



HAL
open science

Plankton food-web functioning in anthropogenically impacted coastal waters (SW Mediterranean Sea): An ecological network analysis

Marouan Meddeb, Boutheina Grami, Aurélie Chaalali, Matilda Haraldsson, Nathalie Niquil, Olivier Pringault, Asma Sakka Hlaili

► **To cite this version:**

Marouan Meddeb, Boutheina Grami, Aurélie Chaalali, Matilda Haraldsson, Nathalie Niquil, et al.. Plankton food-web functioning in anthropogenically impacted coastal waters (SW Mediterranean Sea): An ecological network analysis. *Progress in Oceanography*, 2018, 162, pp.66-82. 10.1016/j.pocean.2018.02.013 . hal-02146358

HAL Id: hal-02146358

<https://hal.science/hal-02146358>

Submitted on 3 Jun 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3
4 Marouan Meddeb^{a*}, Boutheïna Grami^b, Aurélie Chaalali^{c,d,e}, Matilda Haraldsson^c, Nathalie
5 Niquil^c, Olivier Pringault^f, Asma Sakka Hlaili^a

6
7 ^aLaboratoire de phytoplanctonologie, Faculté des Sciences de Bizerte, Université de Carthage,
8 7021 Zarzouna, Bizerte, Tunisie.

9 ^bLaboratoire de Recherche "Bioressources : Biologie Intégrative & Valorisation" BIOLIVAL,
10 Institut Supérieur de Biotechnologie de Monastir, Université de Monastir, Avenue Taher
11 Hadad, 5000, Tunisie.

12 ^cNormandie Université UNICAEN, UMR BOREA (MNHN, UPMC, CNRS-7208, IRD-207),
13 CS 14032, Caen, France

14 ^dIFREMER, Ecology and models applied to fishery resources, Nantes, France

15 ^eESE, Ecology and Ecosystem Health, Agrocampus Ouest, INRA, 35042 Rennes, France

16 ^fInstitut de Recherche pour le Développement (IRD), MARBEC, Marine Biodiversity,
17 Exploitation & Conservation, BP 434 1004 Tunis, Tunisie, UMR IRD (n° 248), Ifremer, Univ.
18 Montpellier, CNRS (n° 9190).

19
20
21 *Corresponding author

22 E-mail: marouan.meddeb@yahoo.fr

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 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 km² 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⁻³, 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⁻¹, Ben Mna

151 et al., 2017), organotins (170 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 μm 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 μm polycarbonate filters and then frozen in acid-washed vials at -20°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°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 μm (met1) and 700 μm (met2)] were sampled using
201 two horizontal net tows with 200 μm and 700 μm 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 (μm^3) of bacteria and picophytoplankton were converted to carbon
207 content (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 μM of
216 doc is equal to 12 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 (mg C m^{-2}) were calculated by vertically integrating the carbon
220 concentration (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, d^{-1}) of bacteria
224 and size-fractionated phytoplankton (pic, nan, and mic), as well as their grazing rates (g, 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⁻³ d⁻¹)
 240 and their consumption rates (*G*, mg C m⁻³ d⁻¹) 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*₀ (mg C m⁻³) 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⁻² d⁻¹) 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, 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, GP_{sub} is the gut pigment concentration (mg pigment m^{-3}) from the subsample, v (m^3) is
262 the volume of the subsample, F is the fraction of subsample processed for gut pigment
263 content, and V_{net} (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 GP (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 WC (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 (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 μm filtered seawater
276 + NaCl at final concentration of 5 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 (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 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-
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 μm
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[®] 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[®] 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 δ test for comparing network indices between sites**

409 As suggested by Tecchio et al. (2016), we use the Cliff δ 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 $1234 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the Lagoon and $966 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the Channel, but only
421 $727 \text{ mg C m}^{-2} \text{ d}^{-1}$ 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 μm (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 μm (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 μm (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 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 μm) 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 μm) 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
713 anthropogenic pressures.

714 **Acknowledgements**

715 This work was supported by IRD through the JEAI-ECOBIZ and the LIM COSYS-Med. MM
716 was financed by an IRD fellowship (ARTS program). The work of Nathalie Niquil on ENA
717 derived indicators for characterizing the stress in food webs is supported by DEVOTES
718 (DEVELOPMENT OF innovative TOOLS for understanding marine biodiversity and assessing
719 Good Environmental Status) funded by the European Union under the 7th Framework
720 Programme, 'The Ocean for Tomorrow' Theme (grant agreement no. 308392), [www.devotes-](http://www.devotes-project.eu)
721 [project.eu](http://www.devotes-project.eu). The English grammar and syntax of the manuscript have been revised by
722 Proof-Reading-service.com. Anonymous referees are warmly acknowledged for triggering
723 substantial enhancements on the early version of this manuscript.

