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1 **A new type of plankton food web functioning in coastal waters revealed by coupling**
2 **Monte Carlo Markov Chain Linear Inverse method and Ecological Network Analysis**

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29

30 **Abstract**

31 Plankton food webs (PFW) typology is based on different categories of functioning, according
32 to the dominant processes and the role played by heterotrophic bacteria, small vs large
33 phytoplankton, and small vs large zooplankton. Investigating the structure and the function of
34 planktonic food webs in two SW Mediterranean waters (inshore and marine sites) at four
35 seasons, using inverse (LIM-MCMC) and ecological network (ENA) analyses, we identified a
36 new type of food web, called the “bacterial multivorous food web”. This food web adds to the
37 conventional trophic continuum as previously reported. The “bacterial multivorous food web”
38 present in winter showed the lowest primary production among seasons, but highest bacterial
39 production. Several food web ratios characterized this new typology e.g. picophytoplankton
40 net primary production to total primary production varied from 0.20 to 0.28; bacterial to
41 primary production ratio is higher than values reported in global scale ($\cong 1$); bacterial net
42 production to the potential protozoan prey net production was high (>0.2). In this special food
43 web, carbon was mostly recycled, with a moderate fraction channeled to deep waters, which
44 lead to a higher retention of carbon inside the ecosystem. This winter PFW also seemed to be
45 the most organized, specialized, stable and mature, as related to common interpretations of
46 ENA. The spring was characterized by herbivorous food web, with highest activity coinciding
47 with low stability. Although less usual, the herbivorous pathway was also observed during
48 summer, in inshore waters. The autumn food webs, which functioned as multivorous or
49 microbial food webs, appeared to be stable and mature. Finally, our study demonstrates the
50 usefulness of food web models derived ratios combined with ecological network analysis
51 indices to conduct evaluation of the structure and functioning of ecosystems and potentially to
52 support management decisions in marine environment.

53

54 **Keywords:** food web modeling, network analysis, trophic structure, coastal waters, seasonal
55 variations, ecology, bacterial multivorous food web.

56

57 **1. Introduction**

58 Marine biological productivity depends on the magnitude of phytoplankton production
59 and its trophic transfer through food webs. The structure and the functioning of the food web
60 can in turn influence the energy flow and the carbon cycling in marine ecosystems (Vargas et
61 al., 2007). In addition, the structure of plankton food webs can vary greatly over seasons,
62 since seasonal change in environmental conditions (mainly the availability of nutrients, light
63 and hydrological conditions) can affect the abundance, the size structure and the composition
64 of plankton communities as well as the tropho-dynamics within the plankton system (Sankar
65 and Padmavathi, 2012; Vajravelu et al., 2017; Rasconi et al., 2017). For temperate regions,
66 there exist a conventional scheme describing the food web dynamics over seasons (Legendre
67 and Rassoulzadegan, 1995). The increasing light during spring and the stratification of the
68 water column, which has already been enriched by nutrients during winter mixing, lead to
69 phytoplankton blooms dominated by micro-sized algae (i.e. diatoms $>10\ \mu\text{m}$). This high
70 production is consumed by herbivorous zooplankton (i.e. copepods) and efficiently channeled
71 to higher trophic levels, or exported to deeper layers (Ryther, 1969; Turner, 2001). In
72 summer, the persistent water column stability causes a depletion of nutrients in the surface
73 waters, causing a decrease in production and a shift in the primary producers, dominated by
74 pico- and nano-sized algae and bacteria. This production is consumed by microbivorous
75 zooplankton (i.e. heterotrophic nanoflagellates and microzooplankton) and transferred to
76 higher consumers through the microbial food web (Calbet and Landry, 2004). In autumn,
77 storms can erode water column stability and amend nutrients in the surface water, resulting in
78 a small autumnal phytoplankton bloom that rapidly decline as light decreases. In this
79 situation, both the microbial pathways and grazing on larger phytoplankton are important,
80 resulting in the multivorous food web (Legendre and Rassoulzadegan, 1995). In winter, under
81 mixed water conditions, the food web can typically function as a microbial pathway (Marquis
82 et al., 2007). Recently, Sakka Hlaili et al. (2014), have proposed two new food webs, based on
83 modeling data of planktonic food webs in oceanic and coastal regions, which adds to the
84 continuum of food web dynamics by Legendre and Rassoulzadegan (1995). They identified
85 the “phyto-microbial food web”, where microzooplankton feeding on phytoplankton is more
86 important than grazing on bacteria, and the “poly-microbial food web”, where
87 microzooplankton consume more or less equally the various types of food.

88 In the Mediterranean Sea, open waters (e.g. Aegean Sea, Levantine basin and Ligurian
89 Sea) are basically oligotrophic supporting low phytoplankton biomass ($<0.2\ \mu\text{g Chl } a\ \text{l}^{-1}$) and

90 primary production ($59\text{--}150 \text{ g C m}^{-2} \text{ y}^{-1}$, Siokou-Frangou et al., 2010). A large part of fixed
91 carbon is channeled to higher trophic levels through microbial organisms, as small-size
92 autotrophs and heterotrophs are dominant in most seasons (Siokou-Frangou et al., 2002;
93 Zervoudaki et al., 2011; Giannakourou et al., 2014). On the contrary, the coastal waters are
94 more productive environments ($200\text{--}400 \text{ g C m}^{-2} \text{ y}^{-1}$, Nixon, 1995), mainly due to the high
95 nutrient availability that promotes intense spring diatom-blooms. Here, phytoplankton
96 production is efficiently transferred to higher trophic levels through the herbivorous food web
97 (Caroppo et al., 2000; Auger et al., 2011; Alekseenko et al., 2014).

98 Establishing the food webs structure in the marine planktonic community is one of the
99 most important steps to predict the ecosystem functioning and to understand the cycling of
100 materials and flows of energy. The structure of the food web is intimately linked to the size
101 structure of the primary producers, which itself depends on the hydrological conditions that
102 control nutrient availability and stratification (Thingstad and Rassoulzadegan, 1999; Irigoien
103 et al., 2005; Marquis et al., 2007). In the present study, an inverse analysis (Linear Inverse
104 Analyses, LIM) approach was used to examine food web interactions in two coastal regions in
105 Southern Mediterranean, the Bay and the Channel of Bizerte in Northern Tunisia. Inverse
106 method, evolved from the physical sciences (Vézina and Platt, 1988), has been used to solve
107 the problem of quantification of missing carbon flows through the plankton food web.
108 Effectively, marine food webs are complex systems with various interactions that are difficult
109 to estimate directly or entirely in field. The LIM approach has been applied to describe food
110 web interactions in various marine ecosystems, as the Gulf of Riga, the Bay of Biscay, the
111 Lagoon of Takapoto, the Northeast Subarctic Pacific and the Baltic Sea (Donali et al., 1999;
112 Vézina and Savenkoff, 1999; Niquil et al., 1998, 2001; Marquis et al., 2007). In the
113 Mediterranean Sea, different modeling analyses have been used to examine the functioning
114 and the structure of food webs and related driving factors. Ecopath with Ecosim (EWE)
115 approach (Coll and Libralato, 2012) is the most used approach in Mediterranean regions,
116 including the Gulf of Gabès (South of Tunisia, Hattab et al., 2013), the Western, Central and
117 Eastern Mediterranean Sea (Tecchio et al., 2015, Heymans et al., 2014), and for the entire
118 Mediterranean Sea (Piroddi et al., 2015, 2017). The three dimensional modeling approach has
119 also been used in the Northwestern Mediterranean basin (Herrmann et al., 2013; Auger et al.,
120 2014) and the Gulf of Lion (Auger et al., 2011). The LIM have been applied in some
121 Mediterranean waters, such as, the Lagoon of Bizerte (Grami et al., 2008) and coastal waters
122 of the Mediterranean Sea (Olsen et al., 2001). This method was modified into the Monte
123 Carlo Markov Chain Linear Inverse method (LIM-MCMC; Van den Meersche et al., 2009).

