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1 **Temporal fluctuations in zooplankton size, abundance and taxonomic**
2 **composition since 1995 in the North Western Mediterranean Sea**

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21 **Abstract**

22
23 In the Gulf of Lions, small pelagic fish have shown reduced body size and body condition after 2007
24 that would result from changes in zooplankton community. We therefore examined zooplankton
25 density, body size and taxonomic composition at the closest long-term monitoring station (1995-
26 2019): the coastal Point-B. To cover a broader spectrum of zooplankton community, samples obtained
27 from two nets, the WP2 (200 µm mesh size) and the Regent (690 µm), were analysed with the imaging
28 Zooscan method. One important result was the high stability through time of the zooplankton
29 community. No long-term monotonous trends in density, size and taxonomic composition were
30 detected. Interannual variations in zooplankton size and density were not significantly correlated to
31 any environmental variable, suggesting the possible importance of biotic interactions. Still, an increase
32 in temperature was followed by a sharp decrease of zooplankton density in 2015, after which only
33 gelatinous groups recovered. No change in the zooplankton community was detected around 2007 to
34 support bottom-up control on small pelagic fish. Whether this derives from different local processes
35 between the Gulf of Lions and Ligurian Sea cannot be excluded, highlighting the need for
36 simultaneous monitoring of different ecosystem compartments to fully understand the impact of
37 climate change.
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45 **1. Introduction**

46 Zooplankton is most often very responsive to environmental changes and could consequently
47 impact upper trophic levels with possible repercussions up to top-predators through different
48 mechanisms (Beaugrand & Kirby, 2010; Cury et al., 2000; Lynam et al., 2017). Changes in
49 plankton phenology (Aberle et al., 2012; Thackeray et al., 2010; Winder et al., 2012) can for
50 instance directly affect planktivorous species recruitment, either positively (match) or
51 negatively (mismatch) (Cushing, 1990). Warming could also decrease net primary production
52 (Bopp et al., 2013) and favor smaller phytoplankton (Daufresne et al., 2009) and zooplankton
53 (Kudela et al., 2006; Medellín et al., 2016) species, modifying the availability of energetic
54 resources in food webs as small zooplankton individuals are generally less energetic than
55 large ones (Barroeta et al., 2017). In upwelling systems, sardine and anchovy regime
56 fluctuations have indeed been related to the size of zooplankton, sardine favoring smaller prey
57 due to higher filtration capacity compared to anchovy (Tam et al., 2008; Van der Lingen et
58 al., 2006). A recent experimental study further showed that Mediterranean sardines feeding on
59 bigger pellets (1.2 mm) were in better body condition (a proxy for energy reserves) and
60 displayed higher growth rate than those feeding on smaller particles (0.1 mm), probably
61 because of a change to a more costly feeding behavior (Queiros et al., 2019), again
62 highlighting the importance of plankton size. In the Gulf of Lions and the bay of Biscay,
63 changes in the zooplankton community and especially the zooplankton quality are suspected
64 to be one of the main drivers of changes in fish size structure and mean body condition
65 (Brosset et al., 2016; Saraux et al., 2019; Véron et al., 2020). Understanding how the plankton
66 community varies in terms of taxonomic composition, body size and density is of primary
67 importance to understand potential impacts on higher trophic levels, especially in a context of
68 climate change.

69 The Mediterranean sea is an oligotrophic semi-enclosed basin under strong anthropic impact
70 (The MerMex Group et al., 2011). In the last 2 decades, different studies highlighted
71 important changes in size, abundance, body condition or spatial distribution of Mediterranean
72 fish populations (Brosset et al., 2017; Sabatés et al., 2006; Saraux et al., 2019; Tsikliras, 2008;
73 Van Beveren et al., 2014). Particularly in North Western Mediterranean sea (NWMS),
74 important demographic changes have been recorded in small pelagic fish since 2007 (Van
75 Beveren et al., 2014; Brosset et al. 2017). Different hypotheses have been formulated and
76 investigated, but top-down controls (due to overfishing or natural predation), emigration of
77 largest individuals or epizootic diseases have all been refuted (Queiros et al., 2018; Van
78 Beveren, et al., 2016a,b, 2017), so that the hypothesis of a bottom-up control has been

79 suggested as the most probable underlying mechanism (Brosset et al., 2016; Saraux et al.,
80 2019).

81 Unfortunately, long time series of zooplankton in the NW Mediterranean are scarce. Using the
82 longest zooplankton time series in the neighboring Ligurian Sea, several studies have shown
83 interannual variability possibly related to large-scale climatic forcing, especially the North
84 Atlantic Oscillation (García-Comas et al., 2011; Molinero et al., 2005; Vandromme et al.,
85 2011; Fullgrabe et al., 2020). According to these studies, interannual variations in winter
86 conditions led to changes in the availability of nutrients resulting in different spring bloom
87 intensities. During favorable years (in the 1980's and early 2000's), increased primary
88 production would favor zooplankton production (especially copepods) for the rest of the year.
89 Coupled atmosphere/ocean/biogeochemical modeling of the central NW Mediterranean sea
90 supported the hypothesis of interannual control of plankton communities by deep winter
91 mixing (Auger et al., 2014). Interannual interactions between filter-feeding gelatinous
92 zooplankton and copepods were suggested to be another key factor (Molinero et al., 2005).
93 The former are more efficient grazers of small phytoplankton than the latter and would over-
94 compete them during warm years, when pico- and nanophytoplankton dominate (Licandro et
95 al., 2006). Finally, it has also been suggested that carnivorous gelatinous, such as
96 *Chaetognatha* or *Siphonophorae* could also have an impact by increasing the top down
97 pressure on copepods (Molinero et al., 2008b).

98 Nonetheless, these studies had investigated zooplankton fluctuation either until 2005 in the
99 northern coastal station (point B) or from 2004 to 2016 in the southern station (Stareso
100 station), but not on a period spanning several years before and after 2007, i.e. when the main
101 changes in NW Mediterranean small pelagic fish population were observed (Saraux et al.,
102 2019). Moreover, most studies had focused on zooplankton densities and did not investigate
103 potential changes in size distribution of the NW Mediterranean zooplankton.

104 The main objective of this work was then to study long-term, interannual and seasonal
105 variations in zooplankton density, body size and taxonomic composition to identify potential
106 changes since 1995. For the first time at the point B station, the long-term variations of
107 zooplankton was studied based on 2 different nets (the WP2 with a small mesh size (200 μm)
108 and the Regent focusing on larger individuals (mesh size of 690 μm) in order to cover a
109 broader spectrum of the zooplankton community. A focus was made on the crustaceans
110 because they are the most abundant zooplankton and the principal prey of many small pelagic
111 fish in the NW Mediterranean sea (Brosset et al., 2016; Plounevez & Champalbert, 2000).
112 The variability of gelatinous carnivorous and gelatinous filter-feeders was also examined, as

113 these two groups could potentially interact with crustaceans through competition or predation.
114 We finally tried to understand the interplays between crustaceans abundance, taxonomic
115 composition, size spectra and environmental changes.

116

117 **2. MATERIAL AND METHODS**

118 **1. Sample collection**

119 Zooplankton samples were collected weekly at Point B (43°41.10'N, 7°18.94'E; 85 m water
120 depth), a coastal monitoring station at the entrance of the bay of Villefranche-sur-Mer (NW
121 Mediterranean Sea, France). Sampling was done by vertical tows (75 m deep to surface) of a
122 Regent net (mesh size of 690 µm, mouth aperture of 0.785 m²) and WP2 net (mesh size of
123 200 µm, mouth aperture of 0.25 m²). For the present study, 919 samples collected once to 4
124 times a month from 1995 to 2019 were used for Regent net and 666 for WP2, from 2004 to
125 2019. All samples were manually fractionated with a Motoda box and then analysed with the
126 Zooscan/Zooprocess system (Gorsky et al., 2010). Samples were fractionated at different
127 levels, depending on zooplankton abundance in the sample, so as to keep around 1500 and
128 500 individuals in the samples for the WP2 and the regent nets, respectively. This process
129 allows having a picture for each individual (avoiding superimposed or touching individuals),
130 from which the identification and size measurements can be performed. Identification was
131 performed using automatic recognition, followed by the validation of each picture by an
132 expert. All the zooplankton data are available on the EcoTaxa platform ([https://ecotaxa.obs-
133 vlfr.fr/](https://ecotaxa.obs-vlfr.fr/)).

134

135 **2. Taxonomy in the WP2**

136 Because of the small size of individuals in the WP2 net, taxonomic identification at fine level
137 was not possible in the frame of this study. 15 groups that presented the finest taxonomic
138 identification homogenous for the whole time were finally retained, i.e., “Eumalacostraca”,
139 “Cladocera”, “Ostracoda”, “Copepoda” and “Other_Crustacea” for the crustaceans ;
140 “Chaetognatha”, “Siphonophorae”, “Other Hydrozoa”, “Salpida”, “Doliolida” and
141 “Appendicularia” for gelatinous species and finally “Harosa”, “Annelida”, “Mollusca” and
142 “Other zooplankton”. The gelatinous were grouped in two functional groups, the
143 “herbivorous” filter feeders (*Doliolida*, *Salpida* and *Appendicularia*) and the carnivorous
144 (*Chaetognatha*, *Siphonophorae* and *Other hydrozoa*) (Acuña, 2001; Dallot et al., 1988).

145 **3. High resolution taxonomy in the Regent**

146 In the Regent, a high resolution taxonomic identification was possible, especially for
147 crustaceans, because of a greater size of the individuals allowing a better recognition
148 compared to smaller one. The taxonomy was determined as a compromise between the
149 resolution allowed by the image quality, preventing high resolution taxonomy for small
150 individuals, and the necessity to aggregate rare groups. Because the Calanoida order was
151 dominant (around 60 % of crustaceans), analyses were performed mainly at the family level
152 for *Copepoda*, including: *Calanidae*, *Centropagidae*, *Candaciidae*, *Metridinidae*, *Temoridae*,
153 *Acartiidae*, *Eucalanidae*, *Euchaetidae*, *Corycaeidae*, *Sapphirinidae*, *Oithonidae* and
154 *Oncaeidae*. Other small *Copepoda* families (e.g. *Clausocalanidae* & *Paracalanidae*) that
155 could not be distinguished with the image resolution were pooled in *Other_Calanoida*.
156 *Decapoda*, *Amphipoda*, *Mysida* and *Euphausiacea* were however only identified at the order
157 levels. Finally, a “Other_Crustacea” group was also kept, representing mainly individuals
158 identified at a low taxonomic resolution, but around 90 % of the individuals of this group
159 were identified as *Eumalacostraca*, at the subclass level. For comparison purposes, Regent
160 results are presented both at the fine taxonomy level and at the same taxonomy level as the
161 WP2 net.