724 **References**

725 Alekseenko, E., Raybaud, V., Espinasse, B., Carlotti, F., Queguiner, B., Thouvenin, B.,
726 Garreau, P., Baklouti, M., 2014. Seasonal dynamics and stoichiometry of the planktonic
727 community in the NW Mediterranean Sea: a 3D modeling approach. *Ocean Dynamics* 64,
728 179-207.
729 Auger, P.A., Diaz, F., Ulses, C., Estornel, C., Neveux, J., Joux, F., Pujo-Pay, M., Naudin, J.J.,
730 2011. Functioning of the planktonic ecosystem on the Gulf of Lions shelf (NW
731 Mediterranean) during spring and its impact on the carbon deposition: a field data and 3-D
732 modeling combined approach. *Biogeosciences* 8, 3231-3261.

733 Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The
734 ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* 10,
735 257-263.
736
737 Baird, D., Mc Glade, J.M., Ulanowicz, R.E., 1991. The comparative ecology of six marine
738 ecosystems. *Philosophical Transactions of the Royal Society of London, Series B. Biological*
739 *Sciences* 333, 15-29.
740
741 Baird, D., Heymans, J.J., 1996. Assessment of ecosystem changes in response to freshwater
742 inflow of the Kromme River estuary, St Francis Bay, South Africa: a network analysis
743 approach. *Water SA* 22, 307-318.
744
745 Baird, D., Luczkovich, J., Christian, R.R., 1998. Assessment of spatial and temporal
746 variability in system attributes of the St Marks National Wildlife Refuge, Apalachee Bay,
747 Florida. *Estuarine Coastal and Shelf Science* 47, 329-34.
748
749 Baird, D., 2012. Assessment of observed and perceived changes in ecosystems over time with
750 special reference to the Sylt-Rømø Bight, German Wadden Sea. *Estuarine Coastal and Shelf*
751 *Science* 108, 144-154.
752
753 Barhoumi, B., LeMenach, K., Dévier, M-H., Ameer, W.B., Etcheber, H., Budzinski,
754 H., Cachot, J., Driss, M.R., 2013. Polycyclic aromatic hydrocarbons (PAHs) in
755 surfacosediments from the Bizerte lagoon, Tunisia: levels, sources and toxicological
756 significance. *Environmental Monitoring and Assessment* 186, 2653-2669.
757
758 Barhoumi, B., Le Menach, K., Dévier, M.H., El megdiche, Y., Hammami, B., Ameer, W.B.,
759 Hassine, S.B., Cachot, J., Budzinski, H., Driss, M.R., 2014a. Distribution and ecological risk
760 of polychlorinated biphenyls (PCBs) and organochlorine pesticides (OCPs) in surface
761 sediments from the Bizerte lagoon Tunisia. *Environmental Science Pollution Research* 21,
762 6290-6302.
763
764 Barhoumi, B., Le Menach, K., Devier, M.H., Ben Ameer, W., Etcheber, H., Budzinski, H.,
765 Cachot, J., Driss, M.R., 2014b. Polycyclic aromatic hydrocarbons (PAHs) in surface
766 sediments from the Bizerte Lagoon, Tunisia: levels, sources, and toxicological significance.
767 *Environmental Monitoring and Assessment* 186, 2653-2669.
768
769 Bejaoui, B., Harzallah, A., 2005. Modèle hydrodynamique de la lagune de Bizerte avec
770 forçage saisonnier. *Atelier de Modélisation des Écosystèmes Marins*, organisé par l'INSTM,
771 Tunis, 27-28.
772
773 Bejaoui, B., Harzallah, A., Moussa, M., Chapelle, A., Solidoro, C., 2008. Analysis of
774 hydrobiological pattern in the Bizerte lagoon (Tunisia). *Estuarine Coastal and Shelf*
775 *Science* 80, 121-129.
776
777 Bejaoui B., Ferjani D., Zaaboub N., Chapelle A., Moussa M., 2010. Caractérisation
778 hydrobiologique saisonnière de la lagune de Bizerte. *Revue des Sciences De l'eau* 23, 215-
779 232.

780 Belgrano, A., Scharler, U.M., Dunne, J., Ulanowicz, R.E., 2005. Aquatic Food Webs. Oxford
781 U 25-40.

782 Ben Ameer, W., Trabelsi, S., El Megdiche, Y., Ben Hassine, S., Barhoumi, B., Hammami, B.,
783 Eljarrat, E., Barceló, D., Driss, M. R., 2013. Concentration of polychlorinated biphenyls
784 and organochlorine pesticides in mullet (*Mugilcephalus*) and sea bass (*Dicentrarchus labrax*)
785 from Bizerte Lagoon (Northern Tunisia). *Chemosphere* 90, 2372-2380.
786

787 Ben Garali, M., Ouakad., Gueddari, M., 2010. Contamination of Superficial Sediments
788 by Heavy Metals and Iron in the Bizerte Lagoon, Northern Tunisia. *Arabian Journal of*
789 *Geosciences* 3, 295-306.
790

