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1 **Plankton food-web functioning in anthropogenically impacted coastal**  
2 **waters (SW Mediterranean Sea): an ecological network analysis.**

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27 **Abstract**

28 The study is the first attempt to (i) model spring food webs in three SW Mediterranean  
29 ecosystems which are under different anthropogenic pressures and (ii) to project the  
30 consequence of this stress on their function. Linear inverse models were built using the Monte  
31 Carlo method coupled with Markov Chains to characterize the food-web status of the Lagoon,  
32 the Channel (inshore waters under high eutrophication and chemical contamination) and the  
33 Bay of Bizerte (offshore waters under less anthropogenic pressure). Ecological network  
34 analysis was used for the description of structural and functional properties of each food web  
35 and for inter-ecosystem comparisons. Our results showed that more carbon was produced by  
36 phytoplankton in the inshore waters ( $966\text{--}1234\text{ mg C m}^{-2}\text{ d}^{-1}$ ) compared to the Bay ( $727\text{ mg C}$   
37  $\text{m}^{-2}\text{ d}^{-1}$ ). The total ecosystem carbon inputs into the three food webs was supported by high  
38 primary production, which was mainly due to  $>10\text{ }\mu\text{m}$  algae. However, the three carbon  
39 pathways were characterized by low detritivory and a high herbivory which was mainly  
40 assigned to protozooplankton. This latter was efficient in channelling biogenic carbon. In the  
41 Lagoon and the Channel, food webs acted almost as a multivorous structure with a tendency  
42 towards herbivorous one, whereas in the Bay the herbivorous pathway was more dominant.  
43 Ecological indices revealed that the Lagoon and the Channel food webs/systems had high  
44 total system throughput and thus were more active than the Bay. The Bay food web, which  
45 had a high relative ascendancy value, was more organized and specialized. This  
46 inter-ecosystem difference could be due to the varying levels of anthropogenic impact among  
47 sites. Indeed, the low value of Finn's cycling index indicated that the three systems are  
48 disturbed, but the Lagoon and the Channel, with low average path lengths, appeared to be  
49 more stressed, as both sites have undergone higher chemical pollution and nutrient loading.  
50 This study shows that ecosystem models combined with ecological indices provide a powerful  
51 approach to detect change in environmental status and anthropogenic impacts.

52 **Keywords:** Food-web modelling, Ecological Network Analysis, Mediterranean coastal  
53 waters, plankton ecology.

## 54 **1. Introduction**

55 Food webs are by definition simple representations of who eats whom in a considered  
56 ecosystem. The common representation of a pelagic food web from the 1920s to the 1970s  
57 consisted of a three level compartment: 1. algae as primary producers of organic matter, 2.  
58 zooplankton (metazoa) as consumers of primary production (grazers), and 3. Ichthyoplankton  
59 (fish larvae) as predators (or secondary consumers). This three-level chain was called  
60 “*herbivorous food chain*” (Steele, 1974). With the discovery of the functional role of  
61 autotrophic and heterotrophic microorganisms as producers and consumers of organic matter  
62 (Pomeroy, 1974), the interactions between the organisms were represented in a more complex  
63 way. Azam et al. (1983) introduced the concept of the “*microbial loop*”, which emphasized  
64 the importance of heterotrophic microbes in the transfer of organic carbon to larger  
65 consumers. Then, Sherr and Sherr (1988) suggested a new food-web structure called the  
66 “*microbial food web*” where autotrophic and heterotrophic microorganisms are dominant and  
67 sustain the functioning of the ecosystem. Legendre and Rassoulzadegan (1995) suggested  
68 complementarily a “*multivorous food web*” where herbivorous and microbial organisms  
69 co-act to transfer organic carbon to larger organisms. Legendre and Rivkin (2002) stressed  
70 that respiration and downward export of particulate and dissolved organic carbon could be a  
71 major way of biogenic carbon export out of the pelagic food web. More recently, food-web  
72 modelling approaches have enabled ecologists to describe new food-web structures such as:  
73 “*phytomicrobial*” where microzooplankton mostly graze on phytoplankton and  
74 “*polymicrobial*” where microzooplankton graze equally on all food resources (Sakka Hlaili et  
75 al., 2014).

76 Food-web models summarize data obtained for any environment into a network of  
77 compartments connected by trophic links. Using any modelling approach, more integrated  
78 and concise information can be obtained on the functioning of pelagic ecosystems and  
79 compared with other modelled ecosystems. Ecosystem models provide a powerful approach  
80 to analyse and predict the consequence of environmental and anthropogenic pressures on food  
81 web structure and functioning. Several methods have been developed to characterize marine  
82 food webs. The Linear Inverse Model (LIM), as defined by Vézina and Platt (1988), allows  
83 the estimation of unknown trophic flows through the pelagic food web and alleviates the  
84 problem of under-sampling using the principle of the conservation of mass, i.e. the quantity of  
85 carbon coming into each compartment considered as equal to the amount leaving it.  
86 Moreover, this approach is considered as sufficient to describe the structure of aquatic  
87 ecosystems (Vézina and Pahlow, 2003; Savenkoff et al., 2004). It has been applied to a wide  
88 range of ecosystems: coastal areas (Vézina and Platt, 1988; Jackson and Eldridge, 1992), bays  
89 (Richardson et al., 2003; Marquis et al., 2007), lakes (Niquil et al., 2011), oceans (Vézina et  
90 al., 1997; Richardson et al., 2004) and gulfs (Vézina et al., 2000; Savenkoff et al., 2004;  
91 Chaalali et al., 2015). This deterministic method had limitations (e.g. Eldridge and Jackson,  
92 1993; Niquil et al., 1998; Donali et al., 1999; Kones et al., 2006), and was therefore modified  
93 into the Monte Carlo Markov Chain Linear Inverse method (LIM-MCMC; Van den Meersche  
94 et al., 2009) based on a sampling procedure that attempts a complete coverage of the range of  
95 possible solutions. This new approach allows the estimation of likelihood distributions of the  
96 flows rather than unique estimates and also takes into account flow variability resulting from  
97 uncertainty in sampling data (Grami et al., 2011; Niquil et al., 2012; Rasconi et al., 2014;  
98 Saint-Béat et al., 2013; 2015; Chaalali et al., 2015; 2016; Tecchio et al., 2016).

99 Ecological Network Analysis (ENA) is a group of algorithms describing food-web structure  
100 and functioning using the output of the calculated flows given by the modelling exercise.

101 ENA is based on a set of indices (i.e. the ENA indices) that describe (i) the connections  
102 between food-web compartments through an analysis of the input and output flows, (ii) the  
103 trophic structure, (iii) the topology, (iv) and the recycling in the network (Ulanowicz, 1996).  
104 When applied to the estimated flows of the food-web model, ENA allows qualitative and  
105 quantitative description of the ecosystem properties (Ulanowicz, 1986; Fath et al., 2007). This  
106 tool has been widely used in coastal ecology to characterize the food-web structure, the level  
107 of organization, the network dependence on external factors, and to evaluate the ecosystem  
108 stress level and its stability (Heymans et al., 2014; Saint-Béat et al., 2015).

109 Mediterranean coastal waters are currently under large anthropogenic pressure, leading to  
110 their eutrophication and chemical contamination (Bianchi et al., 2000; Boudouresque et al.,  
111 2002; Mzoughi et al., 2005; Sakka Hlaili et al., 2007; Sahraoui et al., 2012). Despite this, a  
112 few studies have addressed change in the structure and functioning of the food webs in some  
113 Mediterranean northern waters such as those in the Catalan continental slope (Tecchio et al.,  
114 2013) and the Gulf of Lions (Auger et al., 2011, Alekseenko et al., 2014). However,  
115 ecosystem-level studies in the South of the Mediterranean Sea are very scarce. Indeed, only  
116 one study using the LIM approach has modelled the plankton trophic pathways in the  
117 semi-enclosed Bizerte Lagoon (Grami et al., 2008), but studies on nearby marine ecosystems  
118 are non-existent. So, in the present study, we have applied the approach LIM-MCMC to  
119 characterize the trophic food-web status and its associated structural and functional properties  
120 in inshore (Lagoon and Channel of Bizerte) and offshore (Bay of Bizerte) coastal waters  
121 located in the south-west of the Mediterranean Sea. The work was carried out in these three  
122 ecosystems, which differ in environmental conditions and anthropogenic pressures, in order to  
123 evaluate if modelling allows us to identify the variability in the structure and the functioning  
124 of each planktonic food web. We specifically addressed the following questions: does  
125 planktonic food web function differently among these coastal waters during spring? Is their

126 primary production efficiently channelled to higher trophic levels? What is the environmental  
127 status of each site with regard to productivity, trophic structure, carbon transfer, stress, and  
128 organisation levels?

