/\text{day}$ (period $\sim \frac{1}{2}$ day), 3)
217 diurnal variability with frequency $\sim 1/\text{day}$ (period ~ 1 day), and 4) sporadic event with frequency $<$
218 $1/\text{day}$ (period > 1 day).

219

220 **RESULTS**

221 **Meteorological and hydrodynamic conditions**

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

227 Concomitant with the strengthening of winds, southwesterly significant wave height (SWH)
228 increased between April 25 and 27 (from 0.5 m to 2 m), then decreased until May 4 (to 0.5 m) and
229 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
231 lag of ~ 1 days (Fig. 2b). Water age also varied spatially from rapid renewal (water age < 1 day)
232 near the reef barrier to slow water renewal (up to 10 days) near the coast and in the bays. For
233 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
236 can be related to the dominant patterns identified in Sous et al. (2017). At the start of the survey (23-
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 Ouarai reef passages and exits from the
239 south through the Ténia Saint Vincent passage. The internal lagoon circulation was mainly
240 southward and fits the “Southward circulation pattern” defined by Sous et al. (2017). Then, from 25
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 Ouarai 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
249 the lagoon varying with the tide from 0 to 0.25 m s^{-1} , and was well correlated with the SWH ($r =$
250 0.923 , $n = 1600$).

251

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

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

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

261 $\mu\text{mol L}^{-1}$) and then between 29 April and 1 May after the rain event (from 0.18 to 0.38 $\mu\text{mol L}^{-1}$)
262 (Fig. 4a). Afterwards, mean daily concentrations remained relatively high between 0.25 and 0.40
263 $\mu\text{mol L}^{-1}$). Despite the lack of data at the beginning and the end of the survey, our results also
264 showed a clear silicate increase after the rain event. In contrast, phosphates showed no clear
265 temporal pattern over the study period (Fig. 4b).

266 Daily chlorophyll concentrations increased at the beginning of the study from 0.32 to 0.57 $\mu\text{g L}^{-1}$,
267 in parallel to the NO_x increase, and then decreased between 30 April and 1 May down to 0.40 $\mu\text{g L}^{-1}$
268 before gradually increasing again (Fig. 4c). On the other hand, microphytoplankton ($> 80\mu\text{m}$)
269 abundance was very low at the beginning, increased sharply on 1 May, mainly due to the
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
272 abundance between 30 April and 2 May, followed by a sharp decrease due to the collapse of
273 tintinnids (Fig. 5a). The total metazooplankton 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
275 well as gelatinous organisms (mainly appendicularians of the genus *Oikopleura*) and other
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
278 older stages of copepods remained fairly stable (around 50 in m^{-3} and 2000 ind m^{-3} , respectively),
279 while nauplii clearly increased from 29 April to 5 May. Appendicularians showed a peak in
280 abundance from 1 to 3 May (up to 3600 ind m^{-3} , Fig. 5d), concomitant with the increase in
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
283 scarce during the first three days, but then increased to a maximum on May 2 (up to 3200 ind m^{-3})
284 before decreasing again to around 500 ind m^{-3} until the end (Fig. 5f). Copepoda (nauplii and older
285 stages) dominated the metazooplankton throughout the survey, accounting for $>70\%$ of total

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

288 Cross-correlation analyses showed no clear relationships ($p > 0.001$) between nutrients (NO_x and
289 PO_4) 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 ($r = -$
296 0.33 , $p < 0.01$; $r = -0.55$, $p < 0.00001$; $r = -0.52$, $p < 0.00001$). Total metazooplankton and main
297 taxonomic groups showed no significant correlation with physical variables with no time lag, except
298 for appendicularians and meroplankton, 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 $< 1/\text{day}$. The
309 variability of nutrients and $\text{Chl}a$ is more balanced between the different processes considered,
310 although the contribution of the day-night cycle is dominant for $\text{Chl}a$. Day-night and tidal cycles
311 have only a small influence on the temporal variability of planktonic component abundance,

312 whereas sporadic events ($< 1/\text{day}$) strongly influence the variability of microphytoplankton,
313 protozooplankton, appendicularians and meroplankton.

314

315 **Space and time variations of environmental variables and plankton abundance during the four** 316 **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, NO_x and silicate concentrations
321 increased at most stations, , while phosphate concentrations showed minor variations between
322 stations or dates (coefficient of variation, $\text{CV} = 17\%$ vs 30 and 36% for NO_x and silicates) (Fig.
323 S3b). Chlorophyll showed a high variability ($\text{CV} = 48\%$) between stations and dates (Fig. S3c). In
324 the lagoon, microphytoplankton was more abundant near the coast (L3) with a predominance of
325 diatoms (mainly *Chaetoceros* spp.), while in the ocean abundance remained low and stable with a
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
336 percentage abundance of cyanobacteria, dinoflagellates and copepods, and the most coastal lagoon
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)_4 , NO_x 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.

Plankton communities: composition and spatio-temporal variations

Classification of microphytoplankton by FlowCAM identified seven groups for the whole set of samples: 3 dinoflagellates (*Ceratium*, *Ostreopsis*, and other), 3 diatoms (*Chaetoceros*, *Rhizosolenia*, and other), and 1 miscellaneous cyanobacteria (mainly, *Trichodesmium*). . NMDS analysis on 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 Os, at all periods) and northern lagoon stations (L1 and L2) at the beginning (25-26 April) (similarity 90), and ii) diatoms correlated with the other lagoon sampling points (similarity 84). Classification of metazooplankton by imagery (FlowCAM and ZooScan) enabled us to identify seventeen taxonomic groups: 6 copepods (eggs + nauplii of copepods, *Oithona*, *Poecilostomatoida*, *Harpacticoida*, others), 3 gelatinous (*Appendicularia*, *Chaetognata* and others), 3 other holoplankton (*Ostracoda*, other *Crustacea*, nematods) and 5 meroplankton (*Polychaeta*, *Teleostei*, *Gasteropoda* and pluteus larvae, and other eggs). In addition to the imagery, microscopy (limited to the ocean and L2) enabled the identification of seventy-seven metazooplankton taxa including 45 copepods, 6 gelatinous, 7 holoplankton and 9 meroplankton (Table 1). The majority of these taxa were present in 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*, *Calanopia aurivii*, *Centropages furcatus*, *Cosmocalanus*, *Nannocalanus*, *Oithona aculeata* and *O.*

