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Oumayma Chkili, Marouan Meddeb, Kaouther Mejri Kousri, Sondes Melliti Ben Garali, Nouha Makhoulf Belkhalia, et al.. Influence of Nutrient Gradient on Phytoplankton Size Structure, Primary Production and Carbon Transfer Pathway in a Highly Productive Area (SE Mediterranean). Ocean Science Journal, 2023, 58 (1), pp.6. 10.1007/s12601-023-00101-6 . hal-03937994

HAL Id: hal-03937994

<https://normandie-univ.hal.science/hal-03937994v1>

Submitted on 30 Mar 2023

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1 **Influence of nutrient gradient on phytoplankton size**
2 **structure, primary production and carbon transfer pathway**
3 **in a highly productive area (SE Mediterranean)**

4
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28 Received: 16 July 2022 / Revised: 30 November 2022 / Accepted: 5 December 2022

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30 (KIOST) and the Korean Society of Oceanography (KSO) and
31 Springer Nature B.V. 2023

32

33 **ABSTRACT**

34 We assessed the spatial variability in the size structure of phytoplankton, community
35 composition, primary production and carbon fluxes through the planktonic food web of the Gulf
36 of Gabès (GG; Southeastern Mediterranean Sea) in the fall of 2017 during the MERMEX-
37 MERITE cruise. High concentrations in nutrients, chlorophyll *a* ($\sim 2\text{--}6 \mu\text{g L}^{-1}$) and primary
38 production ($1816\text{--}3674 \text{ mg C m}^{-2} \text{ d}^{-1}$) revealed an eutrophic status of the studied stations in the
39 GG. In accordance with hydrodynamic features, inorganic nutrients showed increases in
40 concentrations from North to South and from coast to offshore, these nutrient gradients
41 impacting the spatial distribution of phytoplankton community. Size-fractionated phytoplankton
42 biomass and production were the lowest in the northernmost zone where they were mainly
43 sustained by pico-sized fraction. Concomitantly, in this area, small aloricate ciliates were
44 dominant leading to a high microbivory. Conversely, higher biomass and production were
45 measured towards the South and offshore with prevalence of larger phytoplankton (nano- and/or
46 micro-sized fractions) supported by diatoms. The herbivorous protozooplankton and
47 metazooplankton were more abundant in these zones, resulting in an increase of the herbivory.
48 The vertical particulate organic carbon flux followed also a north-south and coast-offshore
49 increasing gradient, with a higher contribution of phytoplankton, and zooplankton fecal pellets
50 to the sinking organic matter in the southernmost area. Our results suggest that even in nutrient-
51 rich and highly productive waters, a continuum of trophic pathways, ranging from microbial to
52 multivorous and herbivorous food webs, may exist, which implies different efficiencies in
53 carbon export and carrying capacity within the ecosystem.

54 **Keywords** Phytoplankton size-structure · Primary production · Zooplankton grazing · Planktonic
55 food web · Mediterranean Gulf

56

57 **1 Introduction**

58 The phytoplankton, through its biomass, diversity and productivity, has a key role in the
59 functioning of marine ecosystems. The size structure of phytoplankton is an important
60 planktonic trait that affects the magnitude of primary production, controls the size of grazers
61 and hence regulates the carbon transfer through the marine food web (Decembrini et al. 2009;
62 Ward et al. 2012; Sakka Hlaili et al. 2014; Negrete-García et al. 2022). Any shift in the size of
63 phytoplankton may largely influence the planktonic food web dynamics and the overall
64 efficiency of the marine system to export primary production (Legendre and Le Fèvre 1989;
65 Legendre and Rassoulzadegan 1996).

66 In general, large phytoplankton (mainly micro-sized cells) is consumed by herbivorous
67 zooplankton (mainly copepods), and primary production is efficiently transferred to higher
68 consumers through the herbivorous food web. At the opposite, small phytoplankton (mainly
69 pico-sized cells) and microbivorous protozooplankton (heterotrophic nanoflagellates and
70 aloricate ciliates) are involved in the microbial food web that channels less carbon to higher
71 consumers, as most of primary production is remineralized in the euphotic zone (Legendre and
72 Le Fèvre 1989; Meddeb et al. 2018). More complex carbon pathways may be present in marine
73 ecosystems. The multivorous food web, in which large and small phytoplankton, as well as
74 herbivorous and microbivorous zooplankton play all together significant roles, can be efficient
75 in carbon transfer (Legendre and Rassoulzadegan 1995). The bacterial-multivorous food web,
76 in which phytoplankton and bacterioplankton contribute together to carbon production, was
77 recently identified and reported to be less efficient in carbon transfer because of the recycling
78 of the latter (Meddeb et al. 2019). Legendre and Rassoulzadegan (1995) reported that the
79 dynamics of planktonic food web was related to that of nutrients and thus described a continuum
80 of trophic pathways between eutrophic and oligotrophic systems, going from herbivorous to
81 multivorous and microbial food webs.

82 The nutrient conditions are controlled by physical processes that ultimately influence the
83 size structure of phytoplankton and the primary production (Estrada et al. 1999; Cermeño et al.
84 2006; Ferland et al. 2011). Previous studies in the Mediterranean Sea have shown that trophic
85 status driven by hydrodynamic forcing can impact the structure of food webs and promote the
86 ecosystem's ability to export biogenic carbon. In highly stratified oligotrophic open waters,
87 where primary production is low, pico- and nano-sized cells dominate the phytoplankton
88 community (Decembrini et al. 2009). Most carbon is then channeled to higher consumers
89 through microbial food web, with a high recycling activity (Giannakourou et al. 2014; Livanou
90 et al. 2019). Changes in the food web structure can occur when vertical deep mixing or
91 upwelling supply nutrients to the euphotic zone that promote large-sized phytoplankton (i.e.,
92 diatoms) and substantially increase primary production (Allen et al. 2002). In that case, the food
93 web shifts to an herbivorous pathway that efficiently transfers carbon to upper trophic levels
94 (Stibor et al. 2019).

95 In the Mediterranean coastal systems, hydrodynamic features (mesoscale structures,
96 tides...) may influence the hydrological and biogeochemical parameters (salinity, temperature,
97 nutrients...) that finally impact the size structure and composition of phytoplankton (Caroppo
98 et al. 2006, 2018; Geyer et al. 2018; Trombetta et al. 2021). Decembrini et al. (2020) have
99 recently shown that the lateral advection of nutrient-rich water in the Gulf of Augusta (Eastern
100 Sicilian coast, Ionian Sea) triggered a change in the size structure of phytoplankton and primary
101 production with a significant ecological effect on the planktonic food web. Besides physical
102 forcing, continental nutrient inputs from anthropogenic activities can influence the
103 phytoplankton structure and alter the relationship between the latter and grazers, with possible
104 changes in trophic pathways (Smith et al. 2006; Decembrini et al. 2021). The coastal
105 Mediterranean environments are typically mesotrophic or eutrophic systems, with relatively
106 high nutrient concentrations and dominance of large-sized phytoplankton (MedECC 2020).
107 Yet, the herbivorous food web is not usually observed and other trophic pathways (such as

108 microbial or multivorous food webs) can occur at spatial and seasonal scales (Grami et al. 2008;
109 Meddeb et al. 2018; Decembrini et al. 2021; Trombetta et al. 2022), probably due to the
110 influence of the hydrological properties of the system. Therefore, the interactions between
111 hydrodynamics and nutrient inputs must be taken into account to describe the structure of
112 marine food web in eutrophic coastal ecosystems (Liu et al. 2018; Decembrini et al. 2021).

113 Although much interest has been given to primary production and its trophic transfer in
114 the Mediterranean Sea (Moran and Estrada 2001; Casotti et al. 2003; Psarra et al. 2005;
115 Decembrini et al. 2009; Kovač et al. 2018; Mayot et al. 2020), data acquired in its Southern
116 basin are scarce (Sakka Hlaili et al. 2008; Grami et al. 2008; Meddeb et al. 2018). Furthermore,
117 little effort has been dedicated to describe how nutrient inputs and physical features affect the
118 phytoplankton community structure and food web dynamics. In the Southeastern Mediterranean
119 Sea, the Gulf of Gabès (hereafter refers to as GG) is a highly dynamical coastal ecosystem,
120 characterized by a large continental shelf with relatively shallow well-mixed and rich-nutrient
121 waters (Bel Hassen et al. 2009; Zayen et al. 2020), which is in contrast to the oligotrophic status
122 of the Eastern Mediterranean basin. The nutrient enrichment results mainly from the
123 anthropogenic inputs (mostly by phosphoric acid industries) (Khedhri et al. 2014; El Kateb et
124 al. 2018) and the atmospheric deposition through Saharan dust (Khammeri et al. 2018) . The
125 GG is also characterized by a complex water circulation, which results from the combination
126 of the general thermohaline circulation (Bel Hassen et al. 2009), the anticyclonic winds and the
127 strong tides (Sammari et al., 2006, Hattour et al. 2010; Othmani et al. 2017) (see details below).
128 This circulation induces North-South and coast-offshore transports, which induce a gradient of
129 particles and dissolved elements (such as nutrients) with accumulation in the Southern part of
130 the GG (Ciglencečki et al. 2020; Mansouri et al. 2020). Previous studies have actually shown
131 that phytoplankton dynamics within the GG was related to the nutrient conditions and water
132 physical properties (Bel Hassen et al. 2008, 2009; Drira et al. 2009, 2014). Spatial distributions
133 were also documented for protozooplankton and copepod communities and were shown to be

134 linked to the combination of hydrodynamic conditions and anthropogenic loads (Hannachi et
135 al. 2008; Drira et al. 2009, 2017; Makhlouf Belkahia et al. 2021). Although nutrient inputs and
136 water circulation are recognized as major drivers in influencing the dynamics of phytoplankton
137 and zooplankton in the GG (Béjaoui et al. 2019), the link between these communities and their
138 functional roles are not well known.

139 The aim of this study is to analyze the size structure of phytoplankton and the size-
140 fractionated primary production, as well as trophic interactions between planktonic components
141 in order to define the main characteristics of carbon transfer pathway. In particular, our work
142 aims to demonstrate how food web structure changes along a nutrients spatial gradient in a
143 highly dynamical environment like the GG. The study will also allow verifying whether the
144 “continuum of trophic pathways” reported by Legendre and Rassoulzadegan (1995) could be
145 found in highly productive waters characterized by a gradient of eutrophic conditions.

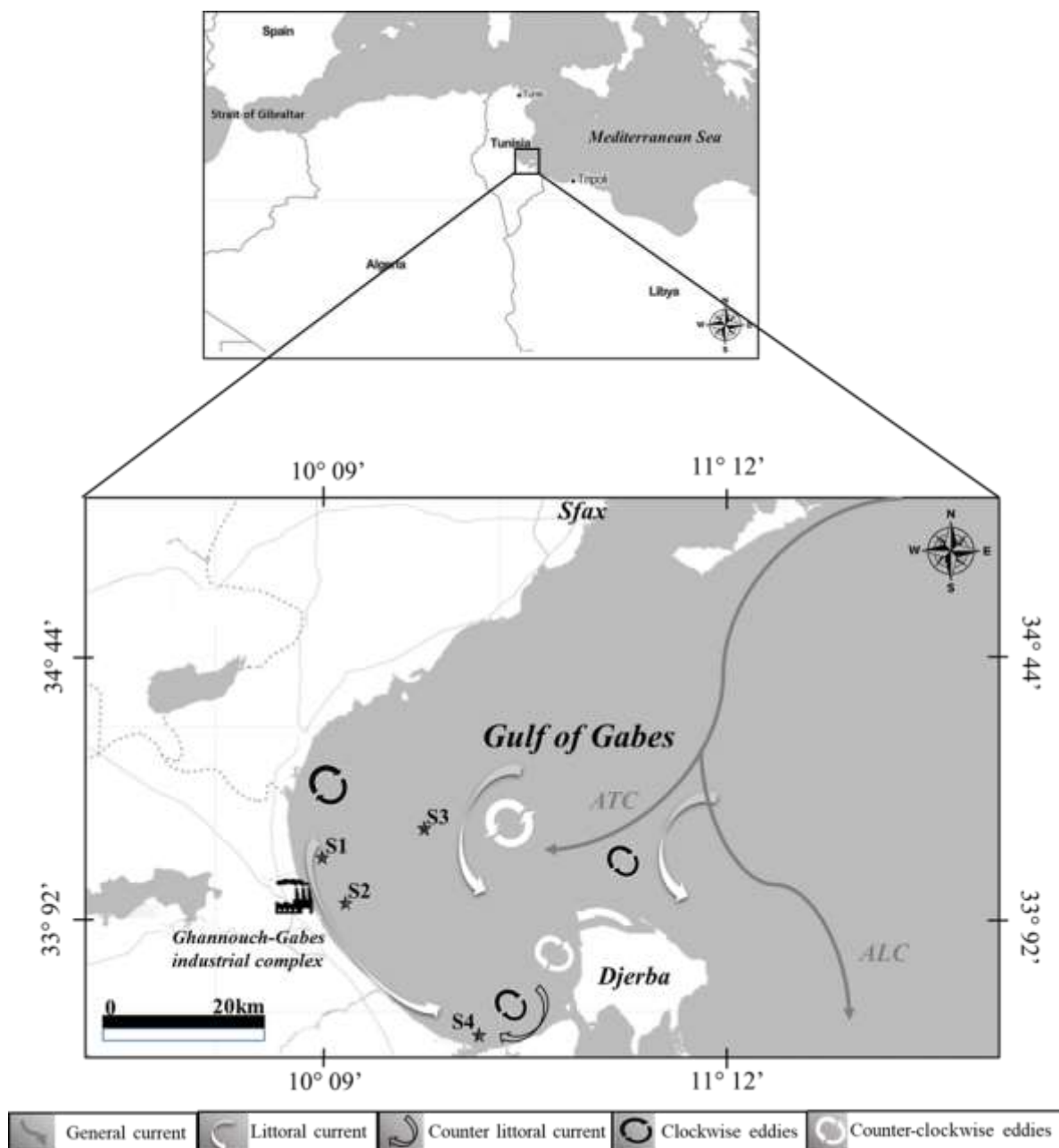
146 **2 Materials and Methods**

147 **2.1 Hydrodynamic features of the study area**

148 The GG is a relatively shallow ecosystem which is strongly influenced by hydrodynamic
149 forcing, mainly driven by the general Mediterranean circulation, the anticyclonic winds and the
150 high tide effects (Hattour et al. 2010; Othmani et al. 2017). The Atlantic Tunisian Current
151 (ATC) is a surface current originating from the Atlantic Ocean. It crosses the Sicilian-Tunisian
152 Channel, flows along the Tunisian continental shelf southward, and splits into two branches
153 (Fig. 1). One coastal branch of the ATC enters the GG and creates an anticyclonic circulation
154 in its Southern part (Ben Ismail et al. 2012; Boukthir et al. 2019). The other branch flows on
155 southeastward along the Libyan shelf, giving rise to the Atlantic Libyan Current (ALC) (Ben
156 Ismail et al. 2015). Furthermore, the hydrodynamics of the GG is deeply influenced by
157 barometric tides (Sammari et al. 2006), which have the highest range of the Mediterranean Sea
158 with a maximal amplitude (~ 2 m) in the Southern region (Abdennadher and Boukthir 2006;

159 Othmani et al. 2017). Concomitantly with our work, Zayen et al. (2020) investigated the
160 hydrodynamic circulation in the GG, and reported an average littoral current flowing North to
161 South and two eddies in the middle of the GG that induce a counter current on the littoral in its
162 Southern part (Fig. 1).