129 The data of standing stocks (bacteria, phytoplankton, protozooplankton, and  
130 metazooplankton) and some *in situ* estimated carbon flows (bacterial and phytoplankton  
131 production, protozooplankton grazing and metazooplankton grazing) were described in  
132 Meddeb et al. (submitted). In the present study, we used these data in addition to a measure of  
133 Dissolved Organic Carbon (DOC) and Particulate Organic Carbon (POC) stocks and vertical  
134 carbon flowing in each ecosystem. All data were integrated in a common view of ecosystem  
135 functioning, and completed, using the inverse analysis LIM-MCMC.

## 136 **2. Material and Methods**

### 137 **2.1. Study sites**

138 Water sampling was carried out during spring 2012 in three south-western Mediterranean  
139 ecosystems, situated in the city of Bizerte (Tunisia, Fig. 1). The sites are the Lagoon (inshore  
140 station L: 37°12'46"N, 09°50'48" E), the Channel (inshore station C: 37°15'04" N, 9°52'34" E)  
141 and the Bay (offshore station B: 37°16'54" N, 9°53'42" E) of Bizerte. The Lagoon, with a  
142 surface area of 121.6 km<sup>2</sup> and a maximum depth of 12 m, is a semi-enclosed ecosystem that  
143 receives a large amount of freshwater, particularly in winter, from several surrounding rivers  
144 and mainly from Lake Ichkeul (Fig. 1). The hydrodynamics are mainly driven by wind  
145 (Harzallah et al., 2003; Bejaoui et al., 2005). The lagoon is experiencing increasing nutrient  
146 concentrations (10.69–17.89 N μM, 0.86–1.33 P μM and 12.30–13.30 Si μM, Sakka Hlaili et  
147 al., 2008) from expanding urban, agricultural, and industrial development, leading in turn to  
148 high Chl *a* concentrations (4.43–5.48 mg m<sup>-3</sup>, Sakka Hlaili et al., 2008). The anthropogenic  
149 activities lead to a contamination of the sediment of the lagoon by several pollutants,  
150 including heavy metals (as Zn, Cd, Co, Cu, Pb, Ni, Cd, Mn, and Fe, 20–598 μg g<sup>-1</sup>, Ben Mna

151 et al., 2017), organotins ( $170 \text{ ng kg}^{-1}$ , Mzoughi et al., 2005), polycyclic aromatic  
152 hydrocarbons (PAHs:  $3042\text{--}9948 \text{ ng g}^{-1}$ , Zmerli et al., 2017), and pesticides ( $1.1\text{--}14.0 \text{ ng g}^{-1}$   
153 of dry sediment, Barhoumi et al., 2013). The Lagoon is one of the most economically  
154 important areas in Tunisia, sustaining large populations of planktivorous fish and shellfish  
155 (mussels, oysters, and clams). The Lagoon is connected northwards to the Mediterranean Sea  
156 through the Bizerte Channel (7 km long, 300 m wide, and 12 m deep). This site supports  
157 eutrophied waters ( $34.40 \pm 12 \text{ N } \mu\text{M}$ ,  $1.30 \pm 0.3 \text{ P } \mu\text{M}$  and  $1.20 \pm 1.05 \text{ Si } \mu\text{M}$ , Sahraoui et al.,  
158 2012) with high Chl *a* concentrations ( $6.20 \pm 4 \text{ mg m}^{-3}$ , Sahraoui et al., 2012) and was  
159 significantly polluted by heavy metals (especially Zn, Cr, and Pb,  $85\text{--}228 \text{ mg g}^{-1}$  of dry  
160 sediment) and PAHs ( $21\text{--}772 \text{ } \mu\text{g g}^{-1}$  of dry sediment) (Pringault et al., 2016). The Bay of  
161 Bizerte, with a depth of 16–20 m, is an open ecosystem directly connected to the  
162 Mediterranean Sea. This site supports lower levels of inorganic nutrients ( $1.19 \pm 0.9 \text{ N } \mu\text{M}$ ,  
163  $0.53 \pm 0.02 \text{ Si } \mu\text{M}$  and  $<1 \text{ P } \mu\text{M}$ ) and Chl *a* ( $0.5\text{--}2.5 \text{ mg Chl } a \text{ m}^{-3}$ ) (Sahraoui et al., 2012),  
164 compared to the two other sites. It is also less contaminated than the Lagoon and the Channel.  
165 The PAHs ( $78 \text{ } \mu\text{g g}^{-1}$  of dry sediment, Boufahja, 2010) are the main pollutants, which are  
166 originated from the oil refinery located on the shore of the Bay (Zrafi-Nouira et al., 2008; Ben  
167 Ameer et al., 2013).

## 168 **2.2. Sampling and water analysis**

169 At each station, water was collected during spring 2012 at four depths using an acid-washed  
170 2.5 L plastic water sampler (Hydro-Bios), which was then pre-filtered through a 200  $\mu\text{m}$  mesh  
171 net to remove meso- and macrozooplankton (except water used for DOC determination)  
172 before storing it in isothermal containers until processing. Five mL subsamples were filtered  
173 on sterilized 0.2  $\mu\text{m}$  polycarbonate filters and then frozen in acid-washed vials at  $-20^\circ\text{C}$  until  
174 analysis for dissolved organic carbon (Knap et al., 1993) using a Shimadzu TOC-5000 carbon  
175 analyser. Subsamples for determination of POC were filtered on pre-combusted (at  $450^\circ\text{C}$ ,



176 during 2 h) GF/F Whatman filters (21 mm) and analysed on a CHN elemental analyser  
177 (Perkin–Elmer 2400), as described in the JGOFS report (Knap et al., 1996). Subsamples were  
178 also taken for plankton enumeration and identification.

179 For the heterotrophic bacteria (bac) count, 20 ml samples were preserved with formaldehyde  
180 (final concentration of 4 %) and kept refrigerated at 4°C. Each sample (2 ml) was labelled  
181 with 0.2 ml of a solution of orange acridine for 2 minutes (Hobbie et al., 1977; Parsons et al.,  
182 1984) and filtered under low pressure on a black filter (0.22 µm, polycarbonate). Counting of  
183 bacteria was performed under a CETI Topic-T epifluorescence microscope using a 100x  
184 objective and the blue filter. The count was done in 20 random fields and by counting 400  
185 cells per slide. To enumerate prokaryotic and eukaryotic picophytoplankton (pic), samples (10  
186 ml) were preserved in 0.22 mm prefiltered formaldehyde (2% final concentration) and stored  
187 for 1 h in darkness at 4°C. The samples were then filtered on 0.22 mm black polycarbonate  
188 filters (Nuclepore), laid over 0.45 mm nitrocellulose backing filters (Millipore). The filters  
189 were mounted on slides using low-fluorescence immersion oil and stored immediately at  
190 20°C. Abundance was determined under a CETI Topic-T epifluorescence microscope (100 x  
191 Fluotar objective), as described in MacIsaac and Stockner (1993), using blue and green  
192 excitation and counting at least 200 cells from 30 random squares. Samples for identification  
193 and enumeration of phytoplankton [nanophytoplankton: 2-10 µm (nan) and  
194 microphytoplankton: 10-200 µm (mic)] and protozooplankton (pro: 5-200 µm, composed of  
195 heterotrophic nanoflagellates, dinoflagellates, and ciliates) were fixed with 4% acid Lugol  
196 solution (Parsons et al., 1984) and 5% alkaline Lugol solution (Sherr and Sherr, 1993),  
197 respectively. Cell abundances were determined under an inverted microscope (100 x  
198 objectives) on 50 or 100 ml settled volumes (Lund et al., 1958). At least 200 cells in each  
199 sample were counted.