124 The LIM-MCMC, allows us to estimate the uncertainty around flows, to perform statistical
125 tests, to compare many marine systems over different seasons and has been applied in many
126 marine ecosystems (De Laender et al., 2010; Grami et al., 2011; Saint-Béat et al., 2014;
127 Chaalali et al., 2015). Nevertheless, the food web structure and the trophic-interaction
128 functioning have so far been poorly described for the southern Mediterranean regions, despite
129 the high plankton diversity and the pronounced productivity observed there (Sakka Hlaili et
130 al., 2008, Bel Hassen et al., 2008; Hafferssas and Seridji, 2010). Up to date, the food web of
131 Bizerte Lagoon has been modeled during summer (Grami et al., 2008), showing an efficient
132 transfer of primary production through the herbivory of microzooplankton. Also, the food
133 webs of the Bay, Channel and Lagoon of Bizerte has been modelled during spring (Meddeb et
134 al., 2018). However, these studies were based on data collected during one season only, and
135 there exist little knowledge about the seasonal variability in food web structures and dynamics
136 in this region and how they fit with the typology of plankton functioning. Using the LIM-
137 MCMC method, our study aims to describe the seasonal dynamics of plankton food webs in
138 the Bay and the Channel of Bizerte in relation to hydrological conditions. We used the ENA
139 to characterize some functional properties of the system and to compare seasonal differences
140 in stress levels and stability of the food webs, two attributes of primary importance in the
141 objective of implementing an ecosystem based management of this environment.

142 **2. Materials and Methods**

143 **2.1. Study areas**

144 The Bay of Bizerte is an important fishing region located in the south-western
145 Mediterranean basin (Fig. 1), with depth varying from 16 to 20 m. The Bay is an open
146 embayment facing the Western Mediterranean basin, which is largely influenced by surface
147 Modified Atlantic Water (MAW) (Millot, 1987, 1999). Throughout the year, this water
148 crosses the Straits of Gibraltar and runs along the North African coasts and reaches the
149 northern Tunisian coasts before branching into two veins, one towards the eastern basin and
150 one towards the Tyrrhenian Sea. The MAW caused a mixed layer of 40–50 m with salinity
151 increasing from Gibraltar (36 psu) to the Algera-Provençal basin (38psu). Consequently, the
152 hydrological structure of the water column in the Bay seems to vary little among seasons. The
153 Bay is located in the semi-humid bioclimatic zone, with significant periods of rainfall
154 (especially in winter) causing an important inputs of terrestrial nutrients. Nutrients are
155 commonly abundant in the surface layers throughout the year (0.1–0.7 P μM ; 1–3.5 N μM ;
156 0.5–2.25 Si μM) (Sahraoui et al., 2009). Seasonal dynamics has previously been shown for
157 phytoplankton, with high chlorophyll biomass (2–4 $\mu\text{g l}^{-1}$) during spring and summer, and

158 lower values in the other seasons ($<1.5 \mu\text{g l}^{-1}$). This coincided with the predominance of
159 diatoms ($10^5 \text{ cells l}^{-1}$) in spring and summer, and of nanoflagellates during the rest of the year
160 (Sahraoui et al., 2009, Meddeb et al., 2018). Diatoms are also present in autumn and winter
161 and may contribute up to 20–35% to the phytoplankton assemblage (Sahraoui et al., 2009).
162 The Channel of Bizerte, 7 km long, 300 m wide and 12 m deep, connects the Lagoon of
163 Bizerte to the Bay, and is therefore influenced by marine inflow from the Bay, particularly
164 during summers.

165 The Lagoon is the most important Tunisian site of fisheries and bivalve culture. The
166 tidal regime in the region is dominated by a semi-diurnal cycle with a low amplitude (<15
167 cm), but the current velocities can reach 1 m s^{-1} in the middle of the Channel (Harzallah,
168 2003; Béjaoui et al., 2008). The Lagoon receives a large amount of freshwater from several
169 rivers and from the big lake of Ichkeul due to strong rains during winter and spring, which
170 also influences the Channel during these seasons (Ben Ismail et al., 2012; Zaaboub et al.,
171 2015). In addition, by receiving high nutrient inputs and effluents from land from several
172 anthropogenic activities ($1\text{--}11.5 \text{ P } \mu\text{M}$; $3.5\text{--}55 \text{ N } \mu\text{M}$; $2\text{--}11 \text{ Si } \mu\text{M}$, Bouchouicha et al., 2012),
173 the Channel is considered as a more eutrophied system than the Bay. Pronounced diatom
174 blooms ($10^6 \text{ cells l}^{-1}$) were previously observed in the Channel during summer. Diatoms are
175 also present in spring together with nanoflagellates. These latter predominated during other
176 seasons (Bouchouicha et al., 2012).

177 **2.2. Sampling and hydrological structure of the water column**

178 Data for the study were obtained from several surveys conducted during four seasons
179 (spring, summer, and autumn 2012, and winter 2013) at a marine station located in the Bay
180 (station B, $37^{\circ}16'54'' \text{ N}, 9^{\circ}53'42'' \text{ E}$) and an inshore station in the Channel (station C,
181 $37^{\circ}15'04'' \text{ N}, 9^{\circ}52'34'' \text{ E}$) (Fig.1). During each season, the sampling was carried out at four
182 depths of each station (0.5, 2.5, 5/6 and 8/16 m) using an acid-washed 2.5-L plastic water
183 sampler (Hydro-Bios). Sampled water was filtered through a $200 \mu\text{m}$ mesh screen to remove
184 meso- and macrozooplankton (except water used for DOC determination) and stored in
185 polyethylene containers until analyses. Metazooplankton, for two size classes ($200\text{--}700 \mu\text{m}$
186 and $> 700 \mu\text{m}$), were sampled using two vertical net tows with $200 \mu\text{m}$ and $700 \mu\text{m}$ screen
187 mesh. Vertical profiles of salinity and temperature were measured *in situ* with a
188 microprocessor conductivity meter (LF 196) (Fig. 2).

189 Nutrient concentrations [NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} and Si (OH)_4] were measured at the
190 four depth of each station (0.5, 2.5, 5/6 and 8/16 m), following the spectrophotometric method
191 (Parsons et al., 1984).

192 **2.3. Linear Inverse Method-Monte Carlo Markov Chain analysis (LIM-MCMC)**

193 To have a complete quantification of the processes in the food web, we used the inverse
194 analysis method to estimate the unknown flows from the known ones. The LIM-MCMC
195 method (Van Den Meersche et al., 2009), derived from the inverse analysis method of Vézina
196 and Platt (1988), was adopted to reconstruct trophic carbon flows through the eight planktonic
197 food webs. This approach is based on four steps: (i) building an *a priori* model including all
198 possible flows between the considered compartments or between the compartments and the
199 outside; (ii) setting mass-balance between flows, for each compartment, as equalities; (iii)
200 setting two groups of inequalities, the first ones based on *in situ* calculated flows, and the
201 second ones consists on a number of biological constraints taken from the literature, to reduce
202 the range of possible values for each flow; and (iv) calculating a large sample of possible
203 solutions for unknown flows.