791 Ben Mna, H., Oueslati, W., Helali, M.A., Zaaboub, N., Added., A., Aley, L., 2017.
792 Distribution and assessment of heavy metal toxicity in sediment cores from Bizerte Lagoon,
793 Tunisia. *Environmental Monitoring and Assessment*, 189-356.
794

795 Berggreen, U., Hansen, B. Kigkhoe, A.T., 1988. Food size spectra, ingestion and growth of
796 the copepod *Acartiu tonsu* during development: Implications for determination of copepod
797 production. *Marine Biology* 99, 341-352.
798

799 Berglund, J., Samuelsson, K., Kull, T., Muren, U., Andersson, A., 2005. Relative strength of
800 resource and predation limitation of heterotrophic nanoflagellates in a low-productive sea
801 area. *Journal of Plankton Research* 27, 923-935.
802

803 Bianchi, C.N., Morri, C., 2000. Marine Biodiversity of the Mediterranean Sea: Situation,
804 Problems and Prospects for Future Research. *Marine Pollution Bulletin* 40, 367-376.

805 Boudouresque, C.F., Verlaque, M., 2002. Biological pollution in the Mediterranean Sea:
806 invasive versus introduced macrophytes. *Marine Pollution Bulletin* 44, 32-38.

807 Boufahja F., 2010. Approches communautaires et populationnelles de biosurveillance
808 d'un milieu marin chez les nématodes libres (lagune et baie de Bizerte, Tunisie). Thèse de
809 doctorat. Faculté des Sciences de Bizerte, Université 7 Novembre Carthage, 422 p.

810 Boufahja, F., Hedfi, A., Essid, N., Aïssa, P., Mahmoudi, E., Beyrem, H., 2012. An
811 observational study on changes in biometry and generation time of *Odontophora villoti*
812 (Nematoda, Axonolaimidae) related to petroleum pollution in Bizerte bay, Tunisia.
813 *Environmental Science and Pollution Research* 19, 646-55.
814

815 Chaalali, A., Saint-Béat, B., Lassalle, G., Le Loc'h, F., Tecchio, S., Safi, G., Savenkoff, C.,
816 Lobry, J., Niquil, N., 2015. A new modeling approach to define marine ecosystems food-web
817 status with uncertainty assessment. *Progress in Oceanography* 135, 37-47.
818

819 Chaalali, A., Beaugrand, G., Raybaud, V., Lassalle, G., Saint-Béat, B., Le Loc'h, F., Bopp, L.,
820 Tecchio, S., Safi, G., Chifflet, M., Lobry, J., Niquil, N., 2016. From species distributions to
821 ecosystem structure and function: A methodological perspective. *Ecological Modelling* 334,
822 78-90.

823 Christensen, V., Pauly, D., 1995. Fish production, catches and the carrying capacity of the
824 world oceans. *Naga* 18, 34-40.
825
826 Cole, J.J., Findlay, S., Pace, M.L., 1988. Bacterial production in fresh and saltwater
827 ecosystems: a cross-system overview. *Marine Ecology Progress Series* 43, 1-10.
828
829 Donali, E., Olli, K., Heiskanen, A.S., Andersen, T., 1999. Carbon flow patterns in the
830 planktonic food web of the Gulf of Riga, the Baltic Sea: a reconstruction by the inverse
831 method. *Journal of Marine Systems* 23, 251-268.
832
833 Duan, L.J., Li, S.Y., Liu, Y., Moreau, J., Christensen, V., 2009. Modeling changes in the
834 coastal ecosystem of the Pearl River Estuary from 1981 to 1998. *Ecological Modelling* 220,
835 2802-2818.
836
837 Eldridge, P.M., Jackson, G.A., 1993. Benthic trophic dynamics in California coastal basin and
838 continental slope communities inferred using inverse analysis. *Marine Ecology Progress*
839 *Series* 99, 115.
840
841 Fath, B.D., Scharler, U.M., Ulanowicz, R.E., Hannon, B., 2007. Ecological network analysis:
842 network construction. *Ecological Modelling* 208, 49-55.
843
844 Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of
845 flows. *Journal of Theoretical Biology* 56, 363-380.
846
847 Grami, B., Niquil, N., Sakka Hlaili, A., Gosselin, M., Hamel, D., 2008. The plankton food
848 web of the Bizerte Lagoon (South-Western Mediterranean): II. Carbon steady state modeling
849 using inverse analysis. *Estuarine Coastal and Shelf Science* 79,101-113.
850
851 Grami, B., Rasconi, S., Niquil, N., Jobard, M., Saint Béat, B., 2011. Functional Effects of
852 Parasites on Food Web Properties during the Spring Diatom Bloom in Lake Pavin: A Linear
853 Inverse Modeling Analysis. *Plos One* 6, 23273.
854
855 Grattepanche, J.D., Vincent, D., Breton, E., Christaki, U., 2011. Microzooplankton herbivory
856 during the diatom *Phaeocystis* spring succession in the eastern English Channel. *Journal of*
857 *Experimental Marine Biology and Ecology* 404, 87-97.
858
859 Harzallah, A., Brahim, M., Sammari, C., Koutitonsky, V., 2003. Water salinity and heat
860 budgets in the lagoon of Bizerte estimated from observations and model simulation.
861 *Proceedings of 3rd JICA*.
862
863 Heymans, J.J., Guénette, S., Christensen, V., 2007. Evaluating network analysis indicators of
864 ecosystem status in the Gulf of Alaska. *Ecosystems* 10, 488-502.
865
866 Heymans, J.J., Coll, M., Libralato, S., Morissette, L., Christensen, V., 2014. Global patterns
867 in ecological indicators of marine food webs: a modelling approach. *Plos One* 9, 95845.
868
869 Hillebrand, H., Dürselen, C.D., Kirschtel, D., Pollinger, U., Zohary, T., 1999. Biovolume
870 calculation for pelagic and benthic microalgae. *Journal of Phycology* 35, 403-424.
871