200 Metazooplankton [two size classes: 200  $\mu\text{m}$  (met1) and 700  $\mu\text{m}$  (met2)] were sampled using  
201 two horizontal net tows with 200  $\mu\text{m}$  and 700  $\mu\text{m}$  mesh net. Samples were then preserved in  
202 borate-buffered formalin (5% final concentration) for identification and counts of organisms,  
203 which were performed under a dissecting stereomicroscope (Leica).

### 204 **2.3. Areal carbon stocks**

205 The carbon biomasses of plankton were calculated as described in full details in Meddeb et al.  
206 (Submitted). Cell volumes ( $\mu\text{m}^3$ ) of bacteria and picophytoplankton were converted to carbon  
207 content ( $\text{pg C cell}^{-1}$ ) using specific conversion factors (Table 1). For phytoplankton and  
208 protozooplankton, biovolumes were estimated by applying standard geometric formulae to  
209 each taxon, as proposed by Hillebrand et al. (1999). Then, the carbon content was obtained  
210 using specific conversion factors or formulae (Table 1). For mesozooplankton, the length and  
211 width of organisms were measured and were converted to carbon content using conversion  
212 factors or formulae corresponding to each taxonomic group (Table 1). The carbon biomasses  
213 of each plankton community (bac, pic, nan, mic, pro, met1, and met2) were estimated by  
214 multiplying their cell carbon by their corresponding abundances.

215 The concentration of dissolved organic carbon (doc) was obtained considering that 1  $\mu\text{M}$  of  
216 doc is equal to 12  $\text{mg C m}^{-3}$  (Grami et al., 2008). The detrital organic carbon (det) was  
217 estimated as total POC, determined from water column, minus the total carbon biomass of all  
218 plankton communities.

219 The final areal carbon stocks ( $\text{mg C m}^{-2}$ ) were calculated by vertically integrating the carbon  
220 concentration ( $\text{mg C m}^{-3}$ ) calculated from the sampling depths.

### 221 **2.4. Areal carbon flows**

#### 222 **2.4.1. Production of bacteria and phytoplankton and their grazing by protozooplankton**

223 Dilution experiments were carried out at each site to estimate growth rates ( $k, \text{d}^{-1}$ ) of bacteria  
224 and size-fractionated phytoplankton (pic, nan, and mic), as well as their grazing rates ( $g, \text{d}^{-1}$ )

225 by protozooplankton (Landry and Hassett, 1982; Sakka Hlaili et al., 2007). Heterotrophic  
 226 nanoflagellates (*Leucocryptos sp.* and *Meringospheara spp.*) and small aloricate ciliates  
 227 (*Strombidium spp.*) were considered as main grazers of bacteria and pico/nanophytoplankton,  
 228 while heterotrophic dinoflagellates (species of *Gyrodinium*, *Gymnodinium*, *Ceratium*,  
 229 *Alexandrium*, and *Protoperidinium*) and tintinnids (*Tintinnopsis corniger*, *Helicostemella*  
 230 *kiliensis*, and *Parafavella gigantea*) were assigned as major grazers of microphytoplankton.  
 231 Details for experimental procedure and calculation are fully provided in Meddeb et al.  
 232 (submitted). In brief, collected water at each sampling station was filtered on a 200 µm mesh  
 233 net to remove meso- and macrozooplankton. Very small metazoa (<200 µm, such as copepods  
 234 nauplii) were extremely rare in the samples and were therefore not considered in the dilution  
 235 experiment. The 200 µm filtered water was mixed with free-particle sea water to give four  
 236 dilution factors (100 %, 75 %, 50 % and 25 % of <200 µm prefiltered water). Each dilution  
 237 mixture was then distributed into three clean 2-l polycarbonate bottles, which were incubated  
 238 at *in situ* temperature (19–22°C) at the sampling depths for 24 h. The estimated rates *k* and *g*  
 239 were used to calculate gross production rates for phytoplankton and bacteria (*P*, mg C m<sup>-3</sup> d<sup>-1</sup>)  
 240 and their consumption rates (*G*, mg C m<sup>-3</sup> d<sup>-1</sup>) as suggested by Moigis (2000) and in more  
 241 recent works (Sakka Hlaili et al., 2008, Grattepanche et al., 2011):

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

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

242 where *C*<sub>0</sub> (mg C m<sup>-3</sup>) is the initial biomass of phytoplankton or bacteria, and *t* (d) is the  
 243 incubation time (1 d).

244 Values of *P* and *G* from the four sampling depths were integrated to determine the areal rates  
 245 (mg C m<sup>-2</sup> d<sup>-1</sup>) of production and consumption.

#### 246 **2.4.2. Grazing of phytoplankton by metazooplankton**

247 Grazing impact of mesoplanktonic metazoa was assessed by the gut fluorescence method  
248 (Mackas and Bohrer, 1976; Slaughter et al., 2006). Since mesozooplankton are known to have  
249 inefficient feeding on  $< 5 \mu\text{m}$  prey (Berggreen et al., 1988; Morales et al., 1993), we have  
250 assumed that they can only consume the nano- and microphytoplankton in our study. The  
251 description of the experiment procedure and calculations have been detailed in Meddeb et al.  
252 (submitted). In brief, vertical sampling of mesozooplankton was undertaken from bottom to  
253 surface in each site using  $200 \mu\text{m}$  and  $700 \mu\text{m}$  mesh net. This allowed the calculation of  
254 phytoplankton grazing by two size fractions of metazoa ( $200\text{-}700 \mu\text{m}$  and  $>700 \mu\text{m}$ ).  
255 Subsamples (0.5 or 1 l) were filtered onto 47 mm GF/F filters, homogenized in 90% acetone  
256 using a motorized tissue homogenizer, and filtered through 25 mm GF/F filters to remove  
257 pulp. The filtrates containing extracted gut pigment were measured before and after  
258 acidification with 10% hydrochloric acid using the spectrophotometric method of Lorenzen  
259 (1967).

260 Gut pigment content (GP,  $\text{mg pigment m}^{-3}$ ) was calculated using the following equation:

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

261 where,  $\text{GP}_{\text{sub}}$  is the gut pigment concentration ( $\text{mg pigment m}^{-3}$ ) from the subsample,  $v$  ( $\text{m}^3$ ) is  
262 the volume of the subsample,  $F$  is the fraction of subsample processed for gut pigment  
263 content, and  $V_{\text{net}}$  ( $\text{m}^3$ ) is the total volume of water filtered during each net tow.

264 Metazooplankton grazing rate (GM,  $\text{mg C m}^{-3} \text{d}^{-1}$ ) was calculated as:

$$\text{GM} = \text{GP} \times \text{WC} \times \text{C:Chl } a$$

265 where  $\text{GP}$  ( $\text{mg pigment m}^{-3}$ ) is the concentration of gut pigment,  $\text{C:Chl } a$  is the  
266 depth-averaged  $\text{C:Chl } a$  ratio determined for  $>2 \mu\text{m}$  phytoplankton (i.e. nano- and  
267 microphytoplankton) at each station, and  $\text{WC}$  ( $\text{d}^{-1}$ ) is the portion of water cleared per day.

268 Finally, GM was multiplied by the vertical depth of the net tow at each site to estimate the  
269 areal rate of consumption of metazooplankton ( $\text{GM}_C$ ,  $\text{mg C m}^{-2} \text{d}^{-1}$ ).

