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1 Temporal dynamics of copepod taxa and 2 trophic groups in a long-term time series in 3 the NW-Mediterranean Sea.

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9 Abstract

10 In the context of structural and functional changes in the pelagic environment, and the
11 oligotrophication and the temperature increase of the NW Mediterranean, this study analyses a 17-
12 year time series (2006-2022) of copepod temporal variability in the Bay of Marseille.
13 Mesozooplankton was sampled bimonthly (0-55 m) together with biotic and abiotic parameters.
14 This study focuses on the temporal dynamics and ecological niches of copepod taxa and trophic
15 groups. In the Bay of Marseille, herbivorous copepods, *Clausocalanus-Paracalanus-Ctenocalanus-*
16 *Pseudocalanus*, dominated the community in abundances. From taxa realized niches, we identified
17 that temperature and trophic conditions drove the seasonal and interannual dynamics of copepods.
18 During the summer months of recent years, the increasing oligotrophication and warming of the
19 seawater favoured carnivorous copepods. A shift in the copepod community structure since the mid-
20 2010s was demonstrated, with a decrease in total copepod abundance and reduced dominance of
21 spring copepod taxa. The trophic groups dynamics were mostly driven by a few dominant taxa in
22 each group. Recent environmental conditions favoured increases in abundance of two warm water
23 affinity species (*Corycaeidae* and *Temora stylifera*) and were unfavourable to a cold-water affinity
24 species (*Calanus helgolandicus*).

25 Keywords: trophic group, niche, ecological succession, interannual trends, environment, Gulf of
26 Lion.

27 Introduction

28 Zooplankton are sensitive to changes in their biotic and abiotic environmental conditions.
29 Monitoring and studying the zooplankton modes of variations, in their structural and functional
30 properties at different temporal scales, is determinant for understanding the impact of ongoing
31 climate change (Richardson, 2008; Ratnarajah et al., 2023) and anthropogenic pressures (Serranito

32 et al., 2016) on pelagic ecosystems. Imaging tools for zooplankton identification are now widely
33 used to rapidly analyse an increasing number of samples (Irisson et al., 2022). However due to
34 technical limitations (e.g., image quality, organism position), this approach fails to identify some
35 organisms at species level. A more precise identification can shed light on complex spatio-temporal
36 dynamics of the community that would have been overlooked when focusing on larger taxonomic
37 groups. One well-known example is the biogeographical reorganization of *Calanus finmarchicus*
38 and *Calanus helgolandicus* described by Beaugrand (2003) in the North Atlantic. However, species
39 level monitoring may be limited by the need for a sustainability and consistency in the identification
40 of species (e.g. different taxonomic analysts). From species identification it is possible to study
41 species traits. The trait-based approach complements the traditional species based approach and
42 aims at characterising the community functioning. Benedetti et al. (2016) compiled a large database
43 of copepod species ecological traits. In the Mediterranean Sea, Benedetti et al. (2018) highlighted
44 that the functioning of the copepod community was spatially changing according to environmental
45 conditions; for example, large carnivorous copepods are found more abundant in oligotrophic and
46 tropical waters whereas herbivorous copepods are more linked to colder and seasonally-marked
47 productive waters. However, the ecological signal (e.g., spatio-temporal patterns) of some taxa may
48 be missed because they are rare in the taxonomic, functional or trophic groups. Assessing the
49 relative abundance of different taxa within such groups is therefore of major concern when
50 discussing the ecological consequences of environmental changes.

51 The ecological niche was defined by Hutchinson (1957) as the range of conditions that favours the
52 development of an organism in a multidimensional environment. To characterize and then identify
53 the main factors that influence the niche occupied by a species in an ecosystem may allow the
54 establishment of a causal link between the biology and ecology of the organism and its biotic and
55 abiotic environment.

56 During the last decades, in the context of global changes and improvements in sewage treatment as
57 required by the European Water Framework Directive, the French metropolitan coastal area
58 experienced lower nutrient intake (Lheureux et al., 2021) which had cascading effects on the
59 phytoplankton community temporal dynamics (Lheureux, 2022). In the Mediterranean Sea,
60 oligotrophication was recently observed in the Gulf of Lion (Feuilloley et al., 2020), although this
61 area was traditionally considered as more productive owing to Rhône river inputs (Durrieu de
62 Madron et al., 2011). In the Bay of Marseille (NW Mediterranean Sea) this decrease of nutrients
63 was hypothesized to be mainly responsible for quantitative and qualitative changes in the
64 zooplankton community (Garcia et al., 2023, 2024), based on imaging analysis and taking into

65 account broad taxonomic groups (e.g., calanoid copepods) encompassing a wide diversity in
66 species, size and trophic traits.

67 Here, we analysed the Bay of Marseille copepod time series identified at species level, when
68 possible, otherwise genus or larger ranks, over the last 17 years (2006-2022). Firstly, the temporal
69 dynamics of taxa and trophic groups were outlined. Then, the realized niches by taxa were
70 characterised. Finally, the temporal dynamics of copepod taxa and trophic groups were discussed
71 with regard to their realized niches.

72 The aim of the present study was to address the following questions: (i) What is the seasonal and
73 interannual variability of copepod taxa and trophic groups? (ii) What is the ecological niche of
74 copepod taxa; and what are the most determinant environmental variables that characterize the
75 copepod ecological niches? (iii) Do species sharing a temporal niche (seasonal and interannual)
76 belong to the same trophic group?

77 **Materials and Methods**

78 1-Study site

79 The Bay of Marseille is located in the eastern part of the Gulf of Lion in the NW Mediterranean Sea
80 (Fig. 1) and is considered as a marine site under strong continental and anthropic influence. The
81 Bay is influenced by multiple regional hydrological factors such as: upwelling events caused by
82 NW winds (Millot, 1979) ; intrusions of oligotrophic waters from the Northern Current (Pairaud et
83 al., 2011) ; intrusions of water rich in nutrients during winter deep convections off the continental
84 shelf of the Gulf of Lion (MEDOC GROUP, 1970); and occasional intrusions of Rhone river inputs
85 (Frayse et al., 2014). In addition, the Bay of Marseille is exposed to local anthropic pressures from
86 the city of Marseille, notably owing to the proximity with a sewage treatment plant (Raimbault et
87 al., 2021).

88 2-Copepod data

89 Zooplankton monitoring was performed at fortnightly frequency in parallel with the long-term
90 national observation program (SOMLIT, www.somlit.fr) at the Frioul station (43.24N, 5.29E, 60 m
91 depth) between 2006 and 2022. Samples were collected by vertical hauls (55 m - surface) with a
92 WP2 net (200 μm mesh size). The samples were preserved in a formaldehyde solution (4%). After
93 sample rinsing, abundance (ind. m^{-3}) and taxonomic composition (from phylum to species level)
94 were determined, according to Rose (1933), Tregouboff & Rose (1957), Razouls et al. (2005-2023)
95 and WoRMS (2024), using a Leica M165C stereo microscope. Taxonomic identification was done
96 by one analyst. Identification was done on aliquots of samples by means of Motoda Box. 12% of a
97 single sample was analyzed on different aliquots (1/128, 1/64, 1/32, 1/16). In total between 300 and

98 1000 individuals were counted per samples. The classification was done up to species when
99 possible. For a significant part of individuals, identification could not be done up to species level for
100 the whole series (e.g. due to sample quality). Therefore, the taxonomy list included lower
101 taxonomic levels such as genera, families, and multispecific taxonomic group (see Supplementary
102 Material 1).

103 The taxa relative abundance index was calculated following Ibanez & Dauvin (1998):

$$\text{Relative Abundance (i)} = \frac{\sum_{j=1}^N A(i, j)}{\sum_{i=1}^P \sum_{j=1}^N A(i, j)} \times 100$$

104 where N and P are respectively the number of samples and species, and A(i,j) the abundance of the
105 ith species in the jth sample. Only species that represent $\geq 0.1\%$ of the relative abundance were
106 considered in the data analysis. This step excluded rare species (61 taxa). A total of 17 copepods
107 taxa were used for data analysis (Table 1). The trophic traits attributed to each taxon were extracted
108 from the review by Benedetti et al. (2016). Carnivores, herbivores, omnivores and detritivores
109 groups were considered. Note that among the taxa studied, all herbivores and detritivores are
110 respectively considered as omnivores-herbivores and omnivores-detritivores in the Benedetti et al.
111 (2016) database.

112 3-Environmental variables

113 The hydrographic monitoring consisted in a vertical CTD cast from bottom (55 m) to surface, and
114 water sampling by means of Niskin bottles at three depths (surface, bottom and maximum of
115 fluorescence). A large set of physical, chemical and biological variables were collected routinely:
116 temperature ($^{\circ}\text{C}$), salinity (practical salinity unit), O_2 (mL L^{-1}), NH_4^+ ($\mu\text{mol L}^{-1}$), NO_3^- ($\mu\text{mol L}^{-1}$),
117 NO_2 ($\mu\text{mol L}^{-1}$), PO_4^{3-} ($\mu\text{mol L}^{-1}$), particulate organic carbon (POC, $\mu\text{g L}^{-1}$), particulate organic
118 nitrogen (PON, $\mu\text{g L}^{-1}$), suspended particulate matter (SPM, $\mu\text{g L}^{-1}$) and chlorophyll *a* (CHLA, μg
119 L^{-1}). The three depths measurements were averaged for the present data analysis. From CTD
120 temperature and salinity casts the mixed layer depth (MLD) was measured following the de Boyer
121 Montégut et al. (2004) method. Precipitations (mm) and wind data were obtained from the closest
122 Météo France station (43.437667°N, 5.216000°E, <https://donneespubliques.meteofrance.fr/>). From
123 wind speed and direction, a wind stress index (unitless) was derived according to a NW-SE axis in
124 order to better represent the two main wind regimes in the zone: north-westerly (Mistral, for
125 positive values) and south-easterly (for negative values).