163



164

165 **Fig. 1** Gulf of Gabès: localization of the sampling stations and hydrodynamic circulation
166 (Atlantic Tunisian Current: ATC and Atlantic Lybian Current: ALC). Modified from Zayen et
167 al. (2020)

168

169 **2.2 Choice of study stations and sampling**

170 The study was carried out within the framework of the MERMEX-MERITE project
171 (*Marine Ecosystems Responses In The Mediterranean Experiment*) campaign from 31 Oct. to
172 3 Nov. 2017. We investigated the overall function of plankton communities based on sampling
173 and field experiments carried out simultaneously, which was not easy to achieve in several
174 stations. Therefore, to meet our objective, we chose to explore several key processes in plankton
175 communities in four relevant stations within the GG (S1, S2, S3 and S4; Fig. 1). The choice of
176 the stations was based on a preliminary work emphasizing a heterogeneous distribution of
177 nutrients in the study region, with increased concentrations from North to South and from the
178 coast to offshore (Fig. S1 in Supplementary Material).

179 Station S2 was located in front of the phosphoric acid plant of the Ghannouch-Gabès
180 industrial complex and was chosen as to represent coastal waters impacted by phosphogypsum
181 loading; Stations S1 and S4 were located on either side of station S2 (North and South,
182 respectively), while S3 was an offshore station in front of S1 (Fig. 1). The characteristics of the
183 stations and sampling are reported in Table 1.

184 In each station, seawater was collected using 2.5 L plastic water sampler (Hydro-Bios),
185 and water temperature, salinity, pH and dissolved oxygen (O₂) were measured *in situ* with a
186 multi-probe sensor (Multi 1970i, WTW) at three depths (between 0.5 and 14 m) depending on
187 the maximal water depth of the stations (Table 1). The collected water was filtered through a
188 200 µm mesh screen to remove large zooplankton, and three subsamples from each depth were
189 taken for nutrients, chlorophyll *a* (Chl *a*), phytoplankton and protozooplankton analyses. At
190 each station, metazooplankton (> 200 µm organisms) was collected with a 28 cm diameter
191 WP2 200 µm net by vertical hauls from the bottom to the surface. A flow meter was used to
192 determine the water volume filtered during the net tow.

193
194

195 **Table 1** Main characteristics, environmental parameters and phytoplankton biomasses of the
 196 sampling stations within the Gulf of Gabès during the fall 2017. Physico-chemical variables and
 197 Chl *a* concentrations are depth-averaged values; carbon biomasses are depth-integrated values
 198 (Mean value \pm SD, N = 9). p-value (ns: not significant; *: 0.01 < p < 0.05; ** 0.001 < p < 0.01, ***:
 199 p < 0.001) indicates the significant level for the ANOVA used to test spatial variation

		S1	S2	S3	S4	p-value
Coordinates	Latitude (N)	34° 01.767'	33° 56.545'	34° 01.491'	33° 52.346'	
	Longitude (E)	10° 06.295'	10° 08.939'	10° 19.940'	10° 11.803'	
Sampling date		30/10	01/11	01/11	03/11	
Tide condition / height (m)		High / 1.6	High / 1.9	Low / 0.7	Low / 0.8	
Maximum water depth (m)		13.5	12.1	18.8	13.6	
Sampled depths (m)		0.5; 2.5; 5	2.5; 4; 7	2; 8; 14	2; 6; 10	
Water temperature (°C)		22.55 \pm 0.64	22.90 \pm 0.37	22.89 \pm 0.21	24.18 \pm 0.52	ns
Salinity		39.43 \pm 0.85	39.56 \pm 0.37	39.48 \pm 0.25	39.42 \pm 0.54	ns
pH		8.31 \pm 0.005	8.24 \pm 0.028	8.27 \pm 0.01	8.25 \pm 0.017	ns
Dissolved O ₂ (mg L ⁻¹)		8.20 \pm 0.05	8.25 \pm 0.02	8.23 \pm 0.04	8.15 \pm 0.11	ns
N _{inorg} (μM)		4.27 \pm 0.36	7.63 \pm 0.43	5.12 \pm 0.31	8.93 \pm 2.11	*
N _{org} (μM)		12.29 \pm 2.42	9.20 \pm 0.27	6.50 \pm 0.11	5.03 \pm 0.49	**
P _{inorg} (μM)		0.91 \pm 0.27	1.77 \pm 0.44	1.52 \pm 0.08	2.20 \pm 0.05	*
P _{org} (μM)		8.23 \pm 1.93	16.95 \pm 2.42	11.45 \pm 0.18	18.32 \pm 0.02	***
Si(OH) ₄ (μM)		4.90 \pm 0.22	5.34 \pm 0.40	6.40 \pm 0.30	8.98 \pm 0.76	***
Chl <i>a</i> (μg L ⁻¹)		1.65 \pm 0.06	3.68 \pm 1.63	5.90 \pm 1.12	6.06 \pm 0.24	**
% of total Chl <i>a</i>						
<i>Microphyt.</i>		35 \pm 3	30 \pm 2	49 \pm 5	74 \pm 5	***
<i>Nanophyt.</i>		28 \pm 5	43 \pm 6	30 \pm 4	15 \pm 5	*
<i>Picophyt.</i>		37 \pm 6	27 \pm 5	21 \pm 4	11 \pm 1	ns
Carbon biomass (mg C m ⁻²)		780.22 \pm 65.60	854.50 \pm 90.19	1300.3 \pm 44.28	1624.57 \pm 134.80	**
<i>Microphyt.</i>		418 \pm 51 (54%)	608 \pm 91 (71%)	951 \pm 30 (74%)	1207 \pm 30 (75%)	***
<i>Nanophyt.</i>		265 \pm 14 (9%)	72 \pm 0.4 (8%)	86 \pm 13 (7%)	265 \pm 13 (16%)	***
<i>Picophyt.</i>		152 \pm 0.1 (38%)	175 \pm 0.1 (21%)	263 \pm 0.1 (20%)	152 \pm 0.1 (9%)	**

200

201 2.3 Nutrient, Chl *a* and plankton analyses

202 Inorganic nitrogen (N_{inorg}: NO₂⁻ + NO₃⁻ + NH₄⁺), inorganic phosphorus (P_{inorg}: PO₄³⁻) and
 203 silicates (Si(OH)₄), as well as total nitrogen (N_{total}) and phosphorus (P_{total}) were analyzed with
 204 a BRAN and LUEBBE type 3 autoanalyzer (Bran + Luebbe Co, Germany). The precision for
 205 all nutrient analyses was \leq 1%. Organic nutrients (N_{org} and P_{org}) were estimated as the difference
 206 between total and inorganic elements.

207 For Chl *a* analysis, water samples (1 L) were successively filtered through 10, 2 and
208 0.2 μm polycarbonate membranes to determine size-fractionated Chl *a* (> 10 , 2-10 and ≤ 2 μm).
209 Filtrations were performed under low vacuum pressure (< 100 mm Hg) and low light intensity.
210 Chl *a* concentrations were estimated using the spectrophotometric method after 24 h extraction
211 in 90% acetone at 4 °C in the dark (Parsons et al. 1984). Total Chl *a* concentration was estimated
212 as the sum of the three size-fractionated Chl *a* concentrations.

213 To enumerate picophytoplankton (≤ 2 μm cells), 2 mL samples were immediately fixed
214 after sampling with 20% paraformaldehyde solution, then placed at 4 °C in the dark for 15 min,
215 and finally frozen at -80 °C in liquid nitrogen until analysis with a CyFlow[®] Space flow
216 cytometer (Partec). Prior to analysis, the samples were filtered on 30 μm pore size filters and
217 enriched with fluorescent beads of 1 and 2 μm in diameter (Polysciences, Inc) as internal cell
218 size standards. Trucount[™] beads were also added to accurately estimate the volume of each
219 sample (BD-Biosciences). Picoprokaryotes and picoeukaryotes were identified and counted on
220 the basis of their relative forward scatter (FSC) and phycoerythrin orange fluorescence (at 488
221 nm) and Chl *a* red fluorescence (at 638 nm), respectively. Cell volumes were determined using
222 equivalent diameters estimated from flow cytometry. The biovolumes (picoprokaryotes:
223 1.77 μm^3 ; picoeukaryotes: 4.19 μm^3) were converted into carbon content using the following
224 conversions: 0.357 pg C μm^{-3} for picoprokaryotes, and 0.433 x (μm^3)^{0.863} for picoeukaryotes
225 (Verity et al. 1992). The cell carbon contents were multiplied by the abundances to estimate the
226 carbon biomass of picophytoplankton (mg C m^{-3}). Depth-integrated biomass (mg C m^{-2}) was
227 obtained from the carbon biomasses estimated for the three depths.

228 Phytoplankton samples (nano-: 2-10 μm ; micro-phytoplankton: > 10 μm) were preserved
229 in 3% acidic Lugol's solution and stored at room temperature in the dark (Parsons et al. 1984).
230 The identification and counting of cells (at least 500 *per* sample) were determined using the
231 Motic AE31E inverted microscope on 100 mL settled volume (Utermöhl 1931; Lund et al.
232 1958). Cell dimensions of phytoplankton taxa were measured using a calibrated ocular

233 micrometer and biovolumes were determined by applying standard geometric formulae to each
234 taxon (Hillebrand et al. 1999). Then, the biovolumes were converted into carbon content using
235 specific conversion factors or formulae (Putt and Stoecker 1989; Menden-Deuer and Lessard
236 2000) for diatoms, autotrophic flagellates and ciliates, as detailed in Meddeb et al. (2018). The
237 carbon biomass of phytoplankton (mg C m^{-3}) was then determined by multiplying the carbon
238 content of different taxa by their specific abundances. Carbon biomasses from the three sampled
239 depths were used to calculate the depth-integrated biomass (mg C m^{-2}).

240 Protozooplankton samples (100 mL) were fixed with 4% basic Lugol's solution (Sherr
241 and Sherr 1993), and organisms were identified and counted (at least 200 cells *per* sample)
242 according to the inverted microscopy technique of Utermöhl (1931). Protozooplankton was
243 composed of heterotrophic nanoflagellates and ciliates including loricate and aloricate species,
244 but also of dinoflagellates (most of which are phagotrophic). Within dinoflagellates,
245 mixotrophic and heterotrophic organisms were distinguished according to several works (Sakka
246 Hlaili et al. 2007; Jeong et al. 2010; Boutrup et al. 2016). The ebridian flagellate *Hermesinium*
247 *sp.* was also considered as a micrograzer since its mixotrophy had been confirmed (Hargraves
248 2002; Jafari et al. 2015).

249 Samples of metazooplankton (250 mL) were fixed with a 5% borate-buffered formalin
250 solution. Metazoan organisms were counted and identified in the whole sample using a Leica
251 M 205C stereo microscope.

252 **2.4 *In situ* dilution experiment**

253 The dilution method (Landry and Hassett 1982) was used to estimate the growth rate of
254 phytoplankton and its grazing rate by protozooplankton at each station and at the same sampling
255 date. Water samples were collected over the water column (5 m for S1, 7 m for S2, 14 m for S3
256 and 10 m for S4) with a submersible pump and then filtered through 200 μm mesh screen (to
257 remove meso- and macroplankton). This screened seawater was diluted with free-particle
258 seawater to achieve four dilutions (25, 50, 75 and 100% of 200 μm screened seawater). The

259 diluting seawater was obtained by gravity filtration using a 0.22 μm sterile filter capsule
260 (polycap 75 AS). Triplicate 2 L polycarbonate bottles (Nalgene[®]) were used for each dilution,
261 and all bottles were incubated *in situ* for one day ($t = 1$ d). The GG is a nutrient-rich environment
262 where nutrients are considered as available throughout the year (Bel Hassen et al. 2008; Béjaoui
263 et al. 2019). Therefore, nutrients were not added to our dilution bottles to avoid the
264 overestimation of growth rates. Furthermore, several authors have found that growth rates in
265 nutrient-enriched bottles were not significantly different from those estimated without nutrients
266 during dilution experiments conducted in nutrient-rich systems (Olson and Strom 2002; Sakka
267 Hlaili et al. 2007; Pecqueur et al. 2022). Subsamples were taken from each dilution bottle at the
268 beginning and the end of incubation to determine initial and final phytoplankton carbon
269 biomasses (C_0 and C_t ; respectively). As protozoans have a prey size-selective feeding activity
270 (Sakka Hlaili et al. 2007; Zhang et al. 2017), size-fractionated biomass of phytoplankton was
271 determined (i.e., pico-: ≤ 2 μm , nano-: 2-10 μm , and microphytoplankton: > 10 μm). The
272 apparent growth rate of each size fraction prey (R) was calculated from the changes in carbon
273 biomass during the incubation period as:

$$274 \quad R(d^{-1}) = \ln\left(\frac{C_t}{C_0}\right) \times t^{-1}$$

275 The coefficients R were plotted against the dilution factor, and a model I linear regression
276 was used to estimate growth rates k (d^{-1}) (i.e., the y-intercept that represented growth in 100%
277 dilution in the absence of grazers) and the grazing coefficient g (d^{-1}) (i.e., the slope of the
278 regression line) (Landry and Hassett 1982). For each size fraction in all stations, the regression
279 lines were tested as significant by Student's t-test ($p < 0.05$) and were represented in the
280 Supplementary Material (Fig. S2).