### 270 **2.4.3. Sinking flux**

271 Sediment traps were used to collect organic particles that settle down along the water column.  
272 Two sediment traps (63 cm high, 6 cm internal diameter) were moored at each site. To avoid  
273 re-suspended material bias as possible, the traps were deployed at two or three meters from  
274 the bottom depending on the station's depth (Lagoon: 7-8 m; Channel: 6-7 m; Bay: 14-16 m).  
275 Prior to their deployment, traps were filled with the dense seawater (0.2  $\mu\text{m}$  filtered seawater  
276 + NaCl at final concentration of 5  $\text{g l}^{-1}$ ) to create a density gradient in order to prevent the  
277 collection of surface particles. After 24 h of mooring, the traps were returned to the laboratory  
278 and stored at 5°C for a night to let the particles settle. For each station, bottom fractions of the  
279 two moored traps were mixed together. Subsamples were taken from the trapped material to  
280 estimate POC as detailed above (section 2.2). The sinking flux ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) of POC was  
281 estimated as the carbon stock collected in the trap (mg C) divided by the area of the trap  
282 ( $6.3 \times 10^{-3} \text{ m}^2$ ) and the duration of deployment (1 day). Other subsamples from the trapped  
283 material were fixed with acid Lugol solution (final concentration of 4%) for nano- and  
284 microphytoplankton cell identification and abundance estimation. Cell abundances were then  
285 converted to carbon biomass ( $\text{mg C m}^{-3}$ ), as explained above (Table 1), which was multiplied  
286 by the volume of trapped material and divide by 2 to get the algal carbon stock collected in  
287 one trap (mg C). This was then divided by the area of the trap and the duration of deployment  
288 to get sinking flux ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) for each phytoplankton fraction (i.e. nano- and  
289 microphytoplankton).

290 Additional subsamples (15–30 ml settled volumes) were preserved in buffered formaldehyde  
291 for faecal pellet enumeration and volume estimation ( $\text{mm}^3 \text{L}^{-1}$ ) using an inverted microscope  
292 (10 x objectives) following the Utermöhl method (1958). The volume sinking flux ( $\text{mm}^3 \text{m}^{-2}$   
293  $\text{d}^{-1}$ ) were then calculated for each category of pellet (cylindrical/conical; ovoid/rounded) as  
294 described by Grami et al. (2008). Then the volume vertical flux was converted to carbon

295 vertical flux ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) using a factor of  $0.057 \text{ mg C mm}^{-3}$  for cylindrical/conical pellets  
296 and  $0.042 \text{ mg C mm}^{-3}$  for ovoid/ rounded ones (Grami et al., 2008).

## 297 **2.5. Model development**

298 Field data were used to construct pelagic food-web models that quantitatively illustrate carbon  
299 pathways in the three study sites. Since the unknown flows outnumbered the known flows, the  
300 LIM-MCMC method (Van den Meersche et al., 2009), derived from the inverse analysis  
301 method of Vézina and Platt (1988) was adopted to reconstruct trophic carbon flows through  
302 the three pelagic food webs. The approach is based on four steps: (1) building an *a priori*  
303 model including all possible flows between the considered compartments or between the  
304 compartments and the outside, (2) setting mass-balance between flows, for each compartment,  
305 as equalities, (3) setting two groups of inequalities, the first ones based on *in situ* calculated  
306 flows and the second ones consists on a number of biological constraints picked from the  
307 literature, to reduce the range of possible values for each unknown flow, and (4) calculating  
308 the possible solutions for unknown flows.

### 309 **2.5.1. Compartments**

310 The number of considered compartments and the possible flows/links between them and the  
311 outside were considered as the same for the three networks (Channel, Lagoon, and the Bay).  
312 Each model contained seven living compartments: heterotrophic bacteria (bac),  
313 picophytoplankton  $<2 \mu\text{m}$  (pic), nanophytoplankton  $2\text{-}10 \mu\text{m}$  (nan), microphytoplankton  $20\text{-}$   
314  $200 \mu\text{m}$  (mic), protozooplankton  $<200 \mu\text{m}$  (including heterotrophic nanoflagellates,  
315 dinoflagellates, and ciliates), metazooplankton  $200\text{-}700 \mu\text{m}$  (met1), and metazooplankton  
316  $>700 \mu\text{m}$  (met2). The non-living compartments were the dissolved organic carbon (doc) and  
317 detrital organic carbon (det).

### 318 **2.5.2. A priori model**

319 The gross primary production of the three size fractions of phytoplankton (pic, nan, and mic)  
320 are the only sources of particulate organic carbon input to the networks (Fig. 2). Carbon  
321 output from the network was driven by respiration of all living compartment and sinking of  
322 all compartments except protozooplankton, picophytoplankton, and heterotrophic bacteria.  
323 Detritus dissolution and doc production by all living compartments contribute to doc input.  
324 Detritus and doc can be lost from the system by advection. Bacteria, were the only  
325 compartment that uses doc, while protozooplankton the only compartment that graze on them.  
326 Production of detritus is assigned to phytoplankton (nan and mic) and protozooplankton  
327 through their mortality and metazooplankton *via* their faecal pellets production. The three size  
328 fractions of phytoplankton were grazed by protozooplankton, while only nano- and  
329 microphytoplankton fractions can be grazed by metazoa. Metazooplankton 200-700  $\mu\text{m}$   
330 (met1) consume protozooplankton and detritus, while metazoa  $>700 \mu\text{m}$  (met2) consume  
331 protozooplankton, small metazoa (met1) and detritus. The *a priori* model is presented in Fig.  
332 2.

### 333 **2.5.3. The set of equalities (mass balances)**

334 Setting equations (equalities) is an essential step to impose the mass balances of the network.  
335 The mass balance equations for all compartments are given in Table 2. The mass balance  
336 equation for each compartment states that the sum of the flows entering any compartment is  
337 equal to the sum of the outflows, meaning that we neglected daily variations of biomass  
338 compared to daily flow values.

### 339 **2.5.4. Biological constraints (inequalities)**

340 Imposing ecological limits (maximum and/or minimum) for each unknown flow helps to  
341 reduce the range of possible solutions. Two ranges of inequalities were adopted. Firstly,  
342 estimated flows derived from field experiments were used as mean values for each model.  
343 These mean values did not allow the model to estimate flows with certainty. For this reason,

344 we proposed to define the minimal and a maximal value for each flow by the calculation of a  
345 confidence interval around the field data, i.e. using the minimum and maximum of the  
346 average value of each flow (Table 3). The production rates ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) of bacteria and  
347 phytoplankton size fractions (pic, nan, and mic), as well as their grazing rates ( $\text{mg C m}^{-2} \text{ d}^{-1}$ )  
348 by protozoa, derived by dilution technique, were integrated as minimum and maximum flows  
349 into the model. Microphytoplankton sedimentation flow was constrained by the minimal and  
350 maximal estimated values for each site. Metazooplankton gut content experiments allowed  
351 constraining (by a minimum and a maximum value) two flows for each model: grazing of  
352 nano- and micro-phytoplankton by metazoan 1 and metazoan 2. Metazoa and detritus  
353 sedimentation were respectively constrained by a minimum and a maximum value estimated  
354 by field experiment for each site. A total of 26 inequalities derived from field experiments  
355 realized for the present study were considered for the Lagoon, the Channel, and the Bay of  
356 Bizerte.

357 A second group of constraints was adopted from previous works to constrain the unknown  
358 flows (Vézina and Platt, 1988; Steinberg et al., 2000; Vézina and Pahlow, 2003), including: the  
359 minimum and maximum respiration rate of phytoplankton, zooplankton, and bacteria; the  
360 minimum and maximum doc production rate by phytoplankton and zooplankton (only the  
361 upper limit was fixed for bacteria); the lower and upper limit of zooplankton and bacteria  
362 growth efficiency; the lower and upper limit of zooplankton assimilation efficiency, detritus  
363 excretion, and detritus dissolution flow upper limit. Forty-four inequalities of this second  
364 group were applied in the Lagoon, the Channel, and the Bay model (See details in Table 4).