126 Abundances of chaetognaths and cnidarians, identified from taxonomic counts, were summed and
127 used as proxy of invertebrate predation pressure on copepods.

128 4-Data analysis

129 Data analyses were performed using the R software (R Core Team, 2022).

130 4.1-Data pre-processing

131 The copepod time series were analysed at monthly scale for a total of 144 months between January
132 2006 and September 2022 (see month/year distribution in Table 1 in Supplementary Material 2).
133 Multiple Imputation with PCA procedure (MIPCA, Audigier et al., 2015) with the R package
134 ‘missMDA’ was performed to substitute missing values (approximately 3%) in the environmental
135 data set.

136 4.2-Copepods ecological niche characterization

137 To study the ecological niches of taxa, dimension reduction approaches (e.g., principal component
138 analysis, outlying mean index, redundancy discriminant analysis, canonical correspondence
139 analysis, etc.) are widely used in the literature. However, from the species position in the reduced
140 space (e.g., principal components of the PCs), it remains difficult to quantify niche optimums and
141 breadth across the most discriminant factors. Recently, Kléparski & Beaugrand (2022) proposed the
142 species chromatogram approach to resolve this issue. Their graphical tool allows the reduction to
143 two dimensions of a complex n-dimensional ecological niche. To assess the ecological niche of
144 copepod taxa, chromatogram analysis was applied (Kléparski & Beaugrand, 2022) with
145 chromatograms representing the standardized abundances of copepods taxa along a discretized
146 gradient of every environmental variable. In chromatogram analysis, each environmental variable
147 was discretized in 20 classes (using quantiles of 0.05). From chromatograms, niche optimum and
148 breadth were calculated for all copepod groups for all environmental variables. The niche optimum
149 was determined by averaging the values of the environmental variables for the samples where the
150 species abundance was higher than the quantile 0.9. This assumes that species abundances are at a
151 maximum for optimum environmental (biotic and abiotic) conditions that correspond to its realized
152 niche. Then, the niche breadth was calculated for all taxonomic groups on all environmental
153 gradients as follows:

$$Amplitude = \frac{U_{max} - U_{min}}{U^*} \times 100$$

154 with U_{max} and U_{min} being respectively the highest and lowest categories with standardized
155 abundance above or equal to 0.4. U^* correspond to the total number of categories with non-zero
156 abundance data.

157 An overlap index (in %) was calculated between every pair of species along every environmental
158 gradient as follows:

$$Overlap_{S1,S2,j} = \frac{100 \times V_{S1,S2,j}}{V_{S1,j} + V_{S2,j} - V_{S1,S2,j}}$$

160 with $V_{S1,S2,j}$ being the number of classes where both species, S1 and S2, reached standardized
 161 abundances above or equal to 0.4 in j environmental variables. $V_{S1,j}$ and $V_{S2,j}$ are the number of
 162 classes where species S1 and S2 reached respectively standardized abundance above or equal to 0.4
 163 along the variable j gradient. To determine the variables that mostly discriminate the niche
 164 realization of the copepod community, the average of the overlap index along environmental
 165 variables was calculated.

166 4.3-Taxa, trophic groups and community structure temporal dynamics

167 Trophic groups dynamics were investigated at interannual and seasonal scales.

168 To analyse the shape of the time series obtained at seasonal and interannual scale, Functional
 169 Principal Component Analysis (FPCA) was used. FPCA is a statistical tool that allows the
 170 ordination of the statistical unit according to the shape of their functional entity. For each taxon, five
 171 B-splines were used to characterize functional objects from (i) the interannual series (144
 172 observations) (ii) and averaged seasonal series (12 observations). The functional objects built on
 173 interannual, and seasonal series aimed at characterizing the taxonomic groups trends.

174 Two FPCA have been performed on the coefficients of the B-splines. A first FPCA (FPCA_int) was
 175 performed to ordinate the interannual trends of taxa, and a second one for seasonal trends
 176 (FPCA_seas). FPCA were performed using the 'fda' package (Ramsay et al., 2009).

177 From FPCA ordination, interpretation was carried out on the basis of univariate times series
 178 analysis. Local polynomial regressions, LOESS (span=0.75), were used to highlight interannual
 179 trends. Interannual trends were considered significant when the confidence interval could not
 180 contain a horizontal line. Boxplots were performed to display the seasonal dynamics.

181 Rank-frequency (log-log) diagrams were realised to study the copepod community structure
 182 (Frontier, 1976). Rank-Frequency diagrams consisted in plotting the frequency (or relative
 183 abundance in y-axis) of each taxon according to their rank (x-axis) in decreasing order of frequency
 184 (i.e. the most abundant taxa plotted in the first rank, the least abundant in the last rank). Linear
 185 regressions on (log-log) rank-frequency diagrams with fixed intercepts were performed. The slopes
 186 of the log-log rank-frequency diagrams were used as an index of the shape of the rank-frequency
 187 diagram.

188 Results

189 1. Community composition

190 The copepod community (Table 1) was mostly dominated by *Clausocalanus-Paracalanus-*
191 *Ctenocalanus-Pseudocalanus* group (60.5%, on average 1123.4 ind.m⁻³), followed by *Centropages*
192 *typicus* (12.7%, on average 234.8 ind.m⁻³) and *Oithona* spp. (12.5%, on average 224.9 ind.m⁻³). The
193 remaining taxa represented less than 15% of the community, none of them exceeded 5% in relative
194 abundance. The copepod community was mostly composed of herbivores (>70%), followed by
195 omnivores (>24%), and to a lesser extent carnivores (3.6%) and detritivores (3.4%). The most
196 abundant taxonomic groups within the trophic groups were *Clausocalanus-Paracalanus-*
197 *Ctenocalanus-Pseudocalanus* group, *Centropages typicus*, Oncaeidae (2.0%, on average 36.3 ind.m⁻³)
198 ³), and Corycaeidae (1.7%, on average 32.1 ind.m⁻³), respectively for herbivores, omnivores,
199 detritivores and carnivores.

200 2. Temporal variability of copepods taxa and trophic groups

201 The abundances of herbivores and omnivores presented a clear seasonal pattern with a peak in
202 April-May (Fig. 2A). Carnivores increased during August-September, whereas detritivores did not
203 present a clear seasonal pattern. In terms of relative abundance (Fig. 2B), the proportion of
204 omnivores tended to increase in spring, and then regularly decrease the rest of the year. Detritivores,
205 carnivores and herbivores did not show strong variations in their relative abundance, except for a
206 small decrease in spring (early spring for detritivores and carnivores and late spring for herbivores).

207 The FPCA_seas (Fig 3) ordinated the taxonomic groups according to their phenology. Taxonomic
208 groups that presented positive values on the first component (explained 60.19% of dataset variance)
209 of the FPCA_seas (Fig 3A) peaked in autumn while taxa with negative values peaked in spring. The
210 second component (explained 25.66% of dataset variance) of the FPCA_seas (Fig 3B) separated
211 taxonomic groups with a summer peak (for negative values) and winter peak (for positive values).
212 The seasonal succession of the taxonomic groups is clearly visible in Fig 3C when moving in a
213 counter-clockwise direction (i.e., starting at positive values on the second PC and null values on the
214 first PC, which corresponded to the winter peak). The succession was presented as follows:
215 *Pleuromamma* spp., *Calocalanus* spp., *Euterpina acutifrons* (winter onset), *Calanus helgolandicus*,
216 *Oithonidae*, *Clausocalanus-Paracalanus-Ctenocalanus-Pseudocalanus* group (early spring onset),
217 *Acartia* spp., *Centropages typicus* (late-spring, summer onset), Corycaeidae, *Temora stylifera*,
218 *Nannocalanus minor* and *Calanus-Mesocalanus-Neocalanus* group (autumn onset). The remaining
219 taxonomic groups (*Candacia* spp., *Isias clavipes*, *Microsetella* spp. and Oncaeidae), in the center of
220 the ordination plot, did not show any significant seasonal pattern. Except for detritivores, the
221 taxonomic groups of a same trophic group may present different seasonal patterns. Thus, the

222 seasonal patterns observed for herbivores, carnivores, and omnivores depend mostly on the most
223 abundant taxonomic group (i.e. respectively *Clausocalanus-Paracalanus-Ctenocalanus-*
224 *Pseudocalanus*, *Corycaeidae* and *Centropages typicus*). The result of the FPCA_seas (Fig 3) are
225 confirmed by the univariate analysis (Fig 4) of the seasonal patterns of the different taxonomic
226 groups. Fig 4 shows in addition the great variability in abundance of the different taxonomic
227 groups.

228 Abundance of carnivores and detritivores increased during the series (Fig. 5A). In contrast,
229 abundance of herbivores and omnivores increased until the early 2010s, then decreased until 2020
230 and then increased significantly in the last two years. In terms of relative abundances (Fig. 5B),
231 carnivores and detritivores increased whereas the other trophic groups did not show any significant
232 variations.