281 For each phytoplankton size fraction, production rates (P_1) and consumption rates by
282 protozooplankton (G_{p1}) were calculated according to several authors (Grattepanche et al. 2011;
283 Meddeb et al. 2018) as:

284
$$P_1 (mg C m^{-3} d^{-1}) = k \times C_0 [e^{(k-g)t} - 1] / (k - g \times t)$$

285 and

286
$$G_{p1} (mg C m^{-3} d^{-1}) = g \times C_0 [e^{(k-g)t} - 1] / (k - g \times t)$$

287 The P_1 and G_{p1} data were multiplied by the sampling depth to get depth-integrated rates of
288 production (P , $mg C m^2 d^{-1}$) and consumption (G_p , $mg C m^2 d^{-1}$), respectively. Depth-integrated
289 production rates for the three size fractions were added to obtain production rate for total
290 phytoplankton. The percentage of production consumed *per* day was estimated as:

291
$$\%Pgrazed d^{-1} = \left(\frac{G_p}{P} \right) \times 100$$

292 2.5 Metazooplankton gut fluorescence analysis

293 The grazing of metazooplankton on phytoplankton was estimated using the gut
294 fluorescence method (Slaughter et al., 2006). Zooplankton was collected as indicated above. To
295 account for vertical migration of zooplankton likely to affect its feeding activity, sampling was
296 carried out around sunset, when zooplankton perform a vertical ascension. Three 500 mL
297 subsamples of the cod content were immediately narcotized with 10% carbonated water (final
298 concentration, v/v) to minimize stress and gut evacuation by zooplankton (Kleppel and Pieper
299 1984) and were kept frozen in the dark to minimize fecal pellet production by the organisms
300 (Saiz et al. 1992). The zooplankton subsamples were thawed and washed with filtered seawater
301 to remove adhering algae and debris, and filtered onto 47 mm diameter GF/F membranes that
302 were extracted in 10 mL of 90% acetone solution maintained at 4 °C in the dark. After overnight
303 extraction, each solution was centrifuged, and the supernatant absorbance was measured using
304 a Jenway spectrophotometer before and after acidification with 10% hydrochloric acid solution
305 (Parsons et al. 1984).

306 The gut pigment content (GP) was calculated according to Slaughter et al. (2006) as:

307
$$GP(mg pigment m^{-3}) = (GP_{sub} \times v) / (F \times V_{net}),$$

308 where GP_{sub} (mg pigment m^{-3}) is the phaeopigment concentration in the subsample, v (m^3) is
309 the volume of the subsample, F is the fraction of subsample processed for gut pigment content,
310 and V_{net} (m^3) is the total volume of seawater filtered during the net tow.

311 Consumption of $> 2\text{-}\mu\text{m}$ phytoplankton by metazooplankton was calculated as:

$$312 \quad G_m (\text{mg C m}^{-2} \text{ d}^{-1}) = [GP \times CR \times C:\text{Chl}a] \times D,$$

313 where D is the depth of the net tow (m), $C:\text{Chl } a$ is the depth-averaged $C:\text{Chl } a$ ratio determined
314 for $> 2 \mu\text{m}$ phytoplankton at each station, and CR is the gut clearance rate of metazooplankton
315 (d^{-1}). The CR was obtained from the gut clearance rate constant (GCRC) vs. temperature (T)
316 relationship ($\text{GCRC} = 0.0117 + 0.001794T$) (Dam and Peterson 1988; Irigoien 1998; Mauchline
317 1998).

318 The impact of metazooplankton grazing on the standing stock and production of
319 phytoplankton were calculated as:

$$320 \quad \% \text{Chl}a \text{ grazed } \text{d}^{-1} = (GP \times CR \times 100) / SC$$

$$321 \quad \%P \text{ grazed } \text{d}^{-1} = \left(G_m / P \right) \times 100,$$

322 where SC is the depth-averaged concentration of $\text{Chl } a$ and P is the production rate of nano-
323 and micro-phytoplankton, estimated by the dilution method.

324 2.6 Vertical carbon fluxes

325 Sediment traps were used to estimate the vertical flux of particles, including
326 phytoplankton, metazooplankton fecal pellets, and detritus. This technique was performed by
327 several authors (Laurenceau-Cornec et al. 2015; Xiang et al. 2022; Kojima et al. 2022) because
328 it is very useful for estimating the particle sinking and gives details in the composition of the
329 sinking fluxes. At each station, two sediment traps (63 cm high, 9 cm internal diameter) were
330 incubated vertically two meters from the bottom. Prior to deployment, the traps were filled with
331 dense seawater ($0.2 \mu\text{m}$ filtered seawater + $\text{NaCl } 5 \text{ g L}^{-1}$) to create a density gradient and avoid
332 collecting surface particles. After 24 h incubation, the traps were closed *in situ*, returned to the
333 laboratory and stored at $5 \text{ }^\circ\text{C}$ overnight to let particles settle. The supernatant was removed from

334 each trap and the bottom contents of the two traps were mixed. Subsamples were taken from
335 the trapped material for further analyses of particulate organic carbon (POC), phytoplankton
336 and fecal pellets.

337 For POC, ~ 500 mL seawater samples were filtered onto precombusted glass fiber filters
338 (450 °C, 24 h) (Whatman GF/F, 25 mm). The filters were oven dried at 50 °C for 24 h and
339 stored in clean glass vials in a desiccator. POC was determined by the high combustion method
340 and mass spectrometry according to Raimbault et al. (2008).

341 Phytoplankton (> 2 µm cells) was enumerated on 500 mL subsamples fixed with acidic
342 Lugol's solution (final concentration 4%), and cell abundances were converted into carbon
343 biomasses as described above.

344 Subsamples (200 mL) were preserved in buffered formaldehyde (final concentration 7%)
345 for counting fecal pellets using an inverted microscope (× 100 magnification). Differently
346 shaped pellets were distinguished (cylindrical, conical; ovoid and round), and their dimensions
347 were measured using a calibrated ocular micrometer.

348 The vertical fluxes of phytoplankton (F_{phyt}) and detritus (F_{det}) were estimated following
349 Grami et al. (2008):

$$350 \quad F_{\text{phyt}}(\text{mg C m}^{-2} \text{d}^{-1}) = 1/2 (C_{\text{phyt}} \times V_{\text{tr}}) / S_{\text{tr}} \times t$$

$$351 \quad F_{\text{det}}(\text{mg C m}^{-2} \text{d}^{-1}) = 1/2 (C_{\text{det}} \times V_{\text{tr}}) / S_{\text{tr}} \times t,$$

352 where C_{phyt} is the carbon biomass of nano- and microphytoplankton (mg C m^{-3}) and C_{det} is the
353 detrital carbon estimate, calculated as the POC concentration minus the carbon biomass of all
354 particles. V_{tr} is the volume of trapped material (m^3), S_{tr} is the trap area (m^2) and t is the duration
355 of incubation (d). The vertical flux of phytoplankton was considered to be the phytoplankton
356 export from the planktonic system towards the benthos, while the vertical flux of detritus was
357 assigned to the sinking flux.

358 The volume of each pellet shape category (V_{pel} , $\text{mm}^3 \text{m}^{-3}$) was estimated from its
359 dimension and abundance. Then, its vertical volume flow (S_{pel}) and vertical carbon flux (F_{pel})
360 were estimated following Grami et al. (2008):

$$361 \quad S_{pel}(\text{mm}^3 \text{m}^{-2} \text{d}^{-1}) = 1/2 (V_{pel} \times V_{tr}) / S_{tr} \times t$$

$$362 \quad F_{pel}(\text{mg C m}^{-2} \text{d}^{-1}) = S_{pel} \times f,$$

363 where f is a conversion factor ($0.057 \text{ mg C mm}^{-3}$ for cylindrical/conical pellets and 0.042 mg C
364 mm^{-3} for ovoid/rounded pellets).

365 2.7 Statistical analyses

366 An analysis of variance (ANOVA) was used to test the significance of the spatial variation
367 of physico-chemical factors, Chl a , plankton concentrations and vertical fluxes. ANOVA was
368 also used to compare (i) environmental factors and plankton concentrations among depths, and
369 (ii) the estimates of rates (k , g , P , G_p , G_m) between phytoplankton size fractions (> 10 , $2-10$ and
370 $< 2 \mu\text{m}$) or stations. The assumptions of normality of data distribution (Kolmogorov-Smirnov
371 test) and homogeneity of variance (Bartlett-Box test) were met. Spearman correlations (r_s) were
372 used to test the relationships between different variables: phytoplankton (Chl a , carbon biomass,
373 growth rate, production rate) and nutrients; growth (k) and grazing (g) rates; coefficients g and
374 G_p and protozooplankton abundances; production (P) and consumption rate by
375 protozooplankton (G_p); consumption rate by metazooplankton (G_m) and phytoplankton biomass
376 and metazoans abundances. ANOVA and correlation analyses were performed in SPSS
377 software 18.0 for Windows.

378 Canonical correspondence analysis (CCA; Ter Braak 1986) was performed to relate the
379 spatial distribution of plankton communities to environmental parameters (P_{org} , P_{inorg} , N_{inorg} ,
380 N_{org} , $\text{Si}(\text{OH})_4$, pH, temperature and salinity). The CCA also elucidated the relationship between
381 the biomass of size-fractionated phytoplankton and different zooplanktonic groups.
382 Phytoplankton and zooplankton data were $\ln(x + 1)$ transformed. The comparison of the
383 canonical inertia associated with the CCA (constrained ordination) and the inertia of the

384 classical correspondence analysis (CA, unconstrained ordination) indicated the extent to which
385 the environmental variables explained the spatial structure of communities. Permutation tests
386 ($n = 999$) were performed to identify the significant axis and to test the significance of the
387 correlations between environmental factors and plankton distribution.

388 **3 Results**

389 **3.1 Environmental conditions**

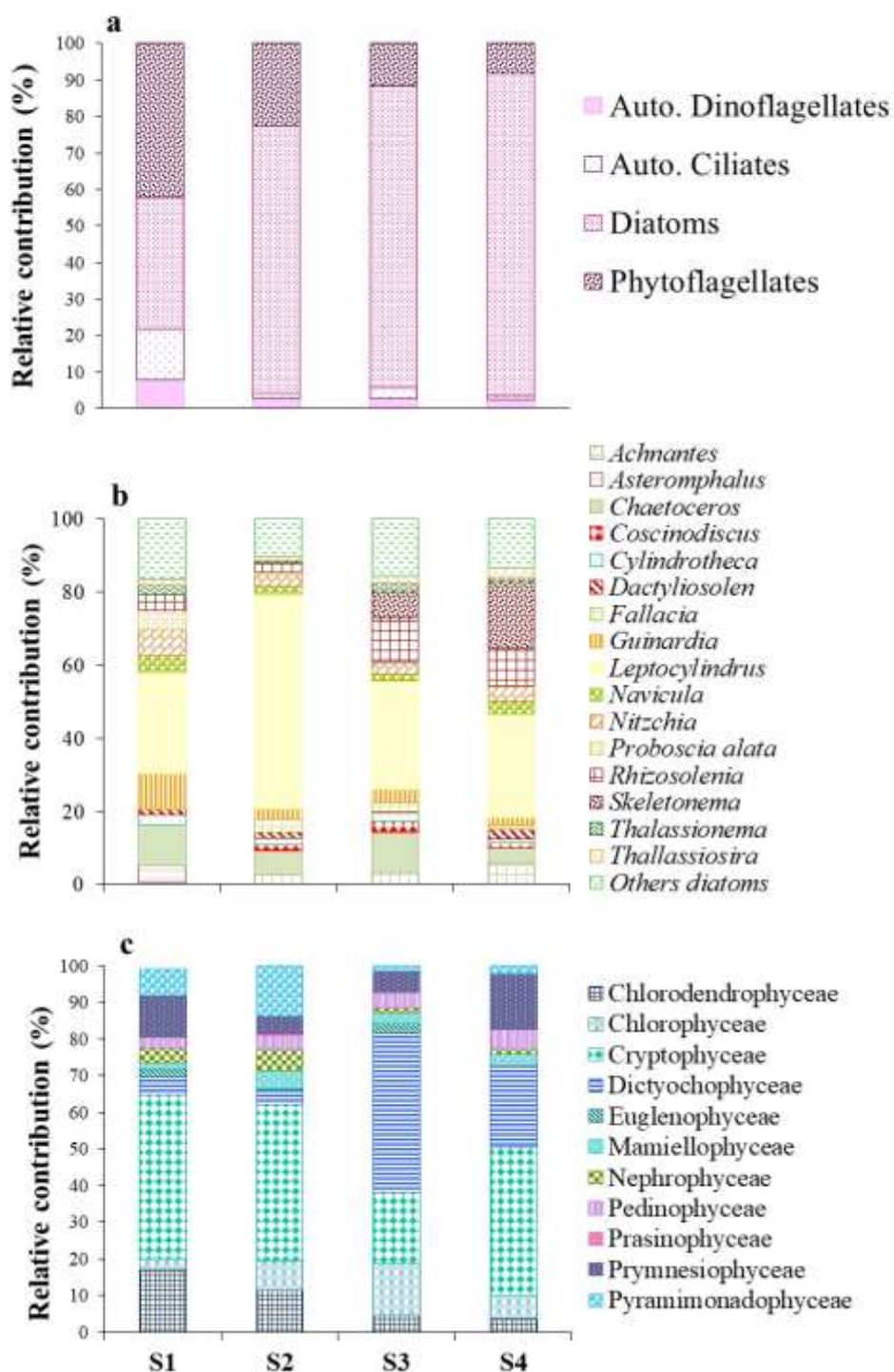
390 Sampling stations were located in the continental shelf of the GG, which is characterized
391 by a shallow (< 20 m) well-mixed water column. Environmental factors showed no significant
392 variations between sampling depths (ANOVA $p > 0.05$), and hence data were presented as
393 depth-averaged values (Table 1). Water temperature (22.6 - 24.2 °C), salinity (39.42 - 39.56), pH
394 (8.25 - 8.31) and dissolved O_2 (8.15 - 8.25 mg L^{-1}) varied little among stations, while nutrient
395 concentrations exhibited significant spatial variations (ANOVA, $p < 0.05$). In S1, inorganic
396 nutrients presented the lowest values (4.27 μM N, 0.91 μM P and 4.90 μM Si) and increased
397 up to 8.93 μM N, 2.2 μM P and 8.98 μM Si in S4. Inorganic nutrient concentrations recorded
398 in S3 were higher than in S1, but lower than the southernmost station (S4). The highest and
399 lowest levels of organic nitrogen (N_{org} : 5.03 - 12.29 μM) were recorded in S1 and S4,
400 respectively. An opposite trend was observed for organic phosphorus (P_{org} : 8.23 - 18.32 μM).