### 365 **2.5.5. Solutions**

366 The last step of the inverse analysis was the calculation of unknown flows. The estimates of  
367 each unknown flow were obtained by the LIM-MCMC method, based on the mirror technique  
368 defined by Van den Meersche et al. (2009). A jump value of  $10 \text{ mg C m}^{-2} \text{ d}^{-1}$  and 300000



369 iterations were adopted to run the models in order to optimize the coverage of all the possible  
 370 solutions (i.e. correct polytope exploration). A Matlab<sup>®</sup> translation by Alain Vézina and  
 371 Lauriane Campo of the R-CRAN project package LIM-Solve was used (Weinbauer, 2002;  
 372 Van den Meersche et al., 2009). More details on the method are available in Van den  
 373 Meersche et al. (2009) and Niquil et al. (2012).

## 374 **2.7. Network analysis**

375 To characterize the food web obtained by the LIM-MCMC approach, Ecological Network  
 376 Analysis (ENA) was applied to the obtained flow values. ENA derived indices are commonly  
 377 used to describe emergent properties of any ecosystem (Ulanowicz, 1986). The algorithms  
 378 used here were written for Matlab<sup>®</sup> by Carole Lebreton and Markus Schartau. A number of  
 379 calculated indices were considered in this study for site comparison and characterization:

380 - Total system throughput (TST): the sum of all the flows circulating through all  
 381 compartments and a measure of the total system activity (Kay et al., 1989).

$$TST = \sum_{i=1, j=1}^n T_{ij}$$

382 where, i: flow out of the system from i,  $i=1, \dots, n$ ; j: flow in to the system to j,  $j=1 \dots n$ ; and  $T_{ij}$ :  
 383 flow from compartment i to compartment j.

384 - Ascendency (A) and Development Capacity (DC):

385 Ascendency represents the organized part of the ecosystem. It is the product of the throughput  
 386 and the Average Mutual Information (AMI: degree of specialization of flows in a network)  
 387 (Ulanowicz, 2004), and merges the quantification of the system activity and the degree of  
 388 specialization (Ulanowicz and Wulff, 1991; Ulanowicz, 2000).

$$A = \sum_{ij} (T_{ij}) \times \log \left( \frac{T_{ij} \times TST}{T_j \times T_i} \right)$$

389 where,  $T_i$ : Total outflow from compartment i;  $T_j$ : Total inflow for compartment j; and  $T_{ij}$ :  
390 Flow from compartment i to compartment j.

391 The development capacity (DC) is the sum of A and Overhead (O), which represents the  
392 maximum possible value of Ascendency that an ecosystem may reach.

$$DC = -TST \times \sum_{ij} \frac{T_{ij}}{TST} \times \log \left( \frac{T_{ij}}{TST} \right)$$

393 where, i: flow out of the system from i; j: flow in to the system to j; and  $T_{ij}$ : flow from  
394 compartment i to compartment j.

395 Ascendency is a more informative metric when it is expressed in relation to development  
396 capacity (relative Ascendency, A/DC). It defines the degree of ecosystem development. High  
397 A/DC ratios are thought to reflect a high degree of organization, highly specialized and less  
398 redundant pathways (Baird et al., 1991; Baird et al., 1998).

$$AC = \frac{A}{DC}$$

399 - Average path length (APL): is the average number of compartments crossed by a unit of  
400 carbon from entering to exiting the ecosystem. It represents a measure of the ecosystem  
401 retention capacity (Kay et al., 1989).

$$APL = \frac{\sum d_{i \leftrightarrow j}}{\frac{N(N-1)}{2}}$$

402 where, i: flow out of the system from i; j: flow in to the system to j; and N is the number of  
403 vertices in graph.

404 - Finn Cycling Index (FCI): is the ratio of carbon flowing in loops to the sum of all carbon  
405 flows. It quantifies the fraction of all flows involved in recycling (Finn, 1976) and can be  
406 considered as a measure of the retentiveness of the system.

$$FCI = \frac{TST_c}{TST}$$

407 where, TSTc is the total flow that is recycled.

## 408 **2.8. Cliff's $\delta$ test for comparing network indices between sites**

409 As suggested by Tecchio et al. (2016), we use the Cliff  $\delta$  method for statistically testing the  
410 ENA index differences between the models. This method is necessary when we have large  
411 sample sizes (here 300000 values for each flow), which precludes us from using other tests  
412 like ANOVA or *t*-tests. For each ENA index, three pairwise comparisons were performed.  
413 Then, the following values were used to define small, medium, and large effects (i.e.  $|\delta|$   
414  $<0.147$  "negligible";  $|\delta|$  0.147-0.33 "small";  $|\delta|$  0.33-0.474 "medium";  $>0.474$  "large"  
415 according to Tecchio et al. (2016).

## 416 **3. Results**

### 417 **3.1. Input, output and throughput**

418 Calculated flows are given in Table 5 and Figure 3. At each site, the food web was only  
419 powered by the phytoplankton gross primary production. The phytoplankton production  
420 reached 1234 mg C m<sup>-2</sup> d<sup>-1</sup> in the Lagoon and 966 mg C m<sup>-2</sup> d<sup>-1</sup> in the Channel, but only  
421 727 mg C m<sup>-2</sup> d<sup>-1</sup> in the Bay. For the three networks, microphytoplankton (mic) exhibited the  
422 highest contribution to total carbon input (70–83%). Picophytoplankton contribution  
423 fluctuated between 8–16%, while nanophytoplankton production varied between 8% and 13%  
424 of total carbon input.

425 Carbon exited the food webs (outputs) either through respiration (res) or dissolved organic  
426 carbon (doc) loss or downward sedimentation flows of detritus (det), phytoplankton (nan and  
427 mic), and zooplankton (met1 and met2). Carbon loss by respiration reached 14–16% of total  
428 carbon circulating for the three sites. It represents the main factor of carbon output at the site  
429 level, i.e. in the Lagoon (39%), the Channel (46%), and the Bay (45%). The highest  
430 respiration flows within a compartment were those from the protozooplankton and  
431 metazooplankton (19–20% and 13–19% of total carbon outputs, respectively, Fig. 4A).

432 Carbon sinking contributed 31% of total carbon loss in the Lagoon, 29% in the Channel, and  
433 25% in the Bay. Microphytoplankton and metazooplankton >700  $\mu\text{m}$  (met2) were the main  
434 living compartment contributing to sinking flows (Fig. 4B).

435 Throughput was defined as the sum of carbon flows incoming or leaving a compartment.  
436 Microphytoplankton followed by protozooplankton and metazooplankton showed the highest  
437 values of carbon throughput (609–868  $\text{mg C m}^{-2} \text{d}^{-1}$ ) among the living compartments of the  
438 three networks (Fig. 5). Detritus also presented relatively high throughput of carbon (230–  
439 531  $\text{mg C m}^{-2} \text{d}^{-1}$ ).

### 440 **3.2. Production of dissolved organic carbon and detritus**

441 The doc production at each site amounted to 334, 274, and 208  $\text{mg C m}^{-2} \text{d}^{-1}$  in the Lagoon,  
442 the Channel, and the Bay, respectively (Fig. 6A). The metazooplankton (met1 and met2) were  
443 the main compartment that contributed (36–40%) to doc in the Lagoon (130  $\text{mg C m}^{-2} \text{d}^{-1}$ ) and  
444 the Bay (76  $\text{mg C m}^{-2} \text{d}^{-1}$ ) (Table 5, Fig. 6A). In the Lagoon, the phytoplankton exudation  
445 (115  $\text{mg C m}^{-2} \text{d}^{-1}$ , i.e. 34% of doc production) was higher than the protozooplankton  
446 excretion (89  $\text{mg C m}^{-2} \text{d}^{-1}$ , i.e. 26% of doc production), whereas both flows were similar in  
447 the Bay (65.9 and 66.4  $\text{mg C m}^{-2} \text{d}^{-1}$ ). For the Channel, the three algal compartments (mic,  
448 nan, and picophytoplankton) contributed almost equally (32, 34, and 35%) to doc (84, 94, and  
449 96  $\text{mg C m}^{-2} \text{d}^{-1}$ ). It is important to highlight here that the microphytoplankton contributed  
450 66–81% to total algal exudation.