233 The FPCA_int (Fig. 6) explained 85.98% of the copepods long-term variations (i.e. calculated in
234 absolute abundances). The first PC (Fig 6A, 51.79% of the variance) ordinated copepods with
235 increasing trends (positive values, red dotted line) and decreasing trends (negative values, blue
236 dashed line). In the second PC (Fig 6B, 34.08% of the variance), copepods associated with positives
237 values (red dotted line) displayed an increasing trend until 2010 before a decrease until 2015, and a
238 following increase (and inverse trends for copepods on positive values, i.e. blue dashed line). This
239 FPCA_int ordination allowed us to classify taxonomic groups in five groups according to their
240 dynamics (Fig 6C): i) the first group was characterized by a constant decreasing trend (negative
241 values on 1st PC and negative on 2nd PC) and included only *Calanus helgolandicus*; ii) the second
242 group composed by *Temora stylifera*, *Oncaeidae* and *Corycaeidae* displayed a monotonous
243 increasing trend (positive values on both axes); iii) *Clausocalanus-Paracalanus-Ctenocalanus-*
244 *Pseudocalanus*, *Oithona* spp. and *Calanus-Mesocalanus-Neocalanus*, associated with negative
245 values on 1st PC and positive on 2nd PC, displayed firstly an increasing trend until 2010 before a
246 decrease.; iv) *Isias clavipes* (positive values on 1st PC and negative values on 2nd PC) displayed an
247 increase in abundance since 2012; v) the taxa present in the center of the ordination plot did not
248 display any significant interannual trend (*Centropages typicus*, *Calocalanus* spp., *Microsetella* spp.,
249 *Nannocalanus minor*, *Acartia* spp., *Candacia* spp., *Pleurommama* spp. and *Euterpina acutifrons*).
250 Within the same trophic group, taxa may display different interannual patterns as shown in Fig. 5.
251 Therefore, the observed patterns at the trophic group level were mostly driven, as for seasonality, by
252 the most abundant taxon. The inspection of the univariate interannual dynamic of the taxonomic
253 groups (Fig 7) confirmed the results of the FPCA_int (Fig 6) and allowed us to refine the
254 interannual pattern for some taxa. The *Clausocalanus-Paracalanus-Ctenocalanus-Pseudocalanus*
255 group (in the third group) displayed a slight increase after 2020 in comparison to *Oithona* spp. and

256 *Calanus-Mesocalanus-Neocalanus*. In addition, as for seasonal patterns, the interannual series of
257 copepods presented a high variability.

258 In the log-log rank-frequency diagram, steep slopes were observed in spring (April-May) when a
259 few taxonomic groups (e.g. *Clausocalanus-Paracalanus-Ctenocalanus-Pseudocalanus*) dominated
260 the copepod assemblage, while flat slopes were found in summer-autumn (Fig. 8 A). Since the mid-
261 2010s slopes flattened (Fig 8B), mainly due by the disappearance of steep slopes during spring (Fig
262 8C).

263 3.Copepods ecological niche along environmental gradients

264 *Centropages typicus*, *Calanus helgolandicus*, *Temora stylifera*, *Candacia* spp., *Calanus-*
265 *Mesocalanus-Neocalanus* group and *Clausocalanus-Paracalanus-Ctenocalanus-Pseudocalanus*
266 group had the narrowest niches in the multidimensional space (i.e. these groups have a high number
267 of dark blue boxes with low abundances in Fig. 9). This observation was confirmed by the lowest
268 values (between 47% and 62%) of niche amplitude calculated for those species (see Table 1).
269 Conversely, *Calocalanus* spp. and Oncaeidae had the highest niche breadths, with 89% and 76% of
270 niche amplitudes, respectively. Copepods groups did not present the same degree of tolerance along
271 the gradient of environmental conditions, e.g. *Calanus-Mesocalanus-Neocalanus* group and
272 *Calanus helgolandicus* presented narrower niches (respectively 21.05% and 26.32%) related to
273 suspended particular matter concentrations compared to *Calocalanus* spp.(94.74%) or *Acartia* spp.
274 (94.74%) (see Table 2 in Supplementary Material 2 for detailed information about the taxonomic
275 groups niche amplitudes for every environmental dimension).

276 The variables that minimize the niche overlap between copepods (i.e. contributed more for
277 taxonomic group niche differentiation) were SPM (56.51%), temperature (56.61%), POC (57.87%),
278 and PON (59.44%) (Table 2). Chromatograms (Fig. 9) showed clearly the discrimination of
279 copepods groups that prefer low temperatures (*Calanus helgolandicus*) and high temperatures
280 (*Temora stylifera*, Corycaeidae, *Nannocalanus minor* and *Isias clavipes*). Temperature optimums
281 were 13.18°C for *Calanus helgolandicus* and >18°C for high temperature taxa (see Table 3 in
282 Supplementary Material 2 for detailed information about the taxonomic groups optimums for every
283 environmental dimension). Conversely, wind stress, Chlorophyll a, MLD and invertebrate predator
284 abundance were the variables that minimised the niche overlap the least, meaning that most of the
285 copepod optimums were in the same range of values for these variables, or that copepods taxa had a
286 wide niche breadth for those variables.

287 Discussion

288 1- Seasonal dynamics and niche realization of copepod taxa

289 The community was dominated by small and medium sized copepods (i.e. *Clausocalanus-*
290 *Paracalanus-Ctenocalanus-Pseudocalanus*, *Centropages typicus*, *Oithonidae*), as generally
291 observed in the Mediterranean Sea (Siokou-Frangou et al., 2010; Donoso et al., 2017; Zingone et
292 al., 2019), and the abundances and relative abundances of trophic groups within the copepod
293 community changed seasonally. Berline et al. (2012) evidenced differences in the seasonal patterns
294 of copepods between Mediterranean sites. The seasonal pattern of total copepods abundance
295 observed in the Bay of Marseille is comparable to those observed at Villefranche sur Mer
296 (Vandromme et al., 2011; Feuilloley et al., 2021), Calvi (Fullgrabe et al., 2020), Athens (Siokou-
297 Frangou, 1996), Stončica (Solic et al., 1997) and Balearic Sea (Fernández De Puelles et al., 2009;
298 Fernandez De Puelles et al., 2023) with a peak between March-May (following phytoplankton
299 bloom) followed by a decrease in summer and autumn. In comparison, in the Gulf of Naples
300 copepods abundance increases in April and remains high during the summer (Ribera d'Alcalà et al.,
301 2004; Mazzocchi et al., 2012, 2023). In the Gulf of Trieste, north Adriatic, a second autumnal peak
302 as strong as the spring peak is usually observed (Berline et al., 2012).

303 In the Bay of Marseille, herbivorous copepods dominated the community all year long. Omnivores
304 and carnivores displayed opposite seasonal trends according to the trophic conditions of the
305 environment. Omnivores were associated with spring phytoplankton bloom and carnivores were
306 associated with oligotrophic conditions, in late summer-autumn, consistent with Benedetti et al.
307 (2018). The seasonal patterns observed at the trophic group level were driven by the most dominant
308 taxonomic groups: *Clausocalanus-Paracalanus-Ctenocalanus-Pseudocalanus* group for herbivores,
309 *Corycaeidae* for carnivores and *Centropages typicus* and *Oithona* spp. for omnivores. If we consider
310 only trophic biotic controls within the zooplankton community, the seasonal variations in relative
311 abundances may indicate a shift in the functioning of the copepod community from bottom-up
312 (during winter-spring) to top-down control (during summer-autumn). This observation is consistent
313 with the seasonal variation of zooplankton stable isotope ratio of nitrogen, a proxy of trophic levels,
314 in the Bay of Marseille (Garcia et al., 2024). In the Bay of Marseille, invertebrate predators, such as
315 chaetognaths and cnidarians, reach their maximum abundance during the summer-autumn period
316 (Garcia et al., 2023). Most copepod groups showed lower abundances when the abundance of large
317 predators was highest (i.e. in summer-autumn) in the Bay of Marseille. These results would
318 suggests a limiting effect of invertebrate predation on the copepod stocks dynamics, as observed in
319 the English Channel (Bonnet et al., 2010).

320 The seasonal succession of zooplankton and copepod trophic groups can be related to water mixing
321 events and phytoplankton blooms as observed at other sites (Ribera d'Alcalà et al., 2004;
322 Romagnan et al., 2015). As commonly observed, temperature seemed to be a major factor

323 influencing copepod seasonal patterns and realized niches (Beaugrand et al., 2002; McGinty et al.,
324 2018; Villarino et al., 2020). Temperature variations are known to affect copepod physiology, in
325 particular its reproduction and development (Halsband-Lenk et al., 2002). However, the copepods
326 assemblages may also depend on other factors such as biotic interactions (e.g. competition)
327 (Barroeta et al., 2022). The seasonal preferences of the taxonomic groups found in the present study
328 are in agreement with earlier results obtained in the Bay of Marseille (Gaudy, 1962). We have
329 classified hereafter the copepod groups into four classes, according to their seasonal dynamics:

330 (i) The winter assemblage is mostly composed of filter feeders herbivorous and omnivorous
331 (*Calocalanus* spp., *Pleuromamma* spp.), and small cruise feeder herbivores (*Euterpina acutifrons*).
332 Winter taxa tend to decline suddenly after the spring phytoplankton bloom (occurring in March).

333 (ii) In the spring, two herbivorous groups (*Calanus helgolandicus* and *Clausocalanus-Paracalanus-*
334 *Ctenocalanus-Pseudocalanus*) and the small active ambush omnivore group (*Oithonidae*) are
335 observed concomitantly with the early spring phytoplankton. Kouwenberg (1994) noted in
336 copepods assemblages of the Gulf of Lion, the association of *Oithona* spp. with large herbivores
337 and suggested a predation of *Oithona* spp. on younger stages of herbivorous copepods.