204 **2.3.1. *A priori* model**

205 The *a priori* model describes all possible carbon flows among the trophic
206 compartments. For all seasons, the model (Fig. 3) includes nine compartments: heterotrophic
207 bacteria (bac), picophytoplankton (pic, $<2 \mu\text{m}$), nanophytoplankton (nan, $2\text{-}10 \mu\text{m}$),
208 microphytoplankton (mic, $10\text{-}200 \mu\text{m}$), protozooplankton (pro = heterotrophic
209 nanoflagellates, dinoflagellates and ciliates, $<200 \mu\text{m}$), metazooplankton $200\text{-}700 \mu\text{m}$ (met1),
210 metazooplankton $>700 \mu\text{m}$ (met2), dissolved organic carbon (doc) and detritus (det). Forty-
211 three flows were considered in the *a priori* model of each season (Fig. 3, Table 3).

212 The gross primary production (gpp) of the three phytoplankton size fractions (pic, nan,
213 and mic) is the only source of carbon input to the network. Carbon loss is driven by
214 respiration of all living compartments and sinking of all compartments except
215 protozooplankton, picophytoplankton and bacteria. We assumed that the very small size of pic
216 and bac did not allow them to generate sinking flux. Detritus dissolution, phytoplankton
217 exudation and zooplankton excretion (i.e. by pro, met1 and met2) contributed to the doc pool.
218 Doc was only used by bacteria, since other potential consumers of doc (such as
219 choanoflagellates) were absent in our samples. All living compartments, except bac and pic,
220 contributed to the detritus pool through mortality, production of feces by metazooplankton
221 (i.e. met1 and met2) and zooplankton sloppy feeding. Protozooplankton grazed on bac, pic
222 and nan, but also on mic, since they have been reported as potential grazers on large preys in
223 several coastal areas, including our study sites (Meddeb et al., 2018). Metazooplankton,
224 known as inefficient grazers on particles $< 5 \mu\text{m}$ (Fortier et al., 1994), consumed nano- and
225 microphytoplankton, but not picophytoplankton. Protozooplankton and detritus represented

226 another food source for the two size classes of metazooplankton (met1 and met2), while large
227 metazoans (met2) consumed smaller ones (met1).

228 **2.3.2. Equalities and inequalities**

229 Establishing the set of linear equalities is an essential step to obtain the mass balances of
230 the network. If the mass of the compartment is stable during the period considered, the sum of
231 the flows entering into this compartment should equal to the sum of the flows leaving it. The
232 mass balance equations for all compartments are given in Table 1.

233 Imposing linear inequalities for each unknown flow helps to reduce the range of
234 possible solutions. Two ranges of inequalities were adopted, as previously considered in
235 Meddeb et al. (2018). Firstly, a bound of an upper and lower values for each flow were
236 considered by the calculation of a confidence interval around the field data, i.e. using the
237 minimum and maximum of the average value of each flows estimated *in situ* (Table 2). More
238 details are given in Meddeb et al. (2018).

239 A second group of constraints was adopted to constrain the unknown flows. For all
240 seasons, the inequalities used for the Channel and the Bay models were described in several
241 previous works (Pace et al., 1984; Vézina and Platt, 1988; Vézina and Pace, 1994; Vézina and
242 Savenkoff, 1999; Steinberg et al., 2000; Vézina et al., 2000; Vézina and Pahlow, 2003). They
243 constrain the respiration of bacteria, phytoplankton, protozooplankton and metazooplankton;
244 the doc production by phytoplankton, bacteria and zooplankton; the growth efficiency of
245 bacteria and zooplankton; the assimilation efficiency of zooplankton; the detritus production
246 by zooplankton and the dissolution of detritus (Table 4).

247 **2.3.4. Solutions**

248 The last step of the inverse analysis was the calculation of unknown flows. The
249 estimations of each unknown flow were obtained by the LIM-MCMC method, based on the
250 mirror technique defined by Van Den Meersche et al. (2009). A jump value of $10 \text{ mgC m}^{-2} \text{ d}^{-1}$
251 and 300000 iterations were adopted to run the models in order to optimize the coverage of all
252 the possible solutions (i.e. correct polytope exploration). A Matlab[®] translation by Alain
253 Vézina and Lauriane Campo of the R-CRAN project package LIM-Solve was used (Van den
254 Meersche et al., 2009). More details on the method are available in Van Den Meersche et al.
255 (2009) and Niquil et al. (2012).

256 **2.4. Data**

257 Data used in the eight models were collected during seasonal samplings at the Bay and
258 the Channel. These data permitted to determine 14 carbon flows for each model. In each sites,
259 sampled water has served for the determination of doc and particulate organic carbon (POC)

260 concentrations as well as the plankton abundance and diversity. See Meddeb et al. (2018) for
261 more details on the preservation of samples and analyses. Briefly, Samples for doc
262 measurement were filtered on sterilized 0.2 μm polycarbonate filters before being analyzed
263 using a Shimadzu TOC-5000 carbon analyser (Knap et al., 1993). The carbon concentration
264 of doc was obtained considering that 1 μM of doc is equal to 12 mg C m^{-3} (Grami et al., 2008;
265 Meddeb et al., 2018). POC was analysed on a CHN elemental analyser (Perkin–Elmer 2400)
266 after filtration of samples through pre-combusted (at 450°C, during 2 h) GF/F Whatman
267 filters (21 mm) (Knap et al., 1996).

268 Heterotrophic bacteria and picophytoplankton (pic= prokaryotes and eukaryotes) were
269 enumerated under a CETI Topic-T epifluorescence microscope on samples filtered through
270 0.22 μm black polycarbonate filters (Nuclepore) laid over 0.45 μm nitrocellulose backing
271 filters (Millipore) (Parsons et al., 1984; Mac Isaac and Stockner, 1993). The mean cell volume
272 of bac and pic was converted into cell carbon using specific conversion factors, 0.35 $\text{pg C } \mu\text{m}^{-3}$
273 3 for bacteria (Bjørnsen, 1986), 0.22 $\text{pg C } \mu\text{m}^{-3}$ for prokaryotic pic (Søndergaard et al., 1991)
274 and 0.22 pg C cell^{-1} for eukaryotic pic (Mullin et al., 1966). Phytoplankton (nan and mic) and
275 protozooplankton were counted and identified under an inverted microscope (Lund et al.,
276 1958) on 100 ml settled samples fixed with 3% acid Lugol solution and 5% alkaline Lugol
277 solution, respectively. The mean cell volume of each taxon of phytoplankton and
278 protozooplankton was determined by applying standard geometric shape, as proposed by
279 Hillebrand et al. (1999). Then, the mean cell volumes were converted to cell carbon using
280 specific formula or factors (see Table 1, Meddeb et al., 2018).