364 *simplex*, *Clytemnestra*, *Macrosetella* and *Porcellidium*). On the other hand, medusa, amphipods and
365 cladocerans were only found in the lagoon. Most of these taxa specific to the ocean or to the lagoon
366 represent a very small percentage of the total abundance ($< 0.5\%$), except for *Oithona simplex* (up to
367 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
369 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
372 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 harpacticoids 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
383 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'),
389 through an integrated strategy coupling physical and biological approaches. The occurrence of two

390 climatic events (wind and rain) during our 15-days survey gave us the opportunity to observe the
391 combined effects of different external and internal physical forcings on the trophic status and on the
392 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.**

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

401 The first climatic event captured in the study was a short-term trade wind event accompanied by
402 nutrient and Chl*a* 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 (NO_x) enrichment at L2, by applying a dilution model

415 based on water age and lagoon/ocean nutrient concentrations (C. Chevalier, Marseille, personal
416 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
425 passage of water above the reef, favoring the direct advection of nutrient-enriched cross-reef water
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).

428 Rivers and runoff are considered important sources of nutrient enrichment for coastal lagoons
429 (Fichez et al., 2010). Here, in the Ouano lagoon, such enrichment was detected at the lagoon scale
430 even during a short rainfall event, and also affected the nearby ocean waters as observed in the south
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
433 river mean silicate value = $310 \mu\text{mol L}^{-1}$ and nitrate value = $6 \mu\text{mol L}^{-1}$; H. Lemonnier, Nouméa,
434 personal communication). The relative influence of oceanic and terrigenous inputs on the nutrient
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

441 by oceanic waters. Then, the lagoon came mostly under terrigenous influence, due to the rain event
442 that occurred in a situation of weak ocean-lagoon exchanges and circulation linked to the decrease
443 of wind, wave and tidal amplitude. This terrigenous influence came mainly from the south via St
444 Vincent bay which receives the waters of three rivers (including La Tontouta). At the end of the
445 survey, the circulation changed again with enhanced flow through the passages towards the lagoon,
446 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
456 terrigenous influences are more restricted to the boundary zones, resulting in higher spatial
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.**

461 The short-term changes in hydrodynamic and trophic conditions at the lagoon scale were
462 accompanied by rapid changes in the plankton community composition. This may be explained by
463 the response time of plankton to changes in trophic conditions which is typically much shorter in
464 tropical than in temperate ecosystems (e.g. Hoover et al., 2006). In a channel lagoon, the rapid
465 changes in local plankton communities may also be related to their mixing with allochthonous
466 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.

Trophic responses. The microphytoplankton quickly responded to the initial N-enrichment of the lagoon associated with the trade wind and swell events, by an increase of its total biomass (Chl a), probably due to the proliferation of pico-nanoplankton, as described by Neveux et al (2010) . In a second step, the silicate and NO x inputs associated with the rain event promote the occurrence and the relative abundance of diatoms (mostly *Chaetoceros* spp.). The link between diatoms and Si is confirmed by a significant relationship between Si and diatom abundance ($\text{Log (diatoms)} = 6.13 \log (\text{Si}) + 1.038$ with $r=0.692$; $p<0.005$) as observed in the SW lagoons (Jacquet et al., 2006). It is well established that external nutrient inputs favor the development of nano- and microphytoplankton to the detriment of picoplankton (Glibert et al., 2016).

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

of New Caledonia; Torretón et al., 2010; Rodier and Arfi, 2021), which are the main prey for these herbivorous zooplankton taxa (Kiorboe, 2011). Appendicularians are blooming organisms that have the capacity to filter large volumes of water (up to $\sim 4 \text{ L ind}^{-1} \text{ d}^{-1}$, Bochdansky et al., 1998) and to graze efficiently on particles from a broad size-range, from pico- to nanophytoplankton (Fernández 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 control of pico- and nanophytoplankton by herbivorous zooplankton may also have favored the proliferation of microphytoplankton by reducing competition for nutrients (Glibert et al., 2016).

501

Advection and community mixing. The abundance and structure of the plankton community can also be modified by advection processes, especially for metazooplankton as shown here by close relationships with some physical parameters (water height, current, wave). Cross-correlation analyses revealed a clear tidal effect on copepod abundance (Fig. 6B), suggesting an alternation between advection of oceanic zooplankton (less abundant) leading to a decrease in abundance during the flood and advection of inner lagoon zooplankton (more abundant) leading to an increase in abundance during the ebb. More generally, the mixing of oceanic plankton with lagoon plankton appears to be more intense when the circulation pattern favours the advection of oceanic water into the lagoon in a period of strong swell and increased exchanges (e.g., at the beginning of our survey). This is shown by the multivariate analyses performed on phyto- and zooplankton taxonomic groups identified by imagery (Fig. 8 and Figs 9A and C). Despite this mixing, the analysis carried out on more detailed taxonomy using microscopy (Fig. 9B) shows that the lagoon zooplankton community always remains clearly distinct from that of the ocean, whatever the forcing. In particular, *O. simplex*, which is the only species that can be qualified as a lagoon-dwelling species because it is a resistant euryhaline species (Grice, 1960; Chew & Chong, 2011), was always abundant in the 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
520 inward cross-reef flows (e.g., “Classical circulation pattern” in our study, Fig. 3). For instance, the
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;
523 Santos et al., 2019 and references therein). The good correlation with a 3-day lag between
524 meroplankton and the SWH and the cross-reef current confirms this trend. The transport of
525 meroplankton from cross-reef to the inner lagoon leads to an enrichment and diversification of the
526 lagoon zooplankton and therefore of the prey for zooplanktophagous organisms. This process favors
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