338 (iii) In late spring and summer, *Centropages typicus* (omnivore) and *Acartia* spp. (here simplified as
339 herbivore) presented highest abundances. They do not belong to the same trophic groups, but both
340 are small mixed feeders (Benedetti et al., 2016). In addition, it is reported that *Acartia* spp. can eat
341 ciliates and switch feeding behavior according to available prey (Calbet & Saiz, 2005). The
342 seasonal maximum abundances are consistent with other coastal Mediterranean sites (Ribera
343 d'Alcalà et al., 2004; Mazzocchi et al., 2007; Fernández De Puellas et al., 2009).

344 (iv) Autumn is characterized by abundance peaks of feeding current taxa (*Temora stylifera*,
345 *Calanus-Mesocalanus-Neocalanus*, *Nannocalanus minor*) that tolerate higher temperatures. These
346 organisms should feed on autumnal phytoplankton blooms that often occur in the NW
347 Mediterranean coasts (Zingone et al., 1995; Garcia et al., 2023), but also switch to omnivory
348 (Razouls et al., 2005). Garcia et al. (2023) showed that phytoplankton presented seasonal variations,
349 in composition and size, which may have shaped the seasonal successions of copepods. The
350 carnivorous copepod Corycaeidae completes the autumn assemblage.

351 No seasonal patterns were observed for *Candacia* spp. (carnivorous), *Isias clavipes* (omnivorous),
352 and two detritivores taxa (Oncaeidae and *Microsetella* spp.). Although WP2 200 µm net may not
353 efficiently sample Oncaeidae and *Microsetella* spp. (Zervoudaki et al., 2006), Benedetti et al.
354 (2018), found that detritivore copepods did not present a typical niche position within the copepod

355 community at a global scale. This is in line with our observed wide niche breadth of detritivores in
356 the Bay of Marseille.

357 Seasonal succession patterns of copepods in the Bay of Marseille are consistent with observations
358 made in other Western Mediterranean Sea series. In the Balearic Sea, Fernández De Puellas et al.
359 (2009) observed seasonal succession of 5 abundant copepods taxa (*Calanus helgolandicus*,
360 *Centropages typicus*, *Acartia clausi*, *Acartia danae* and *Temora stylifera*) which is similar to our
361 observations. In the Bay of Villefranche sur Mer and in the Gulf of Naples, *Centropages typicus*
362 tended to peak earlier (April-July) compared to *Temora stylifera* (July-October) (Molinero et al.,
363 2005; Mazzocchi et al., 2007).

364 **2-Copepods' interannual dynamics and their links with environmental changes**

365 Over the last 17 years the copepod assemblage in the Bay of Marseille has changed. One of the
366 main results is the decrease of total copepod abundance during the 2010 decade (with a slight
367 recovery after 2020). This change occurred in parallel with a reduced dominance of small copepods
368 during the spring period, since the mid-2010s, and concerned mainly the taxonomic groups,
369 *Clausocalanus-Paracalanus-Ctenocalanus-Pseudocalanus* group and *Oithonoidae*. Since these
370 taxonomic groups include numerous species, the trend observed may not be the same for all species
371 that belong to the taxon. In fact, during the last decades, in the Balearic Sea, opposite interannual
372 trends were observed between *Paracalanus parvus* (i.e. decreasing) and *Clausocalanus arcuicornis*
373 (i.e. increasing)(Fernandez De Puellas et al., 2023). Nonetheless, the decrease in the dominance of
374 *Clausocalanus-Paracalanus-Ctenocalanus-Pseudocalanus* group and *Oithonoidae* in the
375 community may be attributed to changes of the biotic and abiotic conditions. Over this period, the
376 Bay of Marseille experienced increasing oligotrophy associated with a decrease in nutrients,
377 suspended particulate matter, and particulate organic matter and an increase in winter temperature
378 (Garcia et al., 2023), as throughout most of the French coastal system (Lheureux et al., 2021).

379 This decrease of abundance during the 2010s was also observed at other sites in the Mediterranean
380 western basin. A decrease in abundance of neritic copepods and *Oithona* spp. were found in the
381 Gulf of Naples (Mazzocchi et al., 2023). A decrease of crustacean abundance (mostly small
382 copepods) was observed after 2015 at Villefranche sur Mer (Feuilloley et al., 2021), leading to a
383 flatter size spectrum and reduced seasonal amplitude. An opposite trend was observed in the
384 Alboran Sea, with higher copepods and nauplii abundances over 2010-2020 compared to 1992-2000
385 (Yebra et al., 2022). Due to the strong influence of Atlantic waters, the Alboran Sea is in a different
386 ecoregion (Berline et al., 2014), and this different trend is not surprising. In addition, in the Bay of
387 Marseille, an increase in the relative abundance of carnivores (mostly due to Corycaeidae trend)

388 was observed. This might be an indicator of a shift in the functioning of the copepod community
389 controls (from a bottom-up to top-down structure) under increasing oligotrophic conditions. This
390 change was concomitant with the recent increase of predators such as chaetognaths and cnidarians
391 (Garcia et al., 2023). The zooplankton community in the Gulf of Naples experienced similar
392 changes : after 2010 copepod abundance decreased, together with an increase of chaetognaths and
393 filter feeders (cladocerans, appendicularians, and thaliaceans) (Mazzocchi et al., 2023). In parallel,
394 the increase in abundance of detritivores Oncaeidae in the Bay of Marseille coincided with the
395 increase of appendicularians (Garcia et al., 2023). This may be due to Oncaeidae preferential
396 feeding on appendicularians houses under oligotrophic conditions (Ohtsuka et al., 1998).

397 Some taxa assemblages may be bioindicators of ecosystem conditions in terms of hydrology,
398 climate, pollution, eutrophication or biological invasions (Beaugrand et al., 2002; Fernández De
399 Puellas et al., 2009; Serranito et al., 2016; Chihoub et al., 2020; Uttieri et al., 2020). Our analyses
400 underlined the importance of the optimum thermal range in the niche realization of copepods.

401 *Calanus helgolandicus*, an offshore species distributed in the North Western Mediterranean basin
402 and associated with cold water masses (optimum 13.18 °C), showed a decreasing abundance over
403 the studied period. Winter conditions have changed in the Bay of Marseille (mostly an increase in
404 seawater temperature), notably since the 2010s (Garcia et al., 2023), possibly as a consequence of
405 the reduced intensity of deep winter convection off the Gulf of Lion (Margirier et al., 2020).

406 Therefore, we hypothesize that the *Calanus helgolandicus* abundance in the Bay of Marseille may
407 be an indicator of large scale hydrological changes in the NW-Mediterranean, due to its sensitivity
408 to temperature changes, as mentioned by Bonnet et al. (2005) and Yebra et al. (2011). Because they
409 cannot migrate northward, cold waters species, such as *Calanus helgolandicus*, would remain in
410 deeper layers (beyond the continental shelf and the Bay of Marseille) within the thermal optimum
411 range (and therefore not included in epipelagic monitoring), supporting the hypothesis of Yebra et
412 al. (2022). In contrast, the increase in temperature was accompanied with the increase in abundance
413 of autumn taxa, Corycaeidae and *Temora stylifera*, (which had a higher optimum on the temperature
414 gradient >18.5°C). Regarding wind events, we observed highest optimum values in wind stress for
415 *Candacia* spp., *Pleuromamma* spp. and *Calanus helgolandicus* (that may live in a deeper layer)
416 which may indicate that those *taxa* were associated with Mistral events. This is similar to earlier
417 observations by Gaudy (1962), in the Bay of Marseille, who described the appearance of taxa
418 coming from a deeper layer, the mesobathypelagic layer, (e.g. *Heterorhabdus*, *Haloptilus*
419 *longicornis*) during upwelling events (i.e. following ‘Mistral’ NW winds).

420 Conclusions and perspectives

421 Our work showed a clear seasonal succession of copepod taxa and trophic group. At the interannual
422 scale, the mid-2010's appeared to be a critical period with change in the community structure of
423 copepods in the Bay of Marseille. Relative abundances of herbivores decreased while carnivores
424 and detritivores increased. Our study showed that within the same trophic group, taxa may display
425 different temporal variation. Thus, the observed patterns at the trophic group level are mostly driven
426 by the most abundant taxa. The analysis of copepod ecological niches highlighted the main factors
427 that discriminate the copepods niches (i.e. temperature, SPM, POC and PON). The joint
428 interpretation of ecological niche analyses and interannual dynamics of copepods taxa revealed that
429 oligotrophication and warming favoured increases in abundance of Corycaeidae (carnivore),
430 Oncaeidae (detritivore) and *Temora stylifera* (herbivore) and were unfavourable to *Calanus*
431 *helgolandicus* (herbivore). Thus, this work demonstrated the interest of combining taxonomic and
432 trophic traits to characterise the temporal changes that occurred in the copepod community.

433 No meta-analyses of zooplankton Mediterranean series have been done since Berline et al. (2012).
434 Over the last two decades, we observed in the Bay of Marseille concomitant and similar changes
435 with other Mediterranean coastal sites. A new re-analysis of Mediterranean time series with recent
436 data, which includes a detailed description of copepods groups (taxonomic and trophic group), may
437 help to improve our understanding of recent concomitant changes in different Mediterranean coastal
438 areas in the context of oligotrophication and climate change.