281 Metazooplankton samples were preserved in borate-buffered formalin (5% final
282 concentration) for identification and counts of organisms under a dissecting stereomicroscope
283 (Leica). For each metazoan organism, the length and the width were converted into carbon
284 content using conversion factors corresponding to each taxonomic group, as detailed in
285 Meddeb et al. (2018). For each plankton group (bac, pic, nan, mic, pro, met1 and met2), the
286 carbon biomass was estimated by multiplying their carbon content by their corresponding
287 abundances. The detrital organic carbon (det) was estimated as total POC, determined from
288 water column, minus the total carbon biomass of all plankton communities. Finally, the areal
289 carbon stocks (mg C m^{-2}) for each living and non-living compartments were calculated by
290 vertically integrating the carbon biomass calculated for each sampling depth. More details of
291 calculations are given in Meddeb et al. (2018).

292 The gross production rate of size-fractionated phytoplankton (pic, nan and mic) and
293 bacteria as well as consumption rate of these living components by protozooplankton were
294 seasonally assessed at each sampling depth of each site by *in situ* dilution experiments
295 (Landry and Hassett, 1982). This method is relatively simple to set up, it minimizes the
296 manipulation and disruption of the micrograzer population and is an appropriate technique for
297 determining total microzooplankton grazing activity (Sakka Hlaili et al., 2008; Grattepanche
298 et al., 2011). Details for experimental procedure and calculation are provided in Meddeb et al.
299 (2018) and Meddeb et al. (submitted).

300 Dilution experiments could be described as mixing free-particle sea water (filtered on 0.2
301 μm) with pre-filtered water on 200 μm mesh net (to remove meso- and macrozooplankton
302 grazing effect) to give four dilution factors (100 %, 75 %, 50 % and 25 %). Each dilution
303 mixture was then distributed into three clean 2L polycarbonate bottles, incubated *in situ* at the
304 sampling depths fortnight. The estimated rates k and g were used to calculate gross production
305 rates for phytoplankton and bacteria (P , $\text{mg C m}^{-3} \text{ d}^{-1}$) and their consumption rates (G , mg C
306 $\text{m}^{-3} \text{ d}^{-1}$) as suggested by Moigis (2000) and in more recent works (Sakka Hlaili et al., 2008,
307 Grattepanche et al., 2011):

$$P = k \times C_0 [e^{(k-g)t} - 1] / (k - g) \times t$$

$$G = g \times C_0 [e^{(k-g)t} - 1] / (k - g) \times t$$

308 where C_0 (mg C m^{-3}) is the initial biomass of phytoplankton or bacteria, k is the growth rates
309 of bacteria and size-fractionated phytoplankton (d^{-1}), g is the grazing rates by
310 protozooplankton (d^{-1}) and t (d) is the incubation time (1 d).

311 The areal rates ($\text{mg C m}^{-2} \text{ d}^{-1}$) of production (P) and consumption (G) were determined
312 by integrating the values obtained from the four sampling depths.

313 The consumption rates of phytoplankton (nan and mic) by metazooplankton (met1 and
314 met2) were estimated by gut content experiments (Slaughter et al., 2006), which were
315 conducted seasonally at each sites. The description of the experiment procedure and the
316 calculation were detailed in Meddeb et al. (submitted).

317 Metazooplankton vertically sampled from bottom to surface in each site allowed the
318 calculation of phytoplankton grazing by two size fractions of metazoa (200-700 μm and >700
319 μm). Subsamples (0.5L or 1L) were filtered (47 mm GF/F), homogenized (90% acetone) and
320 filtered through 25 mm GF/F filters to remove pulp. The filtrates containing extracted gut

321 pigment were measured before and after acidification with 10% hydrochloric acid using the
322 spectrophotometric method of Lorenzen (1967).

323 Gut pigment content (GP, mg pigment m⁻³) was calculated using the following equation:

$$GP = (GP_{\text{sub}} \times v) / (F \times V_{\text{net}})$$

324 where, GP_{sub} is the gut pigment concentration (mg pigment m⁻³) from the subsample, v (m³) is
325 the volume of the subsample, F is the fraction of subsample processed for gut pigment
326 content, and V_{net} (m³) is the total volume of water filtered during each net tow.

327 Metazooplankton grazing rate (GM, mg C m⁻³ d⁻¹) was calculated as:

$$GM = GP \times WC \times C:Chl\ a$$

328 where GP (mg pigment m⁻³) is the concentration of gut pigment, C:Chl *a* is the
329 depth-averaged C:Chl *a* ratio determined for >2 μm phytoplankton (i.e. nano- and
330 microphytoplankton) at each station, and WC (d⁻¹) is the portion of water cleared per day.

331 Finally, GM was multiplied by the vertical depth of the net tow at each site to estimate the
332 areal rate of consumption of metazooplankton (GM_C, mg C m⁻² d⁻¹).

333 Sediment traps were used to measure sinking rates of particles and faecal pellets, during
334 each season and at each site, as described in Meddeb et al. (2018).

335 **2.5. Ecological Network Analysis**

336 Ecological network analysis (Ulanowicz, 1997) was used to describe and to characterize
337 the structural properties and function of plankton food webs resulted from the LIM-MCMC
338 analysis. The MATLAB[®] algorithms, written by Carole Lebreton and Markus Schartau
339 (GKSS Research Center, Geesthacht Germany), were used to calculate the indices that
340 characterize food webs in term of activity, organization, specialization, recycling, maturity
341 and stability (Table 5). The ENA indices used in this work as trophic functioning indicators
342 were the total system throughput (TST), the ascendancy (A), the development capacity (DC),
343 the relative ascendancy (A/DC), the average path length (APL) the Finn cycling index (FCI)
344 and the detritivory/herbivory ratio (D/H). The definition and the formulae calculation of these
345 indices are presented in Table 5.

346 **2.6. Cliff's δ test for comparing network indices between seasons**

347 The statistical comparison between the four seasons, concerning the set of indices
348 calculated under Matlab (TST, DC, A, A/DC, APL, FCI and D/H) was performed with Cliff's
349 δ test, which is usually used when having large sample sizes (here 300000 values for each
350 flow) (Tecchio et al., 2016). For each ENA index, six pairwise comparisons were performed
351 (comparing seasons) using the effsize package under R (version 3.4.3, www.r-project.org).

352 Then, the following values were used to define small, medium, and large effects according to
353 Romano (2006). No p values can be calculated based on delta.

354 **3. Results**

355 **3.1. Hydrodynamic status**

356 Water temperatures, which were similar among stations and over depths, showed a
357 seasonal cycle, ranging between a minimum in winter (12–13.7 °C) and a maximum in
358 summer (25.7–27.1 °C). In the Bay, the salinity showed little variation within and between
359 depths and seasons (36.9–37.4 psu). The water column of the Channel was vertically
360 homogenous regarding the salinity during summer, autumn and winter (36.5–37.5 psu). In
361 contrast, there was a haline stratification of the inshore water during spring due to low saline
362 surface water coming from the Bizerte Lagoon. During this season, there was an exceptional
363 decrease of salinity in the Lagoon (14–24 psu) caused by important river runoff associated
364 with a large amount of rain during the winter 2012 (213 mm, INM, 2013). Further, high levels
365 of nutrients were recorded in the Channel (Fig. 4). In both stations, pronounced
366 concentrations of NO_2^- , NO_3^+ , and NH_4^+ were detected in spring, summer and autumn (10–
367 24 μM) compared to the winter (3–4 μM) (Fig. 4A). PO_4^{3-} (0.14–0.99 μM) and Si(OH)_4 (0.84–
368 2.86 μM) were available throughout the year in both stations (Fig. 4 B, C).

369 **3.2. Primary and bacterial production**

370 The LIM-MCMC analysis allowed the estimation of 44 carbon flows for each study site
371 during each season (Table 3).