162 **4. Time series analyses of the zooplankton density**

163 Because both changes in plankton phenology and density could affect upper trophic levels, we
164 investigated crustaceans and gelatinous (herbivorous and carnivorous) densities at a monthly
165 time scale. Data were expressed in individuals/m³ and log-transformed to stabilize the
166 variance (Curran-Everett, 2018). A wavelet analysis was performed to quantify the main
167 patterns of variability (Carey et al., 2016; Chatfield, 2003). Wavelet analysis is a frequency-
168 analysis technique that can be used to reveal the frequency components of signals and identify
169 where a certain frequency exists in the temporal domain (e.g. seasonal signal would be seen at
170 a frequency of 12 months). By looking for regions where the Wavelet Power Spectrum (WPS)
171 is of large power, we can determine which features of the signal are important. The
172 significance of the wavelet spectrum was performed against white noise, as the time series
173 displayed variance at both high and low frequencies (Rouyer et al., 2008). The long-term
174 trend was extracted with the Eigen Vector Filtering (EVF), which allowed us to estimate the
175 percentage of variance associated to this trend (Ibanez & Dauvin, 1988). To do this, a
176 Principal Component Analysis (PCA) was performed on a matrix of the time series lagged
177 from 0 to n time lags (in this study, n being equal to 36 months, which allowed us to
178 investigate interannual variations without considering seasonal variability). The analyses were
179 performed using the “pastecs” R package (Grosjean et al., 2014). The breakpoint analysis was

180 performed to identify potential regime shifts (i.e. major discontinuities) in the time series
181 using the “strucchange” R package and an algorithm testing structural changes in time series
182 (Kleiber et al., 2002). Optimal number of segment partitions was based on Bayesian
183 Information Criterion (BIC) in order to compute only the most relevant changes (Schwarz,
184 1978).

185 **5. Time series analyses of the zooplanktonic community**

186 To study the variations in the composition of the zooplanktonic community, monthly time
187 series of densities of each group were constructed (see Sections 2.2 and 2.3). Monthly
188 densities of each group were then plotted on stacked plots to depict both the interannual
189 variations, the phenology of the zooplanktonic community and the proportion of each group.
190 The long-term trends of each group were further extracted by means of EVF analysis (see
191 above). Note that the proportion of each group per year (or month) was calculated on the raw
192 data (without log transformation) and represented in “stacked plot” as the log density of total
193 zooplankton multiplied by the proportion of each group.

194 **6. Time series analyses of crustaceans size spectra**

195 Because crustaceans are mostly ellipsoid, size of each individual was defined as the primary
196 axis of the best fitting ellipse calculated during the Zooprocess (Gorsky et al., 2010;
197 Romagnan et al., 2016). A sensitivity analysis was run to determine the minimal number of
198 individuals within a sample to perform a reliable size spectrum. The results led us to keep a
199 minimum of 200 and 45 individuals/sample for the WP2 and the Regent, respectively (See
200 ESM – Figure S1). Monthly and annual size spectra were then computed by means of
201 Normalized Density Size Spectra (NDSS), which is similar to the well-known Normalized
202 biomass size spectra (Sheldon et al., 1977; Zhou et al., 2010), but based on density instead of
203 biomass. To do so, the density of each size class was calculated and divided by the width of
204 the size class in order to normalize the spectra. Size classes increased each time by a factor of
205 1.3 in order to have both details in smaller size and avoid empty size classes in higher body
206 size. Analyses based on monthly crustaceans size spectra, investigating the distribution of all
207 size spectra mode from 1995 to 2019 for Regent and from 2004 to 2019 for WP2 showed that
208 the nets accurately sampled individuals measuring at least 1.5 mm and 0.65 mm for the
209 Regent and the WP2 respectively (see ESM for details). For that reason, individuals lower
210 than 1.5 mm for Regent and 0.65 mm for WP2 were not considered in any of the following
211 analyses. For both nets, the upper limit of spectra (2.7 mm for WP2 and 3.7 mm for Regent)
212 was defined as the one representing at least 1% of total individuals and contained all the
213 individuals larger than this limit. For each monthly spectrum, the slope was estimated through

214 a linear regression. The time series of the slopes of the monthly NDSS were finally
215 constructed and analysed through EVF to extract the trend (see above) and breakpoint
216 analysis to identify potential regime shifts (i.e. major discontinuities) in the time series. The
217 breakpoint analysis was performed using the “strucchange” R package and an algorithm
218 testing structural changes in time series (Kleiber et al., 2002). Optimal number of segment
219 partitions was based on BIC criterion in order to compute only the most relevant changes.
220 Additional analyses based on functional PCA have been further performed and showed that
221 the slopes of the NDSS carefully tracked changes in size spectra of the zooplanktonic
222 community collected by the WP2 or by the Regent (see ESM for further details).

223 7. Dealing with missing data

224 The minimal number of individuals by sample necessary to construct reliable size spectrum
225 (see above) led to some months with missing values, i.e., 14 of the 300 months in the slopes
226 time series of Regent were missing, while 6 of the 192 months were missing for the WP2.
227 Furthermore, 4 of 192 monthly densities of the WP2 were also missing. Missing values were
228 scattered over the whole period allowing to fill them with an algorithm based on iterative
229 PCA from the MissMDA package (Josse & Husson, 2012). First, the monthly time series was
230 transformed in a year x month matrix and missing values were replaced by the mean of the
231 variable (here the months). Then a PCA was performed and mean values inserted to fill
232 missing data were replaced by the values estimated by the PCA. A second PCA was
233 performed and values estimated by the first PCA were replaced by the one of the second
234 PCA. Following this scheme, iterative PCA were performed until the values estimated
235 stabilised.

236 8. Environment data and analyses

237 *Environmental data*

238 Because one of the objectives was to investigate whether the interannual variability observed
239 in crustaceans density and size spectra could be explained by environmental parameters, we
240 gathered a set of environmental variables that are known to affect plankton dynamics at both
241 the local and the regional scales. All the local environmental data have been sampled weekly
242 since 1995 at the same location as the plankton tows (the “Point B”) at 5 different depths (1
243 m, 10 m, 20 m, 30 m and 50 m). Water for nutrients and chlorophyll-a (Chl-a) analyses was
244 sampled by Niskin bottles. Nitrate ($\text{NO}_3 \mu\text{mol.l}^{-1}$) and Silicate ($\text{SiOH}_4 \mu\text{mol.l}^{-1}$) nutrients
245 were considered, but not Phosphorus because concentrations were at the limit of the detection
246 threshold. Nutrient data at the 1m and 50m layers were averaged, as those two depths were
247 the only ones with complete data from 1995 to 2019. Chl-a was considered as a proxy of

248 phytoplankton biomass and was averaged over the 5 available depths from 1 to 50m. A
249 Seabird SBE25 CTD was used to measure sea water temperature, which was also averaged
250 over the 5 available depths from 1 to 50m. Finally, the stratification of the water column was
251 calculated as the difference of water density between the 10m layer and the 50m layer, as in
252 Vandromme et al., (2011). All these environmental data were provided by SOMLIT
253 (<http://somlit-db.epoc.u-bordeaux1.fr/bdd.php>).

254 As winter water mixing could favour planktonic production (García-Comas et al., 2011;
255 Vandromme et al., 2011), a winter water mixing index was constructed. To do so, a PCA was
256 performed on the winter temperature, winter stratification (Vandromme et al., 2011), winter
257 salinity and winter water density at the “Point B” (see ESM-Fig S2; Vandromme et al., 2011).
258 All winter time series were constructed by averaging monthly values from December to
259 March. The first axis of this PCA, which represented 56.6% of the total variance, was
260 considered as the winter water mixing time series (see also Vandromme et al., 2011).

261 Finally, the large scale Western Mediterranean Oscillation (WeMO) index (Martin-Vide &
262 Lopez-Bustins, 2006) was also considered, rather than the North Atlantic Oscillation (NAO)
263 index (as used in past studies, such as Molinero et al. 2005) because of its better
264 representation of the environmental conditions of the North Western Mediterranean sea
265 (Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012). This index represents differences
266 in standardized surface atmospheric pressure between San Fernando (Spain) and Padua (Italy)
267 and reflects changes in regional weather conditions, especially in rainfall, river flow, wind
268 strength and direction and temperature. Positive values of the index are associated to lower
269 temperature and higher river flow and wind, thought to be favourable for plankton
270 productivity (Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012).

271

272 *Environmental drivers of the variations in zooplanktonic densities and*
273 *size spectra*

274 To identify the potential relationships between environmental variables and the log-density or
275 size spectra of crustaceans, linear models (LM) were investigated, as these two biotic
276 variables were normally distributed. Environmental time series of local temperature, Chl-a,
277 nitrate, silicate and the winter water mixing index as well as the WeMO index were used as
278 explanatory variables. The linear models were based on annual time series for both the
279 environmental and zooplanktonic variables to avoid the strong autocorrelation in the monthly
280 time series due to the seasonal cycle. A stepwise forward and backward selection was run to
281 select the most explanatory and significant variables based on corrected Akaike Information

282 Criterion (AICc) (Burnham & Anderson, 2004) . Variance Inflation Factor values (VIF) were
283 checked in order to avoid multicollinearity between variables (Zuur et al., 2010). Finally,
284 residuals and the goodness of fit of each model were then investigated through standard tests.
285 Because relationships between zooplankton and environment could be nonlinear, potential
286 synchronicity between breakpoints in environmental time series and zooplankton community
287 was also investigated.