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464 Data archiving

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Table

Table 1: Summary of the different taxonomic group studied, their trophic regime, abbreviations used in the manuscript (abbr), abundance (sample average) and the niche amplitudes derived from the chromatogram analysis (2006-2022). The niche amplitudes correspond to the average amplitude over the 16 environmental variables. The details of the composition of every taxonomic groups is

687 given

Trophic group / Taxonomic group	abbr	Abundance (ind.m ⁻³) mean	Relative Abundance (%)	Niche amplitude (%)
Herbivores				691
<i>Clausocalanus</i> - <i>Paracalanus</i> - <i>Ctenocalanus</i> - <i>Pseudocalanus</i> group	CPCP	1123.4	60.5	62 692 693 694 695
<i>Acartia</i> spp.	Acar	84.1	4.5	75 696
<i>Calocalanus</i> spp.	Calo	34.9	1.9	88 697
<i>Temora stylifera</i>	TSty	27.7	1.5	50 698
<i>Euterpina acutifrons</i>	EAcu	11.5	0.6	76 699
<i>Calanus helgolandicus</i>	CHel	9.2	0.5	47 700
<i>Calanus</i> - <i>Mesocalanus</i> - <i>Neocalanus</i> group	CMN	4	0.2	60 701 702 703
<i>Nannocalanus minor</i>	NaMi	2.6	0.1	71
Omnivores				
<i>Centropages typicus</i>	CTyp	234.8	12.7	51
<i>Oithona</i> spp.	Oith	224.9	12.1	63
<i>Pleuromamma</i> spp.	Pleu	8.3	0.4	71
<i>Isias clavipes</i>	ICla	3.8	0.2	63
Detritivores				
Oncaeidae	Onca	36.3	2.0	76
<i>Microsetella</i> spp.	Micr	2.8	0.1	67
Carnivores				
Corycaeidae	Cory	32.1	1.7	63
<i>Candacia</i> spp.	Cand	6.8	0.4	62

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704 Table 2: Summary of the average overlap among taxonomic units for all environmental variables.

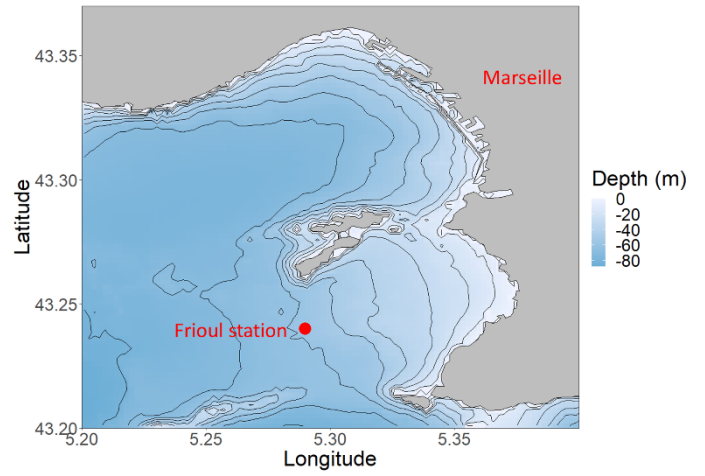
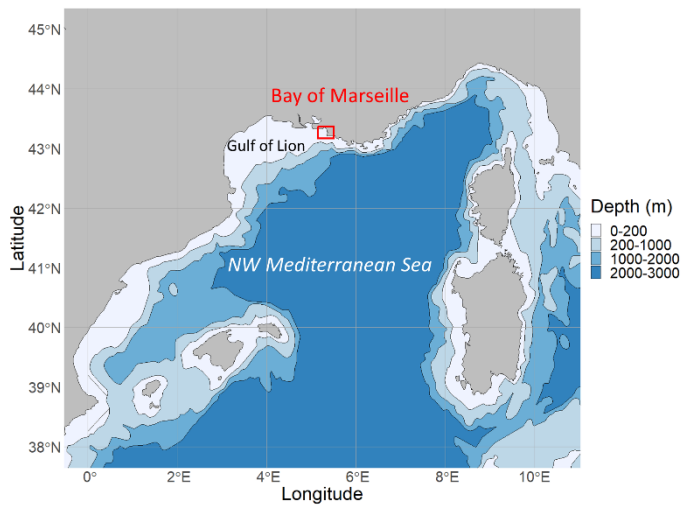
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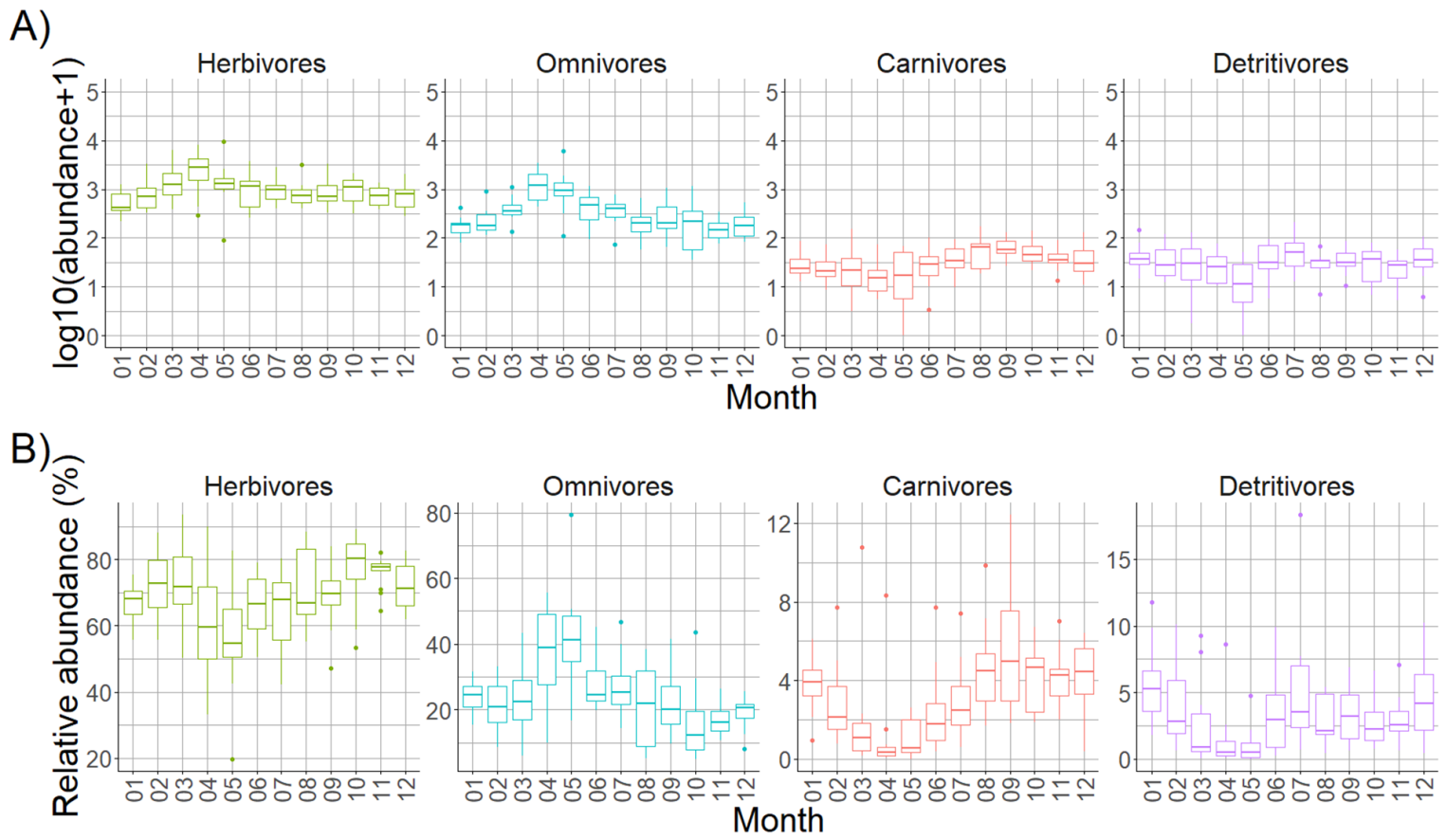
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Variable	Overlap (%)
SPM	56.51
T	56.61
POC	57.87
PON	59.44
PO ₄	59.7
NO ₂	60.52
Prec	60.68
NH ₄	61.49
O ₂	62.79
NO ₃	62.89
S	63.18
large predators	65.5
CHLA	66.39
MLD	73.99
wind stress	76.3