372 The primary production was relatively high during spring (966–727 $\text{mg C m}^{-2} \text{d}^{-1}$), moderate
373 in summer and autumn (394–571 $\text{mg C m}^{-2} \text{d}^{-1}$) and low in winter (160–256 $\text{mg C m}^{-2} \text{d}^{-1}$)
374 (Fig. 5). During most seasons and in both stations, microphytoplankton (mic) contributed
375 significantly to total production (Bay: 48–84%; Channel: 60–82%), except in the inshore
376 station during autumn, when the proportion of picophytoplankton production was high 60%.
377 During the rest of the year, the picophytoplankton contribution ranged from 10 to 29%.
378 Nanophytoplankton production had low proportion during spring-summer (8–29%) and even
379 lower (0.29–3.03%) in autumn-winter in all stations.

380 In both sites, bacterial production was low from spring to autumn (48–117 $\text{mg C m}^{-2} \text{d}^{-1}$)
381 and significantly increased in winter (135–274 $\text{mg C m}^{-2} \text{d}^{-1}$). Bacterial production was very
382 low relative to primary production (5 to 15 times less) in most cases, but in winter, it almost
383 equaled the phytoplankton production at inshore and marine stations.

384 **3.3. Carbon outflows**

385 Respiration constituted the major carbon outflow from the eight model systems, with
386 higher proportion during winter (66–84% of gross primary production) compared to the other
387 seasons (45–53%) (Fig. 6). Carbon sinking contributed from 26–31% and 14–29 % of gross
388 primary production, respectively, in the inshore and marine stations (Fig. 6A, B). Added to
389 these two carbon loss pathways, the remaining carbon could be available for trophic transfer
390 *via* the predation on metazooplankton. This trophic transfer was high during spring, summer
391 and autumn (21–31% of gross primary production), but did not exceed 2% in winter at both
392 stations (Fig. 6A, B).

393 **3.4. Carbon flows to grazers**

394 In the eight plankton food webs, the diet of protozooplankton was mainly composed of
395 autotrophs during spring (90–97%), summer (86–88%) and autumn (86–93%), but equally
396 shared between bacteria and phytoplankton in winter (i.e. mic and pic) (Fig.7A).
397 Microphytoplankton formed the main prey of protozoa in both stations during spring (73–
398 77% of total diet) and summer (36–47% of total diet). During autumn, microalgae remained
399 the major food source in the marine station (66% of total diet), but in the inshore food web,
400 picophytoplankton supplied 67% of carbon demand. The proportion of nanophytoplankton to
401 protozoan diet was low in spring and summer (3–22 %) and even lower during autumn and
402 winter (<2%).

403 In both sites, metazooplankton was mainly carnivorous, since protozooplankton and
404 small metazoan (met1) formed their major food source in all seasons (40–62% of total diet).
405 Herbivory of metazooplankton was low (<15% of total diet), but increased slightly (20–25%
406 of total diet) in some cases (i.e. in spring and winter, in the inshore and marine stations).
407 Detritus formed almost half of the food for the mesozooplankton during summer. The detritus
408 contributed little to the metazoan diet in spring and autumn (26–45%) and even lower in
409 winter (15–20%) (Fig. 7B).

410 **3.5. Structural and functional proprieties of food webs**

411 The total system throughput (TST) varied proportionally to the total input in the
412 plankton food web system. This index, related to the total activity of the system, was high in
413 spring (2934–3818 mg C m⁻² d⁻¹), moderate in summer and autumn (1733–1743 and 1710–
414 2384 mg C m⁻² d⁻¹) and low in winter (879–1562 mg C m⁻² d⁻¹) (Fig. 8). The two food webs in
415 spring exhibited the highest development capacity (DC)(Channel: 11.106 mg C m⁻² d⁻¹; Bay:
416 8489 mg C m⁻² d⁻¹, Fig. 8, Table 6) compared to the other seasons (2634–6951 mg C m⁻² d⁻¹)
417 (Fig. 8). The ascendancy showed similar pattern as DC, with higher values in spring (4838–
418 6054 mg C m⁻² d⁻¹) in comparison to the rest of the year (1566–3963 mg C m⁻² d⁻¹, Fig. 8,

419 Table 6). The A/DC ratio, which quantifies the degree of organization (information) of the
420 system, reached higher values in winter (59.4–59.6%, Fig. 8) and decreased from autumn
421 (57–58%) to spring (54.5–56%) and summer (53.4–53.9%) (Fig. 8). The highest values of
422 APL, that quantifies the capacity of retention of the system, were detected in winter (4.48–
423 5.09) in both sites, while the lowest ones were recorded during spring in both sites (2.95–
424 3.03) and during summer in the Channel (3.20). Similarly, the Finn cycling index was highest
425 in winter (41–46%). During autumn (for both sites) and summer (for the channel), this index
426 reached higher values (16–17%) than in spring (for both sites) and summer (for the Bay) (13–
427 14%) (Fig. 8, Table 6). Finally, the detritivory/herbivory ratio (D/H) showed significant
428 increases during summer (0.59–0.66, Fig. 8, Table 6) in both sites and moderate (0.22–0.48,
429 Fig. 8, Table 6) to lower values (0.05–0.12, Fig. 8, Table 6) were observed respectively
430 during the spring, autumn and winter in all study sites.

431 **4. Discussion**

432 **4.1. Hydrodynamics and nutritional status over seasons**

433 The Bay of Bizerte is characterized by marine water mainly originated from the surface
434 Modified Atlantic Water (MAW) (Millot, 1987, 1999), which flow into the Bay throughout
435 the year. Even in winter, the freshwater discharges from the rivers surrounding the Lagoon of
436 Bizerte only partly reaches the Bay. These conditions can lead to little variation of
437 hydrological structure throughout the year. Consequently, nutrients were available throughout
438 the year inside the Bay. In contrast, the Channel was influenced both by the marine water
439 from the Bay (mostly in summer) and by lagoonal water (mostly in winter). Hence, the spring
440 situation within the Channel was characterized by a strong halocline resulting from low saline
441 surface water coming from the Lagoon of Bizerte, which was caused by an important river
442 runoff during late winter (Fig.2A). In summer, the direction of the current was reversed, with
443 an inflow of marine water from the Bay resulting in well mixed water (Fig. 2A). In autumn
444 vertical mixing became more important, resulting in a well-mixed water column rich in
445 nutrients (Fig. 3). This hydrological situation was maintained in winter with lower nutrient
446 levels (particularly for nitrogenous nutrients).

447 **4.2. Description of the new type of planktonic food web**

448 To identify the dominant trophic pathway in marine environment, Sakka Hlaili et al.
449 (2014) have proposed a specific ratio: the ratio of picophytoplankton net production to total
450 phytoplankton net production (R7 ratio). This ratio was proposed by the authors to
451 discriminate between herbivorous ($R7 \leq 0.1$), multivorous ($R7: 0.1-0.6$), and microbial food
452 webs ($R7 \geq 0.6$). Based on this ratio, the spring food webs encountered in the Channel ($R7 =$

453 0.1) acted almost as a multivorous structure with a tendency towards herbivorous one, and the
454 Bay ($R7 = 0.07$) functioned as herbivorous pathways. During the summer food web
455 functioned as herbivorous pathway in the Channel ($R7 = 0.1$), and as multivorous in the Bay
456 ($R7 = 0.27$). The situation in autumn was different between the sites (Fig. 9A, B). In the Bay,
457 the food web did not change much in structure from that in summer and continued to function
458 as a multivorous pathway ($R7 = 0.21$), while, it functioned approximately as a microbial
459 pathway in the Channel ($R7 = 0.7$). More explanations in the evolution of food webs in both
460 sites during spring, summer and autumn were reported in the supplement annex.

