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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  $\mu\text{M}$ ; 1–3.5 N  $\mu\text{M}$ ;  
156 0.5–2.25 Si  $\mu\text{M}$ ) (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  $1 \text{ m s}^{-1}$  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 [ $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$  and  $\text{Si}(\text{OH})_4$ ] 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<sup>®</sup> 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  $\mu\text{m}$  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  $\mu\text{M}$  of doc is equal to 12  $\text{mg C m}^{-3}$  (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  $\mu\text{m}$  black polycarbonate filters (Nuclepore) laid over 0.45  $\mu\text{m}$  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  $\text{pg C cell}^{-1}$  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 ( $\text{mg C m}^{-2}$ ) 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  $\mu\text{m}$ ) with pre-filtered water on 200  $\mu\text{m}$  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 ( $G$ ,  $\text{mg C}$   
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  $C_0$  ( $\text{mg C m}^{-3}$ ) is the initial biomass of phytoplankton or bacteria,  $k$  is the growth rates  
309 of bacteria and size-fractionated phytoplankton ( $\text{d}^{-1}$ ),  $g$  is the grazing rates by  
310 protozooplankton ( $\text{d}^{-1}$ ) 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  $\mu\text{m}$  and >700  
319  $\mu\text{m}$ ). 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<sup>-3</sup>) was calculated using the following equation:

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

324 where, GP<sub>sub</sub> is the gut pigment concentration (mg pigment m<sup>-3</sup>) from the subsample, v (m<sup>3</sup>) is  
325 the volume of the subsample, F is the fraction of subsample processed for gut pigment  
326 content, and V<sub>net</sub> (m<sup>3</sup>) is the total volume of water filtered during each net tow.

327 Metazooplankton grazing rate (GM, mg C m<sup>-3</sup> d<sup>-1</sup>) was calculated as:

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

328 where GP (mg pigment m<sup>-3</sup>) 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<sup>-1</sup>) 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<sub>C</sub>, mg C m<sup>-2</sup> d<sup>-1</sup>).

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<sup>®</sup> 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  $\text{NO}_2^-$ ,  $\text{NO}_3^+$ , and  $\text{NH}_4^+$  were detected in spring, summer and autumn (10–  
367 24  $\mu\text{M}$ ) compared to the winter (3–4  $\mu\text{M}$ ) (Fig. 4A).  $\text{PO}_4^{3-}$  (0.14–0.99  $\mu\text{M}$ ) and  $\text{Si(OH)}_4$  (0.84–  
368 2.86  $\mu\text{M}$ ) 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<sup>-2</sup> d<sup>-1</sup>), moderate in summer and autumn (1733–1743 and 1710–  
414 2384 mg C m<sup>-2</sup> d<sup>-1</sup>) and low in winter (879–1562 mg C m<sup>-2</sup> d<sup>-1</sup>) (Fig. 8). The two food webs in  
415 spring exhibited the highest development capacity (DC)(Channel: 11.106 mg C m<sup>-2</sup> d<sup>-1</sup>; Bay:  
416 8489 mg C m<sup>-2</sup> d<sup>-1</sup>, Fig. 8, Table 6) compared to the other seasons (2634–6951 mg C m<sup>-2</sup> d<sup>-1</sup>)  
417 (Fig. 8). The ascendancy showed similar pattern as DC, with higher values in spring (4838–  
418 6054 mg C m<sup>-2</sup> d<sup>-1</sup>) in comparison to the rest of the year (1566–3963 mg C m<sup>-2</sup> d<sup>-1</sup>, 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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