872 Hobbie, J.E., Daley, R.J., Jasper, S., 1977. Use of Nucleopore filters for counting bacteria by
873 fluorescence microscopy. *Applied and Environmental Microbiology* 33, 1225-1228.
874

875 Huertas, I. E., Navarro, G., Rodríguez Gálvez, S., 2005. The influence of phytoplankton
876 biomass on the spatial distribution of carbon dioxide in surface sea water of a coastal area of
877 the Gulf of Cádiz (southwestern Spain). *Canadian Journal of Botany* 83, 929-940.
878

879 Jackson, G.A., Eldridge, P.M., 1992. Food web analysis of a planktonic system off Southern
880 California. *Progress in Oceanography* 30, 223-251.
881

882 Kay, J., Graham, L.A., Ulanowicz, R.E., 1989. A detailed guide for network analysis. In:
883 Wulff, F., Field, J.G., Mann, K.H. (Eds.), *Network Analysis in Marine Ecology. Methods and*
884 *Applications*. Springer-Verlag Berlin, 15-61.
885

886 Knap, A.H., Michael, A.F., Dow, R.L., Johnson, R.J., Gundersen, K., Sorensen, J.C., Close,
887 A.R., Howse, F.A., Hammer, M., Bates, N., Doyle, A., Waterhouse, T., 1993. *BATS Methods*
888 *Manual*. US Joint Global Ocean Flux Planning. Office, Woods Hole Massachusetts, A 3, 1-
889 108.
890

891 Knap, A., Michaels, A., Close, A., Ducklow, H., Dickson, A., 1996. Protocols for the Joint
892 Global Ocean Flux Study (JGOFS) Core Measurements, JGOFS Report No. 19, 170 pp.
893 Reprint of the IOC Manuals and Guides No 29, UNESCO 1994.
894

895 Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J.O., Mavuti, K., 2006. Gaining insight
896 into food webs reconstructed by the inverse method. *Journal of Marine Systems* 60, 153-166.
897

898 Lafabrie, C., Hlaili, A.S., Leboulanger, C., Tarhouni, I., Othman, H.B, Mzoughi, N., Chouba,
899 L., Pringault, O., 2013. Contaminated sediment resuspension induces shifts in phytoplankton
900 structure and function in a eutrophic Mediterranean lagoon. *Knowledge and Management of*
901 *Aquatic Ecosystems* 410, 1-16.
902

903 Lafferty, K.D., Hechinger, R.F., Shaw, J.C., Whitney, K., Kuris, A.M., 2006. Food webs and
904 parasites in salt marsh ecosystem. Chap. 9, *Disease ecology: community structure and*
905 *pathogen dynamics*, Oxford University Press, 119-134.
906

907 Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., Leo, G., 2008. Parasites in food webs: the
908 ultimate missing links. *Ecology Letters* 11, 533-546.
909

910 Landry, M.R., Hassett, R.P., 1982. Estimating the Grazing Impact of Marine Micro-
911 zooplankton. *Marine Biology* 67, 283-288.
912

913 Leboulanger, C., Bouvy, M., Carre, C., Cecchi, P., Amalric, L., Bouchez, A., Pagano, M.,
914 Sarazin, G., 2011. Comparison of the effects of two herbicides and an insecticide on tropical
915 freshwater plankton in microcosms. *Archives of Environmental Contamination and*
916 *Toxicology* 61, 599-613.
917