461 During winter, the intensification of vertical mixing and the low light condition in both
462 sites were accompanied with a sharp decrease of primary production, which reached the
463 lowest rates registered throughout the year ($160\text{--}256 \text{ mg C m}^{-2} \text{ d}^{-1}$, Fig. 9). These levels were
464 very low compared to the one found in coastal areas. Instead, the bacterial production
465 increased (especially in the Bay) and almost equalled the primary production (bacterial to
466 primary production ratio, $PB:PP = 0.85\text{--}1.07$). This differed from that observed for the other
467 seasons ($PB:PP$ ratio $0.06\text{--}0.21$), which were in the range of values found in other coastal
468 areas, such as the Arcachon Bay (0.17 , Tortajada et al., 2012: spring), the Bay of Biscay
469 (0.23 , Marquis et al., 2007, 2011: spring), and the lagoon of Bizerte ($0.23\text{--}0.26$, Grami et al.,
470 2008: summer). Bacteria supplied 50% of the C demand of protozooplankton, which were
471 mainly composed of aloricate ciliates and HNF in both sites during winter ($50\text{--}70\%$, Meddeb
472 et al., submitted). Consequently, the microbivorous activity of protozooplankton increased
473 relatively to their herbivory (Fig. 9 B), while metazooplankton consumed more
474 microphytoplankton than during the other seasons. For these reasons, we were cautious to use
475 only the $R7$ ratio to identify the dominant food web during winter, because bacteria seemed to
476 play a stronger role in the winter food web than during the other seasons. In this case, another
477 ratio was calculated, the $R5$ proposed by Sakka Hlaili et al. (2014) to determine the bacterial
478 contribution to the production of potential microzooplankton food. The $R5$ is defined as the
479 ratio between the net bacterial production to the net production of potential protozoan food
480 (i.e. sum of net production of bacteria, phytoplankton, detritus and doc). $R5$ values showed
481 that, in all sites, the bacteria contributed largely to the production of potential
482 microzooplankton food during winter ($0.26\text{--}0.29$) than the other seasons ($0.03\text{--}0.1$). The $R7$
483 ratio calculated for winter (0.20 and 0.28 for the Channel and the Bay, respectively) suggested
484 that the winter structure acted as a multivorous food web, but with the use of the $R5$ ratio, we
485 preferred to call it “bacterial multivorous food web”. In this food web, bacteria and

486 microphytoplankton were the main actors and together fuelled the system. This newly defined
487 food web type, which seems to be highly unusual, was not reported in the meta-analysis by
488 Sakka Hlaili et al. (2014), who summarized and defined planktonic food webs from various
489 regions. We propose that the bacterial multivorous food web should be added to the typology
490 proposed by Legendre and Rassoulzadegan, (1995) and Sakka Hlaili et al. (2014) (Fig. 10).

491 For the determination of this “bacterial multivorous food web”, we here propose to
492 researchers and managers, new criteria that they could use to identify quantitatively the
493 trophic pathways that dominate the multivorous food web. The first criterion was the R7 ratio
494 (i.e, picophytoplankton to total phytoplankton production), which separated the three main
495 types of food web: herbivorous < 0.1 , multivorous $0.1-0.6$, and microbivorous > 0.6 . The
496 second criterion was the R5 ratio (i.e. net bacterial production to the net production of
497 potential microzooplankton food), which is used into the multivorous interval and
498 discriminates between the multivorous (low R5 < 0.1) and bacterial multivorous food web
499 (high R5 > 0.2). By using these two ratios in succession, researchers and managers can
500 identify the newly defined food web type, “bacterial multivorous food web”.

501 Despite the impact of many factors on the seasonal evolution of planktonic food webs
502 functioning, it is possible to identify an overall pattern of evolution. The accumulation of
503 nitrates in the water column during winter allows the development of a spring bloom of
504 phytoplankton when light and temperature conditions become more favorable. Thereafter, the
505 mesozooplankton species develop rapidly and the ‘herbivorous’ food web is set up. This
506 carbon pathway cannot persist in time (Legendre and Rassoulzadegan, 1995). The grazing
507 activity of heterotrophic organisms enriches the pool of carbon and dissolved nitrogen (DOC
508 and DON) and ammonium (excretion). DON promotes remineralization of ammonium by
509 bacteria and their associated predators (protozoa) and a microbial food web settles while the
510 classical herbivorous food web persists, leading to the formation of a ‘multivorous food web’
511 (Legendre and Rassoulzadegan 1995). This scenario was observed in the offshore site from
512 the summer to the autumn (Fig. 10B). Phytoplankton communities are dominated by diatoms
513 more suitable for non-limiting conditions of nitrates as was previously observed in other
514 systems (Reynolds 2000, Alves de Souza et al., 2008). Smaller producers dominate when
515 nitrates decrease, which was observed in our inshore station during autumn. Other conditions
516 may favor proliferation of small producers leading to their dominance in relation the total
517 primary production. This leads to the increase of the grazing activity of microzooplankton on
518 the small cells and thus causes the installation of a microbial food web (Fig. 10C). In winter,

519 the fall of temperature and light was not favorable to the development of phytoplankton and
520 therefore caused the decrease of the primary production. In this season, nitrogen was still
521 quite low, and bacteria fed on these nutrients and did not use the remineralization process.
522 This led to the increase of the bacterial production which became equal to the primary
523 production accentuating the installation of the “bacterial multivorous food web” (Fig. 10G).

524 **4.3. Ecosystem indicators and emergent properties**

525 Ecological ratios (R7 and R5) are useful to discriminate between types of planktonic
526 food webs and to identify “bacterial multivorous food web”. In complement, the calculation
527 of Ecological Network Analysis indices are effective tools for characterizing the functioning
528 of the food webs and especially of the new one (Ulanowicz 1986, 1997, Ulanowicz et al.,
529 2009).

530 For both sites, all ENA indicators have obviously varied over seasons parallel to the
531 change of trophic type (Fig. 8). The ENA variation showed also that there is a seasonal
532 pattern of ecosystem properties, which coincides with specific food web, as illustrated by
533 Fig 11. The highest ecosystem activity, indicated by TST, was observed in spring (2933–3818
534 $\text{mg C m}^{-2} \text{ d}^{-1}$), when algal blooms occurred and primary production dominating by
535 microphytoplankton (Table 3) resulting to the herbivorous food web. In the opposite, the
536 winter “bacterial multivorous web” showed the lowest activity. The ascendancy (A) and the
537 development capacity (DC) are strongly related to the TST (Table 5, Ulanowicz, 2004) and
538 showed the same pattern of variation. The relative ascendancy (A/DC) is an essential
539 indicator of the degree of ecosystem organization and specialization (Ulanowicz, 1997;
540 Patrício et al., 2004). The A/DC decreased from spring to summer and then rose in
541 autumn/winter, which perfectly followed the seasonal change in the activity of the observed
542 trophic structures over seasons. In other words, the increase of the amount of carbon
543 circulating (i.e. TST) seemed to favor the direct pathways. Consequently, the carbon flows
544 through few particular flows (bac-pro, mic-pro, pro-met; Fig. 10G) leading to an increase in
545 carbon transfer efficiency and a better organization and specialization (Fig. 11). Other
546 emergent properties of ecosystems (i.e. stability, maturity, resilience...) should also vary
547 among seasons. For example, Legendre and Rassoulzadegan (1995) stated that an herbivorous
548 food web could be considered as a system of low stability, since it is of transient nature and
549 thus inherently unstable. In contrast, the multivorous and microbial food webs have higher
550 stability and thus are longer lasting and will dominate the pelagic environment in most
551 oceans. Our result are coherent with this proposition. Effectively, the FCI and APL indexes