401 **3.2 Spatial distribution of planktonic communities**

402 **Phytoplankton.** The depth-averaged Chl *a* concentrations and the depth-integrated
403 carbon biomasses were different among stations (ANOVA, $p < 0.05$; Table 1), increasing
404 gradually from S1 (1.7 μg Chl *a* L^{-1} , 780 mg C m^{-2}) to S4 (6.07 μg Chl *a* L^{-1} , $1,624$ mg C m^{-2}).
405 Positive correlations were found between inorganic N, P and Si and Chl *a* concentrations
406 ($r_s = 0.64$ - 0.84 , $p < 0.01$) and carbon biomass ($r_s = 0.67$ - 0.78 , $p < 0.01$). Microphytoplankton
407 was the main source of Chl *a* in S4 (74%) and contributed to $\sim 50\%$ of it in S3. The contribution

408 of picophytoplankton to Chl *a* was higher in S1 (37%) than in the other stations (11-27%), while
409 nanophytoplankton contributed to a large fraction of Chl *a* in S2 (43%) (Table 1). In terms of
410 carbon biomass, micro-sized fraction (418-1207 mg C m⁻²) formed the most of phytoplankton
411 (54-75%), while nano-sized fraction (70-265 mg C m⁻²) contributed only by 9-16%. The pico-
412 sized fraction (152-292 mg C m⁻²), which formed only 9% of phytoplankton carbon in S4,
413 showed increased contributions in S2 and S3 (20-21%) and mostly in S1 (38%).

414 The composition of > 2 µm phytoplankton community changed also among stations.
415 Diatoms showed different contributions to the community according to the station, and their
416 biomass was positively correlated with inorganic N, P and Si ($r_s = 0.79-0.67$, $p < 0.01$). Diatoms
417 were dominant in S2, S3 and S4, showing depth-averaged contribution of 73-88% (Fig. 2a).
418 They were mainly represented by *Leptocylindrus minimus* (30-60% of diatoms) in the three
419 stations. Large chains of *Skeletonema costatum* and *Rhizosolenia setigera* showed increased
420 contribution to diatoms (18-28%) only in S3 and S4 (Fig. 2b). The small phytoplankton were
421 particularly abundant in S1 (45%; Fig. 2a), and were represented by nano-sized Cryptophyceae
422 (*Hillea fusiformis* and *Rhodomonas marina*). Within the phytoplankton, the micro-sized
423 Dictyochophyceae (i.e., *Dictyocha fibula*) were more important in S3 and S4 than in the other
424 stations (Fig. 2c). In all stations, photosynthetic ciliates (*Mesodinium rubrum*) and
425 dinoflagellates (*Prorocentrum gracile*) only accounted for 2-13% of the > 2 µm phytoplankton
426 community (Fig. 2a).



427

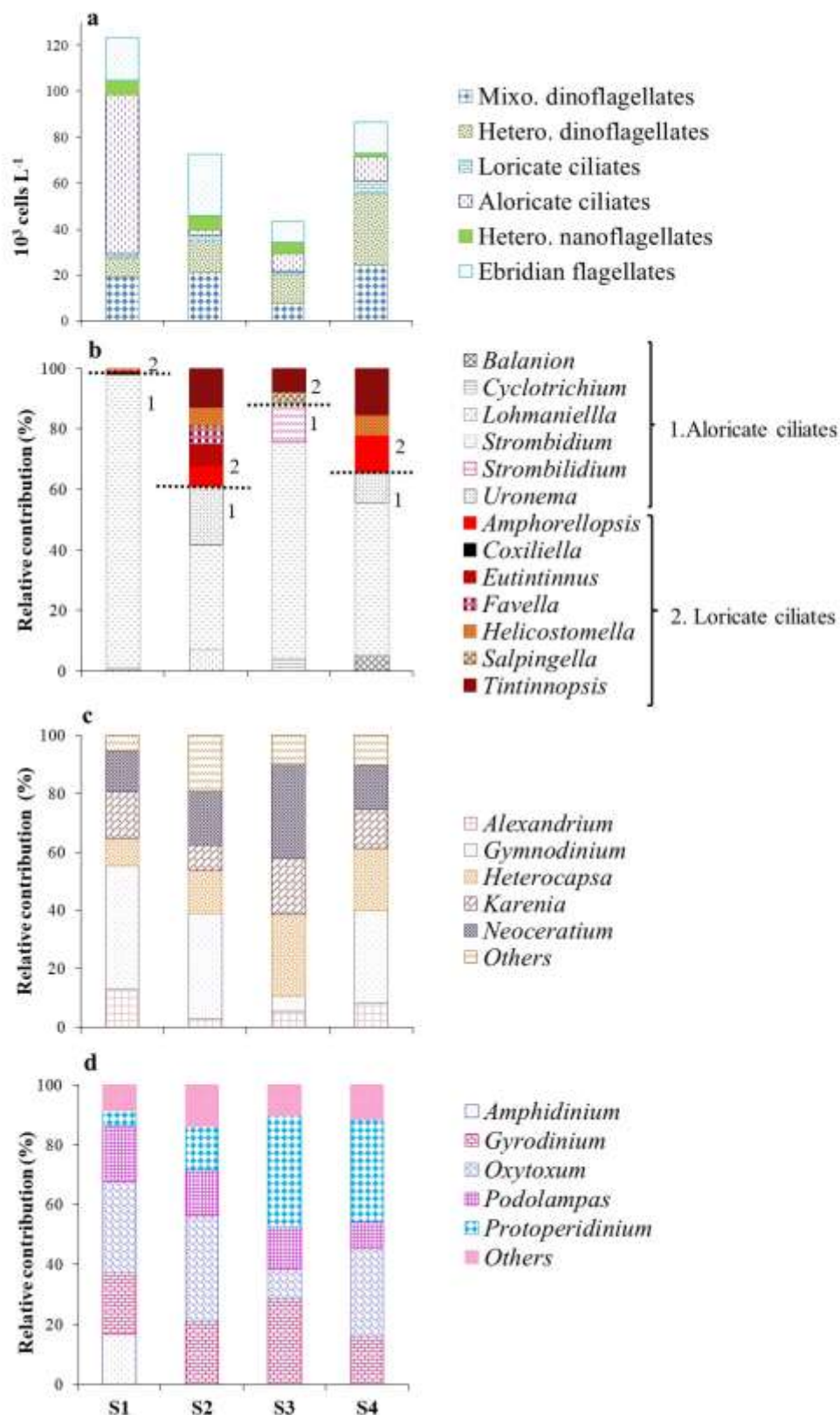
428 **Fig. 2** Composition of > 2 μm phytoplankton (a), diatoms (b) and phytoflagellates (c) in the
429 sampling stations during fall 2017. Values are the means of the three depths at each station.

430

431 **Protozooplankton.** The depth-averaged abundance of total protozooplankton was
432 significantly different between stations (ANOVA, $p < 0.05$), varying from 43×10^3 cells L^{-1} (in
433 S3) to 123×10^3 cells L^{-1} (in S1) (Fig. 3a). Aloricate ciliates, mainly composed of *Strombidium*
434 spp. (Fig. 3b), were dominant in S1 (~60%; 70×10^3 cells L^{-1}). Loricated ciliates displayed a
435 relatively low abundance ($1.5\text{--}6 \times 10^3$ cells L^{-1}) and were most abundant in S4, where
436 *Tintinnopsis*, *Helicostomella* and *Amphorellopsis* occurred (Fig. 3b). Dinoflagellates were
437 abundant in S2, S3 and S4 ($20\text{--}55 \times 10^3$ cells L^{-1}), contributing to 48–64% of protozooplankton.
438 Mixotrophic dinoflagellates including *Gymnodinium*, *Heterocapsa*, *Karenia* and *Neoceratium*
439 (Fig. 3c) were dominant in S2 (59% of dinoflagellates), whereas large heterotrophic
440 dinoflagellates (mainly *Protoperidinium*) mostly occurred in S4 (60%). The heterotrophic
441 nanoflagellate *Commatia cryoporinum* ($0.75\text{--}5.78 \times 10^3$ cells L^{-1}) and the ebridian flagellate
442 *Hermesinium sp.* ($8.7\text{--}26.7 \times 10^3$ cells L^{-1}) contributed 2–12% and 15–37% to protozooplankton,
443 respectively (Fig. 3a).

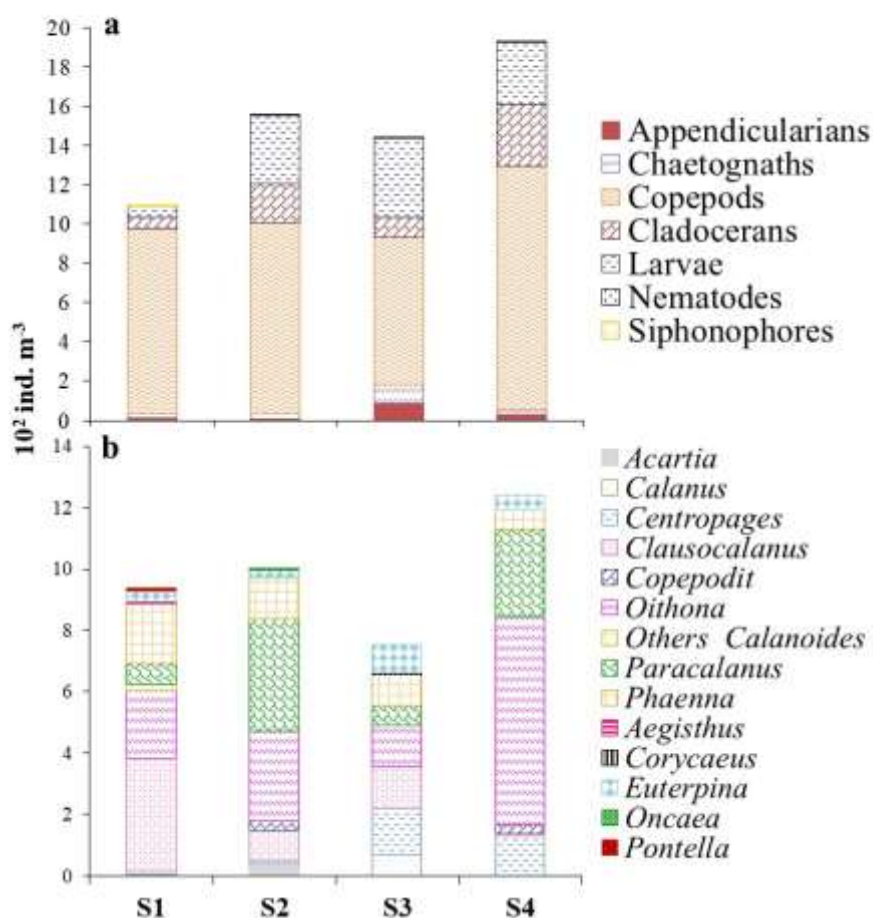
444 **Metazooplankton.** Metazooplankton abundance significantly varied among stations
445 (ANOVA, $p < 0.05$) from 11×10^2 ind. m^{-3} in S1 to 20×10^2 ind. m^{-3} in S4 (Fig. 4a). Copepods
446 ($7.5\text{--}12.5 \times 10^2$ ind. m^{-3}) were dominant in all stations, forming 53–86% of total
447 metazooplankton (Fig. 4a). Calanoida (*Centropages*, *Clausocalanus*, *Paracalanus* and
448 *Phaenna*) and Cyclopoida (*Oithona*) contributed to the majority of copepods, but with different
449 percentages according to the station (Fig. 4b). The harpacticoid *Euterpina* was relatively
450 abundant in S3 (12%). Cladocerans (*Penilia sp.*) mainly occurred in S4 (forming 16% of
451 metazoans), while decapod, polychaete and crab larvae as well as, crustacean nauplii were
452 observed at moderate concentrations in S2, S3 and S4. Other metazoan groups, e.g.,
453 chaetognaths, appendicularians, nematodes and siphonophores were observed in all stations,
454 but at much lower densities.

