Zooplankton biodiversity and temporal dynamics (2005–2015) in a coastal station in western Portugal (Northeastern Atlantic Ocean)

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Long-term monitoring of zooplankton assemblages provides essential knowledge to assess key factors impacting marine ecosystems. Despite the importance of this type of data, monitoring stations worldwide are spatially and temporally limited due to the difficulty of maintaining them operational on a frequent basis. In the northeastern Atlantic area, Cascais-Watch is one monitoring site operating since 2005, despite some constraints throughout the years, and has allowed the collection of important data on the zooplankton communities of the area. The present work summarizes the knowledge collected until 2015 on the biodiversity and dynamics of zooplankton in the site. The results showed a year-round high productivity of the zooplankton abundance, biomass and diversity for the area, with no significant general trends or periodicity, despite the relatively lower winter and higher spring values. The results revealed two main transition periods with marked changes in species composition and dominance of the most abundant taxa. This shift was tentatively attributed to the extended annual dry season verified in Portugal after 2011, the low values of upwelling and precipitation, and the warmer waters. The zooplankton abundance presented an interannual increase for spring periods, and the proportion of Copepoda, the dominant taxa, was lower during summer months, corresponding to increased abundances of Mollusca, Diplostraca (Cladocera) and Cnidaria. In particular, the study shows an increasing abundance of the gelatinous species (particularly Cnidaria) for spring/summer months in recent years, suggesting changes in primary production and prey dynamics. Other relevant tendencies were the higher abundance of meroplankton, such as Bivalvia and fish larvae/eggs, and the decreasing trend in the abundance of the meroplanktonic coastal crustaceans, Decapoda and Cirripedia taxa, highlighting possible changes in the benthic coastal populations in the study region. The present study highlights probable changes and trends in the zooplankton community that should be

monitored in the following years.

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19 **Short title**

20 Zooplankton patterns in western Portugal

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22 **Keywords**

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25 **Abstract**

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28 assess key factors impacting marine ecosystems. Despite the importance of this type of data,

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30 maintaining them operational on a frequent basis. In the northeastern Atlantic area, Cascais-

31 Watch is one monitoring site operating since 2005, despite some constraints throughout the

32 years, and has allowed the collection of important data on the zooplankton communities of the

33 area. The present work summarizes the knowledge collected until 2015 on the biodiversity and

34 dynamics of zooplankton in the site. The results showed a year-round high productivity of the

35 zooplankton abundance, biomass and diversity for the area, with no significant general trends or

36 periodicity, despite the relatively lower winter and higher spring values.

37   The results revealed two main transition periods with marked changes in species

38 composition and dominance of the most abundant taxa. This shift was tentatively attributed to

39 the extended annual dry season verified in Portugal after 2011, the low values of upwelling and

40 precipitation, and the warmer waters. The zooplankton abundance presented an interannual

41 increase for spring periods, and the proportion of Copepoda, the dominant taxa, was lower

42 during summer months, corresponding to increased abundances of Mollusca, Diplostraca

43 (Cladocera) and Cnidaria. In particular, the study shows an increasing abundance of the

44 gelatinous species (particularly Cnidaria) for spring/summer months in recent years, suggesting

45 changes in primary production and prey dynamics.

46   Other relevant tendencies were the higher abundance of meroplankton, such as Bivalvia

47 and fish larvae/eggs, and the decreasing trend in the abundance of the meroplanktonic coastal

48 crustaceans, Decapoda and Cirripedia taxa, highlighting possible changes in the benthic coastal

49   populations in the study region. The present study highlights probable changes and trends in the

50   zooplankton community that should be monitored in the following years.

51

52   **1. Introduction**

53

54   Coastal areas are complex systems influenced by both marine and land processes, being

55   among the most ecologically and socio-economically vital ecosystems in the world. Given their

56   importance, coastal areas are under major concern regarding the potential impact of climate

57   change and anthropogenic pressures (Harley et al. 2006). Changes in the physical and chemical

58   properties of the marine environment may alter the physiological functioning and behavior of

59   organisms, leading to changes in population dynamics. Consequent modifications in the

60   community structure affect both the bottom-up and top-down processes within the food web

61   (Doney et al. 2012).

62   Zooplankton play a key role in the coastal pelagic food webs, transferring the energy

63   from primary producers to top predators. Given its quick response to environmental changes,

64   these organisms are good indicators of ecosystem changes (e.g., Muñoz-Colmenares, Soria &

65   Vicente 2021). Therefore, species succession and community shifts may emerge as an outcome

66   of climate change. Long-term changes in zooplankton biomass, diversity and community

67   structure have been frequently associated with climate change and anthropogenic impacts (e.g.,

68   Richardson 2008). These factors may have severe effects on the zooplankton communities

69   (including fish eggs and larvae), potentially reducing food availability or modifying the

70   nutritional quality of these organisms for higher trophic levels (Wright, Pinnegar & Fox 2020).

71   For these reasons, long-term observations of population and community composition dynamics

72   are regarded as research priorities (Pitois & Yebra 2022).

73   Upwelling areas are paramount sources of primary productivity, supporting substantial

74   abundances of zooplankton and prosperous food webs, which ultimately promote favorable

75   conditions for populations of commercially important fish species (Pires & Dos Santos, 2020).