552 have increased from spring (FCI: 13–14%; APL: 2.95–3.20) to summer/autumn (FCI: 16–
553 17%; APL: 3.27–3.33) and then showed the highest value in winter (FCI: 41–46%; APL:
554 4.48–5.09). Moreover, during the same succession, the A/DC values have slightly increased,
555 and the maximum value reached is slightly inferior to 60%, hence. With this situation, the
556 maximum possible specialization was not reached, letting a reserve of redundancy, important
557 for the robustness of the food web as underlined by Ulanowicz et al. (2009). This indicates a
558 concomitant increase of ecosystem stability and maturity, when the trophic typology has
559 evolved from the herbivorous web to multivorous and microbial webs and reached the
560 “bacterial multivorous web”. This new trophic pathway based on a high heterotrophic
561 bacterial production had the strongest carbon recycling, which lead to a higher retention of
562 carbon inside the ecosystem and then appears to be the most stable and mature.

563 The D/H ratio is often considered as another index that could bring an important
564 information to complete the description of the food web functioning. This ratio has effectively
565 showed a seasonal shift in the food source used by consumers inducing an alternation between
566 a system based on primary production pathway in spring, autumn and winter (lower D/H:
567 0.05–0.48, Fig. 9) and a system based on detrital energy pathways in summer (higher D/H:
568 0.59–0.66, Fig. 9). In our modelling work, the local information was limited on the detrital
569 pathway toward mesozooplankton. So, detritivory flows were not enough constrained when
570 calculating the unknown flows, which made us uncomfortable on linking the new typology of
571 functioning and D/H values. Therefore, more experiments should be done to help limiting
572 detritivory unknown flows before investigating the link between plankton food web typology
573 and D/H index.

574 An important emergent property of each food web, highly related to the internal
575 organization described with the ENA indices, is the distribution of carbon as transfer from the
576 planktonic system, to non-planktonic pelagic consumers or down to the benthic consumers.
577 The fate of biogenic carbon is dependent on the amount of primary production, the size of
578 primary producers and the structure of the food web (Legendre and Rassoulzadegan, 1995;
579 Vézina and Savenkoff, 1999; Legendre and Rivkin, 2002). Herbivorous food webs, based on
580 large producers with high production rate, are considered as having the highest capacity to
581 channel C to higher pelagic and benthic consumers, whereas in microbial food webs, most
582 organic carbon is expected to be lost through respiration and trophic transfer will be low
583 (Legendre and Rassoulzadegan, 1995, Rivkin et al., 1996; Legendre and Le Fèvre, 1995).
584 Interestingly, a specific situation has been found in winter during which the “bacterial
585 multivorous web” was acting that differs from others seasons (Fig. 6). In spring, summer and

586 autumn, the respiration was around 50% of gpp and a substantial fraction of primary
587 production could reach higher pelagic consumers (21–31% of gross primary production, gpp).
588 Meanwhile, another significant part of the production sank down to the benthic food web (20–
589 30% of gpp), mainly due to the downward flow of metazoan faecal pellets (50–72% of total
590 sinking material). These important proportions of sinking was in accordance to the
591 assumptions made above for the herbivorous and multivorous food webs found in the Channel
592 (during spring/summer) and the Bay (during spring/summer/autumn), but was unexpected for
593 the Channel in autumn. During this season, the microbial pathway was observed and
594 picophytoplankton dominated the primary production, which typically results in carbon
595 leaving the plankton food web mainly through respiration (Legendre and Rassoulzadegan,
596 1995; Rivkin et al., 1996; Legendre and Le Fèvre, 1995). In our case, it seems that the
597 capacity of the food web to channel carbon to higher trophic levels does not depend so much
598 on the size of the producers, but rather on the amount of primary production, as stated
599 previously (Rivkin et al., 1996, Marquis et al., 2007, 2011). The pronounced capacity of
600 spring, summer and autumn food webs in channeling carbon to pelagic and benthic consumers
601 may result from their high activity, as shown by a high value of TST, but also from the low
602 recycling (FCI) and the low retention of carbon associated with low path length (APL) in the
603 system (Fig. 11).

604 When the “bacterial multivorous food web” was observed, during winter, most
605 produced carbon was lost by respiration (66–84% of gpp), leaving a little amount available for
606 higher pelagic consumers (2–2.32% of gpp, Fig. 6). Obviously, this was a consequence of the
607 functioning of the “bacterial multivorous web”, which was characterized by a strong recycling
608 activity and long internal food chains, as supported by the highest values of FCI and APL
609 (Fig. 11). The loss by sinking during winter (14–31% of gpp) did not differ that much from
610 other seasons, but the sedimentation was mainly due to sinking of phytoplankton (59–75% of
611 total sinking material). Thus, the winter food web exported carbon to the benthic system, just
612 as the herbivorous pathway, and in the same time showed high cycling activity, as a microbial
613 pathway. This reinforces our suggestion about a new type of functioning during winter, the
614 so-called “bacterial multivorous food web”. This understanding of emergent properties
615 determining the functioning of the system and in particular the fate of carbon is primordial as
616 it impacts directly ecosystem services, such as shellfish farming or fishing which are the main
617 activities in both study sites. This is of first importance for environment managers.

618 **4.4. Ecological indicators, ecosystems health monitoring and management outlook**

619 The present results highlight the importance of selecting the right indicators and that
620 this directly links with management needs. ENA indices have been proposed as ecosystem
621 health indicators (Niquil et al 2014) and proved to be sensitive to different impacts on marine
622 ecosystems (Baird et al., 2009; Tecchio et al., 2016; Pezy et al., 2017; de la Vega et al.,
623 2018a, b). In line with these former studies, our results showed significant implications of
624 these approaches for the understanding of the ecosystem dynamics and for adaptive
625 management. Some types of food webs can be considered as indicators of trophic status (Fath
626 et al., 2019, Safi et al., 2019) and ecosystem services (Schückel et al., 2018). Thus, the present
627 study appears as a relevant track for managers to develop indicators of health status of
628 ecosystems. Based on the present results, we propose to researchers and managers new
629 criteria (R7 and R5) to consider, in complement to ENA, and that they could use to identify
630 quantitatively the newly defined food web type, “bacterial multivorous food web” which we
631 suggest to be added to the existing typologies of planktonic food webs proposed by Legendre
632 and Rassoulzadegan (1995) and modified by Sakka Hlaili et al. (2014).