451 Detritus production by all living compartments was high in the Lagoon (531  $\text{mg C m}^{-2} \text{d}^{-1}$ )  
452 compared to the Channel (229  $\text{mg C m}^{-2} \text{d}^{-1}$ ) and the Bay (285  $\text{mg C m}^{-2} \text{d}^{-1}$ ) (Fig. 6B). Half  
453 of the detritus production derived from microphytoplankton in the Lagoon and the Bay. In  
454 these sites, protozooplankton (16 and 22%) and metazooplankton (i.e.; met1 and met2, 23 and  
455 25% respectively) presented almost similar contributions to detritus production. In the  
456 Channel, most of the detritus production resulted from protozooplankton (41%) and

457 metazooplankton (40%) activities whereas phytoplankton had a lower contribution (19%)  
458 (Fig. 6B).

### 459 **3.3. Zooplankton diets**

460 The protozooplankton diet was mainly based on herbivory, as microalgae constituted the main  
461 prey for these protozoa in the three sites (60–77% of the protozooplankton diet, Fig. 7A).  
462 Nanophytoplankton formed only 3–13% of total carbon consumed by protozooplankton in all  
463 sites, while picophytoplankton contributed more to the consumption of protozooplankton (11–  
464 23%). Protozooplankton showed very weak bacterivory, since bacteria formed only 10% of  
465 their diet in the Channel and not more than 5% in the Lagoon and the Bay.

466 In the Lagoon and the Bay, the metazooplankton 200-700  $\mu\text{m}$  (met1) were mainly  
467 detritivorous, since detritus represented 52–58% of their diet (Fig. 7B). At both sites,  
468 protozooplankton contributed 32–39% of the met1 consumption while phytoplankton  
469 guaranteed only 5%. In the Channel, the smaller metazooplankton was carnivorous, with a  
470 diet that relied mainly on protozooplankton (54%) (Fig. 7B). Detritus and phytoplankton  
471 formed 31 and 10% of met1 diet, respectively, in this site.

472 At the three stations, the metazooplankton  $>700 \mu\text{m}$  (met2) was mainly carnivorous, since  
473 48–62% of their diet were composed of protozoa and metazoa 200-700  $\mu\text{m}$  (Fig. 7C). The  
474 remaining source of carbon came principally from detritus in the Lagoon (42%) and the Bay  
475 (38%), where herbivory did not represent more than 10%. In the Channel, phytoplankton and  
476 detritus contributed almost equally (21 and 26%, respectively) to the carbon demand of met2  
477 (Fig. 7C).

### 478 **3.4. Ecosystem indicators and Ecological Network Analysis indices.**

479 Flow estimates obtained from the LIM-MCMC were used to calculate ecological networks  
480 indices (Fig. 8). This showed that the total system throughput (TST) was higher in the Lagoon  
481 ( $4798 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) compared to the Channel ( $3818 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and the Bay ( $2934 \text{ mg C}$

482  $\text{m}^{-2} \text{d}^{-1}$ ), due to higher primary production by phytoplankton. Also the development capacity  
483 (DC) in the Lagoon ( $14195 \text{ mg C m}^{-2} \text{d}^{-1}$ ) significantly exceeded those of the Channel ( $11106$   
484  $\text{mg C m}^{-2} \text{d}^{-1}$ ) and the Bay ( $8489 \text{ mg C m}^{-2} \text{d}^{-1}$ ) (Table 6, Fig. 8). Ascendency showed a  
485 similar pattern as DC, with higher values for the Lagoon ( $7686 \text{ mg C m}^{-2} \text{d}^{-1}$ ) and the Channel  
486 ( $6054 \text{ mg C m}^{-2} \text{d}^{-1}$ ) compared to the Bay ( $4839 \text{ mg C m}^{-2} \text{d}^{-1}$ ). Conversely, a high relative  
487 ascendency was founded in the Bay ( $A/DC = 57\%$ , Fig. 8) in comparison to the Lagoon and  
488 the Channel ( $A/DC = 55\%$ ).

489 The average path length (APL) differed significantly between the Lagoon (2.95) and the  
490 Channel (2.88) (Table 6). While the Bay had the highest APL value (3.03), suggesting that a  
491 unit of carbon crossed more compartments during its path through the trophic system (from  
492 input e.g. gross primary production, to output: e.g. respiration) compared to the Lagoon and  
493 the Channel. The Finn cycling index (FCI) showed slightly higher and significant cycling  
494 activity in the Channel (14%) compared to the Bay (13%) or the Lagoon (12%) (Table 6, Fig.  
495 8).

## 496 **4. Discussion**

### 497 **4.1. Plankton food webs of the study sites**

498 Mediterranean coastal waters are currently under several anthropogenic pressures, including  
499 eutrophication and pollution, but few studies have addressed the impact of these stressors on  
500 their functioning and food web structure. Here, we have presented new results concerning the  
501 food web and its associated properties in three coastal waters habitats in the SW  
502 Mediterranean Sea. Although these sites are closely located, they are different in eutrophic  
503 status, contamination levels, hydrology, and geomorphology (Bejaoui et al., 2008; Boufahja et  
504 al., 2012; Louati et al., 2013; Barhoumi et al., 2014a, b). These factors may impact plankton  
505 diversity and dynamics as well as productivity (Smayda and Reynold, 2001; Sakka Hlaili et

506 al., 2006; Leboulanger et al., 2011; Lafabrie et al., 2013). Therefore, variability in the  
507 structure and functioning of the plankton food web among sites may be suspected. Indeed, the  
508 LIM-MCMC approach revealed that the three ecosystems differed in their productivity which  
509 could be reflected in their planktonic system functions.

510 The photosynthetic carbon input was sufficient to support the functioning of the three  
511 food-web models. As expected, the inshore waters with substantial nutrients loading (Sakka  
512 Hlaili et al., 2008; Ben Garali et al., 2010; Sahraoui et al., 2012) exhibited high production  
513 rate ( $1234 - 966 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). Similar production rates were previously found for the Lagoon  
514 of Bizerte ( $1872 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Grami et al., 2008) and the Bay of Biscay (French Atlantic  
515 Gulf;  $1145 - 1666 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Marquis et al., 2007). These values are however low  
516 compared to other values recorded in temperate ecosystems, like the shelf of the Gulf of  
517 Cadiz (Spanish South Atlantic Gulf;  $4500 \text{ mg C m}^{-2} \text{ d}^{-1}$ ; Huertas et al., 2005). The production  
518 rate in the Bay ( $727 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) was similar to those of Arcachon Bay (French Atlantic  
519 Coast;  $433 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Tortajada et al., 2012) and the Bay of Biscay during late spring  
520 (French Atlantic Gulf;  $631 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Marquis et al., 2007). For all study sites,  
521 phytoplankton production ( $727 - 1234 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) was higher than the bacterial production  
522 ( $34.5 - 116.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). The bacterial to primary production ratio exhibited very low  
523 values in the Lagoon (0.03) and the Bay (0.06), which was close to those found in other  
524 coastal systems such as the Bay of Biscay (0.03–0.04, Marquis et al., 2007), the northern  
525 Spanish coast (0.04; Teira et al., 2003), and the Arcachon Bay (0.02, Tortajada et al., 2012).  
526 In the Channel, this ratio amounted to 0.12 but it was still lower than the value reported at a  
527 global scale (0.3; Cole et al., 1988).