531 ***In summary***, the short-term temporal variability of planktonic communities observed in this type of
532 narrow lagoon is closely related to sporadic phenomena (i.e., winds, waves, and precipitation) that
533 can blur the tidal and diel components, that are generally dominant in wider lagoon environments
534 such as in the southwestern lagoon (Le Borgne et al., 2010; Torreton et al., 2010) and in open
535 coastal ecosystems (Goswami et al., 2000, Vineetha et al, 2015; Yelton et al, 2022). This short-term
536 temporal variability also tends to mask the spatial variability, which here is mainly expressed by
537 higher plankton abundances in the most confined coastal zone (L3), as previously observed in two
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).

542

543 CONCLUSIONS

544 This study highlights the tight coupling between physical processes and nutrient dynamics, and
545 the rapid (on the order of a day), lagoon-scale responses of plankton to these forcings in shallow and
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
548 situation observed in large coral-reef lagoons (e.g., SL and SWL in New Caledonia) which are
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
554 forcing on the nutrient and plankton dynamics in these lagoons is reinforced in New Caledonia by
555 the occurrence of coastal upwelling events along the western reef barrier (Hénin & Creswell, 2005)
556 and by the predominance of the effect of waves over that of tides in this region of the South Pacific
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.

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

569 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 AVAILABILITY**

585 Data are available upon request to the corresponding author

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778

780 **Figure legends**

781

782 Fig. 1. Sampling stations (stars) during the OLZO cruise aboard the R/V ALIS (from 24 April to 8
783 May, 2016). The black dots refer to the position of ADCP moorings.

784 Fig. 2. (a) Time series of significant wave height (from model), cross-reef current speed (measured)
785 and water age at station L2; horizontal grey rectangles indicate the strong SE wind period and the
786 yellow lighting the rainy event. (b) Cross-correlograms between water age, current speed, wind
787 velocity and wave height. Significant values for p: $p=0.05$ (grey dotted lines), $p=0.001$ (grey dashed
788 lines), $p=0.00001$ (grey solid lines).

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

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

797 Fig. 5. Time series at station L2 of abundances of (a) total protozooplankton, (b) total
798 metazooplankton, (c) copepods, (d) appendicularians, (e) other holoplankton groups and (f)
799 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)
803 and water height, current speed, and wave height. Significant values for correlation: $p=0.05$ (grey
804 dotted line), $p=0.001$ (grey dashed line), $p=0.00001$ (grey solid line).

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807 1/day) and processes of higher (>2/day) or lower frequency (<1/day) associated with punctual
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810 spatial surveys: plots of the sampling points (a) and the variables (b) on the first factorial plane. The
811 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).

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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)
817 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).