455



456

457 **Fig. 3** Abundance and composition of protozooplankton (a), and specific structure of the main
 458 protozoan groups (b-d) in the sampling stations during the fall 2017. Values are the means of
 459 the three depths at each station



460

461 **Fig. 4** Abundance and composition of metazooplankton groups (a), and copepod taxa (b) in
462 the sampling stations during the fall 2017

463

464 **Relationship between environmental conditions and plankton communities.** The

465 influence of physico-chemical factors on phytoplankton (the three size fractions) and

466 zooplankton distribution, as well as relationships between phytoplankton and zooplankton were

467 summarized by the CCA. The first two canonical components extracted 69% of the canonical

468 variance (Fig. 5). A Monte Carlo permutation test showed that all canonical axes were highly

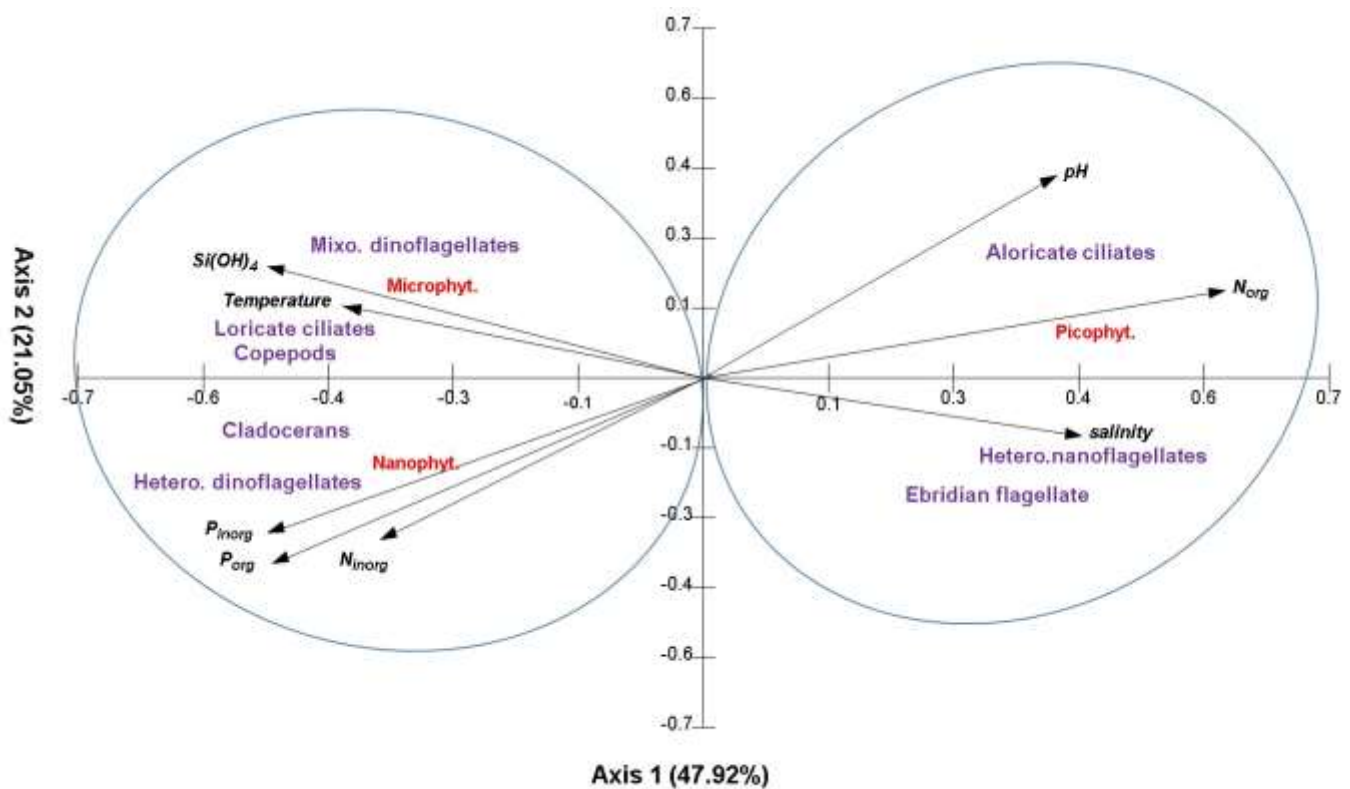
469 significant ($p < 0.0001$). The positive pole of axis 1 was correlated with salinity (0.53, $p < 0.05$)

470 and organic nitrogen (0.73, $p < 0.01$), while the negative pole was correlated with temperature

471 (-0.51, $p < 0.05$), inorganic phosphorus (-0.61, $p < 0.05$), inorganic nitrogen (-0.50, $p < 0.05$),

472 silicates (-0.61, $p < 0.05$) and organic phosphorous (-0.65, $p < 0.05$). Axis 2 was positively
473 correlated with the pH (0.53, $p < 0.05$).

474 The CCA discriminated two groups. The first axis positively selected picophytoplankton
475 with abiotic variables such as salinity and organic nitrogen, while nano- and
476 microphytoplankton were related to organic and inorganic phosphorus, silicates, inorganic
477 nitrogen, and temperature. The CCA also showed that pico-sized cells were associated with
478 aloricate ciliates, as well as heterotrophic and ebridian nanoflagellates. In contrast, nano- and
479 microphytoplankton prevailed when dinoflagellates (mixo- and hetero-trophic organisms),
480 loricate ciliates, copepods and cladocerans largely occurred. Dinoflagellates, loricate ciliates
481 and copepods showed a positive correlation with temperature but were negatively correlated to
482 salinity. Loricata ciliates and flagellates protozoans followed, however, the opposite trend.

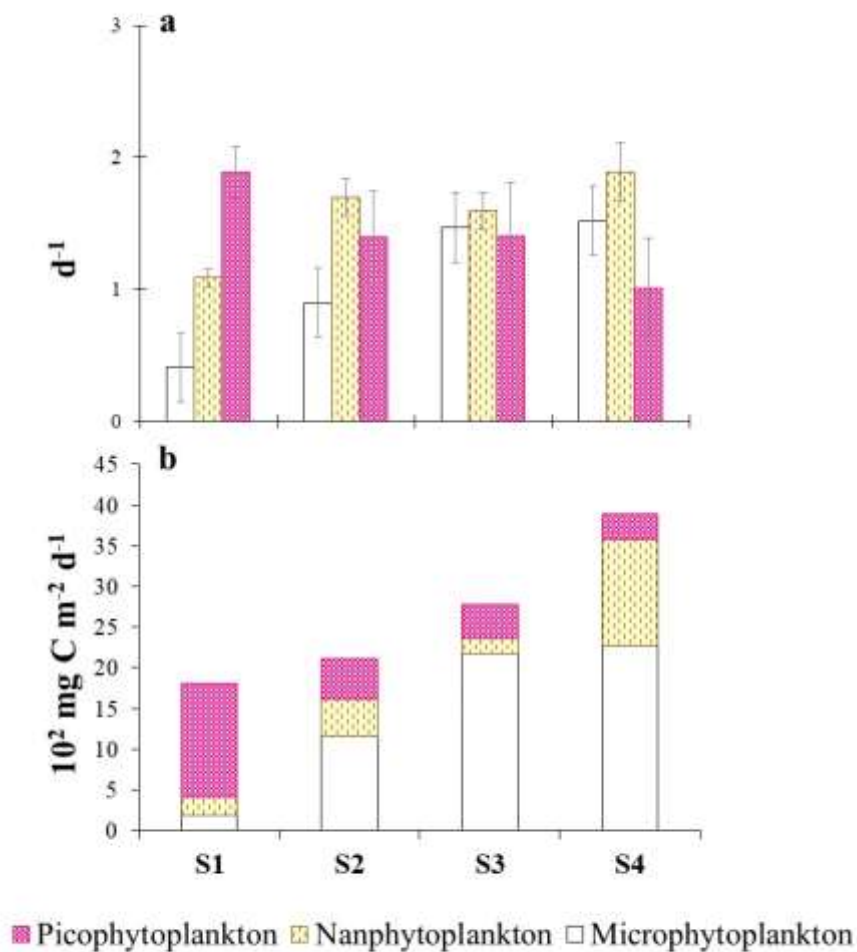


484 **Fig. 5** Canonical correspondence analysis (CCA) ordination diagram showing the relationship
485 between phytoplankton (the three size fractions), zooplankton, and physico-chemical factors

486 3.3. Phytoplankton growth and production

487 The growth rates varied significantly (ANOVA, $p < 0.01$) among stations and size
488 fractions (micro-: 0.41-1.52 d^{-1} ; nano-: 1.09-1.89 d^{-1} ; pico-phytoplankton: 1.01-1.89 d^{-1}) (Fig.
489 6a). The highest rate for the pico-sized fraction was recorded in S1, whereas for nano- and
490 micro-phytoplankton, the highest rates were observed in S4. The growth rate of
491 microphytoplankton was positively correlated with inorganic N and P ($r_s = 0.73-0.76$, $p < 0.01$),
492 while that of picophytoplankton showed negative correlations with these nutrients ($r_s = -0.62 -$
493 0.73 , $p < 0.01$).

494 Production rates for size fractionated and total phytoplankton varied significantly among
495 stations (ANOVA, $p < 0.05$; Fig. 6b). Picophytoplankton displayed a very high production rate
496 in S1 (1412 $mg\ C\ m^{-2}\ d^{-1}$) in comparison to other stations (300-496 $mg\ C\ m^{-2}\ d^{-1}$).
497 Microphytoplankton showed an opposite trend, with higher production rates in S2, S3 and S4
498 (1160-2075 $mg\ C\ m^{-2}\ d^{-1}$) than in S1 (188 $mg\ C\ m^{-2}\ d^{-1}$). The production rate for the micro-
499 sized fraction was positively correlated to diatom biomass ($r_s = 0.83$, $p < 0.01$). Production rate
500 for nanophytoplankton was low in S1 and S3 (188-215 $mg\ C\ m^{-2}\ d^{-1}$). Higher value was
501 observed in S2 (452 $mg\ C\ m^{-2}\ d^{-1}$) and the highest in S4 (1301 $mg\ C\ m^{-2}\ d^{-1}$). Production rate
502 for total phytoplankton showed an increasing trend from S1 (1816 $mg\ C\ m^{-2}\ d^{-1}$) to S4 (3873
503 $mg\ C\ m^{-2}\ d^{-1}$), and was positively correlated to all inorganic nutrients ($r_s = 0.68-0.81$, $p < 0.01$).
504 In S2, S3 and S4, microphytoplankton was the main carbon producer (55-78%), whereas in S1
505 picophytoplankton provided 78% of total carbon production. Nanophytoplankton contributed
506 only 7-12% of produced carbon in S1 and S3, and 21-34% in S2 and S4.



507

508 **Fig. 6** Growth (a) and production (b) rates of the three phytoplankton size fractions
509 (picophytoplankton: $< 2 \mu\text{m}$, nanophytoplankton: $2\text{-}10 \mu\text{m}$, microphytoplankton: > 10
510 μm) in the sampling stations during the fall 2017

511 3.4 Phytoplankton grazing

512 **Grazing by protozooplankton.** The grazing and consumption rates by protozooplankton
513 varied significantly among size fractions and across stations (ANOVA, $p < 0.01$; Table 2).
514 Picophytoplankton was grazed at higher rates ($0.82\text{-}1.30 \text{ d}^{-1}$) than the other size fractions
515 (micro-: $0.18\text{-}0.54 \text{ d}^{-1}$; nano-phytoplankton: $0.51\text{-}1.01 \text{ d}^{-1}$) in stations S1, S2 and S3. However,
516 microphytoplankton was the most grazed in S4 (0.84 d^{-1}). The highest consumption rate for
517 picophytoplankton was recorded in S1 ($762.96 \text{ mg C m}^{-2} \text{ d}^{-1}$) and the lowest in S4 (137 mg C

518 $\text{m}^{-2} \text{d}^{-1}$). In the opposite, nano- and micro-phytoplankton were consumed at low rates in S1
519 (92 and 71 $\text{mg C m}^{-2} \text{d}^{-1}$, respectively). Their consumption increased in other stations,
520 particularly in S4 (318 and 1049 $\text{mg C m}^{-2} \text{d}^{-1}$, respectively). For each size fraction, the
521 consumption rates showed positive correlations to the production rates ($r_s = 0.73-0.95$, $p <$
522 0.05). The consumption rate for micro-sized fraction was positively correlated with the
523 abundances of heterotrophic dinoflagellates ($r_s = 0.85$, $p < 0.01$) and loricate ciliates ($r_s = 0.60$,
524 $p < 0.05$). Protozooplankton removed a substantial fraction of daily production for
525 picophytoplankton in most stations ($\sim 60\% \text{ P grazed d}^{-1}$), except in S4 ($40\% \text{ P grazed d}^{-1}$). The
526 protozooplankton grazing corresponded to daily remove of 23-62% of nanophytoplankton
527 production. Protozooplankton grazing impact on microphytoplankton was higher in S4 (47%
528 P grazed d^{-1}) than in the other stations ($22-41\% \text{ P grazed d}^{-1}$). Furthermore, microbivory (carbon
529 from picophytoplankton) contributed to carbon ingestion of protozooplankton by only 9% in
530 S4, but by 24-34% in S2 and S3, and up to 82% in S1. Conversely, herbivory played a
531 significant role in the feeding of protozooplankton in the other stations, as microphytoplankton
532 alone represented 54-70% of their diet (Table 2).