528 In these three locations, the primary production was mainly sustained by microphytoplankton  
529 (70–80%). Diatoms and autotrophic dinoflagellates were the main microphytoplankton taxa at  
530 all stations and dominated the algal biomasses (Sakka Hlaili et al., 2007; Meddeb et al.,

531 submitted). Since microphytoplankton known to be selected by herbivorous zooplankton, the  
532 dominance of the herbivorous pathway from the typology of Legendre and Rassoulzadegan  
533 (1995, 1996; redefined in Sakka Hlaili et al. 2014) is suspected at the three sites.  
534 Nevertheless, a previous study has reported the dominance of the microbial food web in the  
535 Bizerte Lagoon during summer, although diatoms were prevailing during this season (Grami  
536 et al., 2008). Similarly, the microbial food web was shown to act in other coastal regions,  
537 where diatoms were abundant (Umani and Beran, 2003; Berglund et al., 2005).

538 At each site, carbon left the pelagic ecosystem firstly by respiration, then by sinking vertically  
539 and finally through doc losses, each loss represented by 39–46%, 25–31% and 24–30% of  
540 total outputs, respectively. Respiration was mainly driven by metazooplankton and  
541 protozooplankton activities (19–20% and 13–19% of total carbon outputs, respectively).  
542 Phytoplankton respiration had a low contribution (5–6%) to total carbon losses. This was  
543 comparable to a previous study in the Bizerte Lagoon (~5%, Grami et al., 2008), but much  
544 less so than in the Bay of Biscay (57–82%; Marquis et al., 2007) and at Lake Pavin (26%,  
545 Grami et al., 2011). Bacterial respiration was very weak, contributing only to 1–3% of carbon  
546 output, which may be related to low bacterial production rates. The two size classes of  
547 metazooplankton (met1 and met2) exhibited the highest vertical sinking flux that represented  
548 14 – 19% of total carbon output. These trophic components produced important fraction (23–  
549 40%) of total detritus.

550 In the Channel, the sinking of phytoplankton (particularly of microphytoplankton) represented  
551 12% of total carbon losses. However, it did not exceed 7% in the Lagoon and the Bay despite  
552 50% of total detritus production made up by microphytoplankton at these sites. This change  
553 may be caused by the high detritivory activity of metazooplankton at these two sites (Fig. 6).  
554 In addition, detritus sinking accounted for only 3.5–5.5% of total carbon output, which  
555 highlighted the important occurrence of detritivorous metazooplankton.



556 When considering the carbon throughput (i.e. activity of each compartment) in the three sites,  
557 the most active compartments were microphytoplankton, followed by protozooplankton and  
558 metazooplankton, suggesting their important role, as producers and grazers. In contrast, the  
559 bacteria exhibited the lowest Throughput value (Fig. 5) which was consistent of their low  
560 production and respiration. The bacterial uptake of doc was also low (Table 5) corresponding  
561 to 8–30% of doc, which resulted from plankton exudation/excretion and from detritus  
562 dissolution. In parallel to the low activity of bacteria, a low fraction of bacterial production  
563 was grazed by protozooplankton at the three sites (29–49% of their total grazing). These  
564 values were in the same range of those reported in previous study for Bizerte Lagoon during  
565 summer (25–50%, Grami et al., 2008), Arcachon Bay (50%, Tortajada et al., 2012) and the  
566 Lake Pavin (48%, Grami et al., 2011). During our study, small protozooplankton, including  
567 aloricate ciliates (*Strombidium* spp.) and heterotrophic nanoflagellates (*Leucocryptos* spp.),  
568 represented less than 5% of total protozooplankton carbon biomass (Meddeb et al.  
569 (submitted). Since protozooplankton have a weak bacterivory, they would satisfy their carbon  
570 demand by consuming large fraction (>80%) of picphytoplankton production. During the  
571 sampling season (i.e. spring), the protozooplankton were mostly composed by >50 µm  
572 heterotrophic dinoflagellates (i.e. *Protoperidinium* spp.) and tintinnid ciliates (i.e. *Paravavella*  
573 *gigantea* and *Tintinnopsis corniger*) (70–95% of total biomass, Meddeb et al., submitted).  
574 This means that their herbivory was suspected to be high. At the same time, these large  
575 protozooplankton could be potential prey for the metazooplankton and hence can contribute to  
576 channel carbon in each site. To elucidate the real role of each grazer's group in the studied  
577 pelagic ecosystems, the composition of each diet of the proto- and metazooplankton were  
578 analysed. This may also permit a characterization of the dominant pathways of biogenic  
579 carbon.

580 As suspected in our hypothesis, during spring the diet of protozooplankton relied mainly on  
581 phytoplankton (90–98%), with large contribution of microphytoplankton (60–77%). The  
582 remaining carbon demand of protozooplankton was supported by bacteria (5–10%). A similar  
583 result was previously reported in the Bizerte Lagoon during the summer season (with 62% of  
584 autotrophs and 17% of bacteria; Grami et al., 2008), in the spring season at Arcachon Bay  
585 (with 84% of autotrophs and 16% of bacteria; Tortajada et al., 2012), and again in spring at  
586 the Bay of Biscay (with 88% of autotrophs and 12% of bacteria; Marquis et al., 2007). In  
587 contrast, in other regions, such as Lake Biwa, the main carbon input to protozooplankton was  
588 detritus (45%) and bacteria (52%) (Niquil et al., 2006). In the Bay of Biscay during spring,  
589 the major food source was picophytoplankton, which contributed 64–83% of total carbon  
590 input; while in the late spring the protozooplankton diet was composed of bacteria and  
591 phytoplankton in roughly equal shares (Marquis et al., 2007).

592 Small metazooplankton (200-700  $\mu\text{m}$ ) seemed to be mainly detritivorous in the Lagoon and  
593 the Bay of Bizerte during spring (detritus formed 52–58% of their diets), whereas in the  
594 Channel, protozooplankton constituted important fraction of their ingested carbon (54%).  
595 Larger mesozooplankton ( $>700 \mu\text{m}$ ) were mostly carnivorous, as protozooplankton and small  
596 metazooplankton (200-700 $\mu\text{m}$ ) formed half of their diets at all sites, but detritus represented a  
597 non-negligible carbon source for the met2 (21–42%). In all sites, diets for both size classes of  
598 metazooplankton relied less on phytoplankton (10, 21, and 5% for Lagoon, Channel and Bay,  
599 respectively). When considering all zooplankton, the detritivory:herbivory (D:H) ratio varied  
600 from 0.25 to 0.77 for the three sites during spring. These values were very similar to those  
601 already reported for the Bizerte Lagoon in spring (0.23–0.74, Grami et al., 2008). Then,  
602 detritus do not have a principal role in channelling carbon through the three planktonic food  
603 webs. The planktonic food webs rely mostly on the herbivory of zooplankton. To stress the  
604 importance of protozooplankton compared to metazooplankton as autotrophic carbon

605 consumer, two specific ratios were adapted from Sakka Hlaili et al. (2014): (1) the ratio of the  
606 consumption rate of phytoplankton by protozooplankton to the total consumption rate by  
607 protozooplankton (R1 ratio) and (2) the ratio of consumption rate of phytoplankton by  
608 protozooplankton to the consumption rate of phytoplankton by proto- and metazooplankton  
609 (R8 ratio). In our case, the R1 ratio varied from 0.83 to 0.94, indicating that protozooplankton  
610 grazed on more phytoplankton than other prey. In parallel, primary producers were consumed  
611 more-so by protozooplankton than metazooplankton, since our R8 ratio varied from 0.82 to  
612 0.99. According to both ratios, the protozooplankton mainly assured the herbivory in the three  
613 pelagic ecosystems. Moreover, the protozooplankton removed 40 –54% of nano- and  
614 microphytoplankton production per day compared to the 3–14% grazed by metazooplankton.  
615 These mesozooplankton seemed to have a small role in herbivory, but instead they can  
616 impose important predatory pressure on protozooplankton and then participate in channelling  
617 biogenic carbon.