819

820 **Table legend**

821 Table 1. Mean values (\pm 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.

825

826 **Supplementary Material**

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

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

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

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

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

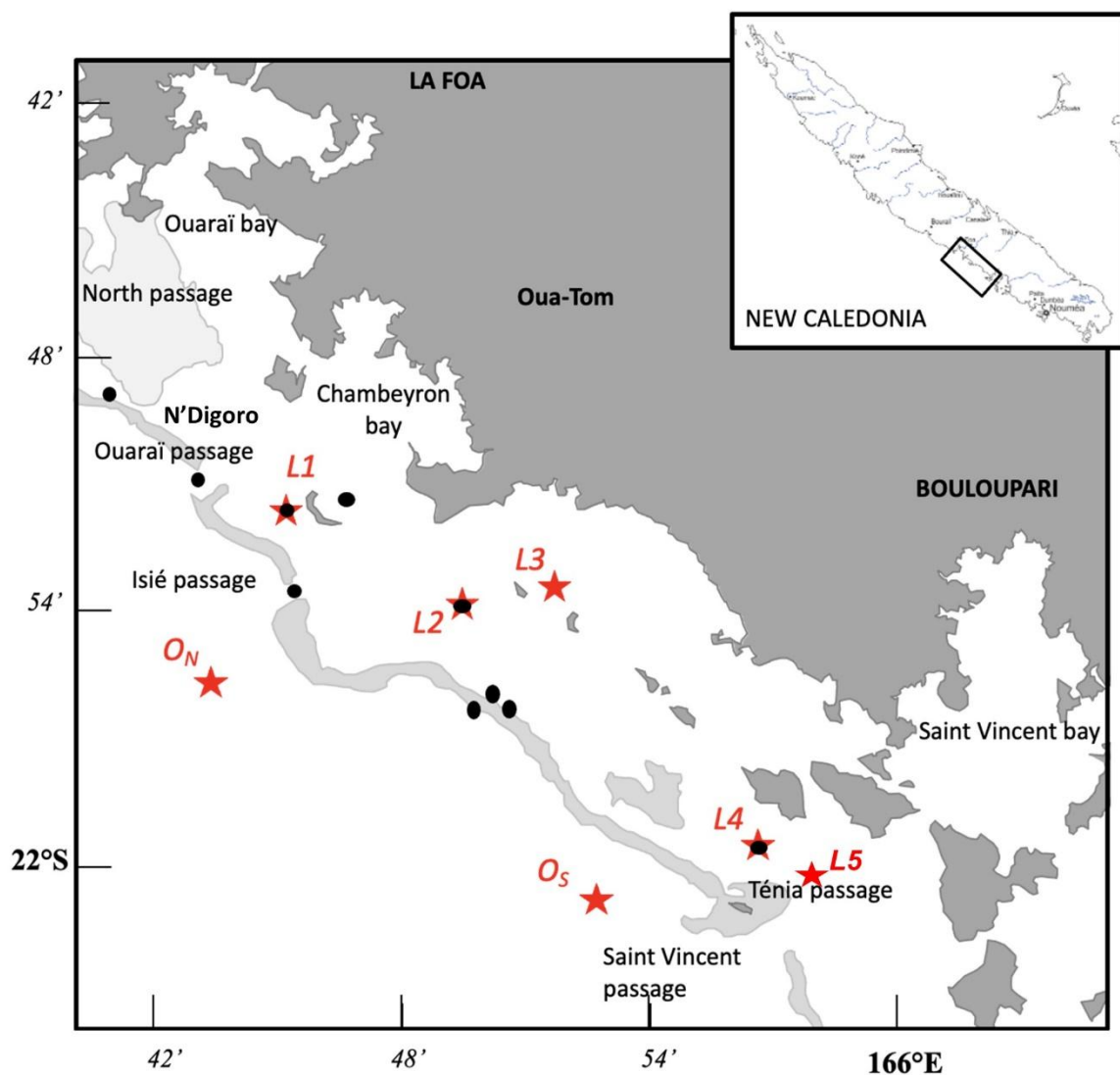
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