288 All the analyses presented above were conducted with R v. 3.4.1.

289

290 **3. RESULTS**

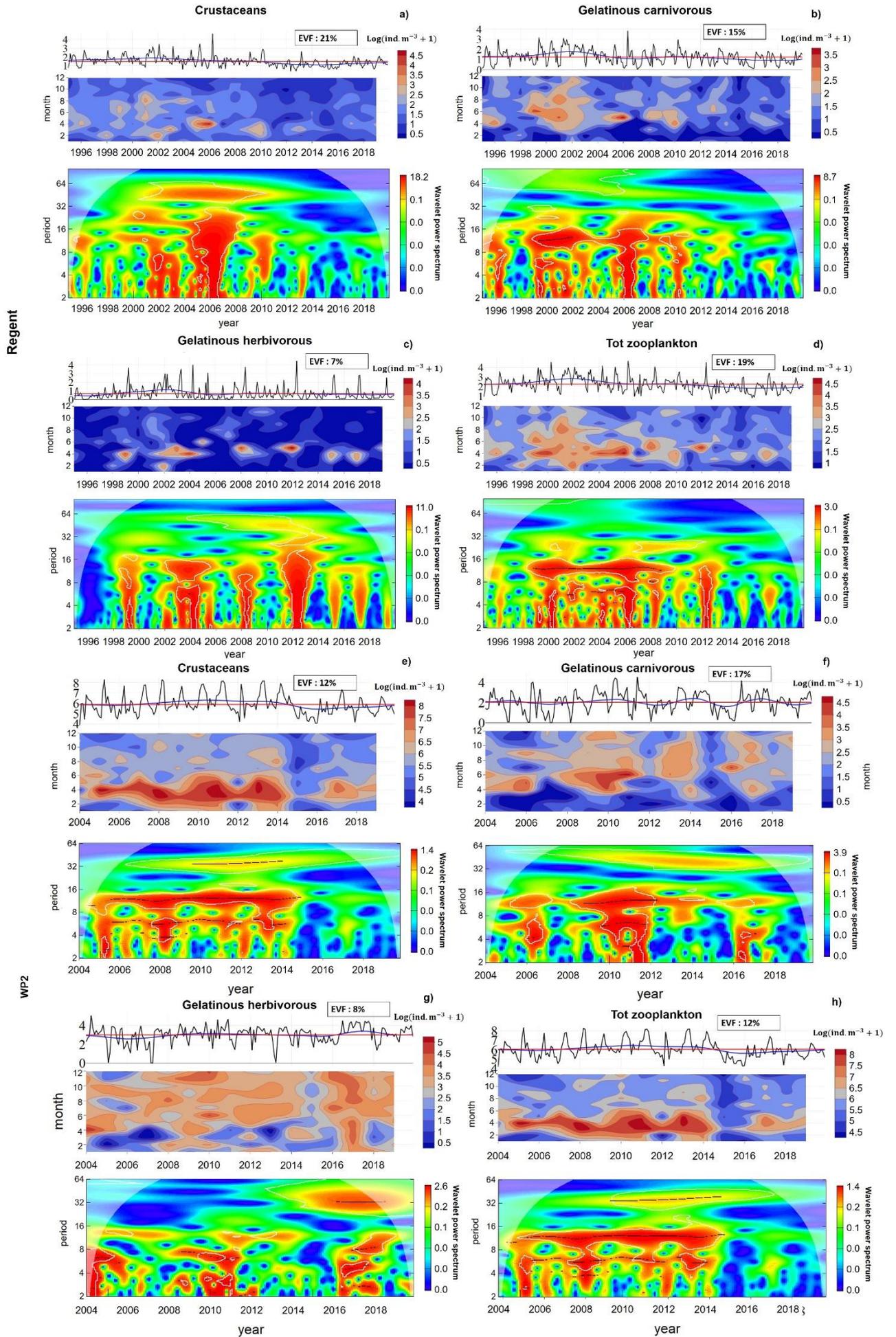
291 **Variability in zooplankton densities**

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293 The long-term trend derived from the EVF explained a rather small proportion of the total
294 variance of the Regent time series, i.e., between 7% and 20% but, the period between 2000
295 and 2005 was marked by higher densities mostly for the total zooplankton and gelatinous
296 carnivorous and secondarily for the 2 other groups. The wavelet analyses performed on total
297 zooplankton showed high power spectrum level (red plume on the wavelet plot) at the 12
298 months frequency highlighting an important seasonal cycle. Important noise was also
299 observed in total zooplankton, revealed by the high power spectrum level in the 2 to 8 months
300 frequencies (Figure 1-d). Both herbivorous and carnivorous gelatinous displayed some
301 seasonality, but less marked than total zooplankton in the Regent. All 3 presented higher
302 densities between April and June, but not all along the time series (Figure 1-b, c and d).
303 However, crustaceans in the Regent did not display any clear seasonal cycle, but short-term
304 variations, as observed in the wavelet analysis with high power spectrum from 2 to 12 months
305 frequencies (even if highest densities seemed to occur generally in spring) (Figure 1-a).

306 Concerning the WP2, the long-term trend derived from the EVF explained between 8% and
307 17% of the total variance of time series (Figure 1-e,f,g and h). The year 2015 appeared very
308 particular, characterized by very low densities for the 3 groups (Figure 1-e, f and g) as well as
309 in total zooplankton abundance (Figure 1-h). Herbivorous and carnivorous gelatinous seemed
310 to recover after 2015, their densities reaching similar (and even higher for herbivorous) levels
311 than before (respectively around $3 \log (ind.m^{-3} + 1)$ and $2 \log (ind.m^{-3} + 1)$), but crustaceans
312 densities stayed at lower values after 2015, at around $5.5 \log (ind.m^{-3} + 1)$. Total zooplankton
313 and crustaceans time series were very similar in the WP2 and presented the same patterns of
314 variation. The wavelet analyses showed high power spectrum level at the 12 months
315 frequency highlighting the presence of a seasonal cycle (however less marked for herbivorous

316 gelatinous). Strong variability was also present at high frequencies (2 to 8 months) for all four
317 time series, indicating also the presence of short-term variations or noise (Fig. 1). Intra-annual
318 (or seasonal) variability was indeed strongly present in crustaceans time series of the WP2,
319 with higher densities between February and May, up to $8 \log(\text{ind.m}^{-3} + 1)$ (Figure 1 - e). Note,
320 however, that this seasonality has been absent since 2015 during the period of lower densities,
321 as indicated by the lower power spectrum at the 12 months frequency after 2015 (Figure 1 -
322 e). The wavelet analyses did not detect any shift in the timing of the seasonal peak of the
323 crustaceans, herbivorous and carnivorous gelatinous of both the Regent and WP2 nets (Figure
324 1).

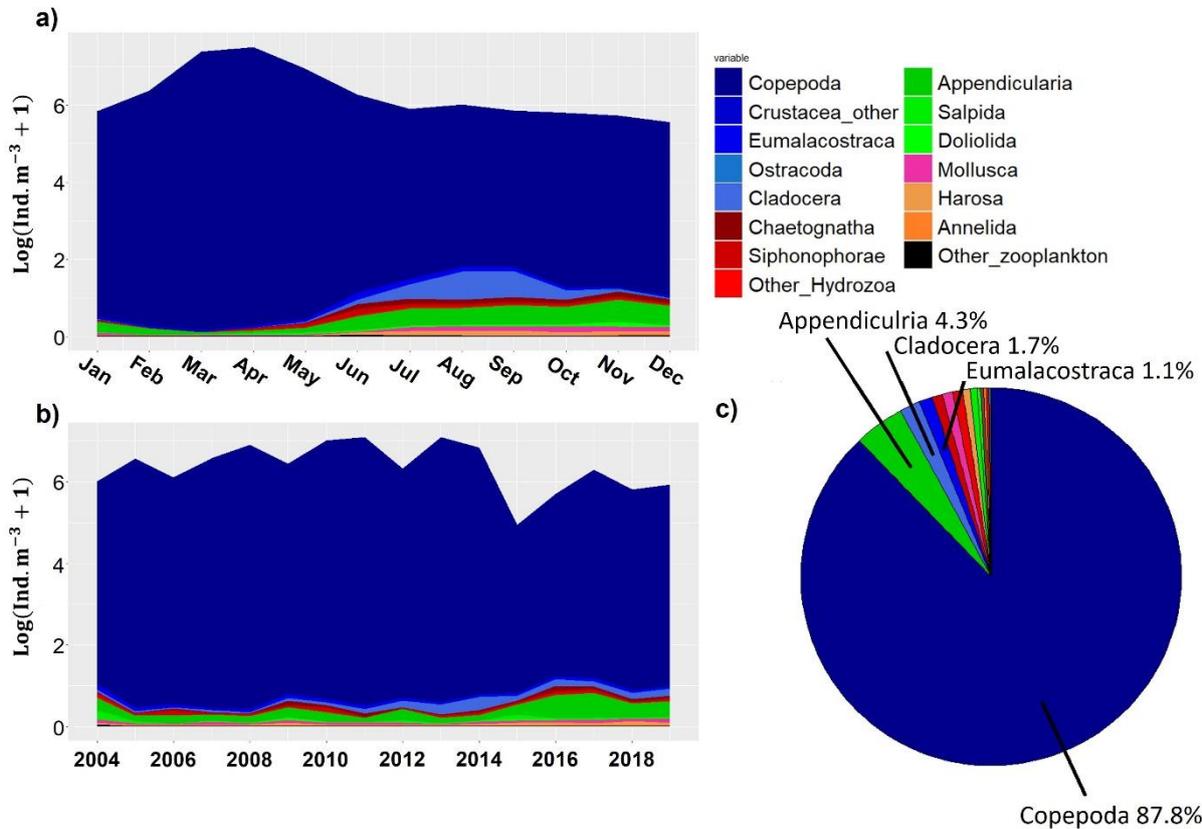


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Figure1: *Monthly log densities ($\ln(\text{ind.m}^{-3} + 1)$) and wavelet analyses of crustaceans, gelatinous carnivorous and gelatinous herbivorous for Regent (upper panels) from 1995 to 2019 and for the WP2 (lower panels) from 2004 to 2019. For each block, the upper panel represents the monthly time series in black with the trend extracted with the EVF (in blue) and the mean over the whole period (in red). In the mid panel, the contour plot of the monthly densities. In the bottom panel, wavelet analyses performed on monthly densities .*

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1. Zooplankton taxonomic composition