533 **Grazing by metazooplankton.** The grazing rate and the impact of metazooplankton were
534 significantly different among stations (ANOVA, $p < 0.01$; Table 3). The consumption rate of
535 phytoplankton by metazooplankton showed the lowest value in S1 ($76 \text{ mg C m}^{-2} \text{d}^{-1}$) and the
536 highest in S4 ($794 \text{ mg C m}^{-2} \text{d}^{-1}$). This rate was positively correlated with nano- and
537 microphytoplankton biomass ($r_s = 0.70-0.78$, $p < 0.01$), and with copepod and cladoceran
538 abundances ($r_s = 0.62-0.76$, $p < 0.05$). Metazooplankton removed 10-24% of phytoplankton
539 production and 22-38% of phytoplankton standing stock (Table 3).

540

541

542 **Table 2** Grazing rates by protozooplankton (g), consumption rates of phytoplankton (G_p),
 543 grazing impact on phytoplankton and protozooplankton diet in the sampling stations within the
 544 Gulf of Gabès during the fall 2017 (Mean value \pm SD, N = 3). p-value (ns: not significant; *:
 545 $0.01 < p < 0.05$; ** $0.001 < p < 0.01$, ***: $p < 0.001$) indicates the significant level for the
 546 ANOVA used to test spatial variation.

547

	S1	S2	S3	S4	p-value
g (d⁻¹)					
<i>Microphyt.</i>	0.18 \pm 0.07	0.54 \pm 0	0.38 \pm 0.09	0.84 \pm 0.03	***
<i>Nanophyt.</i>	0.88 \pm 0.21	0.51 \pm 0.15	0.71 \pm 0.10	0.65 \pm 0.21	*
<i>Picophyt.</i>	1.30 \pm 0.04	0.88 \pm 0.48	0.82 \pm 0.80	0.68 \pm 0.11	**
G_p (mg C m⁻² d⁻¹)					
<i>Microphyt.</i>	71.07 \pm 17.46	463.79 \pm 6.96	461.91 \pm 103.73	1048.77 \pm 48.25	**
<i>Nanophyt.</i>	91.74 \pm 12.49	102.12 \pm 29.80	119.45 \pm 46.56	317.73 \pm 16.81	*
<i>Picophyt.</i>	762.96 \pm 6.35	293.91 \pm 39.01	204.79 \pm 30.00	137.50 \pm 16.73	**
%P grazed d⁻¹					
<i>Microphyt.</i>	35 \pm 15	40 \pm 5	22 \pm 4	47 \pm 7	***
<i>Nanophyt.</i>	42 \pm 5	23 \pm 7	62 \pm 20	40 \pm 15	**
<i>Picophyt.</i>	60 \pm 1	57 \pm 6	56 \pm 13	40 \pm 4	**
Diet (%)					
<i>Microphyt.</i>	8 \pm 3	54 \pm 8	62 \pm 7	70 \pm 7	**
<i>Nanophyt.</i>	10 \pm 3	12 \pm 1	14 \pm 8	21 \pm 6	*
<i>Picophyt.</i>	82 \pm 7	34 \pm 7	24 \pm 3	9 \pm 1	*

548

549

550 **Table 3** Phytoplankton (nano- and micro-sized fractions) consumption rates by
 551 metazooplankton and grazing impact in the sampling stations within the Gulf of Gabès during
 552 the fall 2017. (Mean value \pm SD, N = 3). p-value (ns: not significant; *: $0.01 < p < 0.05$; **
 553 $0.001 < p < 0.01$, ***: $p < 0.001$) indicates the significant level for the ANOVA used to test
 554 spatial variation

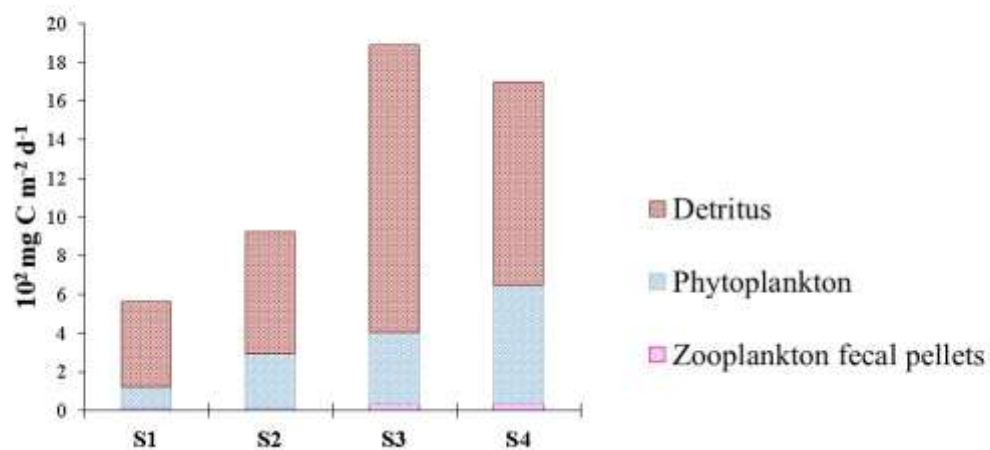
	S1	S2	S3	S4	p-value
G_m (mg C m⁻² d⁻¹)	76.26 \pm 0.65	313.36 \pm 6.58	225.84 \pm 2.40	794.28 \pm 72.20	***
% P grazed d⁻¹	19 \pm 1	20 \pm 1	10 \pm 5	24 \pm 6	**
% Chl a grazed d⁻¹	22 \pm 1	38 \pm 3	32 \pm 1	37 \pm 4	ns

555

556

557 3.5 Vertical fluxes of particulate organic matter

558 The vertical fluxes of particles varied significantly among stations, from 561 mg C m⁻² d⁻¹
559 in S1 to 1891 mg C m⁻² d⁻¹ in S3 (ANOVA, $p < 0.05$; Fig. 7). These fluxes only accounted for
560 30% of primary production in S1, but reached 43-45% in S2 and S4, and 70% in S3. Detritus
561 was the dominant sinking flux from S1 (78%) to S3 (79%), but contributed less to the vertical
562 carbon flux of S4 (62%). The phytoplankton carbon exported towards the benthos followed an
563 increasing trend from S1 (111 mg C m⁻² d⁻¹) to S4 (611 mg C m⁻² d⁻¹). Zooplankton fecal pellets
564 were non-significant in S1, S2 and S3, and made only 2% of the vertical carbon flux in S4 (38
565 mg C m⁻² d⁻¹).



566

567 **Fig. 7** Vertical fluxes of particulate organic carbon in the sampling stations during the fall
568 2017

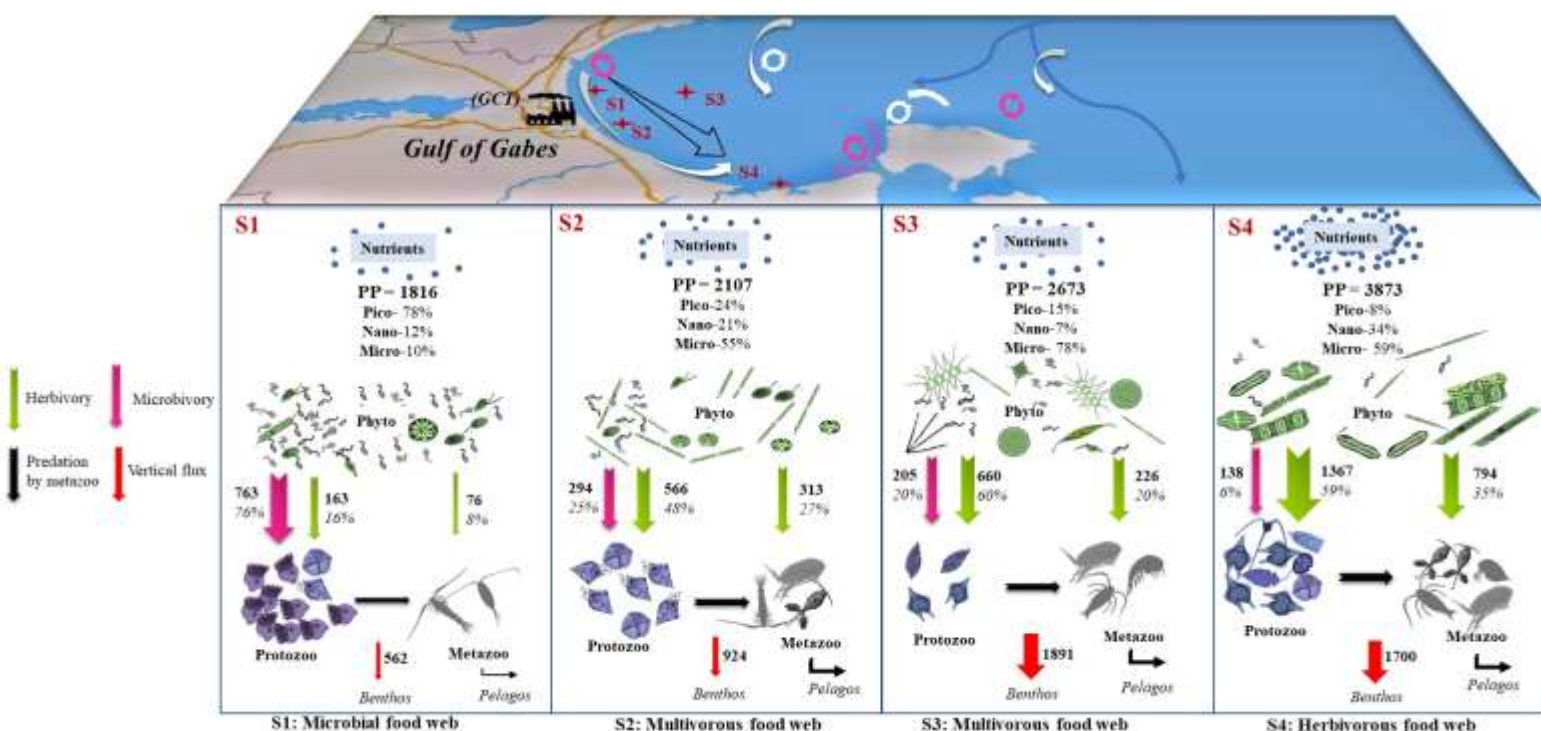
569 3.6 Planktonic interactions

570 Based on data of size-fractionated production, prey-grazers relationships and carbon
571 vertical flux, conceptual diagrams of planktonic interactions were established for all sampling
572 stations (Fig. 8). The importance of the zooplankton microbivory and herbivory in the carbon
573 transfer (i.e., total consumption by proto- and meta-zooplankton) were considered in each
574 station.

575 In station S1, the primary production ($1816 \text{ mg C m}^{-2} \text{ d}^{-1}$) was lower than in the other
576 stations, and mainly sustained by picophytoplankton (78%). These small producers were under
577 strong grazing pressure by protozooplankton, which was dominated by aloricate ciliates.
578 Consequently, a large amount of carbon ($763 \text{ mg C m}^{-2} \text{ d}^{-1}$) entered the food web *via* the
579 microbivory of protozooplankton, which represented 76% of carbon transfer. However, $> 2 \mu\text{m}$
580 phytoplankton (i.e., nano- and microphytoplankton), which was mainly composed by nano-
581 sized phytoflagellates and to a lesser extent by diatoms, participated weakly to primary
582 production (22%). Moreover, protozooplankton grazing on $> 2 \mu\text{m}$ phytoplankton supplied
583 small amounts of carbon to higher consumers ($163 \text{ mg C m}^{-2} \text{ d}^{-1}$). Metazooplankton had also
584 low feeding on nano- and microphytoplankton ($76 \text{ mg C m}^{-2} \text{ d}^{-1}$). Consequently, herbivory of
585 proto- and metazooplankton together represented only 24% of channeled carbon. Similar to
586 primary production, the amount of carbon particles that settled down and could reach benthos
587 was low ($562 \text{ mg C m}^{-2} \text{ d}^{-1}$).

588 In comparison to station S1, stations S2 and S3 had an increased production of $> 2 \mu\text{m}$
589 phytoplankton, particularly of microphytoplankton forming more than 70% of the total primary
590 production, simultaneously to an increase of the diatom abundance. This was accompanied by
591 an increase in the herbivory of protozooplankton (48-60% of carbon transfer), which was
592 dominated by mixotrophic and heterotrophic dinoflagellates and ebridian flagellates. Thus, a
593 high amount of $> 2 \mu\text{m}$ phytoplankton production ($566\text{-}660 \text{ mg C m}^{-2} \text{ d}^{-1}$) fueled the food web.
594 Conversely, grazing impact of protozooplankton has decreased for picophytoplankton, which
595 contributed moderately to primary production (15-24%), and hence protozooplankton
596 microbivory ($205\text{-}294 \text{ mg C m}^{-2} \text{ d}^{-1}$) supplied 20-25% of carbon to food web. Herbivory of
597 metazooplankton was relatively important ($226\text{-}313 \text{ mg C m}^{-2} \text{ d}^{-1}$), corresponding to 20-27% of
598 carbon transfer. Similarly, vertical flux of particles increased in both stations to reach higher
599 value ($924\text{-}1891 \text{ mg C m}^{-2} \text{ d}^{-1}$) than in S1.

600 In station S4, the production of picophytoplankton had further decreased, compared to
 601 other stations, to reach the lowest rate (8% of total PP) in detriment of an increase of the
 602 production of $> 2 \mu\text{m}$ phytoplankton, which was characterized by the abundance of large
 603 diatoms (such as *Rhizosolenia setigera* and *Skeletonema costatum*). Therefore, herbivorous
 604 protozoans, such as the diatom-consumer *Protoperidinium*, were abundant, leading to increased
 605 herbivory for proto- (59%) and meta-zooplankton (35%), which supplied substantial quantities
 606 of carbon (1367 and 794 $\text{mg C m}^{-2} \text{d}^{-1}$, respectively) to food web. A significant carbon flux
 607 towards benthos was also observed in this station ($1700 \text{ mg C m}^{-2} \text{d}^{-1}$).