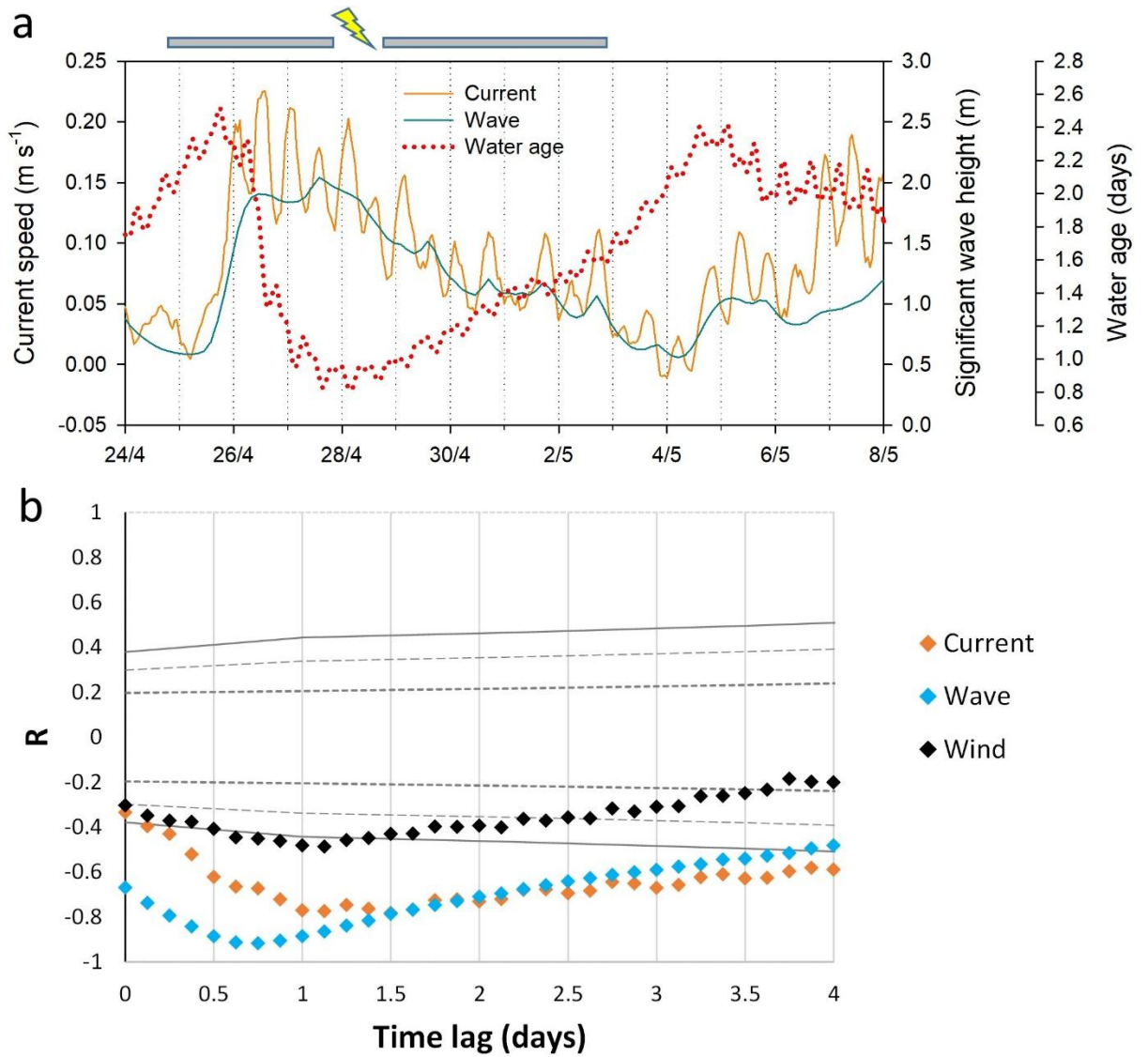
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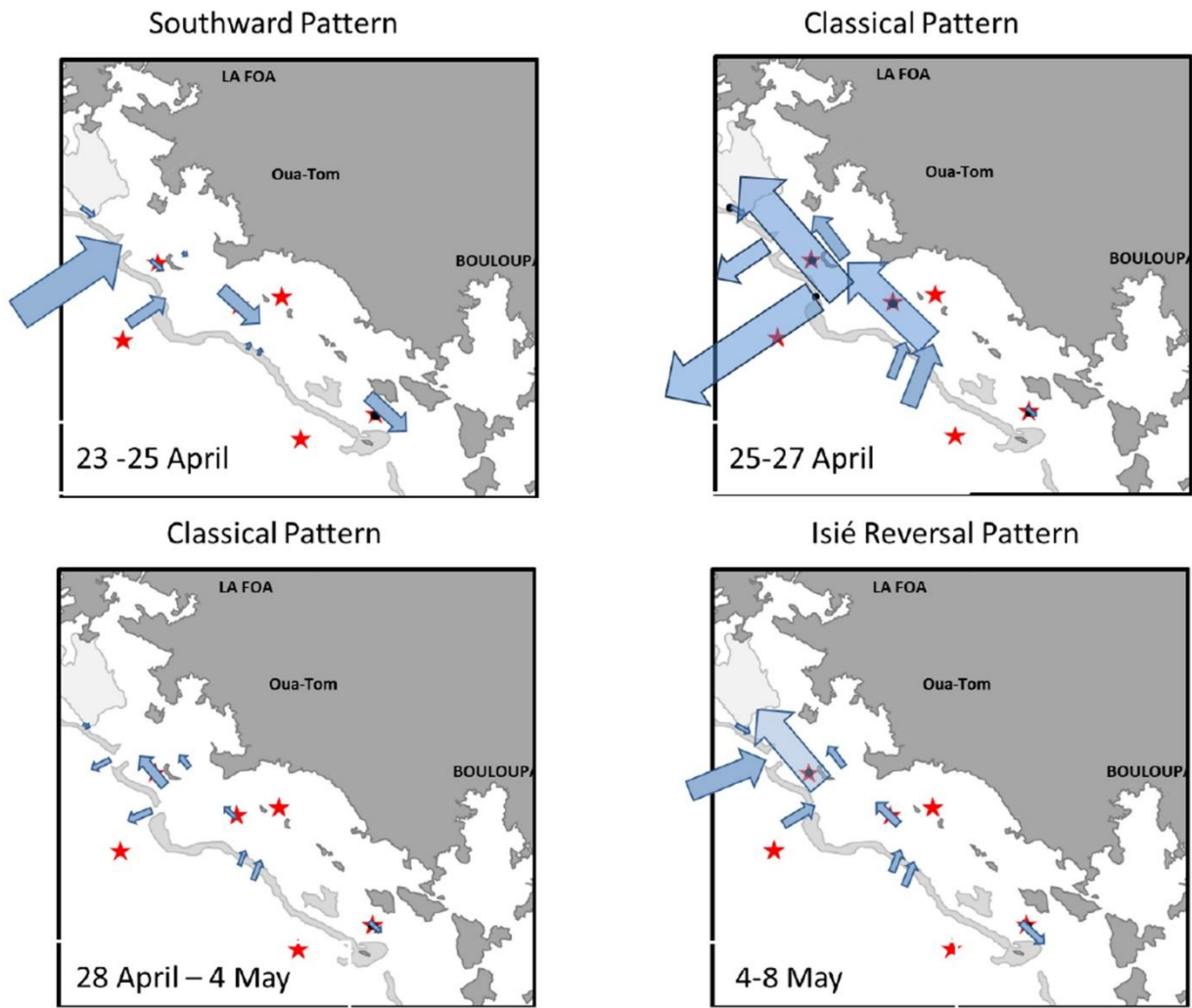
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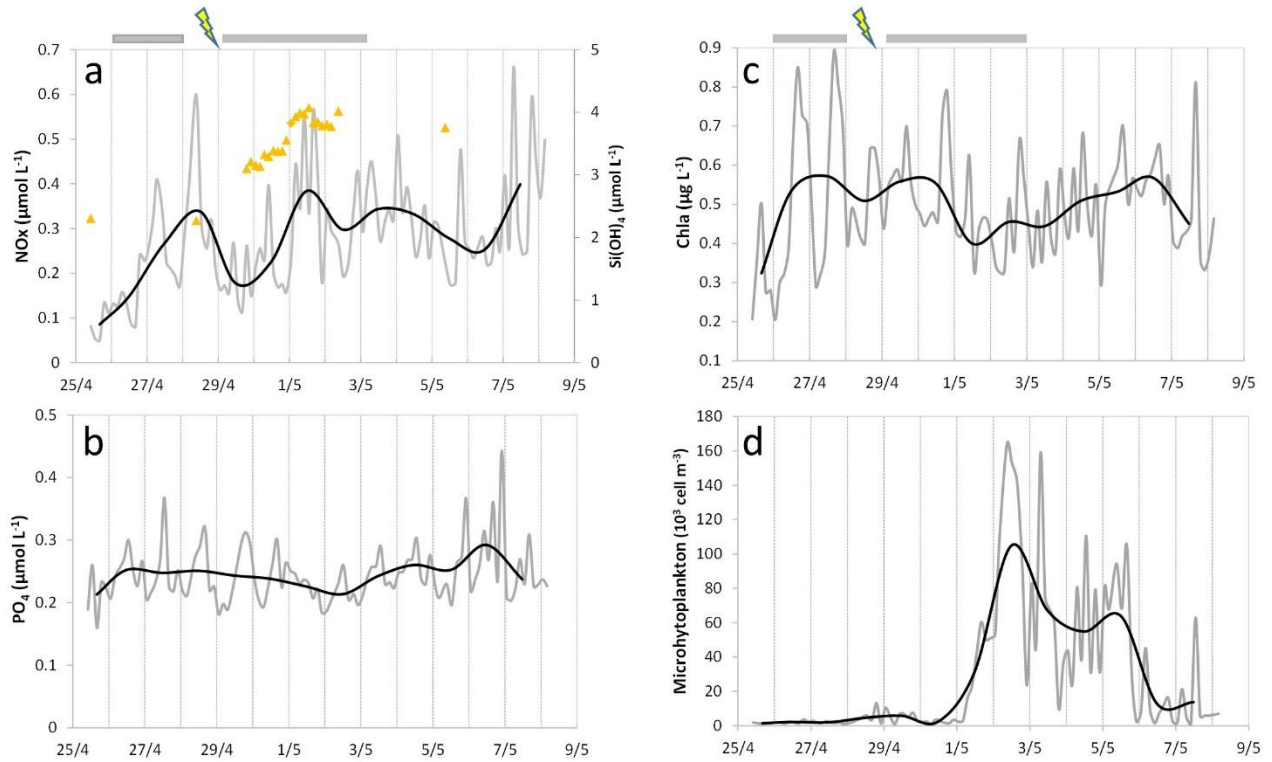