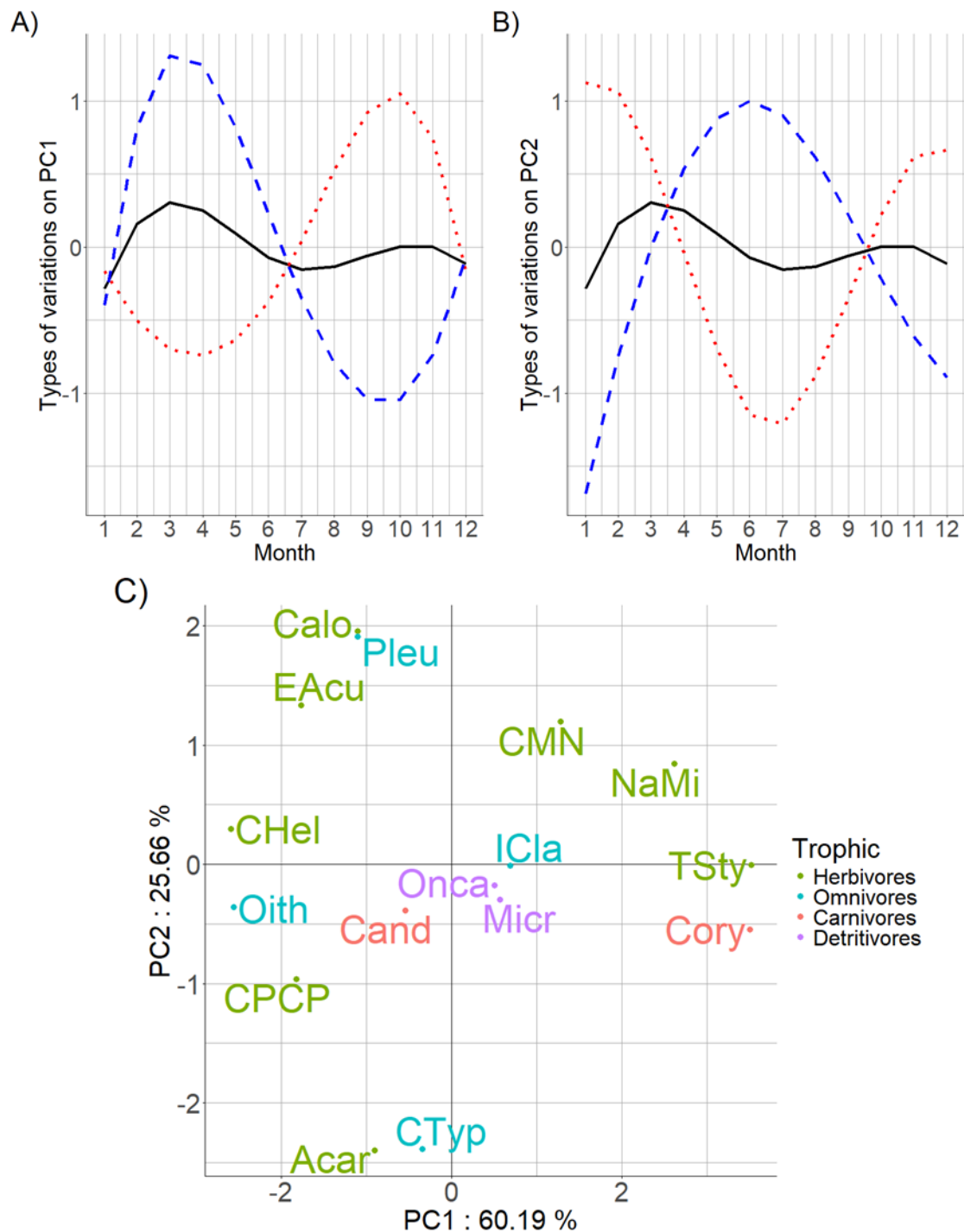


709 **Figures**

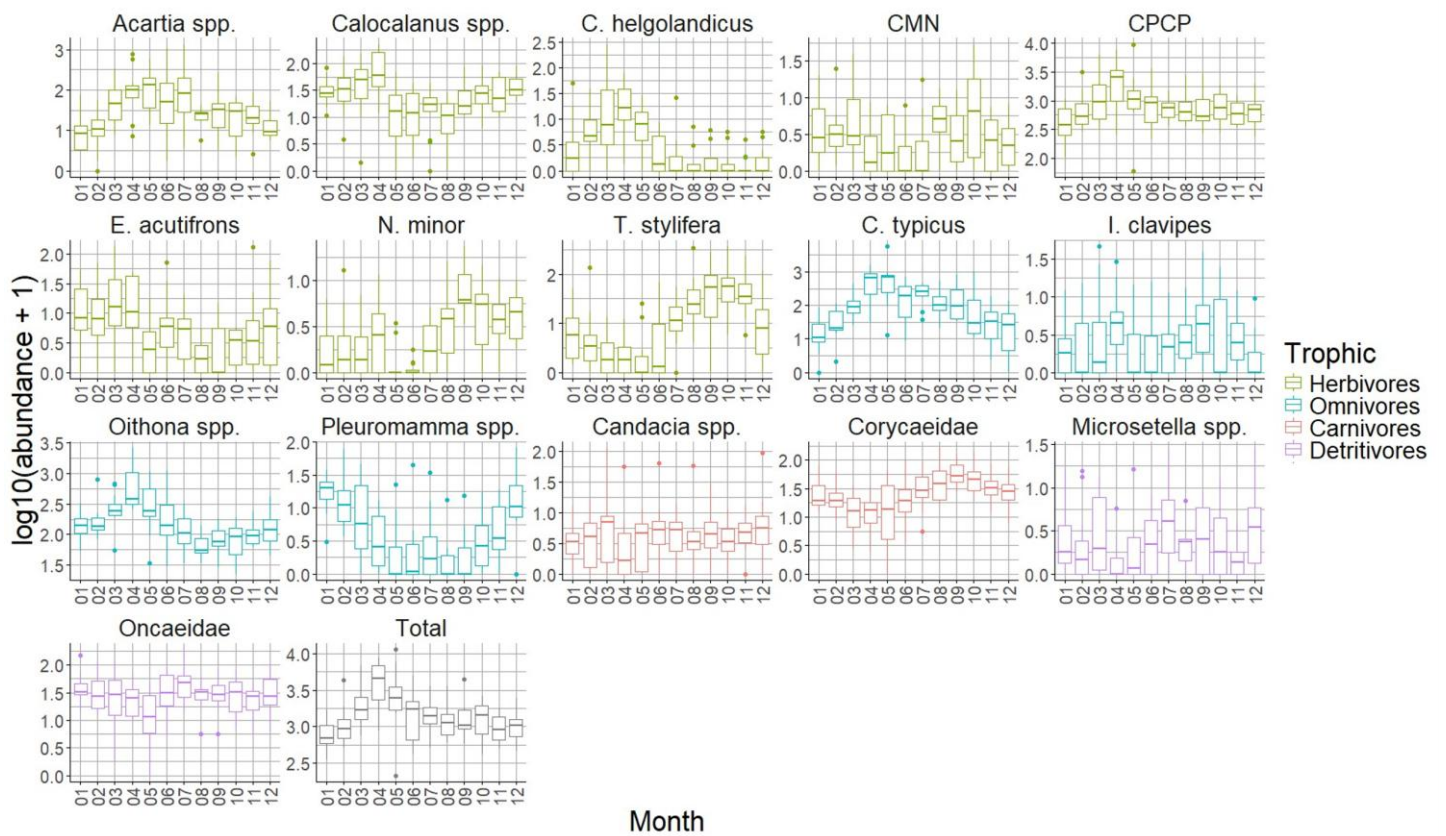
710 Fig. 1: Location of the Bay of Marseille (red square) in the Gulf of Lion (NW-Mediterranean Sea)
 711 and the Frioul station in the Bay of Marseille (red dot).



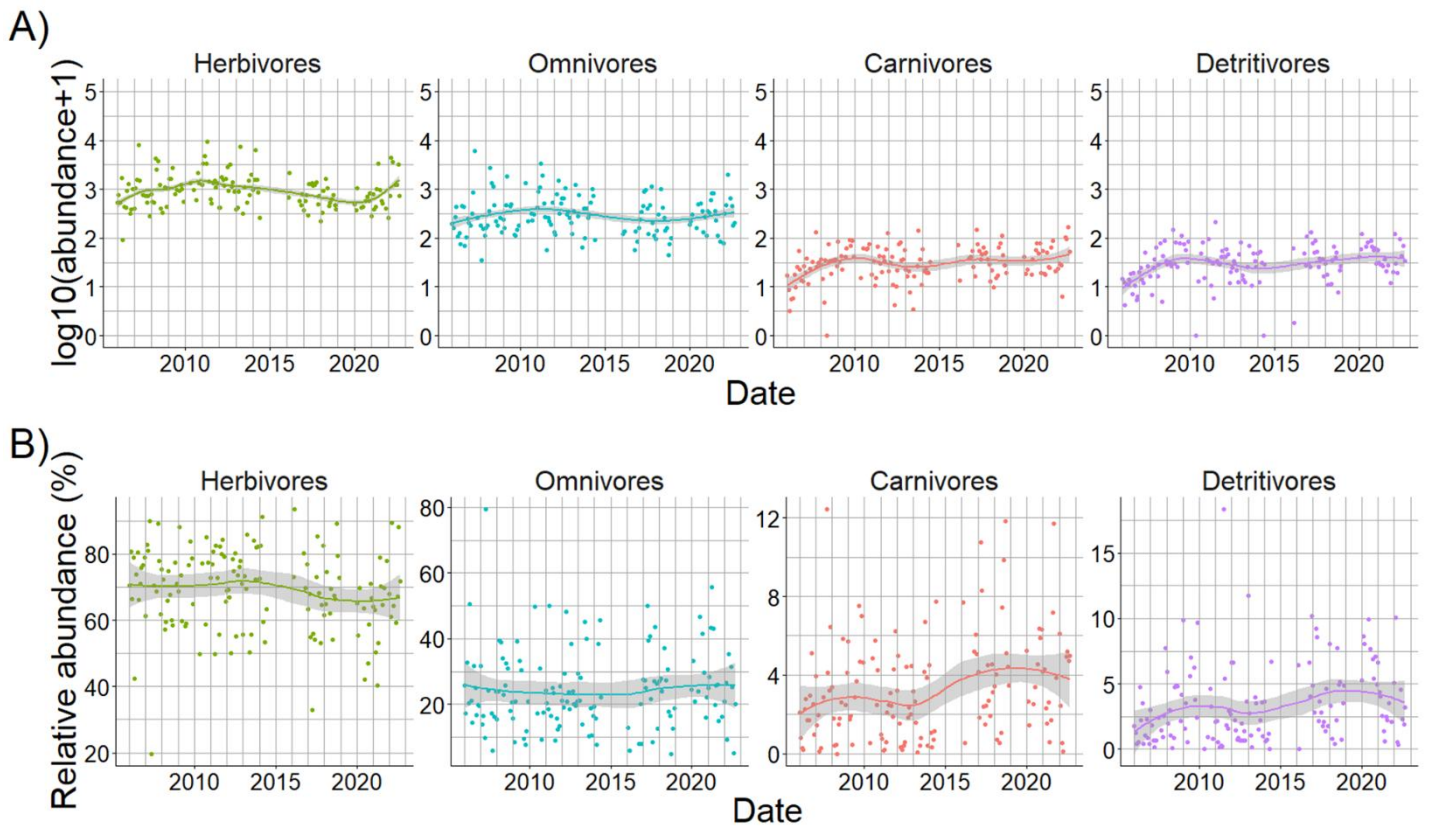
712 Fig. 2: Seasonal dynamics of trophic groups as Boxplots of A) log transformed abundance (ind.m⁻³),
 713 log₁₀(abundance+1), and B) relative abundances.