76   The coast of Portugal, in the northern limit of the Northeastern Atlantic Upwelling System (e.g.,

77   Relvas et al. 2007), sustains large populations of planktivorous fish such as sardines (*Sardina*

78   *pilchardus*), anchovies (*Engraulis encrasicolus*) and horse mackerel (*Trachurus trachurus*), with

79   great economic value (Santos et al. 2007). For instance, catches of sardine, the most

80   commercially important and dominant fish species in the area, fluctuates around 150 thousand

81   tonnes per year (Santos et al. 2007). The recruitment of these species is tightly dependent on

82   upwelling (Santos et al. 2001), given the favorable conditions provided for fish larvae in terms of

83   the high food availability (i.e., zooplankton). Nevertheless, despite the acknowledged importance

84   and the works already available (e.g. Lindley & Daykin 2005, Sobrinho-Gonçalves et al. 2013,

85   Stehle, Dos Santos & Queiroga 2007, Domínguez et al. 2017, Cruz et al. 2020), studies assessing

86   the seasonal and interannual variability of the composition of zooplanktonic communities off

87   Portugal are still required, given that established monitoring for wider spatial and temporal scales

88   is still not fully implemented in Portuguese waters.

89   Future climate predictions suggest an intensification of the upwelling events, with

90   potentially severe consequences for planktonic communities (Bakun et al. 2010). The nutrient

91   enrichment effect of stronger upwelling can be counteracted by an increased rate in the offshore

92   transport of organisms (Bakun et al. 2010), such as fish larvae (Santos et al. 2001). Furthermore,

93   under climate change scenarios for Portugal, the decrease in both precipitation (Soares et al.

94   2015) and the runoff of rivers such as the Tagus have been predicted, with the latter expectedly

95   promoting more saline environmental conditions (Kilsby et al. 2007).

96   The present study uses data on diversity and temporal variability of zooplankton

97   communities obtained in a highly productive coastal station, Cascais-Watch (hereafter

98   designated as CCW), located in the Cascais Bay (Site 54, O'Brien et al. 2011), in the

99   northeastern Atlantic. The station is under the influence of seasonal upwelling, promoted by

100   favorable northerly winds, which are strongest between June and August (Relvas et al 2007,

101   Pires & Dos Santos, 2020). In addition, it is also influenced by the Tagus estuarine plume that,

102   induced by wind and river runoff, is advected offshore (Vaz et al. 2009, Relvas et al. 2007). Both

103   processes, together with the conspicuous local topographical structures, create complex

104   mesoscale circulation features, shaping the ecosystem and the dynamics of the zooplankton

105   communities. The study station is placed in the northern region of the Lisbon Bay, which was

106   previously suggested as a retention area (e.g., Moita et al. 2003), driven by the sheltering effect

107   of the Estremadura headland (Raso/Roca and Espichel Capes) from the direct influence of the

108   offshore circulation features.

109   This study represents the first long term comprehensive research for the zooplankton

110   community on the Portuguese coast. Our purpose is to describe the dynamics and composition of

111   the zooplankton community at the CCW station from 2005 to 2015, and assess its temporal

112   (monthly, seasonal and interannual) differences. Considering the available environment

113   variables, we analyzed and discussed their effect on the abundance and taxa composition of the

114   local zooplankton community. The CCW is in a temperate zone and thus our hypothesis is that

115   we will notice a difference between spring/summer and winter periods at least in terms of

116   zooplankton abundance and composition. Since the CCW station is under the influence of coastal

117   upwelling, we also expect to have high productivity during these periods. On the other hand, as

118   the CCW station is placed outside the Tagus estuary, whose discharge flow is dependent on the

119   precipitation regimes, and considering the effects of climate changes, we expect to detect signs

120   of shifts on the taxa composition and abundance through the years.

121

122   **2. Materials & Methods**

123

124   A zooplankton monitoring program has been carried out at the CCW station, off the coast

125   of Portugal, since 2005. The sampling station is located around 2.5 nautical miles off Cascais, at

126   36 m depth and near the Tagus River mouth (38º 40'N, 09º 26.2'W) (Fig.1). Whenever possible,

127   samples were collected monthly, between February 2005 and June 2015 with some gaps, such as

128   the absence of samplings for 2011 and 2012, and the limited sampling frequency from 2009

129   onward (4 samples collected in 2009; 1 to 2 samples from 2010 onward, with no sampling during

130   winter seasons). To reduce the influence of the Tagus River, samples were collected circa 2 h

131   before the high tide. Samples collected 4 h before and 3 h after high tide were not considered in

132   the data analysis. A total of 49 samples were examined.

133   Zooplankton was sampled with a WP-2 plankton net (0.56 m diameter, 200 µm mesh

134   size) fitted with a flowmeter, towed obliquely between the surface and 5 m above the bottom.

135   Each sample represented on average 48.9 ± 18.2 m^3 of filtered sea water. Samples were

136   immediately preserved with 4 % borax buffered formaldehyde, prepared using seawater.

137   Vertical profiles of temperature, salinity and fluorescence were also registered with a

138   CTD SBE 19p and a Chelsea Instruments fluorometer, deployed right before the biological

139   sampling. However, due to the irregularity in the acquisition of these environmental data, we

140   chose not to use them in the present analyses. Satellite-derived data of sea surface temperature

141   (SST) and chlorophyll a surface concentration (Chl a) for the years 2005 to 2015 were obtained

142　from MODIS ocean color products distributed through http://oceancolor.gsfc.nasa.gov/ and using

143　SeaDAS program, Version 7.3.1. The upwelling index (2005−2015) from Cape Roca was

144　obtained from http://www.indicedeafloramiento.ieo.es/HCRoca/ (FNMOC 6h 1-degree

145　Transports model; center position: 38.5 N, 9.5 W), while daily and monthly precipitation

146　(2005−2015) was acquired from the "Sistema Nacional de Informação de Recursos Hídricos"

147　(SNIRH, Monte da Caparica station) and considered as a proxy for river runoff and salinity.