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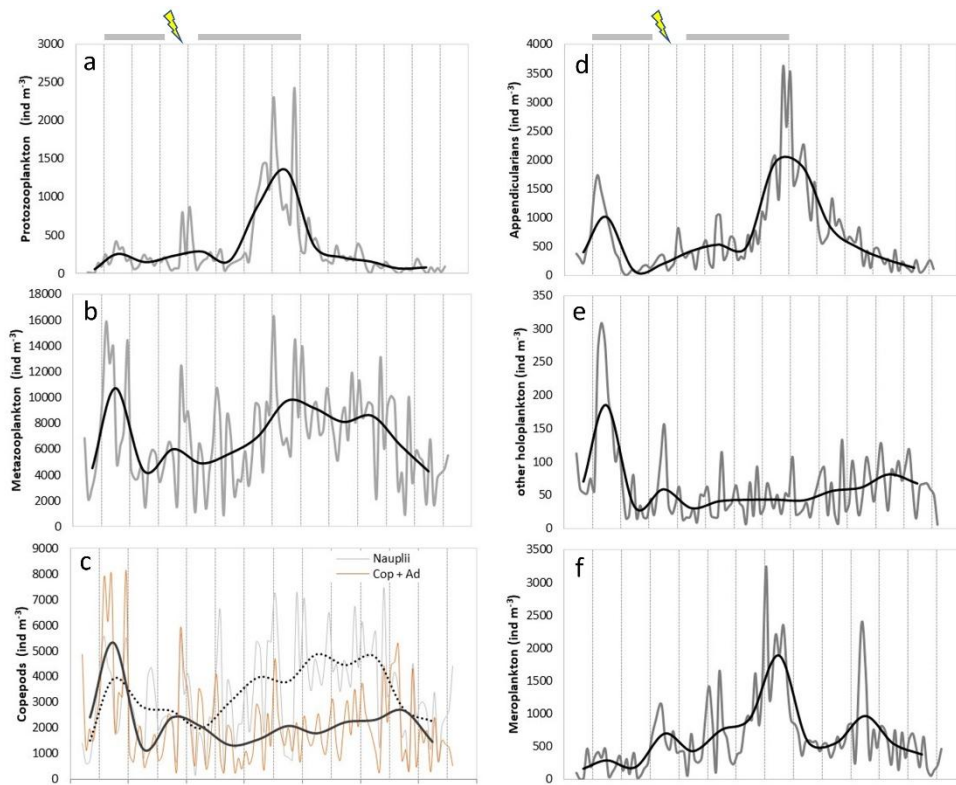
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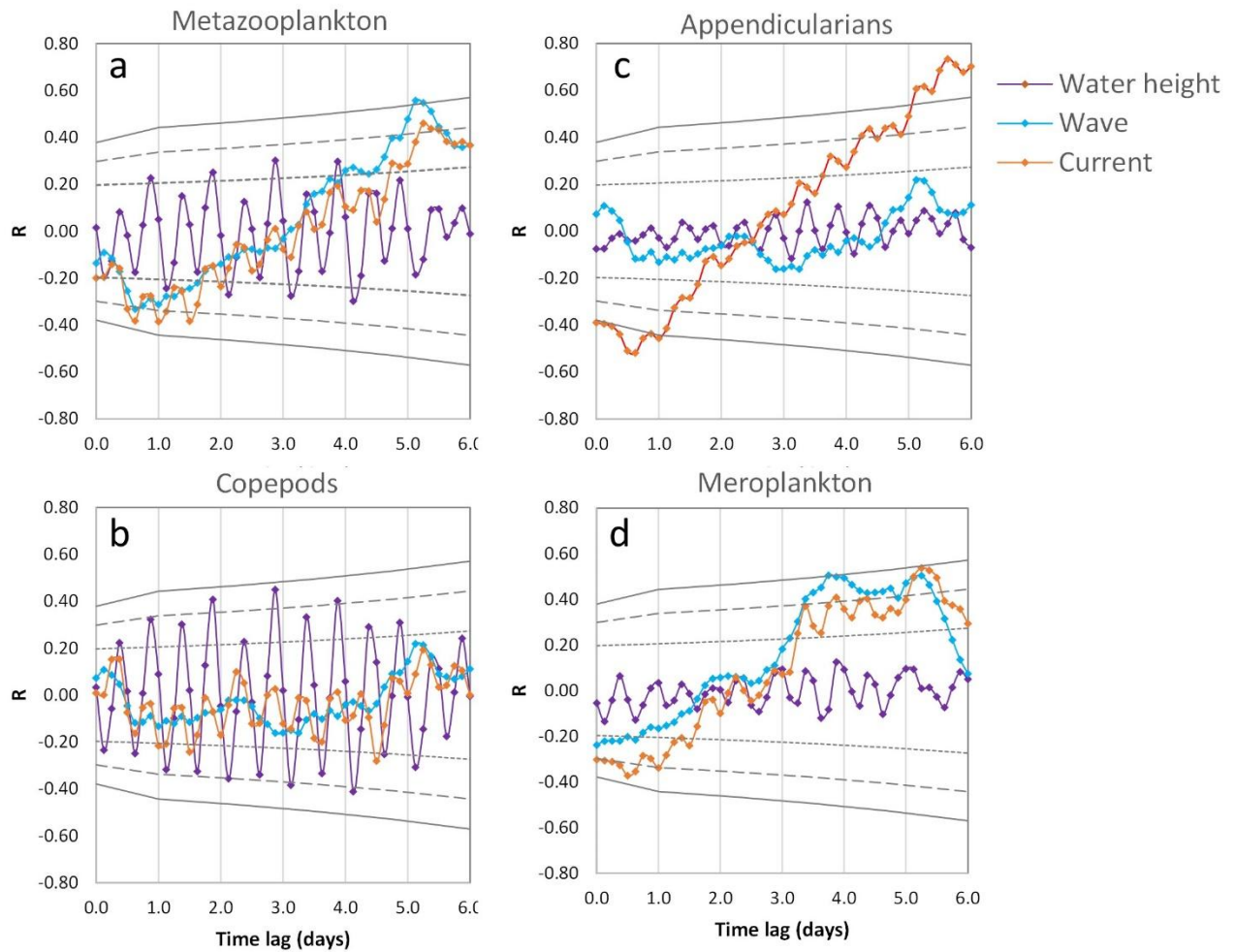
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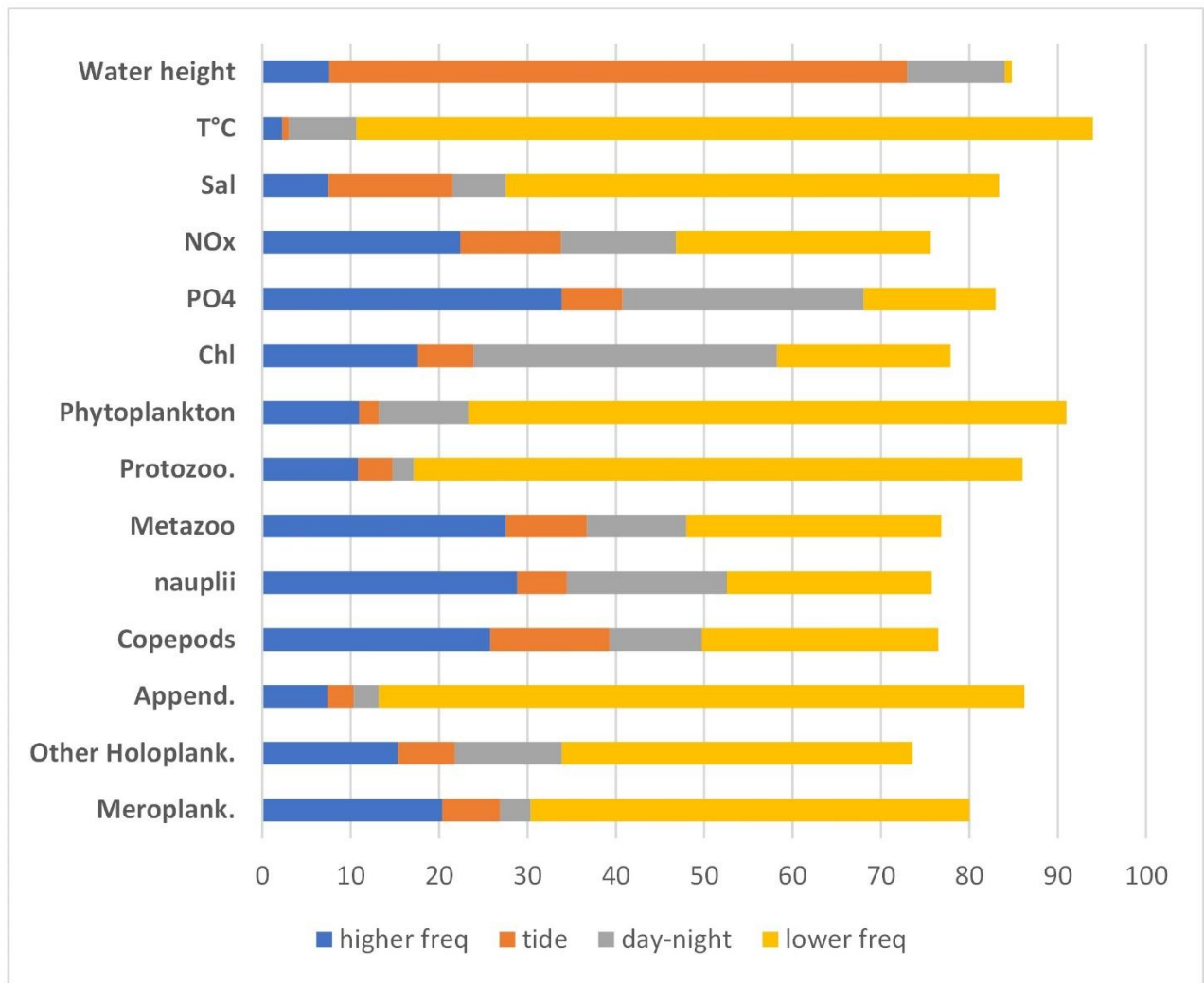