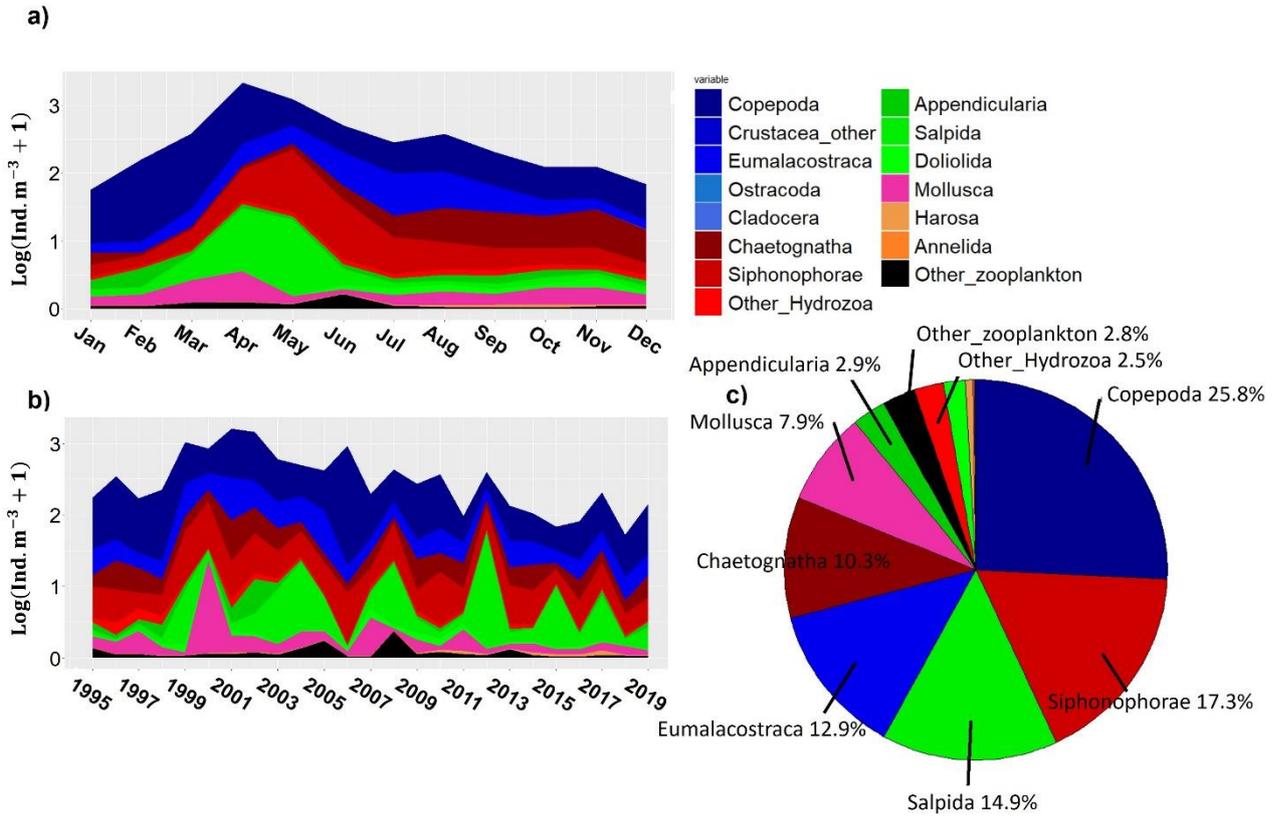
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Figure 2: Stacked mean densities in the WP2 net (for individuals over 0.65 mm body length) of each group for each month (a), stacked yearly densities of each group from 2004 to 2019 (b) and mean proportion of the different groups for the whole period (c). Blue colors represent the crustaceans, red colors the gelatinous carnivorous and green colors the gelatinous herbivorous. For clarity, only groups representing more than 1% of the total community are indicated in panel c.

346 *Copepoda* was the most abundant group, highly dominant in the WP2 both at seasonal and
347 interannual scales. This group represented 87.8% of total density of the zooplankton collected
348 by this net from 2004 to 2019 (Figure 2-c). The main temporal pattern in total zooplankton
349 density was a sudden drop in 2015, mainly due to decline in *Copepoda* density. In opposition,
350 *Appendicularia* increased at the same moment, but not enough to counterbalance the decrease
351 of *Copepoda*. Phenological differences were observed among groups, with *Copepoda* more
352 abundant in spring (March and April), whereas *Appendicularia* and *Cladocera* were more
353 abundant in summer (between July and October, Figure 2-a). This was confirmed when
354 looking more precisely at the monthly time series of the different groups, mostly classified in
355 2 categories: (i) those displaying high densities in spring until early summer, such as

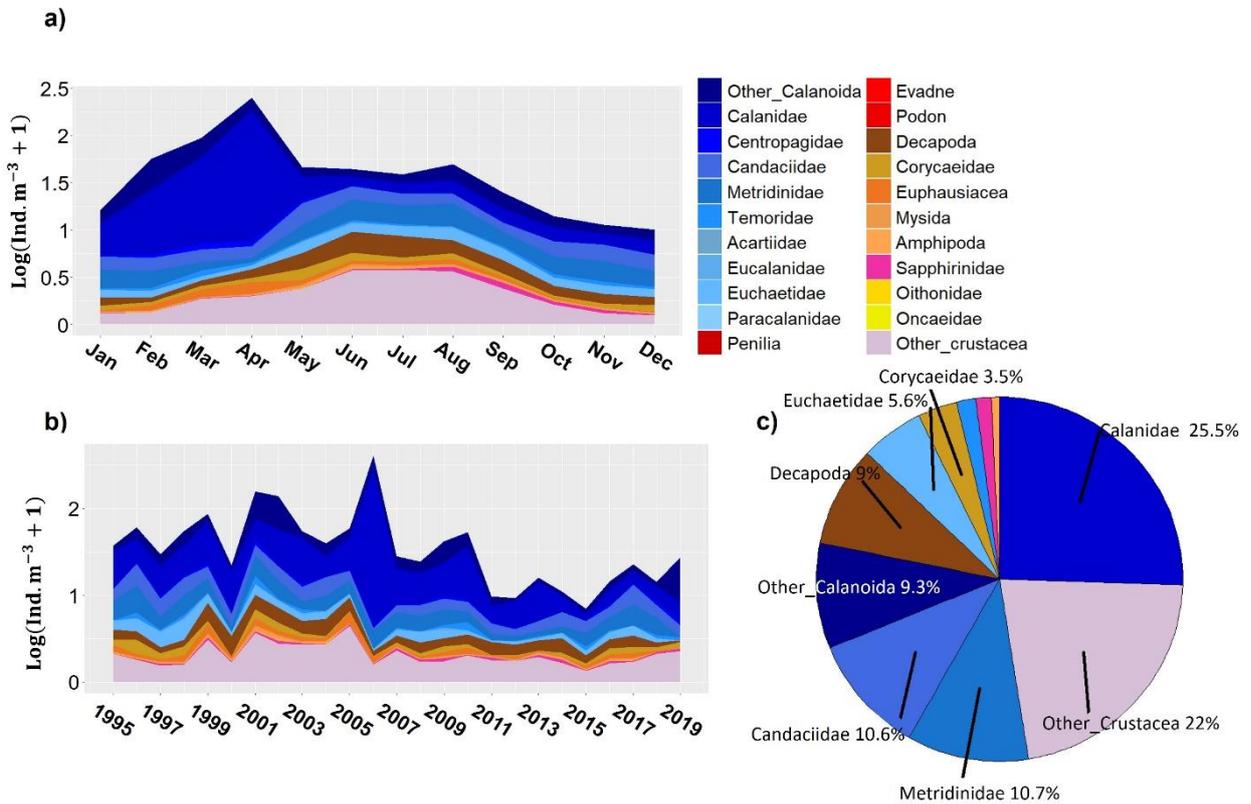
356 *Copepoda*, *Salpida*, *Siphonophorae* and *Eumalacostraca*, and (ii) those having high densities
357 in summer and early autumn, such as *Cladocera*, *Doliolida* and gelatinous carnivorous with
358 *Chaetognatha* and other *Hydrozoa* (ESM - Fig S3). As in previous analyses, no change in
359 phenology (i.e., shift in the timing of the seasonal peak) was observed over the two decades.
360 In the Regent, *Copepoda* were also the most abundant group, but not as dominant (25.8%).
361 Gelatinous zooplankton as a whole accounted for higher percentage (50%) than crustaceans
362 (40%, Figure 3-c). Total zooplankton slightly increased from 1995 to 2001 and then
363 decreased until 2019. There were also strong year-to-year variations, such as peaks of
364 *Copepoda* in 2006, *Mollusca* in 2000 or *Salpida* in 2013 (Figure 3-b). The peaks of
365 zooplankton densities were observed in April, with *Copepoda* and *Salpida*, just followed by
366 *Hydrozoa* in May and then *Eumalacostraca* from June to September and *Chaetognatha* from
367 July to December (see also ESM-Fig S4). Here again, no shift in phenology was observed
368 over the three decades. Due to the large mesh size of the net, some groups were poorly
369 represented and even totally absent in the Regent net samples, such as *Ostracoda* and
370 *Cladocera* (Figure 3; ESM-Fig S4).

371 The crustaceans' community in the Regent that could be investigated at the family level (see
372 Material & Methods) was well diversified with no strong dominance. *Calanidae* was the most
373 abundant family, representing about 25% of total densities, followed by the other crustaceans
374 (22%). A decrease in total densities has been observed since 2002, but again with strong year-
375 to-year fluctuations. In 2001, all the groups increased while *Calanidae* displayed a strong
376 peak in 2006, which represented more than 60% of the total crustaceans community (Figure
377 4-b). Highest densities occurred between March and April, around $2.4 \log (\text{ind.m}^{-3} + 1)$,
378 mainly with *Calanidae* (Figure 4-a). *Eumalacostraca*, which represent an important part of
379 other crustaceans (see section 2.3), and *Decapoda*, were more abundant in late spring and
380 summer. *Metridinidae* and *Candacidae* (each one representing around 10% of the
381 community) were stable over time, with no seasonality and no interannual changes (Figure 4).
382 Some taxa were however poorly represented, such as *Penilia*, *Oithonidae*, *Oncaeiidae* and
383 *Acartiidae*, and could therefore hardly be analyzed (see ESM-Fig S5). As for the other taxa,
384 no shift in phenology was observed over the three decades (see ESM-Fig S5).



385

386 **Figure 3:** Stacked mean densities in the Regent net samples (for individuals over 1.5 mm body
 387 length) of each group for each month (a), stacked yearly densities of each group from 1995 to
 388 2019 (b) and mean proportion of the different groups for the whole period (c). Blue colors
 389 represent the crustaceans, red colors the gelatinous carnivorous and green colors the
 390 gelatinous herbivorous.



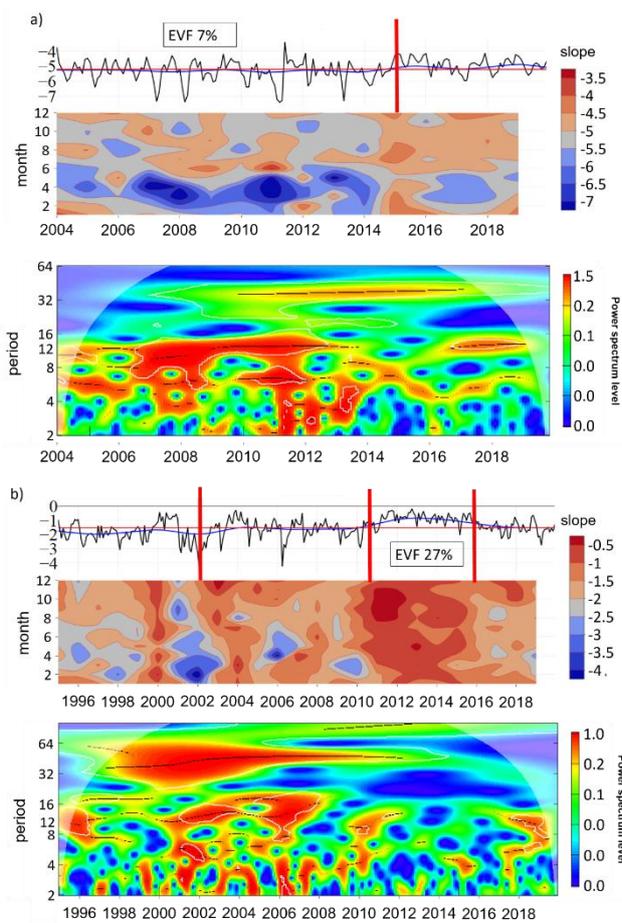
391

392 **Figure 4:** *Stacked mean densities in the Regent net samples (for individuals over 1.5 mm body*
393 *length) of each crustaceans' order, family and genera for each month (a), stacked yearly*
394 *densities of each group from 1995 to 2019 (b) and mean proportion of the different groups for*
395 *the whole period (c). Blue colors represent the Calanoida families, red colors the Cladocera*
396 *and brown to orange colors the Eumalacostraca families.*
397

398 **3.3 Crustaceans size spectra analysis**

399 The long-term trend of WP2 crustaceans NDSS slope (extracted by EVF) only accounted for
400 7% of the total variations of the series. The series of the NDSS slopes was quite stable from
401 2004 to 2014, with values at around -5.5. In 2015, the values of slopes increased (i.e. spectra
402 became flatter) and remained at higher values around -5.2 afterwards. This change in 2015
403 was confirmed by the breakpoint analysis which detected a significant discontinuity in that
404 year. Seasonal variations were also detected in that time series of NDSS slopes, with steeper
405 spectra in spring and flatter spectra in summer and autumn (Figure 5a). This seasonality was
406 confirmed by the wavelet analysis with high power values at around 12 months. However,
407 this seasonality also disappeared in 2015, when spectra became flatter all through the year
408 (including spring, Figure 5a). As previously, no phenological change was observed, steeper
409 spectra were always in spring between March and May.