918 Legendre, L., Rassoulzadegan, F., 1995. Plankton and nutrient dynamics in marine waters.
919 *Ophelia* 41, 153-172.

- 920 Legendre, L., Rassoulzadegan, F., 1996. Food-web mediated export of biogenic carbon in
921 oceans: hydrodynamic control. *Marine Ecology Progress Series* 145, 179-193.
- 922 Legendre, L., Rivkin, R.B., 2002. Fluxes of carbon in the upper ocean: regulation by food-
923 web control nodes. *Marine Ecology Progress Series* 242, 95-109.
- 924 Lorenzen, C. J., 1967. Determination of chlorophyll and phaeo-pigments: spectrophotometric
925 equations. *Limnology and Oceanography* 12, 343-346.
- 926 Louati, H., Ben Said, O., Got, P., Soltani, A., Mahmoudi, E., Cravo-Laureau, P., Duran, R.,
927 Aissa, P., Pringault, O., 2013. Microbial community responses to bioremediation treatments
928 for the mitigation of low-dose anthracene in marine coastal sediments of Bizerte lagoon
929 (Tunisia). *Environmental Science and Pollution Research* 20, 300-310.
- 930 Lund, J.W.G., Kipling, C., LeCren, E.D., 1958. The inverted microscope method of
931 estimating algal numbers and statistical basis of estimations by counting. *Hydrobiologia* 11,
932 143-170.
- 933 MacIsaac, E.A., Stockner, J.G., 1993. Enumeration of phototrophic picoplankton by
934 autofluorescence microscopy. In: Kemp, P.F., Sherr, B.F., Sherr, E.B., Cole, J.J. (Eds.),
935 *Handbook of Methodology in Aquatic Microbial Ecology*. Lewis Publishers, Boca Raton, FL,
936 pp 187-197.
- 937 Mackas, D., Bohrer, R., 1976. Fluorescence analysis of zooplankton gut contents and an
938 investigation of diel feeding patterns. *Journal of Experimental Marine Biology and Ecology*
939 25, 77-85.
- 940
- 941 Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F., Herbland, A.,
942 Labry, C., Sautour, B., Laborde, P., Vézina, A., Dupuy, C., 2007. Inverse analysis of the
943 planktonic food web dynamics related to phytoplankton bloom development on the
944 continental shelf of the Bay of Biscay, French coast. *Estuarine Coastal and Shelf Science* 73,
945 223-235.
- 946
- 947 Moigis, A.G., 2000. Photosynthetic rates in the surface waters of the Red Sea: the radiocarbon
948 vs. the non-isotopic dilution method. *Journal of Plankton Research* 22, 713-727.
- 949
- 950 Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three U.S.
951 mid-Atlantic estuaries. *Marine Ecology Progress Series* 161, 239-254.
- 952
- 953 Morales, C.E., Harris, R.P., Head, R.N., Tranter, P.R.G., 1993. Copepod grazing in the
954 oceanic northeast Atlantic during a 6 week drifting station: the contribution of size classes and
955 vertical migrants. *Journal of Plankton Research* 15, 185-211.
- 956
- 957 Mzoughi, N., Lespes, G., Bravo, M., Dachraoui, M., Potin-Gautier, M., 2005. Organotin
958 speciation in Bizerte lagoon (Tunisia). *Science of the Total Environment* 349, 211-222.
- 959
- 960 Niquil, N., Jackson, G.A., Legendre, L., Delesalle, B., 1998. Inverse model analysis of the
961 planktonic food web of Takapoto Atoll (French Polynesia). *Marine Ecology Progress Series*
962 165, 17-29.

963 Niquil, N., Bartoli, G., Urabe, J., Jackson, G.A., Legendre, L., Dupuy, C., Kumagai, M.,
964 2006. Carbon steady state model of the planktonic food web of Lake Biwa, Japan. *Freshwater*
965 *Biology* 51, 1570-1585.

966

967 Niquil, N., Kagami, M., Urabe J, Christaki, U., Viscogliosi, E., Sime-Ngando, T., 2011.
968 Potential role of fungi in plankton food web functioning and stability: a simulation analysis
969 based on Lake Biwa inverse model. *Hydrobiologia* 659, 65-79.

970

971 Niquil, N., Chaumillon, E., Johnson, G.A., Bertin, X., Grami, B., David, V., Bacher, C.,
972 Asmus, H., Baird, D., Asmus, R., 2012. The effect of physical drivers on ecosystem indices
973 derived from ecological network analysis: Comparison across estuarine ecosystems. *Estuarine*
974 *Coastal and Shelf Science* 108, 132-143.

975

976 Niquil, N., Baeta, A., Marques, J.C., Chaalali, A., Lobry, J., Patrício, J., 2014. How does an
977 estuarine food web react to disturbances? Lindeman's perspective *Marine Ecology Progress*
978 *Series* 512, 141-154.

979

980 Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262-270.

981

982 Parsons, T.P., Maita, Y., Lalli, C.M., 1984. A manual of Chemical and Biological Methods for
983 Seawater analysis. Pergamon Press, Oxford, England 1, 173.