618 To identify the dominant trophic pathway in the three planktonic ecosystems, a specific ratio  
619 was proposed by Sakka Hlaili et al. (2014): the ratio of picophytoplankton net production to  
620 total phytoplankton net production (R7 ratio). This ratio was proposed by the authors to  
621 discriminate between herbivorous ( $R7 \leq 0.1$ ), multivorous ( $R7: 0.1-0.6$ ), and microbial food  
622 webs ( $R7 \geq 0.6$ ). In the Lagoon and the Channel, the ratio values (0.13 and 0.11, respectively)  
623 are very close to the lower limit of R7 (0.1) that discriminates the multivorous structure of the  
624 herbivorous one. Therefore, food webs in both sites during spring can be considered to be  
625 approximately multivorous but tend towards the herbivorous pathway. In the Bay of Bizerte,  
626 the herbivorous pathway was more dominant, at 0.08.

#### 627 **4.2. Structural and functional proprieties of identified food webs**

628 The ENA indices have proved to be very useful to characterize ecosystem functioning, to  
629 describe the activity and the retention capacity as well as the level of organization and

630 maturity of the food webs, and to detect any change in their environments (Proulx et al., 2005;  
631 Heymans et al., 2007). These indicators have been frequently used, especially to assess the  
632 impact of natural and anthropogenic pressures on coastal marine ecosystems (Belgrano et al.,  
633 2005; Niquil et al., 2014; Piroddi et al., 2015; Chaalali et al., 2016). They also provide useful  
634 information on the degree of stress and stability of food webs (Grami et al., 2008; Heymans et  
635 al., 2014; Saint-Béat et al., 2015). Besides, ENA indices were potentially very valuable in  
636 inter-ecosystem comparisons.

637 Considering the total system throughput (TST), the highest values were observed for the  
638 Lagoon ( $4798 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and the Channel ( $3818 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) (large and medium  
639 difference) compared to the Bay ( $2934 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) (Table 6; Fig. 8). This means that the  
640 Lagoon and the Channel were most active as they had high productivity, which can be related  
641 to their high degree of eutrophication. These semi-enclosed ecosystems are closer to sources  
642 of nutrient discharges compared to the Bay that has larger exchange with the Mediterranean  
643 Sea (Fig. 1). Previously, Grami et al. (2008) have also shown high TST within the Lagoon of  
644 Bizerte, which was directly related to the proximity of the study station to sources of nutrient  
645 discharge (urban and shellfish farming input). Our results are in line with the estimates  
646 obtained for other eutrophic ecosystems. For example, some South African ecosystems are  
647 very active with high TST values (Niquil et al., 2012) reflecting high production, which rely  
648 on the strong activity of the benthic compartments (macrophytes as main primary producers  
649 in salt marshes) (Scharler et al., 2005).

650 The relative ascendancy (A/DC) represents the total activity that has been converted into  
651 organized complexity. It equalled 57% in the Bay and 55% in the Lagoon and the Channel of  
652 Bizerte (Fig. 8), suggesting that the Bay is more organized than the two other ecosystems.  
653 Some ecosystems, such as Kromme Estuary (South Africa), exhibited low A/DC (35%,  
654 Scharler et al., 2005) because of severe limitations in freshwater inflow that caused a decline

655 of the internal organization and maturity (Baird and Heymans, 1996). On the Italian coast,  
656 higher relative ascendancy values appeared to be related to the impact of human and industrial  
657 activities focused in the southern part of the Apulian peninsula (Vassallo et al., 2006).

658 According to Monaco and Ulanowicz (1997), recycling is considered to be an important  
659 indicator of an ecosystem's ability to maintain its structure and integrity through positive  
660 feedbacks, and has been used as an indicator of stress (Ulanowicz, 1986) and ecosystems  
661 maturity (Odum, 1969; Christensen, 1995; Vasconcellos et al., 1997). Cycling reduces the  
662 impact of a perturbation on an ecosystem by acting as a buffer and it seems to increase the  
663 resistance of the system (Saint-Béat et al., 2015). Therefore, the Finn's cycling index (FCI,  
664 Finn, 1976) has been shown to be correlated with ecosystem maturity, resilience, and stability  
665 and high FCI is a feature of mature ecosystem (Christensen et al., 2005; Duan et al., 2009,  
666 Niquil et al., 2012). In our study, the FCI was generally quite low (12–14%), suggesting that  
667 the study sites are disturbed ecosystems and that they are not mature. This may be due to  
668 anthropogenic stresses, such as eutrophication and chemical contamination. Patrício et al.  
669 (2004) has shown that FCI decreased from 20.24% to 19.46% between moderate and strongly  
670 eutrophic waters. Similarly, Duan et al. (2009) have reported a drastic decrease of the FCI for  
671 the Pearl River Estuary between 1981 (9.21%) and 1998 (2.72%) due to a continuing  
672 pollution since 1980. Piroddi et al. (2015) showed that the Amvrakikos Gulf (Western  
673 Greece) was an immature and perturbed ecosystem (FCI = 16%), typical of “closed”  
674 ecosystems (e.g., like estuaries, lagoons, and bays) where bottom-up prevail over top-down  
675 processes, and where possibly high levels of community stress are induced by anthropogenic  
676 and environmental forces. In a previous study, conducted in the Bizerte Lagoon in 2004  
677 (Grami et al., 2008), the FCI was found to be higher (21%) than our estimate (12%). During  
678 last decade, the Lagoon has undergone increasing anthropogenic pressure, as several new  
679 industrial factories are located on its shores and the number of shellfish farms has tripled. This

680 has obviously contributed to an increase of eutrophic and polluted status of the Lagoon, which  
681 was confirmed by a decrease of the FCI from 2004 to 2012. Unfortunately, no previous data  
682 existed for the Channel and the Bay, so our study is a first report modelling the perturbed  
683 status of these waters.

684 To compare the degree of perturbation among the study sites, the average path length (APL)  
685 was used. This descriptor is expected to be longer in systems with high degree of flow  
686 diversity and cycling (Christensen, 1995; Thomas and Christian, 2001). Increasing the  
687 number of links increases the robustness of interactions of an ecosystem (Lafferty et al.,  
688 2008), and its overall organization (Lafferty et al., 2006). The APL reached higher value in  
689 the Bay (3.03 components per average food cycle) than the two other sites (2.88 –2.95).So,  
690 compared to the Bay, the Lagoon and the Channel were more stressed. As mentioned, both  
691 sites have undergone higher chemical pollution and nutrient loading than the Bay (Bejaoui et  
692 al., 2010; Sahraoui et al., 2012; Barhoumi et al., 2014a, b; Pringault et al., 2016)

## 693 **5. Conclusion**

694 Modelling can be used to investigate, analyse, and compare the functioning of ecosystems  
695 subjected to various anthropogenic stresses at different periods. This integrated approach  
696 provides many indications on ecosystem health and stability. Several modelling technique  
697 exists and are already used for management objectives (e.g: Ecopath, Osmose, Atlantis). More  
698 specifically, the LIM-MCMC approach has important complementary features, since it takes  
699 into account microbial processes and which can provide confidence intervals for statistical  
700 comparisons. Our study has highlighted the status and the functioning of three interconnected  
701 sites during the spring of 2012 (Lagoon, Channel, and Bay of Bizerte), subjected to various  
702 anthropogenic pressures. The main results showed that (i) carbon input came from autotrophic  
703 primary production, by microphytoplankton, (ii) herbivorous and almost multivorous  
704 food-webs were the dominant carbon pathways in the study sites during spring, and (iii) the

705 herbivorous activity was mainly driven by the protozooplankton, which played a major role in  
706 the transfer of biogenic carbon to higher trophic levels.

707 The different indices used in our study showed that the Lagoon and the Channel seemed to be  
708 more stressed, more active, and less organized compared to the Bay of Bizerte. This directly  
709 reflects the difference in the degrees of anthropogenic pressure (as eutrophication and  
710 chemical pollution) among these ecosystems. Finally, this study supports that inverse  
711 modelling combined with ecological network analysis may offer an effective tool for  
712 management and assessment of ecosystems health, and to diagnose the occurrence of  
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