148　　　In the laboratory, the biovolume was determined by displacement volume, which was

149　afterwards converted to dry weight according to the equations on Wiebe (1988). Zooplankton

150　samples were fractionated with a Folsom plankton splitter, and the identification of the

151　specimens was conducted in the smallest fraction, totaling at least 500 organisms for the

152　common taxa, although all fractions were searched for the less abundant ones. The identification

153　of the specimens was made to the lowest possible taxonomic level. Abundance values were

154　expressed as the number of individuals per cubic meter (ind.m^{-3}).

155

156　**2.1. Statistical analysis**

157

158　　　Average abundance and biomass values were tested for differences among months,

159　seasons (hereafter referring to astronomical seasons) and years using one-factor fixed effects

160　ANOVA models, when the homogeneity of variance was verified in the Levene test. For non-

161　significant homogeneity of variance, Kruskal-Wallis analyses were conducted instead. Pairwise

162　tests (Tukey or Mann-Whitney) were used to identify the factors contributing to the statistical

163　differences. The grouping of the data intended to reflect the irregularity in the sampling effort, by

164　using the most uniform points of comparison possible. For all the statistical analysis, taxa, when

165　necessary, were considered by major groups (mollusca, diplostraca, decapoda, etc.). To uncover

166　the dominant taxa/species responsible for the observed differences in the community

167　composition, a Principal Component Analysis (PCA) was performed. Additional PCA analyses

168　were performed with standardized data (zero mean and unit variance, i.e., dimensionless data) to

169　examine correlations among the environmental (temperature, chlorophyll *a* concentration,

170　upwelling index and precipitation) and biological (biomass, abundance of zooplankton and taxa

171　groups) parameters. The abundance ratios of Holoplankton:Meroplankton,

172　Gelatinous:Crustaceans and Cyclopoida:Calanoida were determined to assess potential shifts in

173   the zooplankton communities. Diversity (Shannon-Wiener; Simpson diversity index, 1-D),

174   species richness (Margalef), eveness (Pielou, J) and taxonomic (Menhinick, D) indices were

175   computed. Significant relationships were further explored with Generalized Linear Models

176   (GLM). For monthly analyses, environmental missing values were replaced by 10-year averages.

177   Lomb-Scargle periodograms and Mann-Kendall trend tests were used on the abundance data to

178   detect periodicities and monotonic tendencies in the occurrence patterns of each taxon,

179   respectively. These methods are useful to explore unevenly sampled data and were applied to

180   values of averaged abundances, adjusted by season and month, and to the entire time-series

181   (excluding non-sampling periods). The statistical analyses were performed using the Statistica

182   (StatSoft, Inc., www.statsoft.com), PAST (Paleontological statistics software package for

183   education and data analysis) (Hammer et al. 2001) and MatLab (www.mathworks.com) software.

184   Complementarily, Dynamic Factor Analysis (DFA) computations were applied to the

185   abundance data of the most abundant taxa identified in the previous analyses, using the Brodgar

186   (Highland Statistics Ltd) software. DFA is an adequate tool to explore patterns in time-series,

187   especially those covering short temporal periods or composed of nonstationary data (Zuur et al.,

188   2003). Although the temporal range of the present data is not the ideal, the missing gaps on the

189   data were one of the main reasons for the application of this technique. Nevertheless, caution is

190   needed when examining these patterns that represent only indications that need to be improved in

191   the future. The method provides smoothed functions through time, trends and relationships

192   between variables. The analyses were performed on transformed data ($\ln[x+1]$) and the missing

193   data identified as such. The environmental factors were used as explanatory variables. The DFA

194   model fit was applied to the entire time-series and specifically to several Copepoda taxa/species.

195   One to three common trends (CTs) were tested, and the best solution was chosen according to

196   the lowest Akaike Information Criterion (AIC).

197

198   **3. Results**

199

200   **3.1. Hydrographic conditions**

201

202   The zooplankton community at the CCW was influenced by the seasonal conditions

203   usually found in temperate regions: high sea surface temperatures during summer and early

204   autumn (average values above 18.1 ºC from June to November), and lower temperatures in late

205   autumn and winter (minimum of 13.5 ± 1.2 ºC, Fig. 2a). Spring and summer months were also

206   characterized by high productivity (Fig. 2a), as well as intense upwelling, which was strongest

207   during July and August (Fig. 2b). The lowest productivity was detected in winter months,

208   associated with the decrease of the upwelling intensity. The recent years were characterized by

209   slightly higher maximum sea surface temperatures and increased variability in the productivity

210   pattern (Fig. 2b). From 2011 onward, extended dry seasons were evident from the precipitation

211   patterns, contrasting with the years prior, characterized by rainy periods from October to March

212   and dry seasons mainly limited to late spring and summer (Fig. 2b).