984

985 Patrício, J., Ulanowicz, R., Pardal, M.A., Marques, J.C., 2004. Ascendency as an ecological
986 indicator: a case study of estuarine pulse eutrophication. *Estuarine Coastal and Shelf Science*
987 60, 23-35.

988

989 Piroddi, C., Teixeira, H., Lynamb, C.P., Smith, C., Alvarez, M.C., Mazik, K., Andonegi, E.,
990 Churilov, T., Tedescog, L., Chifflet, M., Chust, G., Galparsoro, I., Garcia, A.C., Kämäri,
991 M., Kryvenko, O., Lassalle, G., Neville, S., Niquil, N., Papadopoulou, N., Rossberg, A.G.,
992 Suslink, V., Uyarra, M.C., 2015. Using ecological models to assess ecosystem status in
993 support of the European Marine Strategy Framework Directive. *Ecological Indicators* 58, 175-
994 191.

995

996 Pomeroy, L. R., 1974. The ocean's food web: A changing paradigm. *Bioscience* 24, 499-504.

997

998 Pringault, O., Lafabrie, C., Avezac, M., Bancon-Montigny, C., Carre, C., Chalghaf, M.,
999 Delpoux, S., Duvivier, A., Elbaz-Poulichet, F., Gonzalez, C., Got, P., Lebourlanger, C.,
1000 Spinelli, S., Sakka Hlaili, A., Bouvy, M., 2016. Consequences of contaminant mixture on the
1001 dynamics and functional diversity of bacterioplankton in a southwestern Mediterranean
1002 coastal ecosystem. *Chemosphere* 144, 1060-1073.

1003

1004 Proulx, S. R., Promislow, D. E. L., Phillips, P. C., 2005. Network thinking in ecology and
1005 evolution. *Trends in Ecology and Evolution* 20, 345-353.

1006

1007 Rasconi, S., Grami, B., Niquil, N., Jobard, M., & Sime-Ngando, T., 2014. Parasitic chytrids
1008 sustain zooplankton growth during inedible algal bloom. *Frontiers in Microbiology* 5, 1-19.

1009

1007 Richardson, T.L., Jackson, G.A., Burd, A.B., 2003. Planktonic food web dynamics in two
1008 contrasting regions of Florida Bay U.S. *Bulletin of Marine Science* 73, 569-591.

1010 Richardson, T.L., Jackson, G.A., Ducklow, H.W., Roman, M.R., 2004. Carbon fluxes through
1011 food webs of the eastern equatorial Pacific: an inverse approach. *Deep Sea Research I* 51,
1012 1245-1274.

1013
1014 Saint-Béat, B., Vézina, A.F., Asmus, R., Asmus, H., Niquil, N., 2013. The mean function
1015 provides robustness to linear inverse modelling flow estimation in food webs: a comparison
1016 of functions derived from statistics and ecological theories. *Ecological Modeling* 258, 53-64.

1017
1018 Saint-Béat, B., Baird, D., Asmus, H., Asmus, R., Bacher, C., Pacella, S.R., Johnson, G.A.,
1019 David, V., Vézina, A.F., Niquil, N., 2015. Trophic networks: How do theories link
1020 ecosystem structure and functioning to stability properties? A review. *Ecological Indicators*
1021 52, 458-471.

1022
1023 Sahraoui, I., Grami, B., Bates, S.S., Bouchouicha, D., Chikhaoui, M.A., Hadj Mabrouk, H.,
1024 Sakka Hlaili, A., 2012. Response of potentially toxic *Pseudo-nitzschia* (Bacillariophyceae)
1025 populations and domoic acid to environmental conditions in a eutrophied, SW Mediterranean
1026 coastal lagoon (Tunisia). *Estuarine Coastal and Shelf Science* 102-103, 95-104.

1027
1028 Sakka Hlaili, A., Chikhaoui, M.A., Grami, B., Hadj Mabrouk, H., 2006. Effects of N and P
1029 supply on phytoplankton in Bizerte Lagoon (western Mediterranean). *Journal of Experimental*
1030 *Marine Biology and Ecology* 333, 79-96.

1031
1032 Sakka Hlaili, A., Grami, B., Hadj Mabrouk, H., Gosselin, M., Hamel, D., 2007.
1033 Phytoplankton growth and microzooplankton grazing rates in a restricted Mediterranean
1034 lagoon (Bizerte Lagoon, Tunisia). *Marine Biology* 151, 767-783.

1035
1036 Sakka Hlaili, A., Grami, B., Niquil, N., Gosselin, M., Hamel, D., Hadj Mabrouk, H., 2008.
1037 The Planktonic food web of the Bizerte Lagoon (South-western Mediterranean): I. Spatial
1038 distribution under different human pressures. *Estuarine Coastal and Shelf Science* 78, 61-77.