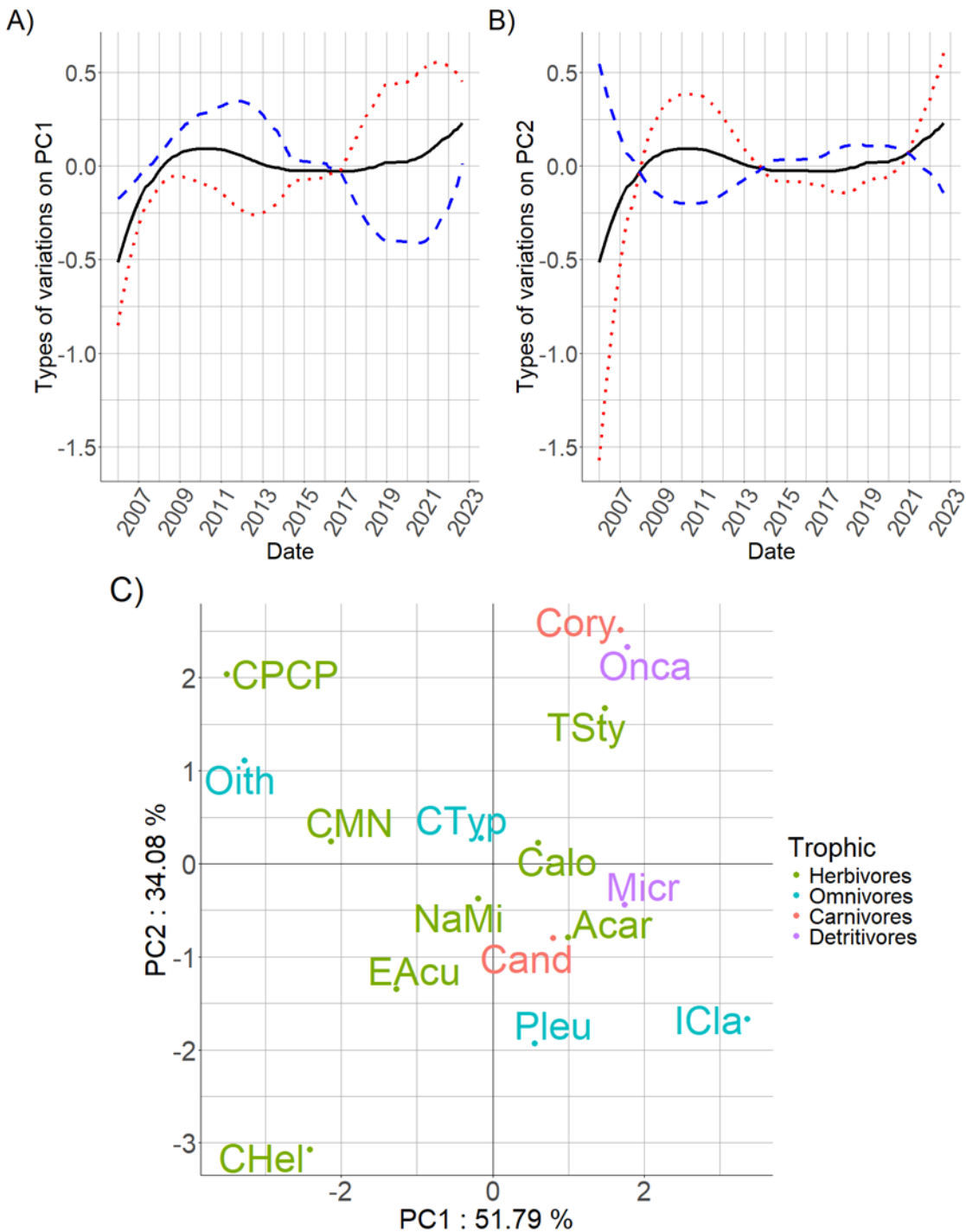
714 Fig. 3: Seasonal series of taxa. Results of FPCA_seasonal. Influence of factorial axis on the shape of the
 715 seasonal trend (functional object) for the first (A) and second (B) principal components
 716 respectively. Black line is the mean functional curve. Blue and red dotted lines represent
 717 respectively the negative and positive influences of the factorial axis on the seasonal dynamic. C)
 718 Plot of individuals of the FPCA. The taxa are ordinated according to the seasonal series modes of
 719 variations. The taxa are coloured according to their trophic group. See Table 1 for taxonomic group
 720 abbreviations.



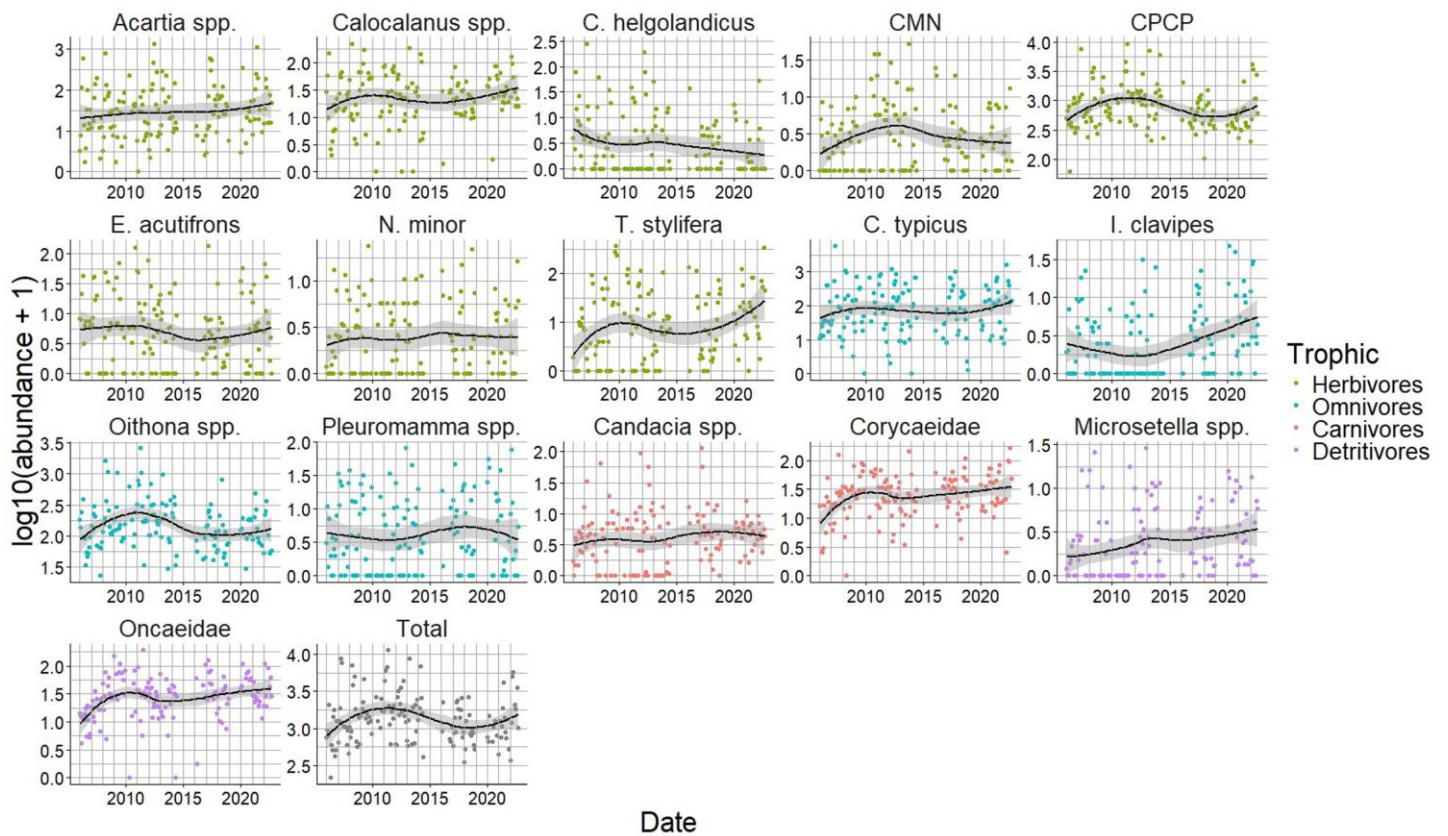
722 Figure 4: Boxplots representing the seasonal dynamics of log transformed, log₁₀(abundance+1),
 723 abundances (in ind.m⁻³) of the different taxonomic unit. CPCP and CMN are respectively
 724 *Clausocalanus-Paracalanus-Ctenocalanus-Pseudocalanus* and *Calanus-Mesocalanus-Neocalanus*
 725 taxonomic groups.



726 Fig. 5: Interannual time series of the different trophic groups, of A) log transformed abundance
 727 (ind.m^{-3}), $\log_{10}(\text{abundance}+1)$, and B) relative abundances. The coloured continuous lines and the
 728 shaded area correspond respectively to the trends depicted by LOESS and the corresponding 95%
 729 confidence interval.