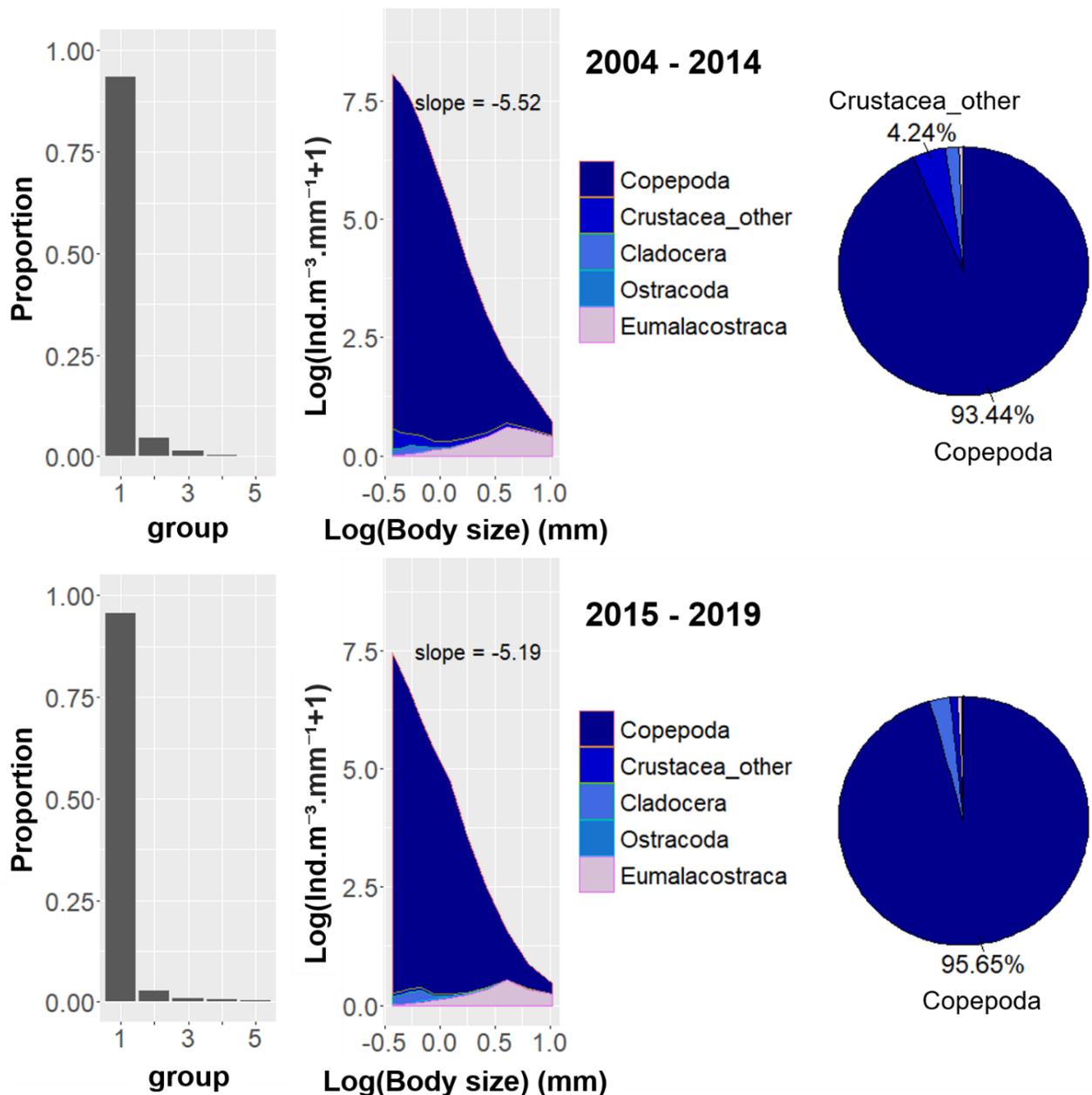
410 Concerning the Regent, the long-term trend of crustaceans NDSS slope presented a higher
411 percentage of the total variability of the series, at around 27% (Figure 5b). The series was
412 rather stable between 1995 and 2002 at values around -2.2 and then increased in 2003, with a
413 breakpoint detected during that year, and spectra becoming flatter (mean slope of -1.8). The
414 slopes of the spectra remained stable until 2010 and a second breakpoint was found in 2011
415 with spectra becoming even flatter (slope around -0.9). Finally, a last breakpoint was
416 observed in 2016, when spectra became steeper, with mean slope at around -1.7 until 2019.
417 No clear seasonal pattern was observed on the contour plot, but the wavelet showed high
418 signal at around 12 months for some years, mainly between 2000 and 2005. Moreover, high
419 frequencies (2 to 8 months) also presented strong signals indicating the presence of short-term
420 variations or noise (Figure 5b).



421

422

423 **Figure 5:** Monthly time series of crustaceans NDSS slopes from 2004 to 2019 in WP2 (a) and
 424 Regent (b). The upper panel represents the monthly time series in black with a 3-year trend
 425 extracted with EVF (in blue) and the mean over the whole period (horizontal red line). The
 426 vertical red line indicates the position of the breakpoint detected. In the mid panel, the
 427 contour plot of the time series and in the bottom panel, wavelet analysis with significant
 428 variance delimited by white lines.



429

430 **Figure 6:** Rank-frequency diagram (left), mean NDSS size spectra (middle) and mean
 431 proportions of crustaceans groups (right) for the 2 time periods identified with breakpoints
 432 performed on monthly time series of crustaceans NDSS slopes in WP2. The slopes of the mean
 433 spectra are indicated in each panel.

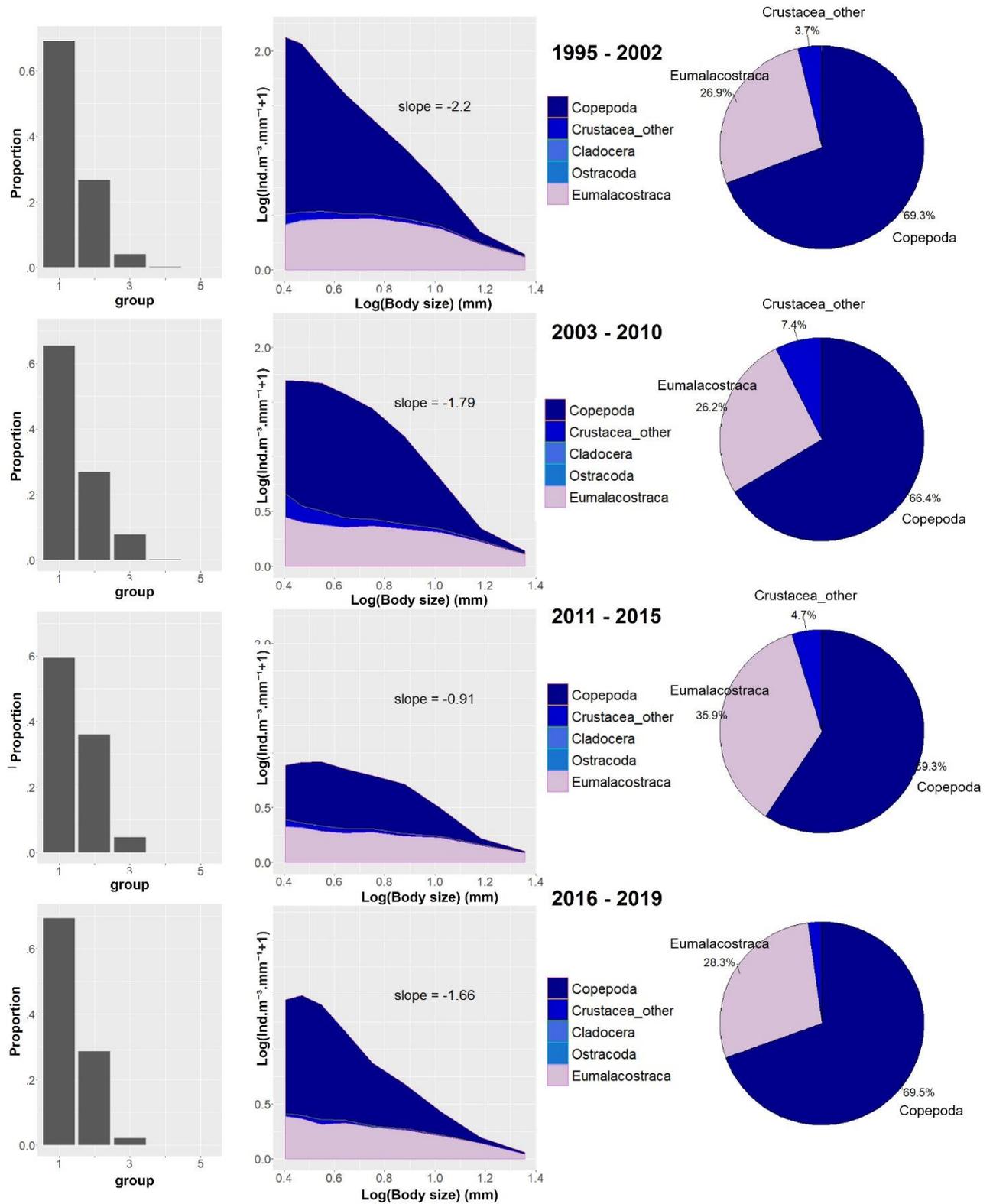
434

435 As already seen above, *Copepoda* was the most abundant group dominating the zooplanktonic
 436 community in the WP2 and represented up to 95% of total densities of the crustaceans
 437 between 2015 and 2019 (Figure 6). The first period between 2004 and 2014 presented steeper
 438 size spectra with a mean slope of -5.5 compared to 2015-2019 period, for which mean slope
 439 of spectra was around -5.2. The size spectra were thus steeper when the densities were higher.