1039
1040 Sakka Hlaili, A., Niquil, N., Legendre, L., 2014. Planktonic food webs revisited: Reanalysis
1041 of results from the linear inverse approach. *Progress in Oceanography* 120, 216-229.

1042
1043 Scharler, U.M., Baird, D., 2005. A comparison of selected ecosystem attributes of three South
1044 African estuaries with different freshwater inflow regimes, using network analysis. *Journal of*
1045 *marine system* 56, 283-308.

1046
1047 Savenkoff, C., Bourdages, H., Swain, D.P., Despatie, S.P., Hanson, J. M., Méthot, R.,
1048 Morissette, L., 2004. Input data and parameter estimates for ecosystem models of the southern
1049 Gulf of St Lawrence (mid-1980s and mid-1990s). *Canadian Technical Report of Fisheries and*
1050 *Aquatic Sciences* 2529, 105.

1051
1052 Sherr, E.B., Sherr, B.F., 1988. Role of microbes in pelagic food webs: a revised concept.
1053 *Limnology and Oceanography* 33, 1225-1227.

1054
1055 Sherr, E.B., Sherr, B.F., 1993. Preservation and storage of samples for enumeration of
1056 heterotrophic protists. In: Kemp, P.F., Sherr, B.F., Sherr, E.B., Cole, J.J. (Eds.), *Handbook of*
1057 *Methods in Aquatic Microbial Ecology*. Lewis Publishers, London, pp 207-212.

1058

1059 Slaughter, A.M., Bollens, S.M., Bollens, G. R., 2006. Grazing impact of mesozooplankton in
1060 an upwelling region off northern California, 2000-2003. *Deep Sea Research II* 53, 3099-3115.
1061

1062 Smayda, T.J., Reynolds, C.S., 2001. Community assembly in marine phytoplankton:
1063 application of recent models to harmful dinoflagellate blooms. *Journal of Plankton Research*
1064 23, 447-461.

1065

1066 Steele, J.H., 1974. *The structure of marine ecosystems*. Harvard University Press, Cambridge.
1067 128 p.

1068 Steinberg, D.K., Carlson, C.A., Bates, N.R. et al., 2000. Zooplankton vertical migration and
1069 the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep Sea*
1070 *Research I* 47, 137-158.

1071 Tecchio, S., Chaalali, A., Raoux, A., Tous Rius, A., Lequesne, J., Girardin, V., Lassalle, G.,
1072 Cachera, M., Riou, P., Lobry, J., Dauvin, J.C., Niquil, N., 2016. Evaluating ecosystem-level
1073 anthropogenic impacts in a stressed transitional environment: The case of the Seine estuary.
1074 *Ecological Indicators* 61, 833-845.

1075

1076 Tecchio, S., Coll, M., Christensen, V., Company, J.B., Ramírez-Llodra, E., Sardà, F., 2013.
1077 Food web structure and vulnerability of a deep-sea ecosystem in the NW Mediterranean Sea.
1078 *Deep Sea Research I* 75, 1-15.

1079

1080 Teira, E., Albade, J., Alvarez-Ossorio, M., Bode, A., Carino, C., Cid, A., Fernandez, E.,
1081 Gonzalez, N., Lorenzo, J., Valencia, J., Varela, M., 2003. Plankton carbon budget in a coastal
1082 wind-driven upwelling station off a Coruna (NW Iberian Peninsula). *Marine Ecology*
1083 *Progress Series* 265, 31-43.

1084

1085 Thomas, C.R., Christian, R.R., 2001. Comparison of nitrogen cycling in salt marsh zones
1086 related to sea-level rise. *Marine Ecology Progress Series* 221, 1-16.

1087

1088 Tortajada, S., Niquil, N., Blanchet, H., Grami, B., Montanie, H., David, V., Gle, C., Saint-
1089 Beat, B., Johnson, G.A., Marquis, E., Del Amo, Y., Dubois, S., Vincent, D., Dupuy, C., Jude,
1090 F., Hartmann, H.J., Sautour, B., 2012. Network analysis of the planktonic food web during the
1091 spring bloom in a semi enclosed lagoon (Arcachon, SW France). *Acta Oecologica* 40, 40-50.

1092

1093 Trabelsi, S., Driss, M. R., 2005. Polycyclic aromatic hydrocarbons in superficial coastal
1094 sediments from Bizerte Lagoon, Tunisia. *Marine Pollution Bulletin* 50, 344-349.

1095

1096 Ulanowicz, R.E., 1980. An hypothesis on the development of natural communities. *Journal of*
1097 *Theoretical Biology* 85, 223-245.