609 **Fig. 8** Primary production (PP, $\text{mg C m}^{-2} \text{d}^{-1}$), trophic relationships and carbon transfer
 610 pathways within the planktonic systems of the sampling stations in link with the nutrient
 611 spatial gradient and hydrodynamic circulation in the Gulf of Gabès during the fall 2017.
 612 Percentage contributions of phytoplankton size fractions to PP are indicated. Values with
 613 arrows show the amount of channeled biogenic carbon ($\text{mg C m}^{-2} \text{d}^{-1}$) and percentages
 614 represent the contribution of zooplankton microbivory or herbivory to carbon transfer.
 615 Width of arrow is proportional to the carbon flow. Microbivory = consumption of Pico-
 616 by Protozoo; Herbivory = consumption of Nano- and Micro- by Protozoo and Metazoo;
 617 carbon transfer = consumption of Pico, Nano and Micro by Protozoo and Metazoo.

618

619

620 **4 Discussion**

621 **4.1 Productivity and nutrient richness**

622 Although the primary production levels are well documented for several Mediterranean regions
623 (Psarra et al. 2005; Kovač et al. 2018), information remains scarce for the Southern
624 Mediterranean (Sakka Hlaili et al. 2008; Meddeb et al. 2018) and even deficient for the GG.
625 Here we provide primary production estimates in the GG based on dilution experiments. This
626 technique has been already used in various marine systems, and has shown production rates that
627 are similar to those measured by ^{14}C method (Moigis and Gocke 2003; Meddeb et al. 2018;
628 Dokulil and Qian 2021). Nutrients were not added to dilution bottles, assuming high nutrient
629 concentrations in the GG during our study period. The estimated growth rates were relatively
630 high for most size fractions ($k \geq 1 \text{ d}^{-1}$; Fig. 6a), indicating that nutrients were non-limiting for
631 phytoplankton growth. Furthermore, our estimates of growth rates for different size fractions
632 ($0.4\text{-}1.9 \text{ d}^{-1}$) are in the range of values reported for fractioned phytoplankton from dilution
633 experiments (with or without nutrient addition) in other coastal ecosystems (Grami et al. 2008;
634 Wickham et al. 2022). Furthermore, Boudriga et al. (2022) recently reported similar growth rate
635 ($0.38\text{-}1.7 \text{ d}^{-1}$) for phytoplankton to our study. Therefore, the growth coefficients and
636 subsequently the calculated production rates measured in the present work are considered as
637 realistic.

638 Previous observations have suggested that the high fish production of the GG was related
639 to a high primary production (Halouani et al. 2016; Béjaoui et al. 2019). Our study reveals
640 indeed high total phytoplankton production rates ($130\text{-}370 \text{ mg C m}^{-3} \text{ d}^{-1}$ or $1816\text{-}3674 \text{ mg C m}^{-2} \text{ d}^{-1}$),
641 which were comparable with estimates from dilution technique in other coastal waters,
642 including Mediterranean ecosystems (Moigis and Gocke 2003; Marquis et al. 2007; Grami et
643 al. 2008). However, the primary production levels determined in the GG, located in the
644 oligotrophic Eastern Mediterranean, far exceed rates currently reported for ecosystems within

645 the same basin, as Ionian Sea, Aegean Sea and Gulf of Trieste (Christaki et al. 2011; Šolić et
646 al. 2010; Cibic et al. 2018). This suggests the influence of anthropogenic nutrient inputs, in
647 addition to natural sources, in the GG leading to its high productivity. Our estimates of Chl *a*
648 concentrations (1.65-6.06 $\mu\text{g L}^{-1}$) also surpassed values reported in Mediterranean open sea
649 areas (Raveh et al. 2015; Salgado-Hernanz et al. 2019), but were in the range found in other
650 coastal waters (Meddeb et al. 2018; Morsy et al. 2022). Our Chl *a* levels were higher than those
651 recorded by previous studies in the offshore part of GG ($< 1 \mu\text{g L}^{-1}$; Bel Hassen et al. 2009;
652 Hamdi et al. 2015), which can be due to several environmental features, such as hydrological
653 conditions, nutrient content, season, and phytoplankton community composition. Most of
654 previous works have been conducted during the summer-stratification period (July-September)
655 or during the transition period from the mixed to the stratified water (May-June), when nutrients
656 were in shortage ($< 3 \text{ N } \mu\text{M}$, $< 1 \text{ P } \mu\text{M}$) resulting in low Chl *a* concentrations. Furthermore,
657 $> 2 \mu\text{m}$ cells dominated the total Chl *a* in all stations (63-89%) and microphytoplankton alone
658 formed $\geq 50\%$ in S3 and S4 (Table 1). Moreover, large diatoms (*Leptocylindrus*, *Skeletonema*
659 and *Rhizosolenia*) were dominant during our sampling period (Fig. 2a, b). All these
660 observations may explain the higher Chl *a* concentrations measured during our study compared
661 to previous works, which reported the dominance of pico- and nano-sized phototrophs and the
662 scarcity of diatoms (Bel Hassen et al. 2009; Hamdi et al. 2015; Khammeri et al. 2020).

663 The high primary production and Chl *a* concentrations in the GG were associated to high
664 nutrient concentrations (Table 1), mainly due to the large supply from anthropogenic discharges
665 and also to tide-induced sediment resuspension and atmospheric deposition (Drira et al. 2016;
666 Khammeri et al. 2018). The GG is exceptionally enriched in inorganic and organic P (Table 1)
667 since it continuously receives large amounts of phosphogypsum (1,000 to 13,000 *t per day* since
668 the 1970's) from the phosphoric acid plant (Béjaoui et al. 2004; Khedhri et al. 2014). The P_{inorg}
669 concentrations measured in all stations exceed those usually observed in Mediterranean coastal
670 waters, like the lagoons of Bizerte (0.15 μM ; Meddeb et al. 2018) and Thau (0.18 μM ;

671 Courboulès et al. 2021), and the Gulf of Lion (0.06-0.12 μM ; Ross et al. 2016). The continuous
672 nutrient enrichment caused by anthropogenic inputs could lead to enhanced eutrophication of
673 the GG, causing ecosystem imbalance in the future. Signs of eutrophication, such as occurrence
674 of harmful algal blooms, have indeed been often reported (Feki- Sahnoun et al. 2017; Ayata et
675 al. 2018).

676 In the GG, a North-South and coast-offshore gradient of nutrients (Fig. S1) and organic
677 matter with accumulation in the Southern part has been already observed (Ciglenc̆ki et al.
678 2020; Mansouri et al. 2020). This spatial pattern can be related to the hydrodynamics of the
679 GG, which is characterized by the presence of a stationary southward current, two great eddies
680 in the middle, and a counter current in the Southern part (Fig. 1; Zayen et al. 2020). During our
681 study, nutrients also showed increasing concentrations from the North (S1) to the South (S4)
682 and from the coast (S1) to offshore (S3). Phytoplankton variables (i.e., production, carbon
683 biomass and Chl *a*) followed the same spatial distribution patterns than nutrients, confirming
684 that spatial distribution of Chl *a* is closely related to nutrient concentrations in the GG (Bel
685 Hassen et al. 2009).

686 **4.2 Spatial dynamics of phytoplankton**

687 There was a clear spatial variability in the size structure of phytoplankton. The dominance
688 of fast-growing picophytoplankton in S1 (Table 1, Fig. 6a, b) confirmed its main functional role
689 in this station. In general, the picophytoplankton is dominant in oligotrophic Mediterranean
690 open sea, such as the Northern Adriatic Sea, the Levantine Basin, the Southern Tyrrhenian Sea
691 and the Southern Adriatic Sea (Totti et al. 2005; Tanaka et al. 2007; Decembrini et al. 2009;
692 Cerino et al. 2012). Our results reveal that picophytoplankton can be an important component
693 within the phytoplankton community in coastal Mediterranean waters, with relatively important
694 nutrient concentrations (i.e., in S1). Unlike S1, large phytoplankton characterized the other
695 stations, even the offshore station (i.e., S3). The micro-sized fraction contributed most of the

696 primary production (55-78%) and carbon biomass (71-75%) in S2, S3 and S4, and dominated
697 the Chl *a* (49-74%) in S3 and S4 (Table 1, Fig. 6b). The nutrient spatial gradient induced by
698 hydrodynamic features has likely influenced the spatial distribution of phytoplankton size
699 fractions. This was evidenced by a positive correlation between the growth rate of micro-sized
700 fraction and inorganic nutrients, and a negative correlation for the pico-fraction growth rate.
701 The CCA showed also that large phytoplankton was associated with all inorganic nutrients
702 while an opposite trend was found for the picophytoplankton (Fig. 5). Jyothibabu et al. (2015)
703 have reported a clear impact of the hydrodynamics (summer monsoon current and associated
704 eddies) on the evolution of nutrients and phytoplankton size structure in the Bay of Bengal
705 (Northeastern Indian Ocean). Recently, Decembrini et al. (2020) have showed that the
706 circulation within the Gulf of Augusta (Western Ionian Sea) allowed the advection of nutrient-
707 rich waters that modified the size structure of phytoplankton and triggered an increase of the
708 micro-sized fraction.

709 The $> 2 \mu\text{m}$ phytoplankton community also displayed a spatial variation in species
710 composition. Generally, nano-sized phytoflagellates, mainly represented by cryptophyceae,
711 dominated in biomass in S1, typified by the least rich waters of the majority of nutrients (lowest
712 concentrations of P_{inorg} , P_{org} , and $\text{Si}(\text{OH})_4$). Conversely, the contribution of diatoms increased
713 from S1 (37%) to S4 (88%) concomitantly with the nutrient increase. Diatom biomass showed
714 a positive correlation with all inorganic nutrients ($r_s = 0.79-0.67$, $p < 0.01$). It is well known
715 that small phototrophs with high surface-to-volume ratio require lower nutrient concentrations
716 for their growth than large cells, which grow well under more nutrient enriched waters (Duarte
717 et al. 2000; Varkitzi et al. 2020). This may explain the high contribution of nano-sized cells to
718 the $> 2 \mu\text{m}$ phytoplankton community and the dominance of picophytoplankton in S1. The high
719 contribution of nano-sized cells, such as chlorophyceae, cryptophyceae and prymnesiophyceae,
720 to phytoplankton community was previously reported in the GG during a period characterized
721 by reduced nutrient supply (Bel Hassen et al. 2009; Ben Ltaief et al. 2015; Rekik et al. 2015).

722 Nano-sized phytoflagellates are typical of waters with low nutrient concentrations, such as
723 Mediterranean open sea areas (Vidussi et al. 2000; Decembrini et al. 2009). In contrast, blooms
724 of diatoms are commonly observed in coastal Mediterranean environments, particularly during
725 late winter-spring (d'Alcalà et al. 2004; Mayot et al. 2017; Leblanc et al. 2018), when the
726 stratification of the water column follows the vertical mixing, thus favoring the growth of small
727 species (such as *Chaetoceros*) (Peters et al. 2006; Trombetta et al. 2021). Other authors have
728 rather reported the presence of diatoms in Mediterranean waters during the period of turbulence
729 (i.e., autumn), with high proliferation of large species (Margalef 1978; Decembrini et al. 2009;
730 Vascotto et al. 2021). This agrees with our finding showing that micro-sized diatoms
731 (*Leptocylindrus*, *Skeletonema* and *Rhizosolenia*) were dominant during our study period.

732 The decrease of picophytoplankton contribution to total primary production and Chl *a*
733 content from S1 to S4, and the increase of micro-sized contribution and diatom proliferation
734 would greatly influence the size and the type of grazers, as well as their feeding activity,
735 suggesting a significant change in carbon transfer pathways between stations. These effects are
736 detailed in the following sections.

737 **4.3 Spatial variation of top-down control by metazooplankton**

738 Copepods were dominant in the GG (Fig. 4a), as previously observed in this area (Drira
739 et al. 2017; Makhlof Belkahia et al. 2021) and in other Mediterranean ecosystems (Sakka
740 Hlaili et al. 2008; Ben Lamine et al. 2015; Gueroun et al. 2020). The abundance of copepods
741 found here ($0.939\text{--}1240 \times 10^3 \text{ ind m}^{-3}$) compared also well with previous reports in the GG (Ben
742 Ltaief et al. 2017; Drira et al. 2017) and in other Mediterranean systems, i.e., Lagoons of
743 Bizerte, Venice and Berre (Riccardi 2010; Siokou-Frangou et al. 2010; Marques et al. 2015;
744 Gueroun et al. 2020). Our study assessed the feeding impact of metazooplankton on
745 phytoplankton using the gut fluorescence method. This simple technique has been widely used
746 for more than several decades because it is useful for revealing the functional role of

747 metazooplankton in various marine environments (Tseng et al. 2008; Meddeb et al. 2018; He
748 et al. 2021). The results show that metazooplankton had an important control on phytoplankton,
749 by consuming 10-24% of the primary production. This feeding effect exceeded that reported in
750 other world oceanic regions (12%, Calbet et al. 2000), but compared with estimates from the
751 gut fluorescence method in other Mediterranean ecosystems (8-30% P grazed d^{-1} in the Lagoon
752 of Bizerte and 9-20% P grazed d^{-1} in the Alboran Sea) (Gaudy et al. 2003; Meddeb et al. 2018).
753 The impact of metazooplankton on phytoplankton biomass (22-38% Chl *a* d^{-1}) was also in the
754 range of percentages found by other authors (using the gut content technique) in coastal
755 ecosystems, such as Gironde estuary, and Gulf of Mexico (Sautour et al. 2000; Landry and
756 Swalethorp 2021). The significant percentages of phytoplankton biomass and production daily
757 consumed by metazooplankton suggested the importance of the metazoan grazers in channeling
758 carbon to higher trophic level in the GG.