213

214   **3.2. Zooplankton composition and temporal distribution**

215

216   Despite the seasonal patterns perceived in the environmental characterization, no

217   significant differences, monotonic tendencies, or periodicities were detected by month or season

218   (Tables SI, SII) in the patterns of the zooplankton abundance, biomass, and diversity at the CCW

219   station, represented in Figs. 3 and S1. The only exceptions were the significant differences found

220   in the zooplankton abundance for the summer and autumn samples, for the first years of

221   sampling (Table SII). Accordingly, the monthly and seasonal patterns were relevant, with high

222   zooplankton abundance and biomass during summer and early autumn months (Fig. 3),

223   especially in July and October (monthly averages of 8956 ± 11981 ind.m^{-3}, 213 ± 193.4 mg m^{-3}

224   and 12321 ± 16283 ind.m^{-3}, 86.2 ± 110.4 mg m^{-3}, respectively). Therefore, slightly higher

225   biodiversity was detected in summer months (Fig. S1), although not statistically significant

226   (Table SII). The zooplankton biomass also peaked in spring (average of 77.8 ± 45 mg m^{-3}, Fig.

227   3b), particularly in April (average of 107 ± 96.4 mg m^{-3}; Fig. 3a). Winter months corresponded

228   to the lowest zooplankton abundances (average of 4116 ± 2769 ind.m^{-3}) and biomass (56 ± 46

229   mg m^{-3}; 10.2 mg m^{-3} in January) (Fig. 3b).

230   Among the 86 taxa found, 43 were identified to family or higher level, 25 to genus and

231   18 to species (Table SIV). The monthly, seasonal and interannual composition of the major taxa

232   found in the samples is presented in Fig. 4.

233   Copepoda dominated the community (71% − 96% of the total), presenting two abundance

234   peaks in July and October. The Copepoda proportion decreased in summer (Figs. 4, 5b),

235   following the increased contribution of Mollusca (up to circa 25–58% of the samples),

236   Diplostraca (Cladocera) and Cnidaria (Figs. 4, 5). Cirripedia, Appendicularia and Decapoda were

237   a relevant component of the winter and spring samples (circa 20%).

238   From the PCA analyses we found that the major contributors for the observed variability

239   in the community composition were *Acartia* spp., *Calanus* spp., *Oncaea* spp., Bivalvia, *Oithona*

240   spp., *Evadne* spp., *Penilia avirostris* and *Centropages* spp. (Fig. S5, Table SIV). Bivalvia,

241   *Acartia* spp. and *Evadne* spp. were associated with the summer samples, while *Penilia avirostris*,

242   *Calanus* spp., *Oithona* spp., *Oncaea* spp. and *Centropages* spp. contributed to the distinction of

243   the autumn samples (Fig. S5, Table SIV).

244

245   **3.3. Zooplankton interannual variability**

246

247   The interannual data, showed a relative increase of the average zooplankton abundance

248   (Fig. 5a). When comparing the years of 2005–2009 with the latter ones, a lower proportion of

249   Copepoda, Decapoda and Cirripedia, and a higher proportion of Mollusca (mostly Bivalvia, see

250   Table SIV) were suggested in the relative abundance (Fig. 4b). The DFA analysis also hinted at

251   an increasing tendency of Mollusca abundance from 2011 onwards (Fig. S2a), similar

252   abundances through the years for Copepoda, despite the decreases in 2009 and 2014, and

253   decreases of Cirripedia and Decapoda larvae (Fig. S2).

254   The average meroplankton/holoplankton ratio has increased since 2009 (Fig. S4),

255   reflecting the increase in the proportion of Bivalvia larvae. Regarding the gelatinous/Crustacea

256   ratio, the Crustacea had a higher contribution to the samples than gelatinous zooplankton (Fig.

257   S4), despite the enhanced abundance of the latter in spring months since 2010 (Table SIV, Figs.

258   5g, S2–S3). Lastly, the Cyclopoida/Calanoida ratio shows a different pattern, with low values

259   registered in 2013–2015 (Fig. S4).

260   In the DFA model fit (Figs. S2, S3), the AIC values obtained for one, two and three

261   common trends (CTs) were, respectively: 1596.6, 1535.3 and 1509.4, for the entire time-series;

262   and 1500.4, 1364.5 and 1317.8, for Copepoda (models with three CTs chosen as the best fit). The

263   models generally depicted increasing trends in the abundance of Mollusca, Cnidaria and

264   Diplostraca, but also of fish larvae/eggs and the total zooplankton abundance.

265   For the Copepoda, no significant monotonic tendencies were detected (Table SI), despite

266   an apparent interannual decrease (Fig. 5b). The statistical analyses showed significant

267   differences in copepod abundance for the period 2005–2009 (Table SII). The copepod abundance

268   was positively correlated with the SST and the upwelling index in the PCA analyses (Figs. 6a,

269   b).

270   *Acartia* spp. (20% of all samples), *Calanus* spp. (14%), *Oncaea* spp. (12%) and *Oithona*

271   spp. (6%) dominated the 2005–2009 samples (from 51 to 96%), decreasing in proportion from

272   2010 onwards (Fig. 7, Table SIV). In the ANOVA and Kruskal-Wallis analyses, these

273   interannual differences were only significant for *Acartia* spp. (Table SII), although a significant

274   monotonic decreasing tendency was detected for *Calanus* spp. in the Mann-Kendall tests (Table

275   SI) and represented in the DFA analyses (Figs. S2, S3). Higher proportions of Calanoida were

276   detected in recent years, with increasing tendencies of *Clausocalanus* spp., *Paracalanus* spp. (up

277   to 3% of the total, only significant for the former, per year; Tables SI, SII, SIV), and

278   *Centropages* spp. (Fig. 7), also generated by the DFA analyses (Figs. S2, S3). In the PCA

279   analyses, *Calanus* spp., *Acartia* spp. and *Paracalanus* spp. showed positive correlations with the

280   SST (Fig. 6c).

281   The observed decrease in the Cyclopoida: Calanoida ratio, with lower proportions of

282   Cyclopoida in the 2013–2014 samples (Table SIV, Fig. S4), followed the decreasing trend of

283   *Oithona* spp. shown in the DFA models (Figs. S2b, S2e, S2f, S3b). On the other hand, the lower

284   proportion of *Oithona* spp. was positively correlated with precipitation, as shown in the PCA

285   analyses (Fig 6c). A positive correlation with precipitation was also obtained for *Oncaea* spp.