1098

1099 Ulanowicz, R.E., 1986. *Growth and Development: Ecosystems Phenomenology*. Springer-
1100 Verlag, New York.

1101

- 1102 Ulanowicz, R.E., Wulff, F., 1991. Comparing ecosystem structures: the Chesapeake Bay and
 1103 the Baltic Sea. In: Cole J, Lovett G, Findlay S (eds) Comparative analyses of ecosystems,
 1104 pattern, mechanism, and theories. Springer-Verlag New York, 140-166.
 1105
- 1106 Ulanowicz, R.E., 1996. Trophic flow networks as indicators of ecosystem stress. In: Polis
 1107 GA, Winemiller KO, Eds. Foodwebs: integration of patterns and dynamics New York.
 1108 Chapman and Hall, 358-68.
 1109
- 1110 Ulanowicz, R.E., 1997. Ecology, the Ascendent Perspective Columbia University Press, New
 1111 York.
 1112
- 1113 Ulanowicz, R.E., 2000. Ascendency: a measure of ecosystem performance. In: Jørgensen,
 1114 S.E., Müller, F. (Eds.), Handbook of Ecosystem Theories and Management. Boca Raton,
 1115 303-316.
 1116
- 1117 Ulanowicz, R.E., 2004. Quantitative methods for ecological network analysis. Computational
 1118 Biology and Chemistry 28, 321-339.
- 1119 Ulanowicz, R.E., Goerner, S.J., Lietaer, B., Gomez, R., 2009. Quantifying sustainability:
 1120 resilience, efficiency and the return to information theory. Ecological complexity 6, 27-36.
 1121
- 1122 Umani, S.F., Beran, A., 2003. Seasonal variations in the dynamics of microbial plankton
 1123 communities: first estimates from experiments in the Gulf of Trieste, Northern Adriatic Sea.
 1124 Marine Ecology Progress Series 247, 1-16.
 1125
- 1126 Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton methodik.
 1127 Mitteilungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie
 1128 9, 1-38.
 1129
- 1130 Van den Meersche, K., Soetaert, K., Van Oevelen, D., 2009. xsample(): An R Function for
 1131 Sampling Linear Inverse Problems. Journal of Statistical Software 30, 1-15.
- 1132 Vasconcellos, M., Mackinson, S., Sloman, K., Pauly, D., 1997. The stability of trophic mass-
 1133 balance models of marine ecosystems: a comparative analysis. Ecological Modelling 100,
 1134 125-134.
 1135
- 1136 Vassallo, P., Fabiano, M., Vezzulli, L., Sandulli, R., Marques, J.C., Jørgensen, S.E.,
 1137 2006. Assessing the health of coastal marine ecosystems: A holistic approach based on
 1138 sediment micro and meio-benthic measures. Ecological Indicators 6, 525-542.
- 1139 Vézina, A.F., Platt, T., 1988. Food web dynamics in the ocean. I. Best estimates using inverse
 1140 Methods. Marine Ecology Progress Series 42, 269-287.
- 1141 Vézina, F.A., Demers, S., Laurion, I., Sime-Ngando, T., Juniper, S.K., Devine, L., 1997.
 1142 Carbon flows through the microbial food web of first-year ice in Resolute Passage (Canadian
 1143 High Arctic). Journal of Marine Systems, 173-189.
- 1144 Vézina, A.F., Savenkoff, C., Roy, S., Klein, B., Rivkin, R., Therriault, J.C., Legendre, L.,
 1145 2000. Export of biogenic carbon and structure and dynamics of the pelagic food web in the
 1146 Gulf of St Lawrence Part 1 Seasonal variations. Deep Sea Research II 47, 585-607.
 1147

- 1148 Vézina, A.F., and Pahlow, M., 2003. Reconstruction of ecosystem flows using inverse
1149 methods: how well do they work?. *Journal of Marine Systems* 40, 55-77.
1150
- 1151 Weinbauer, M.G., Winter, C., Höfle, M.G., 2002. Reconsidering transmission electron
1152 microscopy based estimates of viral infection of bacterioplankton using conversion factors
1153 derived from natural communities. *Aquatic Microbiol Ecology* 27, 103-110.
- 1154 Zmerli Triki, H., Laabir, M., Lafabrie, C., Malouche, D., Bancon-Montigny, C., Gonzalez, C.,
1155 Deidun, A., Pringault, O., Kéfi Daly-Yahia, O., 2017. Do the levels of industrial pollutants
1156 influence the distribution and abundance of dinoflagellate cysts in the recently-deposited
1157 sediment of a Mediterranean coastal ecosystem?. *Science of the Total Environment* 595, 380-
1158 392.
- 1159 Zrafi-Nouira, I., Khedir-Ghenim, Z., Zrafi, F., Bahri, R., Cheraeif, I., Rouabhia, M., 2008.
1160 Hydrocarbon pollution in the sediment from the Jarzouna-Bizerte coastal area of Tunisia
1161 (Mediterranean Sea). *Bulletin of Environmental Contamination and Toxicology* 80, 566-572.