440 The rank frequency analyses presented only low variability between periods, the mean
441 proportion of the first group ranging from 0.94 to 0.96 (Figure 6).

442 In the Regent, *Copepoda* was also the most abundant group, representing between 60% and
443 70% of the crustaceans densities while *Eumalacostraca* was the second group representing
444 between 26% and 36% of the crustaceans densities (Figure 7). The first period between 1995
445 and 2002 was characterized by the steepest spectra, with a mean slope of -2.2 and also the
446 highest densities (up to 2.1 log(densities.mm⁻¹)). In opposition, the third period between 2011
447 and 2015 displayed the flattest spectra, with mean slope of -0.91 and also the lowest densities
448 (0.9 log(densities.mm⁻¹)). Rank-frequency analysis showed few variations, the first group
449 representing between 59.1% and 69.2% of the community. Interestingly, the third period,
450 which was the less abundant, was also the less dominated by the first group (Figure 7).

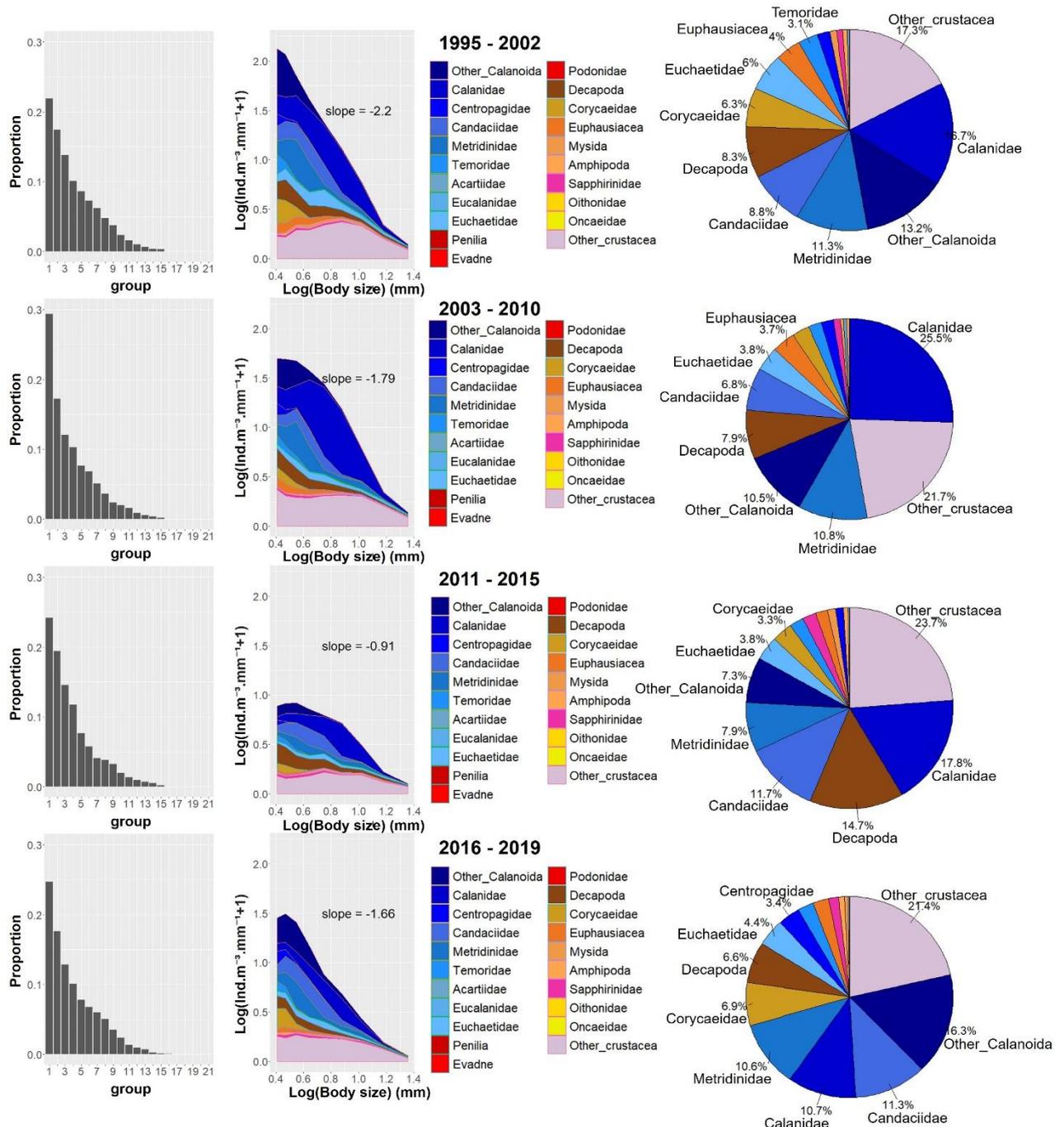
451 The same analysis was also performed at a higher taxonomy level for the Regent. The
452 community was rather diversified, as indicated by the shape of the rank-frequency diagram
453 and the rather low percentage of first taxa (<30% for all periods). A high stability was
454 observed in the composition of the community with the same dominant taxa, i.e., other
455 crustaceans (*Eumalacostraca*) and *Calanidae* always the first 2 except in the last period
456 where other-*Calanoida* was in second position. The following most important groups were
457 *Metridinidae*, *Candacidae*, *Corycaeidae* and *Decapoda*, which represented between 6% and
458 11% of the community. No replacement of groups was observed except for *Calanidae* which
459 was partly replaced by other-*Calanoida* in the last period (Figure 8). Crustaceans community
460 appeared thus fairly stable and rather diversified, with no strong changes over time, despite
461 changes in the size spectra slopes.



462

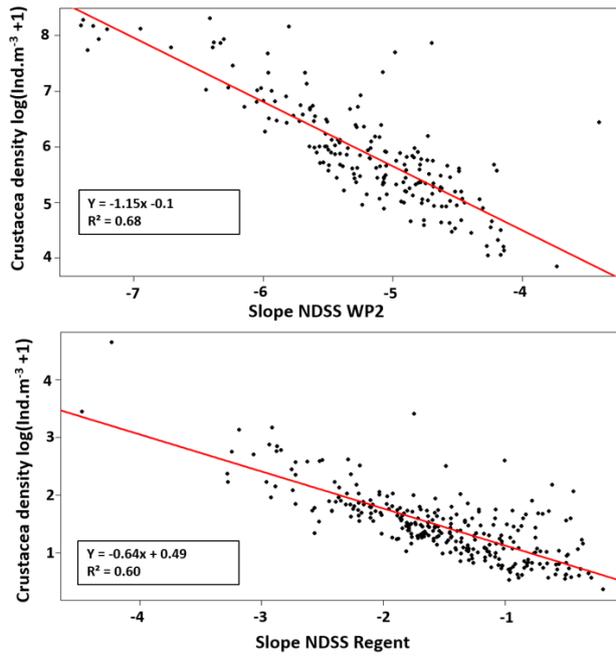
463 **Figure 7:** Rank-frequency diagram (left), mean NDSS size spectra (middle) and mean
 464 proportions of crustaceans groups (right) for the 4 time periods identified with breakpoints
 465 performed on monthly time series of crustaceans NDSS slopes in Regent net samples. The
 466 slopes of the mean spectra are indicated in each panel.

467



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Figure 8: Rank-frequency diagram (left), mean NDSS size spectra (middle) and mean proportions of crustacean taxa (right) for the 4 time periods identified with breakpoints performed on $PC1_{size}$ in Regent net. Calanoida are represented with blue colors, Cladocera in red and Eumalacostraca in brown to orange colors. The slopes of the mean spectra are indicated in each panel. In each pie chart, the percentage of Eumalacostraca in “Other_Crustacea” group is indicated in parentheses.

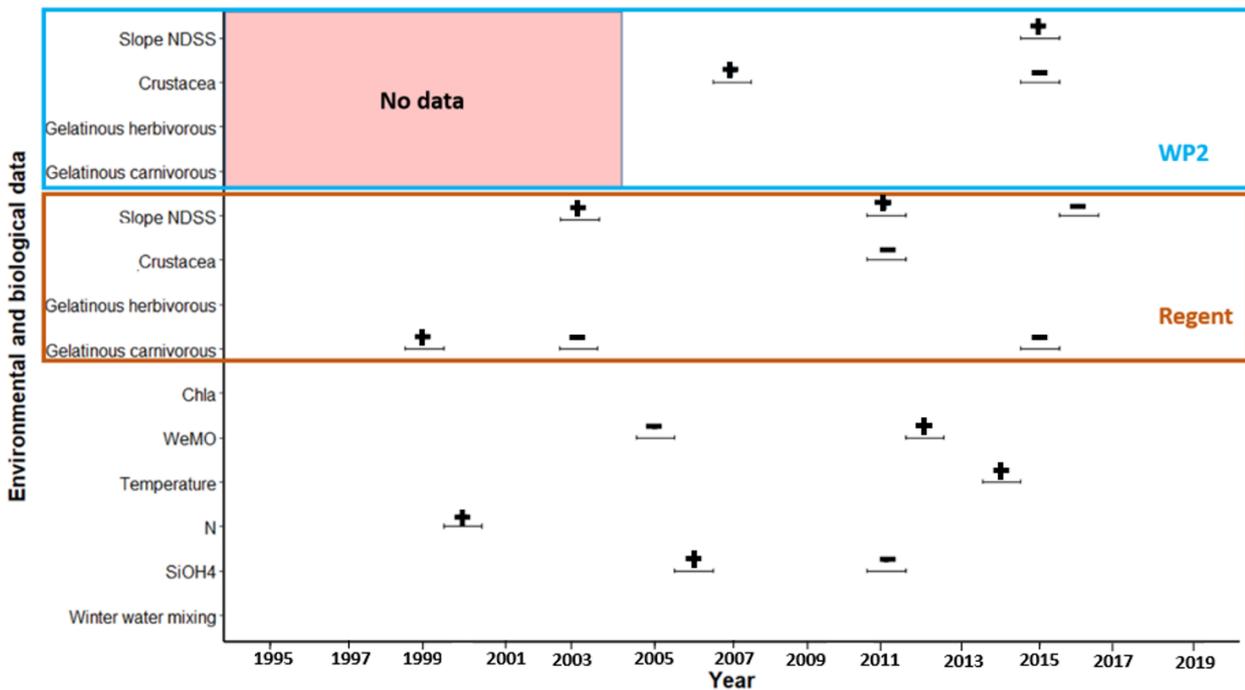


478

479 **Figure 9:** Linear regression between the monthly time series of crustaceans density and the
 480 slopes of monthly crustaceans NDSS for WP2 (top) and Regent (down).
 481