286   (Fig. 6c). Additionally, *Oithona* spp. was positively correlated with the upwelling index in the

287   GLM analyses (Table SV).

288   The increasing monotonic tendency of Mollusca (circa 10% in the total samples; Table

289   SI), was significantly different for late spring and summer months (Fig. 5c), with positive

290   correlations with year, upwelling intensity, and SST in the PCAs (Figs. 6a, b). Bivalvia, the most

291   represented (average of 97% of the samples; Table SIV), showed a monotonic increasing

292   tendency per season and month (MK $p<0.02$ in all cases; not shown), and a significant

293   correlation with SST (Table SV). For Mollusca, significant differences were found between the

294   first and later years of sampling (Table SII).

295   Abundance peaks of Diplostraca (Cladocera) were detected in July and October (Fig. 4a).

296   No monotonic tendencies were observed (Table SI), despite the apparent autumn and summer

297   interannual decrease (Fig. 5d). The slight increase for spring periods (Figs. 4b, 5d) was also

298   hinted at in the DFA analyses (Figs. S2, S3). Positive PCA-based correlations were obtained

299   with SST and the upwelling intensity (Figs. 6a). *Evadne* spp. and *Penilia avirostris* were the

300   most abundant taxa (48 and 43% of the total, respectively) (Table SIV) and the latter showed

301   significant correlations with SST and the upwelling intensity (Table SV).

302   Cirripedia registered the highest abundances in late winter and spring (Fig. 4a), with

303   monotonic decreasing tendencies (Table SI, Fig. 5f), that were not entirely represented in the

304   DFA analyses (Figs. S2, S3). The PCA analyses revealed negative correlations with SST and

305   chlorophyll *a* (Fig. 6a).

306   For Cnidaria, mainly siphonophores (circa 60%) and hydromedusae (39%) were

307   identified (see Table SIV). July registered the highest abundances (Fig. 4a) and, the apparent

308   spring/autumn interannual increase (Figs. 4b, 5g), depicted in the DFA analyses (Figs. S2, S3),

309   did not manifest in monotonic tendencies (Table SI). Positive PCA-based correlations were

310   obtained with year, SST and upwelling intensity (Figs. 6a, 6b).

311   Decapoda showed decreasing monotonic tendencies (Table SI), and significant

312   differences for winter samples and the first year of sampling (Table SII). Abundance peaks were

313   detected in winter and spring (Fig. 4b), as well as March (Fig. 4a), showing a significant

314   correlation with SST in the GLM analyses (Table SV).

315

316   **4. Discussion**

317

318   The study presents a relevant analysis of the information available for the seasonal and

319   interannual variability of the zooplankton community in the CCW coastal station from 2005 to

320   2015 and their potential long-term changes. Given the scarcity of recent samples, the patterns

321   must be carefully considered. Nevertheless, given the lack of knowledge for the region, the

322   analyses highlight some shifts in the local community that need to be verified and monitored in

323   the following years through the maintenance and the increase of the sampling frequency in the

324   CCW.

325

326   **4.1. General patterns of zooplankton biomass, abundance and composition**

327

328   High year-round productivity was observed for the study area, without major significant

329   trends or periodicities detected in the zooplankton abundance, biomass, and diversity, even

330   despite the relatively lower winter values. The high chlorophyll levels during the entire year

331   were undeniable, when compared with values obtained in other works (e.g., Bode et al. 2009,

332   Eloire et al. 2010, Bresnan et al. 2015, Yebra et al. 2020), namely for Galician waters (Buttay et

333   al. 2016). The average zooplankton biomass followed the values reported by Domínguez et al.

334   (2017) for the northern Portuguese coast. Nevertheless, the present study detected spring/summer

335   and autumn peaks in zooplankton abundance, complying with the common seasonal shifts

336   reported for zooplankton communities of temperate latitudes and for the region (e.g., Valdés &

337   Moral 1998).

338   The composition of the zooplankton community at CCW was alike to what has been

339   reported for the Iberian coast (e.g., Valdes et al. 1990, Valdés & Moral 1998, Valdés et al. 2007,

340   Bode et al. 2009, Sobrinho-Gonçalves et al. 2013, Domínguez et al. 2017). The dominance of

341   Copepoda also followed the results of works for other areas of the northeastern Atlantic and

342   adjacent seas (e.g., Eloire et al. 2010, Bresnan et al. 2015, Valdés et al. 2021). The

343   spring/summer decrease observed in the Copepoda proportion was not accompanied by the taxa

344   abundance, which was higher during these periods, much due to the greater diversity of other

345   zooplankton groups and the dominance of certain copepod taxa. *Acartia* spp., *Paracalanus* spp.,

346   *Clausocalanus* spp., and *Oncaea* spp., highly abundant in the samples, have also been described

347   as widely distributed and frequent in the northwestern Iberian coast (e.g., Bode et al. 2012),

348   being some of the most common taxa recorded in the northeastern Atlantic (e.g., Valdés et al.