759 The consumption by metazooplankton varied significantly among stations (Table 3), in
760 relation with spatial variations of metazoan abundance ($r_s = 0.62-0.76$, $p < 0.05$) and prey
761 biomass ($r_s = 0.70-0.78$, $p < 0.01$). Besides, change in size structure of phytoplankton seemed
762 to influence the feeding of metazooplankton. Consumption rates of phytoplankton measured
763 from S2 to S4 were 3-10 folds higher than that in S1, where the phytoplankton production was
764 dominated by the pico-sized fraction, which is inefficiently consumed by copepods (Berggreen
765 et al. 1988; Morales et al. 1993; Callieri and Stockner 2002). Conversely, the highest feeding
766 activity of metazooplankton was observed in the southernmost station (S4), where large
767 phytoplankton dominated the Chl *a* and primary production (Table 1, Fig. 6b). This coincided
768 with a high proliferation of herbivorous copepods (e.g., *Centropages*, *Clausocalanus* and
769 *Paracalanus*) and herbivorous cladocerans (e.g., *Penilia*, Katechakis et al. 2004) (Fig. 4a). The
770 CCA also showed a clear association between the two metazoan groups and nano- and
771 microphytoplankton (Fig. 5), which might be due to trophic relationships. As explained, the
772 complex circulation in the GG favoured the accumulation of particles towards the South –

773 among which zooplankton and phytoplankton – leading to increased trophic interactions
774 between the two planktonic components. Similarly, a recent work highlighted the role of
775 hydrodynamics in the retention of metazooplankton in the Southern area of the GG and in the
776 enhancement of its potential control of phytoplankton (Makhlouf Belkahia et al. 2021).

777 **4.4 Spatial variation of top-down control by protozooplankton**

778 Our study examined the impact of protozooplankton grazing on phytoplankton using the
779 standard dilution method. This simple technique, which gives simultaneous estimations of
780 growth and grazing rates, has been used over the past decades in open and coastal environments,
781 including Mediterranean systems (Calbet and Landry 2004; Calbet et al. 2008; Griniené et al.
782 2016; Leruste et al. 2019; Pecqueur et al. 2022; Wickham et al. 2022). However, the dilution
783 method has been employed to a lesser extend for the estimation of protozooplankton grazing in
784 the Southern Mediterranean (Sakka Hlaili et al. 2008; Grami et al. 2008; Meddeb et al. 2018).
785 Furthermore, the functional role of protozooplankton is poorly documented in the GG, although
786 previous studies have reported high abundances of ciliates, heterotrophic and mixotrophic
787 flagellates (Hannachi et al. 2008; Drira et al. 2008; Kchaou et al. 2009; Hamdi et al. 2015; Ben
788 Ltaief et al. 2017; Rekik et al. 2021).

789 Different size fractions of phytoplankton were measured in our dilution bottles rather than
790 total phytoplankton in order to give an insight into the size-selective protozooplankton feeding.
791 The dilution experiments provided statistically significant grazing estimates for different
792 phytoplankton size fractions in all stations (Fig. S2 in Supplementary Material). Grazing rates
793 may be over-estimated, if nutrient limitation occurs during experiment (Landry and Hassett
794 1982). In our work, although nutrients were not added, the phytoplankton growth was kept
795 under unlimited conditions. Moreover, our estimates of grazing rates for pico-sized fraction
796 were in the range of values reported from dilution experiments (with or without nutrients) in
797 other coastal waters (Dong et al. 2021; Pecqueur et al. 2022). Using the same method, several

798 authors have also found grazing rates for nano- and microphytoplankton (Sakka Hlaili et al.
799 2007; Dong et al. 2021) comparable to our estimates (Table 2).

800 In general, there is a close and a positive trophic interaction between the growth of prey
801 and their grazing by protozooplankton (Shinada et al. 2000; Martin-Cereceda et al. 2003;
802 Dopheide et al. 2011; Chen et al. 2020). Indeed, for each size-fraction, significant and positive
803 correlations were found between prey production and protozooplankton consumption rates.
804 Several studies have shown that protozoan organisms were able to modify their growth
805 according to the availability of their potential prey and that the change in phytoplankton size
806 structure may influence the community composition of protozooplankton and its grazing
807 pressure (Sherr and Sherr 2007; Mansano et al. 2014; Horn et al. 2020; Corradino and Schnetzer
808 2022; Li et al. 2022). The high proliferation of picophytoplankton in S1 was associated with a
809 clear dominance of small aloricate ciliates (20-50 μm *Strombidium* spp.; Fig. 3a), which are
810 known to have large predation on pico-sized cells (Rassoulzadegan et al. 1988; Sakka 2000;
811 Meddeb et al. 2018). Heterotrophic nanoflagellates (*Commotion cryoporinum*) and ebridian
812 flagellates (*Hermesinium* sp.), which can actively consume pico-sized prey (Hargraves 2002;
813 Calbet and Landry 2004; Berglund et al. 2007), were well represented in S1 (Fig. 3a). The CCA
814 analysis showed likewise a strong association, likely through feeding links, between
815 picophytoplankton biomass and the abundances of all these microbivorous consumers (Fig. 5).
816 Accordingly, the protozooplankton displayed high consumption rate and grazing impact on the
817 pico-sized fraction in S1 (60% P grazed d^{-1}), testified by the large contribution of the
818 picophytoplankton to the protozoan diet (82%) (Table 2). Our result is consistent with the
819 finding of high grazing pressure of protozooplankton on picophytoplankton in other
820 Mediterranean coastal systems, such as the Bizerte Channel (84% P grazed d^{-1}) and Thau
821 Lagoon (71% P grazed d^{-1}) (Bec et al. 2005; Meddeb et al. 2018). Grazing and consumption
822 rates for the pico-sized fraction showed a decreased trend from S1 to S4, where the
823 protozooplankton community has clearly changed towards a dominance of heterotrophic and

824 mixotrophic dinoflagellates (Fig. 3a), concomitantly to the increase of large phytoplankton
825 proliferation (Table 1, Fig. 6). In S4, heterotrophic dinoflagellates were dominated by species
826 of *Protoperidinium* and *Oxytoxym* (Fig. 3d), which are known as potential grazers of chain-
827 forming diatoms and small diatoms, respectively (Seong et al. 2006; Girault et al. 2013; Kase
828 et al. 2021). Mixotrophic dinoflagellates were dominated by *Heterocapsa* and *Gymnodinium*
829 (Fig. 3c) that can feed on small diatoms and nano-sized cells (Du Yoo et al. 2009; Jeong et al.
830 2010). The loricate ciliates, mainly *Tintinnopsis*, *Helicostomella* and *Amphorellopsis*, which
831 commonly feed on large algae (Dolan et al. 2012; Yang et al. 2019), were more abundant in S4
832 than in other stations (Fig. 3a). All these herbivorous protozoans seemed to be tightly
833 associated, probably *via* feeding links, to nano- and micro-phytoplankton (CCA analysis,
834 Fig. 5). Thus, the highest consumption rates for nano- and micro-sized fractions were recorded
835 in S4. In this station, the protozoan's diet mainly relied on microphytoplankton (70%), which
836 accordingly was under the greatest protozooplankton grazing effect ($\sim 50\%$ P grazed d^{-1})
837 (Table 2). In S4, although metazoans displayed increased abundance and very high
838 consumption rates (Table 3; Fig. 4), their grazing impact (24% P grazed d^{-1}) remained lower
839 than that of protozooplankton, which daily consumed 48% of the $> 2\text{-}\mu\text{m}$ phytoplankton
840 production. Our finding is in good agreement with several authors stating that protozooplankton
841 is the major grazer of phytoplankton in productive waters dominated by large phytoplankton
842 (Aberle et al. 2007; Vargas et al. 2007; Meddeb et al. 2018; Yang et al. 2022). In S2 and S3,
843 nano- and micro-sized fractions formed large proportions of phytoplankton production and
844 biomass (Chl *a* and carbon). The contribution of picophytoplankton was not as low, reaching
845 $\sim 20\%$ of biomass and production of phytoplankton (Table 1; Fig. 6a). Accordingly,
846 microbivorous protozoans (i.e., aloricate ciliates, heterotrophic nanoflagellates and ebridian
847 flagellates) and herbivorous organisms (i.e., dinoflagellates) were both important components
848 of the protozooplankton in both stations (Fig. 3). This resulted in significant protozooplankton
849 top-down control on large and small phytoplankton in S2 and S3 (Table 2).

850 **4.5 Implication for carbon transfer pathway**

851 Anthropogenic nutrient inputs coupled with a complex hydrodynamic circulation in the
852 GG led to a clear spatial gradient in nutrients, associated with spatial changes in composition
853 and size structure of phytoplankton and selective zooplankton grazing. Microbivory and
854 herbivory would therefore have different roles in carbon transfer (Fig. 8), inducing different
855 trophic structures among stations.

856 In the northernmost station (S1), characterized by less nutrient-rich waters, the high
857 contribution of picophytoplankton (78%) to the primary production was associated with a high
858 microbivory of protozooplankton, representing 76% of carbon transfer. Therefore, the feeding
859 of the microbivorous protozoans played the main role in carbon transfer to upper consumers
860 (76%), as the herbivory of proto- and meta-zooplankton contributed together only 24% of the
861 channeled carbon. These trophic interactions suggest the prevalence of the microbial food web
862 in S1 (Legendre and Rassoulzadegan 1995; Sakka Hlaili et al. 2014), which is different from
863 the traditional view regarding the presence of the microbial pathway in oligotrophic waters.
864 Nevertheless, there is increasing evidence that microbial food web can be significant for
865 eutrophic coastal areas (Grami et al. 2008; Viñas et al. 2013; Paklar et al. 2020). The situation
866 has changed in S2 and S3, evidenced by the increased contribution of microphytoplankton to
867 primary production (55-78%), albeit the pico-sized cells remained as substantial contributor to
868 carbon production (15-24%). Parallel to the increase of large phytoplankton production, the
869 herbivory of proto- and metazooplankton increased, forming 75-80% of biogenic carbon
870 channeling. The consumption of picophytoplankton allowed 20-25% transfer of biogenic
871 carbon. Therefore, pico-, nano- and micro-phytoplankton potentially contributed to the
872 production of biogenic carbon, which reached higher consumers through the microbivory and
873 the herbivory of zooplankton. This suggests that a multivorous food web (Legendre and
874 Rassoulzadegan 1995) was present in both stations. The multivorous pathway was already

875 observed in other productive waters (Vargas and González 2004; Siokou-Frangou et al. 2010;
876 Masclaux et al. 2015; Meddeb et al. 2018). In the southernmost nutrient-rich station (S4), the
877 herbivorous food web seemed to be dominant, since the high primary production was mainly
878 sustained by microphytoplankton (~60%) and the biogenic carbon was mainly channeled to
879 higher trophic levels through the proto- and meta-zooplankton herbivory, which represented
880 94% of total carbon transfer. The herbivorous pathway was reported in several coastal waters
881 with high trophic level and abundant diatoms (Sakka Hlaili et al. 2008; Masclaux et al. 2015;
882 Meddeb et al. 2018; D’Alelio et al. 2022). The co-existence of different and contrasted
883 planktonic food webs during the same period in a highly productive system (i.e., the GG)
884 diverges from the traditional view that large phytoplankton and herbivorous pathway usually
885 dominate in nutrient-rich waters.

886 The spatial variability in planktonic food webs has an ecological implication, as biogenic
887 carbon can be exported with different efficiency to pelagos and benthos (Legendre and
888 Rassoulzadegan 1995; Sakka Hlaili et al. 2014). The microbial food web is known to be
889 inefficient in exporting organic matter, as most of the carbon is recycled and a small amount of
890 carbon can be exported to higher consumers or outside euphotic system (Legendre and
891 Rassoulzadegan 1995; Decembrini et al. 2009). This was consistent with the low vertical carbon
892 flux found in S1, which only accounted for 30% of total primary production. In the other
893 stations, the increase of primary production and of the dominance of large phytoplankton was
894 associated with the increase of vertical flux of organic particles (43-70% of primary
895 production). Furthermore, phytoplankton and zooplankton fecal material showed increased
896 contribution to the carbon flux toward the benthos (Fig. 7). This confirms that more biogenic
897 carbon is exported towards multivorous and herbivorous food webs (Legendre and
898 Rassoulzadegan 1995; Meddeb et al. 2019). The highest phytoplankton export to benthos was
899 observed in S4, coinciding with the largest contribution of microphytoplankton to primary

900 production. Conversely, the highest detritus sinking flux was not measured in S4 but in S3. This
901 indicates that some of the sinking detrital material in S3 could be transported from elsewhere.

902 The hydrodynamic and hydrological features of this area change across seasons, which
903 can impact the plankton dynamics (Bel Hassen et al. 2008, 2009; Makhoulf Belkahia et al.
904 2021) as well as planktonic interactions within the ecosystem. Thus, it is important to consider
905 the seasonal variations in further investigations to better understand the overall functioning of
906 this high dynamical and productive Mediterranean area.

907 **5 Conclusion**

908 Our study provides a detailed analysis of the plankton communities and the trophic links
909 between size fractionated phytoplankton and proto/metazooplankton in a nutrient-rich and
910 highly productive Mediterranean system, the GG. The complex hydrodynamic circulation
911 within the GG seemed to induce a spatial gradient in nutrient concentrations driving a spatial
912 changes in size structure and production of phytoplankton and trophic interactions, ultimately
913 leading to various food webs structure with different efficiency in carbon export. Our results
914 allows changing our traditional view concerning the dominance of the herbivorous pathway in
915 highly productive areas and evidencing the presence of a trophic pathway continuum, with other
916 types of planktonic food webs. Our study gives relevant insight on the functional roles of
917 phytoplankton size fractions, proto- and meta-zooplankton and proposes a first description of
918 carbon transfer pathways in the Southeastern Mediterranean area, where such information is
919 deficient. These results can improve the understanding of the dynamics of marine food webs,
920 particularly in ecosystems strongly impacted by anthropogenic nutrient inputs and strong
921 hydrodynamics.

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924 **References**

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