633 Results of ENA analyses contribute to a better knowledge of the impacts of seasonal
634 variations and anthropological pressures on food webs. They also allow defining
635 recommendations for environmental managers and industry in terms of monitoring the effects
636 on marine ecosystems by the limitation of nutrient and pollutant loads in coastal zone and
637 ensuring restoration and increasing ecosystem resilience. Effectively, some ecological
638 indicators, such as TST, A/DC, APL and FCI are already used to examine the impact of
639 anthropization on marine ecosystems. Previous studies have considered TST as an indicator of
640 eutrophication (Niquil et al., 2012; Grami et al., 2008; Scharler and Baird, 2005). Our results
641 reported also very high TST values in spring, related to the high productivity of the
642 ecosystems during this season, and especially to that of the autotrophic organisms (i.e.
643 phytoplankton). The increase in TST could be interpreted as eutrophication and affiliated to
644 the presence of a higher biodiversity of sources of carbon in the ecosystem and also to the
645 proximity of the study stations to sources of nutrient discharges (urban, agricultural and
646 shellfish farming input). Effectively, eutrophication events has been always reported for the
647 Bay and the Channel sites (Sakka Hlaili et al., 2007). The relative ascendancy (A/DC),
648 considered as a proxy for maturity, is supposed to decrease with an increase of stress
649 (Ulanowicz, 1997). In our study, we found that A/DC followed trends predicted by this
650 theory. The observed pattern mean that the least disturbed systems (autumn, winter) appeared
651 to be less vulnerable to disturbance, more tightly organized, resistant and more efficient in
652 processing energy (high A/DC) than perturbed systems (spring, summer). In addition, relative

653 indices (e.g. A/DC) appeared to be less affected by equilibrium process than the absolute
654 indices (e.g. A). This confirms that the relative information indices appear more suitable for
655 monitoring the effects of anthropogenic impact (as pollution, eutrophication...) on an
656 ecosystem level than the absolute indices (Ulanowicz et al., 2009) and are preferred by many
657 authors (Baird et al., 1991; Baird and Ulanowicz, 1993; Christensen 1995; Monaco and
658 Ulanowicz, 1997; Rybarczyk and Elkaïm 2003; Rybarczyk et al., 2003; Patricio et al., 2004)
659 because it excludes throughputs effects and allows comparison between ecosystems
660 (Heymans et al., 2002).

661 It was also stated that stressed ecosystems show high FCI (Finn, 1976; Heymans, 2002;
662 Richey et al., 1978; Ulanowicz, 1996; Mann et al., 1989). For example, Baird and Ulanowicz
663 (1993) have shown that FCI index was higher in the most polluted estuary and lower in the
664 less stressed systems, assessing that this index can be viewed as an indicator of pollution.
665 Regarding findings based on chemically polluted and eutrophied ecosystems, FCI values were
666 high in comparison to more pristine systems (Baird et al., 2004; Patricio et al., 2004; Scharler
667 and Baird, 2005) and the structure of cycling changed dramatically between the unimpacted
668 and the eutrophic systems (Patricio et al., 2004), consequently, FCI can be considered as a
669 good candidate index for comparing stress states of many ecosystems. In the Bay and the
670 Channel of Bizerte, chemical contamination by different pollutants has been widely described
671 (Derouiche et al., 2004; Boufahja, 2010; Pringault et al., 2016). Effectively, the high FCI
672 values of the winter (0.41–0.46) and those lower but still high compared to literature values,
673 in other seasons (0.13–0.17), revealed that both systems could be considered as stressed over
674 all the year. Furthermore, for both sites and over all seasons the APL responded to the
675 environmental perturbation to the same gradient as FCI, thus suggesting that either index
676 would be sufficient for evaluating the ecological status of studied ecosystems.

677 The differences observed in the functioning of the studied sites (the Channel and the
678 Bay of Bizerte) indicate that those ecosystems, strongly impacted by human activities, must
679 be monitored based on several representative sites, chosen regarding their main habitat type
680 and environmental status. In addition, further comparative studies for the same sites should be
681 made in different stations and seasons in term of food web monitoring development
682 perspective. Monitoring programs covering the majority of ecosystem compartments and for
683 the different habitats should be applied. Presently, there are major gaps in knowledge and
684 data, in particular for higher trophic levels such as fish, birds, mammals ... and for lower
685 trophic levels such as meiofauna or benthic diatoms. For this purpose, we advise managers to
686 study and to integrate information about complete trophic systems by recommending a field

687 monitoring that covers plankton as well as fish and benthos compartments. Moreover, some
688 other trophic strategies are important to be considered and studied for trophic transfer in
689 planktonic environment (e.g. mixotrophy, parasitism, saprothitism). Integrating all these
690 processes into a single food-web model gathering all carbon flows will allow a complete
691 understanding of the ecosystem functioning. Such an approach is essential for applying a
692 holistic ecosystem management strategy. Finally, we propose the use of well-studied areas as
693 reference sites, selected according to available data (research projects) and existing
694 monitoring programs (sampling takes place regularly, e.g. at least annual basis) for
695 comparison.

696 **5. Conclusion**

697 Based on series of physico-chemical and plankton measurements along a seasonal
698 gradient and using the LIM-MCMC approach, this study presents the dynamics and
699 functioning of plankton food webs in inshore and marine waters of SW Mediterranean Sea
700 during all seasons. These waters were characterized by specific environmental and
701 hydrological conditions that were reflected in the food web structures, which showed seasonal
702 dynamics that diverged from the conventional scheme proposed by Legendre and
703 Rassoulzadegan (1995). The herbivorous food web dominated during spring, and showed the
704 highest gross primary production that was largely dominated by microphytoplankton. This
705 coincided with high availability of nutrients and light and stratification of the water column,
706 caused by an increased freshwater inflow in the inshore waters. More surprisingly, the
707 herbivorous food web was also identified during summer, as nutrient and light conditions
708 remained favorable for microphytoplankton production. The multivorous pathway was
709 dominant in the marine site during summer and autumn, when microalgal production
710 decreased and picophytoplankton became more productive. In contrast, the autumn food web
711 in inshore site functioned as microbial pathway, as primary production was mainly dominated
712 by picophytoplankton. The microphytoplankton exhibited the lowest production in autumn,
713 probably due to the decrease of light. The winter situation corresponded to a new type of
714 pathway, the “bacterial multivorous food web” which we suggest can be added to the existing
715 typologies of plankton food webs. In this newly defined food web, bacterial production
716 equalled that of primary production, hence bacteria and microphytoplankton were the main
717 actors that together fuelled the system.

718 The seasonal change in food webs structure resulted in a shift in the system properties
719 and functioning of the ecosystem summarized in Figure 11. Comparing the ENA indices

720 among different seasons showed that the spring trophic pathway (herbivorous food web) was
721 the most active with pronounced total system throughput (TST). In opposite, they showed
722 lower stability in comparison to the systems encountered during summer (multivorous
723 pathway) and autumn (microbial and multivorous pathways), with relatively high cycling
724 activity and path length. The strongest carbon recycling coincided with the “bacterial
725 multivorous food webs” observed in winter. This pathway was the most stable and mature,
726 with pronounced capacity to retain carbon inside the system, leading to low export. The
727 winter ecosystem also seemed to be most organized and specialized, as indicated by the high
728 relative ascendancy (A/DC), with a probable more direct carbon pathways (Fig. 11).

729 Finally, this study propose appropriate indicators and evaluation tools to be used by
730 managers and researchers for the assessment of the structure, functioning and emergent
731 properties of ecosystems in natural and in disturbed conditions. The suggestion is to combine
732 the use of R5 and R7 ratios to identify the newly defined food web type “bacterial
733 multivorous food web” and ENA indices, to distinguish different states of the food web
734 functioning across natural evolution and anthropogenic pressures.

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