349   2007, Sobrinho-Gonçalves et al. 2013, Domínguez et al. 2017). The importance of Copepoda as

350   intermediaries between distinct trophic levels across the marine food web is undeniable, namely

351   for planktivorous fish (e.g., Garrido et al. 2015) that usually decrease in abundance following the

352   lower availability of Copepoda (e.g., Heneghan et al. 2020).

353

354   **4.2. Interannual shifts in the zooplankton community**

355

356   The spring/summer and autumn zooplankton abundance peaks followed the seasonal

357   variation of the environmental variables, namely the sea surface temperature and upwelling

358   index, which had relevant impacts in some of the taxa (see below). The link between the

359   zooplankton abundance and the upwelling intensity is not surprising, given its well-known

360   importance for zooplankton productivity (e.g., Pires & Dos Santos 2020). In the Portuguese

361   coast, wind-driven upwelling of colder and richer deep waters is frequent in spring/summer

362   months, when temperature increases and north/northwestern winds and southward currents

363   dominate, contrasting with the winter prevalence of southwestern winds and northward slope

364   flows (e.g., Relvas et al. 2007). The upwelling regimes, together with the influence of the Tagus

365   plume, especially when coupled with high precipitation (e.g., Vaz et al. 2009), enhance

366   chlorophyll concentration and phytoplankton production at surface coastal waters, leading to

367   increased zooplankton abundance. The local sheltered dynamics, with slower currents and

368   recirculation features, result in the coastal retention of plankton (e.g., Moita et al. 2003) thus

369   contributing to the high productivity and biodiversity observed herein. Indeed, previous works

370   pointed to distinct inshore and offshore communities of zooplankton in the Portuguese coast

371   (e.g., Bartilotti et al. 2014, Domínguez et al. 2017), stressing the importance of the coastal

372   environmental conditions in shaping zooplankton communities. This may have important

373   implications for the regional ecosystem yield capacity, since the frequent local generation of

374   upwelling filaments (e.g., Haynes et al. 1993) may contribute to the transfer of productivity

375   towards offshore areas.

376   The slightly increasing interannual zooplankton abundances detected herein for spring

377   periods, contrast with the general declining trends reported for the North Atlantic (e.g., Iriarte et

378   al. 2022, McQuatters-Gollop et al. 2022). Nonetheless, our observations parallel the increasing

379   zooplankton trends detected for the Benguela upwelling region (Verheye & Richardson 1998).

380   Inhabiting a transition area between temperate and tropical environments (e.g., Boaventura et al.

381   2002) that comprise the northern/southern limit of distribution of many species, the CCW

382   zooplankton communities may experience less drastic effects than those reported for the North

383   Atlantic. On the other hand, the upwelling regimes, as one of the drivers of long-term increase of

384   crustacean zooplankton (Verheye & Richardson 1998), may also explain the observed trend. In

385   the long-term analyses for the western Atlantic by Morse et al. (2017), the spring community

386   shifts detected in the composition and abundance of zooplankton were associated with

387   environmental changes mediated by the North Atlantic Oscillation (NAO).

388   We report two main periods (2006 and 2009/2010) of lower abundance of zooplankton,

389   particularly for Copepoda, fish larvae, Cnidaria, Diplostraca and Cirripedia, that apparently

390   induced shifts in the community. The 2009/2010 period was characterized by unusual climatic

391   variability throughout the North Atlantic, including warmer and more saline waters, driven by a

392   strong negative NAO (e.g., Hughes, Holliday & Beszczynska-Möller 2011). During this period,

393   in Portugal, heatwaves were registered from spring to autumn, extending the annual dry season

394   (IPMA 2010, 2011).

395

396   **4.2.1. Copepoda**

397

398   Concerning the Copepoda, our results suggest that the periods 2006 and 2009/2010 may

399   mark changes in species composition and dominance of the most abundant taxa, namely lower

400   abundances of *Acartia* spp. and *Calanus* spp., and increased abundances of *Paracalanus* spp. and

401   *Clausocalanus* spp.. Similar results, particularly the replacement of *Acartia* species, dominant in

402   spring, by *Paracalanus* spp., highly abundant in summer, were obtained by Iriarte et al. (2022)

403   for the Bay of Biscay. These and other authors (e.g., Buttay et al. 2016, Dessier et al. 2018)

404   reported points of regime shifts and high variability for the Copepoda species composition in the

405   northeastern Atlantic throughout the 2002–2018 year span, particularly 2006 and 2010.

406   The decrease in proportion of larger Copepoda such as *Calanus* spp. is an important shift that

407   may impact the community structure (Barton et al. 2013), as well as the trophic links and the

408   energy transfer through the food web (Heneghan et al. 2020), influencing for example the

409   regimes of planktivorous fishes (Verheye & Richardson 1998). Northward expansions of the

410   distribution limits of *Calanus helgolandicus* in the north Atlantic associated with climate

411   variability and driven by warmer southern currents have been suggested (e.g. Bonnet et al. 2005,

412   Bode et al. 2009).

413   *Acartia* spp., typical inhabitants of estuarine and coastal areas (e.g., Bode et al. 2005),

414   were the most abundant Copepoda. Although no significant trends were detected, the apparent

415   interannual decrease may represent changes both in the food web and the environmental

416   conditions. Impacts in the trophic transfer were previously suggested for *Acartia tonsa* in a long-

417 term monitoring for Chesapeake Bay (Kimmel et al. 2012), given the importance of the taxa for

418 planktivorous fish. The location of CCW, at the mouth of the Tagus River, may explain the

419 abundance of the taxa. Previous studies suggested that *Acartia* species have a diverse range of