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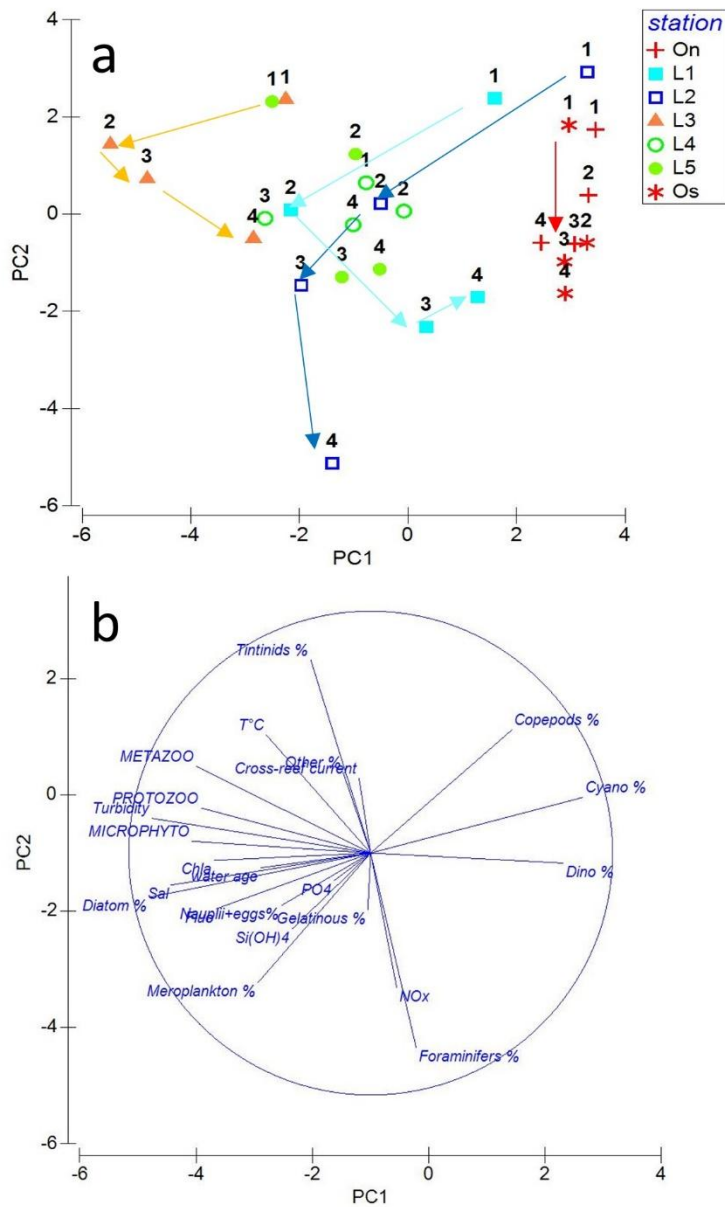
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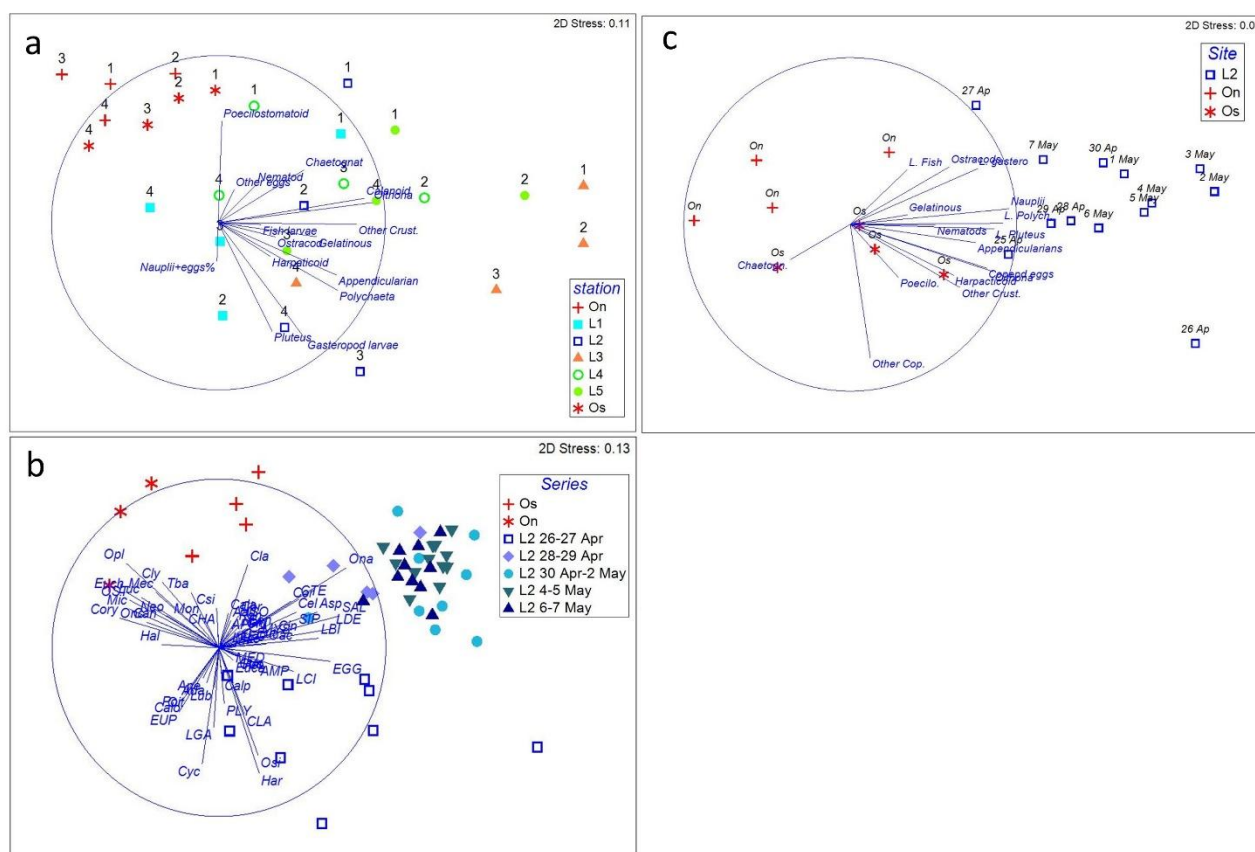
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