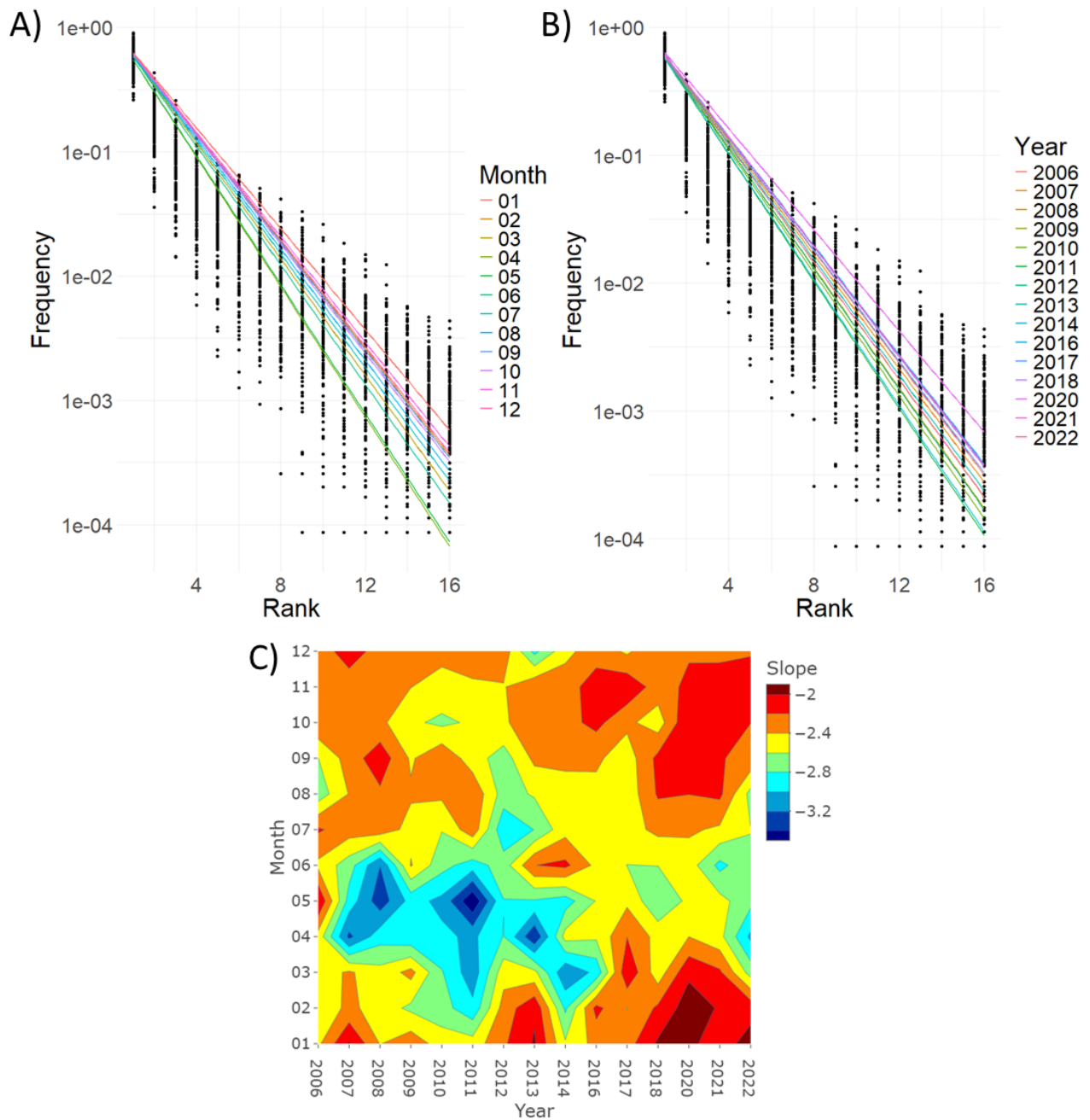
730 Fig. 6: Interannual series of taxa. Results of FPCA_int. Influence of factorial axis on the shape of
 731 the interannual trend (functional object) for the first (A) and second (B) principal components
 732 respectively. Black line is the mean functional curve. Blue and red dotted lines represent
 733 respectively the negative and positive influences of the factorial axis on the interannual dynamic. C)
 734 Plot of individuals of the FPCA. The taxonomic group are ordinated according to the interannual
 735 series modes of variations. The species are colored according to their trophic group. See Table 1 for
 736 taxonomic group abbreviations.



738 Figure 7: Interannual time series of the different taxonomic units. Dots correspond to the
 739 $\log_{10}(\text{abundance}+1)$ values. Abundances are expressed in ind.m^{-3} . The colored continuous lines and
 740 the shaded area correspond respectively to the trends depicted by LOESS and the 95% confidence
 741 interval corresponds. CPCP and CMN are respectively *Clausocalanus-Paracalanus-Ctenocalanus-*
 742 *Pseudocalanus* and *Calanus-Mesocalanus-Neocalanus* taxonomic groups.

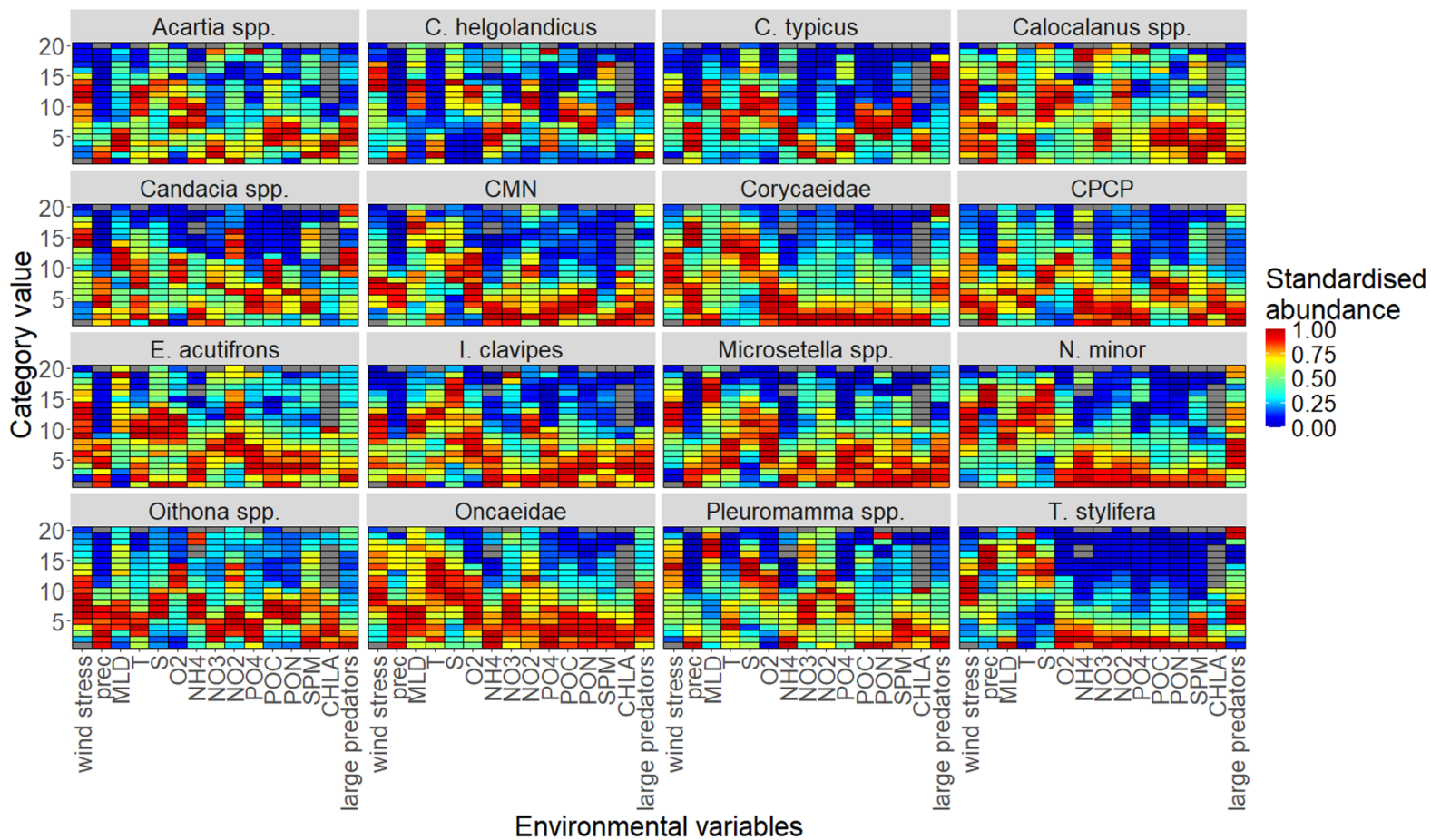
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745 Fig. 8: Rank-Frequency diagram of copepod community. Colored lines correspond to smoothed
 746 regressions (LOESS) between frequency and rank values of month (A) and in year (B). Note that
 747 the y-axis of both figures is log transformed. C) Slope of rank-frequency diagrams as contour plot
 748 (months in y axis, year in x axis). The slopes were computed on log transformed (ln) rank and
 749 frequencies.

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751 Fig. 9: Chromatograms representing the multidimensional niche of the taxonomic groups in the Bay
 752 of Marseille. Taxonomic group standardized abundance is represented along a gradient of 20 classes
 753 (from low to high) for the 15 environmental variables. Blue and red colors correspond respectively
 754 to the lowest and highest abundances of taxonomic groups, and grey color when no value is
 755 available in the class. CPCP and CMN are respectively *Clausocalanus-Paracalanus-Ctenocalanus-*
 756 *Pseudocalanus* and *Calanus-Mesocalanus-Neocalanus* taxonomic groups.