420 prey (Bollens & Penry 2003), adapting their feeding preferences according to the oceanic

421 conditions (Kiørboe, Saiz & Viitasalo 1996). Moreover, previous evidence showed that climate

422 change may promote earlier peaks in the occurrence of zooplankton, as reported for some

423 Copepoda and meroplankton (e.g. Edwards & Richardson 2004).

424   Our results suggest a strong link between the abundance of Copepoda and the environmental

425 factors, given the correlation with SST and the upwelling intensity. The relative interannual

426 decrease of Copepoda reported herein is mainly accompanied by the lower proportion of

427 Cyclopoida, such as *Oithona* spp. in recent years, against the enhanced abundance of Calanoida

428 species (*Clausocalanus*, *Paracalanus* and *Centropages*). This shift in the abundance of copepod

429 taxa composition, namely the decrease of *Oithona* spp., is also related with the extension of the

430 dry season discussed above, as shown by the positive correlation with precipitation. The effect of

431 warmer temperatures and negative correlations with SST were previously reported for *Oithona*

432 *similis* (Castellani et al. 2016). Similarly, the observed interannual decrease of *Oncaea* spp. from

433 2010 onwards, followed the correlation found with precipitation, especially considering that the

434 recent years were characterized by warmer and dry periods, with the occurrence of frequent heat

435 waves. As follows, *Oncaea* spp. dominated the autumn period, which can also be related with the

436 decreased relative abundance of *Acartia* and *Paracalanus*/*Clausocalanus* species. *Oncaea* spp.

437 are widely distributed in the northeastern Atlantic (Valdés et al. 2007) and are considered as

438 indicators of coastal upwelling (Blanco-Bercial, Álvarez-Marqués & Cabal 2006). Nevertheless,

439 in the present study they were found when the upwelling intensity was lowest. However,

440 consistently high abundances were recorded annually, with higher seasonal values than the

441 spring peak recorded by Sobrinho-Gonçalves et al. (2013). *Oncaea* spp. are thermophilic,

442 omnivore and opportunistic species, adapting to warmer and more stratified conditions (Valdés

443 et al. 2007), typical conditions in summer and autumn, when the taxa dominate the northwestern

444 Iberian zooplankton communities (Valdes et al. 1990, Blanco-Bercial, Álvarez-Marqués & Cabal

445 2006), as suggested by our data.

446

447 **4.2.2. Gelatinous zooplankton**

448

449   The increasing importance of the gelatinous fraction (particularly Cnidaria) for

450 spring/summer months in recent years, closely linked with SST, hint at changes in primary

451 production and prey dynamics. The same pattern was previously reported in the region (e.g.,

452 Valdes et al. 1990, D'Ambrosio et al. 2016), contrasting with autumn periods when this

453 component is less relevant (Dominguez et al. 2017). D'Ambrosio et al. (2016) detected

454 interannual increasing trends and earlier occurrences of gelatinous zooplankton since 2007, as

455 reported for other areas where these patterns were linked with climate changes (e.g., Molinero,

456 Casini & Buecher 2008). As suggested by our results, these patterns were particularly related to

457 warmer water temperatures (e.g., Purcell et al. 2012), and enhanced variability of both upwelling

458 and NAO. Temperature is known to enhance the reproductive efficiency of many species of

459 gelatinous zooplankton, increasing the magnitude and frequency of their occurrences (e.g.,

460 Purcell et al. 2012). In addition, their ability to survive in conditions that may be detrimental to

461 other taxa results in large outbreaks in coastal areas (Richardson 2008). Thus, the environmental

462 variability is regarded as the main driver of the abundance of gelatinous zooplankton, especially

463 regarding upwelling and water temperature (e.g., Lucas et al. 2014).

464   Siphonophores, the most abundant Cnidaria in the CCW, are avid predators of

465 zooplankton and their abundance follows that of their preys, such as Copepoda or Diplostraca

466 (e.g., D'Ambrosio et al. 2016). Indeed, Diplostraca and the most represented of this group,

467 *Penilia avirostris*, showed a preference for warmer waters, agreeing with what was reported by

468 Dominguez et al. (2017) for the adjacent northern coastal area. Thus, the increased abundance of

469 the cnidarians complies with the interannual Copepoda decrease, further highlighting the

470 importance of trophic interactions in our study site. These trends may have important ecological

471 implications, since gelatinous zooplankton play a key role in the food web, comprising the prey

472 of several fishes, especially when other food resources are scarce (Brodeur et al. 2019).

473 However, this implies lower nutritional value and growth potential for higher trophic levels,

474 potentially affecting some ecosystem services (e.g., fisheries).