482 As already suggested from Figures 6 and 7, there was a significant relationship between the
 483 monthly crustaceans total densities and the monthly slopes of the size spectra for both the
 484 WP2 and Regent ($p < 0.001$, Figure 9). High densities of crustaceans were associated with
 485 steeper spectra and *vice versa*.
 486

3.4 Environmental and zooplankton variability



487

488 **Figure 10:** *Synthesis of breakpoints detected in annual time series of crustaceans NDSS*
489 *slopes, densities of crustaceans, gelatinous herbivorous and carnivorous and the*
490 *environment. “+” indicate an increase of densities or environmental variables and spectra*
491 *becoming flatter and inversely for “-”, with a decrease of densities or environmental*
492 *variables and spectra becoming steeper. Biological data in the WP2 are in the blue box and*
493 *in the brown box for Regent.*
494

495 Breakpoint analyses were also performed on annual time series of the environmental
496 variables, i.e. Chl-a, WeMO, Temperature, N, SiOH₄ and winter water mixing (see ESM Fig-
497 S8 for annual time series) and no clear synchrony could be detected, as the breakpoints were
498 observed at different dates for the different variables. Concerning the biological variables
499 (crustacean size and density and gelatinous and herbivorous and carnivorous densities),
500 several breakpoints were observed around 2015 when crustaceans decreased in the WP2
501 concomitant with a flattening of the crustaceans size spectra and a decrease of gelatinous
502 carnivorous in the Regent (Figure 10). No clear link was made with the environment, albeit a
503 sudden increase of temperature was observed a year before (in 2014). We further noted the
504 co-occurrence of some breakpoints in crustaceans density and size spectra and SiOH₄
505 concentration in 2011 (Figure 10). Before 2007, only changes in N and WeMO were observed
506 in the environment with an increase of N and a decrease of WeMO. Carnivorous gelatinous
507 also presented changes but not synchronous with N and WeMO.

508

509 **3.5 Relationship between crustaceans and environment**

510 To determine the potential environmental drivers of interannual variations in total crustaceans
511 log-density and size spectra, linear models were run considering 5 environmental explanatory
512 variables: N and SiOH₄ local concentrations, mean annual sea temperature, mean annual
513 WeMO and the winter water mixing index. Chl-a was not incorporated in the complete model
514 because of high level of Variance Inflation Factor (VIF>4) with the winter water mixing
515 index, revealing collinearity between both variables. After model selection based on AICc,
516 the best model retained for WP2 crustaceans log-densities was the one with mean annual
517 temperature (but with a low probability level, $p = 0.091$, Table 1). This model only explained
518 19% of the amount of deviance. Residuals of the model were moderately satisfactory due to
519 the presence of a few outliers, but the predicted *versus* observed values were reasonable (see
520 ESM-Fig S10). Concerning the crustaceans density in the regent, only the winter water
521 mixing was retained (at a higher probability level than the previous model, $p=0.018$, Table 1),
522 positively related to the crustaceans log-densities. This model nonetheless only explained
523 22% of the amount of deviance. Residuals of the model were relatively satisfactory as well as

524 the plot of the predicted *versus* observed values but here also 3 outliers were detected (see
525 ESM-Fig S10).

526 Regarding the size, no environmental variables were retained for the WP2 and only the
527 WeMO index was kept after selection for the Regent (but with a low probability level, $p =$
528 0.118, Table 1). It was negatively related to the time series of slopes, indicating that strong
529 values of WeMO could be related to steeper size spectra, but this model only explained 10.3%
530 of the amount of deviance. The residuals of the model were rather normally distributed
531 however the plot of the predicted *versus* observed values presented quite strong dispersion
532 (see ESM-Fig S10).

533

534 **Table 1:** *Statistics of the explanatory variables retained in the best model of crustaceans*
 535 *densities and size in the WP2 and Regent nets. Variable with grey areas were not retained in*
 536 *the best GLM model after variable selection*

	<i>Crustacea WP2</i>				<i>Crustacea Regent</i>				<i>NDSS slopes Regent</i>			
PARAMETER	Estimate	SE	t	p	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	19.251	7.142	2.696	0.017	1.643	0.074	22.263	<0.001	-1.744	0.163	-10.720	<0.001
Temperature	-0.747	0.411	-1.815	0.091								
WeMO									-0.393	0.242	-1.626	0.118
Winter water mixing					0.128	0.050	2.552	0.018				

537

538

539 **4. Discussion**

540 The objective of this study was to investigate the main patterns of temporal variations of
 541 zooplankton density, size spectra and taxonomic composition, with a focus on crustaceans,
 542 weekly sampled at Point B at the entrance of the bay of Villefranche-sur-Mer (NW
 543 Mediterranean Sea) from 1995 to 2019. If the density variability had already been studied
 544 until early 2005 at this location (see García-Comas et al., 2011; Molinero et al., 2008a;
 545 Vandromme et al., 2011), it was the first time that total density, size and community
 546 composition were studied all together. Those 3 indicators are of primary importance to
 547 understand trophic interactions, as size and community composition could modulate predator-
 548 prey relationships and in the case of crustaceans also energy transfer to higher trophic levels
 549 (Barroeta et al, 2017; Chen et al., 2019; Scharf et al., 2000). It was also the first time that such
 550 a time series analysis was based on zooplankton samples simultaneously collected by 2
 551 different nets, which allows us to cover a broader spectrum of the zooplankton community.

552

553 **Nets selectivity and individual's identification**

554 Like most zooplankton studies, this one relies on zooplanktonic individuals collected by nets
 555 which are size selective (Mack et al., 2012; Pansera et al., 2014). To collect a large size range
 556 of zooplankton, we used two nets with different mesh sizes: the WP2 and the Regent. The
 557 WP2 has been widely used to study crustaceans and mostly copepods variability as
 558 recommended by the UNESCO manual (Cook & Hays, 2001; Raybaud et al., 2008; Tranter,
 559 1968; Vandromme et al., 2014), while the Regent has been mostly used to sample gelatinous
 560 organisms (Buecher & Gibbons, 1999; Licandro et al., 2001). The Regent net has a larger

561 mesh size than the WP2 (690 μm against 200 μm) and our analyses showed that
562 zooplanktonic organisms measuring at least 1.5 mm and 0.65 mm were accurately sampled by
563 the Regent and the WP2, respectively. Similar size threshold was estimated by Vandromme et
564 al., (2012) for the WP2, with a maximum of biovolume around 0.029mm^3 corresponding to
565 length (major axis) of around 650 μm . In the literature, the threshold between small and large
566 crustaceans is generally fixed at 1 mm (Hassel et al., 1991; Svensen et al., 2011; Wahlström et
567 al., 2000), so that WP2 analyses embraced both small and large crustaceans while the Regent
568 solely focused on large ones. So even if we covered a larger spectrum of zooplankton size
569 using samples from two nets than usually done, the variability of smaller individuals could
570 not be investigated with those nets. For instance, *Microsetella*, an important zooplankton
571 group of Mediterranean sea (Siokou-Frangou et al., 2010), was absent in both nets because of
572 its small size.

573 The Zooscan imaging methods used in this work has the advantage of measuring the size of
574 each individual providing consistent and repeatable results among samples, but it has a lower
575 taxonomic definition than traditional observations under microscopes (Gorsky et al., 2010).
576 Therefore in this study most zooplankton were sorted to the Order and sometimes to the
577 family when the morphological details were present, as done in many past studies on
578 zooplankton reported in Lombard et al., (2019).

579

580 **WP2 versus Regent**

581 The zooplanktonic community sampled by the WP2 was strongly dominated by copepods
582 (87% on average), while this sampled by the Regent was more diversified, with gelatinous in
583 general representing up to 50% of total zooplankton in the net. Still, when comparing
584 zooplankton densities in both nets considering individuals greater than 1500 μm , the Regent
585 underestimated the densities of all the groups (including gelatinous ones) compared to the
586 WP2. This result was unexpected, especially for the gelatinous, as Regent net is supposed to
587 be more performing and less damaging for those groups (Buecher & Gibbons, 1999). The
588 WP2 net appeared to be a better choice to sample the zooplankton community at the broad
589 taxonomic level at the point B of Villefranche-sur-mer, both for crustaceans and gelatinous
590 taxa.

591 Because size spectra were normalised, the slopes of NDSS in both nets could be compared
592 considering different size range of individuals. Crustacean NDSS in the WP2 appeared
593 steeper than in the Regent net, revealing a higher proportion of small individuals compared to
594 larger ones in the WP2. NDSS in the WP2 was however less variable, possibly because of a

595 higher number of individuals considered to construct size spectra compared to Regent. NDSS
596 differed also in term of variability with different breakpoints identified in the time series of
597 both nets. For instance, high proportions of large individuals (inducing a flatter size spectrum)
598 were observed from 2016 to 2019 and 2011 to 2014 for the WP2 and the Regent, respectively.
599 Those differences could be explained by the differences in the proportion of the different taxa
600 sampled by each net. Indeed, *Eumalacostraca* (among the largest crustaceans) represented
601 one third of the community in the Regent, but less than 1% in the WP2. Conversely,
602 *Cladocera*, such as *Penilia*, *Podonidae* or *Evadne* (of relatively small size) were present in the
603 WP2, but absent in the Regent net. Such differences between two nets are not so surprising
604 and Calbet et al., (2001) also observed strong differences in the zooplankton community
605 sampled by nets of 53 μm and 200 μm mesh size at the same time.

606 Nevertheless, the identification of individuals at the family level for crustaceans in the Regent
607 provided useful additional information (see below) that was not available for the WP2
608 because of the difficulty to precisely and rapidly identify small individuals on automatically-
609 generated images. However, even in the Regent, the identification of individuals at the family
610 level was only available for copepods and not for the other groups partly limiting our vision
611 of the community variability. It appears then crucial to develop higher resolution sensor and
612 new process to semi-automatically identify at the species level smaller crustaceans individuals
613 sampled by the WP2, and more generally zooplankton net samples, to better understand the
614 links with the environment and interactions with upper trophic levels.

615

616 **Temporal stability of the zooplankton community**

617 One of the most striking results of this analysis is the strong stability through time of the
618 zooplankton community (in both the WP2 and Regent) and when zooplankton total densities
619 varied, the taxa varied most often synchronously. The examination of the crustaceans
620 community at a higher taxonomic resolution in the Regent led to the same conclusion of a
621 high stability and diversity in the taxonomic composition (with similar proportions of
622 *Calanidae*, other-*Calanoida*, *Metridinidae*, *Candacidae* *Corycaeidae* and *Decapoda* through
623 time). Similarly, the crustaceans and gelatinous densities as well as size spectra slope of
624 crustaceans presented strong long-term stability, as documented by the low percentage of
625 variance explained by the long-term trend. Some interannual variability was observed in
626 zooplankton size, as depicted by the flattening of spectra in the WP2 in the last years
627 suggesting an increase of the proportion of larger individuals. However, this flattening was
628 not induced by an increase in the density of larger individuals but rather by a reduction of

629 smaller individuals, potentially leading to lower energy transfer to higher trophic levels.
630 Different changes of slopes were also observed in the Regent but the only notable variation
631 was the decrease in crustaceans densities in the last years. Such stability and high resilience in
632 the zooplankton community was unexpected, especially in a context of global warming of the
633 Mediterranean waters, but this has been also reported in several other Mediterranean locations
634 (see Berline et al., 2012; Fullgrabe et al., 2020; Mazzocchi et al., 2011; 2012).

635

636 **Zooplankton long-term variability and global warming**

637 This strong stability of the community could be surprising in a context of global change and
638 long-term changes in phytoplankton and zooplankton phenology or size have been already
639 observed in several areas and related to increasing temperature (Aberle et al., 2012; Herrmann
640 et al., 2014; Winder et al., 2012). Our study did not display any clear relationships between
641 environmental and planktonic variables, albeit a negative (but statistically fragile) relationship
642 between crustaceans density in the WP2 and annual temperature. Such a relationship between
643 crustaceans densities and temperature had been documented in some studies in the
644 Mediterranean sea (Fernández De Puellas & Molinero, 2008a; Fernández de Puellas et al.,
645 2004). No link was observed between the crustaceans size spectra and the temperature in this
646 study, as in other studies (Dziuba et al., 2017; García-Comas et al., 2014). Concerning the
647 gelatinous community, a usual expectation from the global warming is the increase in
648 gelatinous densities, with potential impact on copepods through competition and/or predation
649 (Molinero et al., 2008a). Warm temperatures are indeed thought to promote an increase of
650 asexual reproduction of hydrozoans and, consecutively, an increase of gelatinous species
651 (Purcell, 2005). However, our results do not support this hypothesis, as herbivorous and
652 carnivorous gelatinous densities were rather stable through time (as crustaceans) and further
653 did not display any positive relationship with temperature. However, disentangling long-term
654 trend from interannual variability with 25 years long time series is not an easy task and longer
655 time series are probably needed to reach more robust conclusion on this issue.

656

657 **Zooplankton interannual variability and winter conditions**

658 Previous studies in the Ligurian sea highlighted the importance of interannual variability
659 rather than monotonous long-term change in the zooplankton community (García-Comas et
660 al., 2011; Molinero et al., 2005; Vandromme et al., 2011) and pointed out the importance of
661 winter conditions. The impacts of winter conditions on phytoplanktonic and zooplanktonic
662 production was shown by Fullgrabe et al., (2020) and Goffart et al., (2015) in the Ligurian sea

663 and to a lesser extent by Mazzocchi et al., (2011) in the Tyrrhenian sea. In the Ligurian sea,
664 quasi-decadal climatic fluctuation, associated to the NAO, was proposed as the driving
665 changes for winter mixing intensity and the input of nutrient at the surface (Molinero et al.,
666 2008a; Garcia-Comas et al., 2011; Fullgrabe et al., 2020). According to those authors, strong
667 winter mixing (such as in the 80s and from 1999 to 2003) would lead to an increase of
668 nutrient input at the surface and a subsequent higher primary and secondary production in
669 spring. While interannual variability was detected in the zooplankton time series (e.g.
670 decrease in crustacean density after 2015 or changes in size spectra slopes in the Regent in
671 2003, 2011 and 2016), our study did not detect any strong relationship between the
672 crustaceans densities or size spectra and winter mixing (and environmental variables). The
673 dates of the breakpoints between the environmental and biological variables were furthermore
674 not synchronous while the percentages of variance explained by the different linear models
675 did not exceed 22%. The relationship between crustaceans density in the Regent and winter
676 water mixing would be the sole result supporting the hypothesis of an impact of winter
677 mixing on zooplankton production, (as raised by Garcia-Comas et al., 2011 and Vandromme
678 et al., 2011). It was however not the case for crustaceans in the WP2, which however better
679 samples the crustaceans than the Regent (see above), but which time series was only 16 years
680 long (probably too short to reflect quasi-decadal variations found by the previous studies).

681

682 **Zooplankton seasonal variability**

683 Both crustaceans size and density presented a clear seasonal cycle in the WP2. This pattern is
684 well documented in the literature, resulting from the phyto- and zooplankton production
685 coupling (Romagnan et al., 2015,2016; Rossi & Jamet, 2009). The development of
686 zooplankton populations follows the spring phytoplankton bloom, with successive
687 development of grazers and carnivorous predators (Sommer et al., 1986). For copepods,
688 recruitment of copepodites occurs mainly in spring, but can be modulated by environmental
689 conditions (Romagnan et al., 2016). This recruitment pattern explained, in the WP2, the
690 presence of higher densities and steeper size spectra in spring for crustaceans, which has
691 probably participated to the strong negative relationship between size spectra slope and
692 densities. This seasonal signal was however less marked for gelatinous in the WP2 and absent
693 in the Regent for both for crustaceans and gelatinous. We postulate that this lack of seasonal
694 pattern in the Regent was due to its large mesh size that prevents catching the small size
695 classes, such as the copepodites that mostly appear in spring during the phytoplankton bloom

696 (Romagnan et al., 2015). No phenological shift was observed in the timing of crustaceans
697 peak, but the seasonal signal totally disappeared since 2015.

698

699 **The 2015 event**

700 Another important result of this study was the identification of the 2015 event, characterised
701 in the WP2 by a sudden and significant drop in crustaceans densities (concomitant to a loss of
702 the seasonal signal) as well as those of the gelatinous taxa (but to a lesser extent). This
703 decrease in the crustaceans (mostly copepods of small size) also led to changes in the size
704 spectra (being flatter). Low densities of crustaceans have been also recorded in 2015 in other
705 areas of the NW Mediterranean sea, such as in the Bay of Calvi and the Alboran sea
706 (Fullgrabe et al., 2020; García-Martínez et al., 2019). This event could be related to the
707 sudden warming in 2015 at the point B station (being the hottest year of the time series), but
708 also more generally in the NW Mediterranean Sea (Margirier et al., 2020). Such an hypothesis
709 needs however to be validated by further work and longer time series, as it is currently
710 supported by only one occurrence. Furthermore, the planktonic dynamics may be more
711 complex than a simple relationship between winter mixing, nutrient concentration (albeit
712 these two variables might be important), as described by the critical depth hypothesis
713 (Sverdrup 1953). Behrenfeld, (2010) indeed stressed the key role of biotic interactions within
714 and between the phytoplanktonic and zooplanktonic communities, especially the balance
715 between phytoplankton growth and grazing in the bloom dynamics. Preliminary analyses on
716 Chl-*a* pigment concentration at point B station suggested a decrease in diatom proportion
717 since 2013, more pronounced in 2015, and an increase in dinoflagellates (Maria Luiza
718 Pedrotti pers.comm). Such changes in the phytoplankton community composition could
719 negatively impact crustaceans and favour appendicularians, which feed on smaller preys
720 (Katechakis et al, 2004; Sommer, et al., 2002a; Sommer et al, 2002b). Competition within or
721 between zooplanktonic groups may thus be an additional key element of their dynamics and
722 need to be deeper investigated.

723

724 **Crustaceans and gelatinous interactions**

725 Top down control of jellyfish on copepods (i.e. predation) has been proposed by Molinero et
726 al. (2005, 2008b) based on time series analyses at the same site, as the densities of the later
727 dropped during the late 80s and early 90s when the former increased. However, using the
728 same time series with 10 more years, Garcia-Comas et al. (2011) found that total copepods
729 recovered around 2003 densities similar as those of the 80s, while jellyfish remained

730 abundant. In this study, we considered two main groups of gelatinous, the carnivorous and the
731 herbivorous (filter-feeders), as they have different interactions with crustaceans (especially
732 copepods), by predation or competition with the first and second gelatinous group,
733 respectively (Molinero et al., 2008b). Densities of crustaceans and carnivorous gelatinous
734 were highly positively correlated in both the WP2 and Regent (see ESM Fig-S9), which does
735 not support the hypothesis of a top-down control of gelatinous on crustaceans through
736 predation. Weak positive covariations between densities of crustaceans and gelatinous
737 herbivorous in both nets also did not support the potential hypothesis of competition between
738 the two groups. The gelatinous herbivory densities did not display any trend and remained
739 rather stable, even during the crustaceans drop around 2015. Overall, the present work did not
740 support the hypothesis of a top-down control of gelatinous on the crustaceans at the point B.

741

742 **Zooplankton and small pelagic fish**

743 Through this study, we wanted to explore the main patterns of zooplankton variations at the
744 point B, with a focus on crustaceans, to investigate if any major changes occurred around
745 2007, when the small pelagic fish community from an adjacent area (the Gulf of Lions)
746 displayed a major regime shift (Saraux et al. 2019). Such bottom-up processes have been
747 already documented (Brosset et al., 2016; Espinoza et al., 2009; Van der Lingen et al., 2006)
748 or strongly suspected (Véron et al., 2020). However, zooplankton data availability is often
749 too limiting to fully investigate potential relationships between plankton and fish. As the rare
750 long-term plankton time series available in the NW Mediterranean tended to indicate
751 synchronous variations at large spatial scale, possibly associated with large or regional ocean-
752 atmosphere oscillations (Brosset et al., 2017; Fullgrabe et al., 2020; Vandromme et al.,
753 2011), it was of interest to explore the long time series of the point B. The present study did
754 not detect any specific changes in the zooplanktonic community around 2007 that would
755 support this bottom-up control hypothesis. It remains however unclear if this indeed results
756 from the absence of bottom-up control on the small pelagic fish or if this results from
757 different dynamics in the plankton communities of those two areas (a preliminary analysis
758 indicating that the zooplankton taxonomic compositions differ between the Gulf of Lions and
759 the Ligurian Sea, (Feuilloley, 2020)). We finally think that a thorough understanding of the
760 impacts of climate change on the functioning of an ecosystem requires simultaneous
761 observations of its different biotic and abiotic compartments (Doray et al., 2018), as this is
762 recommended by the ecosystemic approach to fisheries (FAO 2003).

763

764

765 Data availability

766 The data underlying this article will be shared on reasonable request to the corresponding
767 author.

768

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