475

476 **4.2.3. Mollusca and other meroplankton**

477

478   The higher abundance of meroplankton in recent sampling years, such as Bivalvia and
479   fish larvae/eggs, in relation to holoplankton, suggests increased inputs of the local adult
480   populations. The importance of the meroplankton fraction for summer zooplankton communities
481   has been widely recognized (e.g., Valdes et al. 1990, Bode et al. 2005, Blanco-Bercial, Álvarez-
482   Marqués & Cabal 2006). In the Cascais area, rocky beaches create diverse habitats available for
483   fishes and invertebrates (e.g., Flores, Cruz & Paula 2002). Considering the adequate conditions
484   for larval survival, namely the access to food, promoted by the link with the Tagus River and the
485   sheltered coastal dynamics, the increase of meroplankton may first represent periods of intense
486   reproductive activity, driven by specific environmental conditions, reflecting seasonal
487   successions in the community. Valdes et al. (1990) reported Bivalvia as one of the most
488   abundant components of the inshore zooplankton community in the Galician coast for
489   spring/summer. The correlation with the coastal upwelling may also explain the high abundance
490   of the taxa, as it implies an enhancement of the supply of meroplankton from benthic habitats
491   into the water column. Furthermore, the relevant abundance and interannual increasing trends of
492   early Copepoda stages (copepodites), prey of sardine and anchovy (Morote et al. 2010), for
493   example, may also explain the higher abundance of fish larvae. Notwithstanding, long-term
494   increases of meroplankton have been detected in the northwestern European shelf across wide
495   spatial scales by Bedford et al. (2020). The authors correlated the increase in meroplankton with
496   the SST and the increased abundance of small Copepoda.
497   We report a conspicuous increase in the abundance of Bivalvia in recent years. Although
498   species specific information could not be obtained from our samples, we hypothesize that this
499   trend may be linked to the increasing abundance of the Manila clam (*Ruditapes philippinarum*)
500   in the Tagus River region. Besides the native species, *Ruditapes decussatus*, whose abundance
501   has declined (Garaulet 2011), the Manila clam is one of the most frequently observed species in
502   the Tagus River (Dias et al. 2019). The species, native from the Indo-Pacific region, dispersed
503   throughout the European estuaries, due to human introductions for aquaculture purposes. In
504   Portugal, despite the limited information available, the species is known to have inhabited the
505   Tagus estuary for more than a decade (Garaulet 2011). Two possible recruitment periods in
506   spring−early summer and autumn−early winter were reported in other areas (Humphreys et al.
507   2007). Considering the lifetime of Bivalvia larvae (ca. 15−30 days reported for *R. decussatus*;
508   Chícharo & Chícharo 2001), the abundance peaks observed in the present study match the

509 recruitment season of the species. In addition, *R. philippinarum* reaches gonad maturation above

510 18°C (Solidoro, Canu & Rossi 2003), temperatures registered in early summer at CCW,

511 corroborating the possibility that this may be one of the species behind the increase. In any case,

512 the great variety of forms and sizes of the Bivalvia detected in the samples suggests a high

513 diversity of species within this group. Attempts to uncover the species driving the Bivalvia

514 increase through molecular techniques are underway.

515   On the contrary, for the meroplanktonic crustaceans, Decapoda and Cirripedia, the

516 decreasing trend in abundance highlighted in the analyses may indicate that the recruitment of

517 benthic crustaceans is decreasing in the study region, contrasting with other regions where

518 crustacean larvae have been increasing and bivalve larvae declining (e.g., Kirby et al. 2008). The

519 higher abundance of crustacean larvae in winter and spring agrees with the exhibited negative

520 correlation with SST. Therefore, it is expected that crustacean larvae (decapods and cirripedes)

521 will decrease in a scenario of increasing SST. However, the reduction of sampling effort since

522 2009 and the lack of data for the 2011–2012 years may be influencing the results. As follows,

523 maintaining the CCW monitoring and increasing the sampling effort is extremely necessary.

524

525 **5. Conclusions**

526

527   The present work adds important knowledge on the zooplankton coastal communities of

528 the northeastern Atlantic, helping to fill the knowledge gap between the northern Iberian margin/

529 Bay of Biscay and the Mediterranean Sea /southern Atlantic. Despite the gaps in the sampling

530 series and the need for caution when examining the trends presented herein, the indications

531 provided are relevant.

532   Contrary to what was expected, the results pointed to a year-round high productivity in

533 the CCW station with no major significant trends or periodicities in the zooplankton abundance,

534 biomass and diversity, although with a perceived seasonal pattern with a peak in summer/early

535 autumn and low values in winter, following the seasonal variability in temperature. An

536 increasing interannual zooplankton abundance was detected for spring periods, in agreement

537 with the Benguela upwelling region (Verheye & Richardson 1998) and contrasting with the

538 general declining trends reported for the North Atlantic (e.g., McQuatters-Gollop et al. 2022).

539 Copepoda dominated the zooplankton community, represented mainly by small size species as

540   *Acartia* spp., *Paracalanus* spp., *Clausocalanus* spp. and *Oncaea* spp., displaying a strong link

541   with SST and the upwelling intensity.

542   The results revealed two main transition periods with marked changes in species

543   dominance for the most abundant taxa, which were tentatively attributed to the extending annual

544   dry seasons in Portugal after 2011, with very low values of precipitation, warmer and more

545   saline estuarine waters. An increasing importance of the gelatinous species (particularly

546   Cnidaria) for spring/summer months in recent years was also evident.

547   Another relevant tendency in recent years, was the higher abundance of meroplankton

548   (Bivalvia and fish larvae/eggs) and the decreasing trend in the abundance of meroplanktonic

549   coastal crustaceans (Decapoda and Cirripedia), highlighting possible changes on the benthic

550   coastal populations in the study region and, contrasting with the scenarios found in other regions

551   (e.g., Kirby et al. 2008).

552   As zooplankton is a key component of marine coastal ecosystems, long-term time series

553   are still the better tool to assess the dynamics of zooplankton communities in all its biological,

554   physical, and chemical components. Monitoring of planktonic communities at the CCW needs to

555   continue through the increasing of the sampling effort, being especially important regarding the

556   predicted climate changes and in face of the results obtained in the present study.

557

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572

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Figure 1

Sampling site location

Western coast of Portugal, indicating the location of Cascais Watch monitoring site (black star).
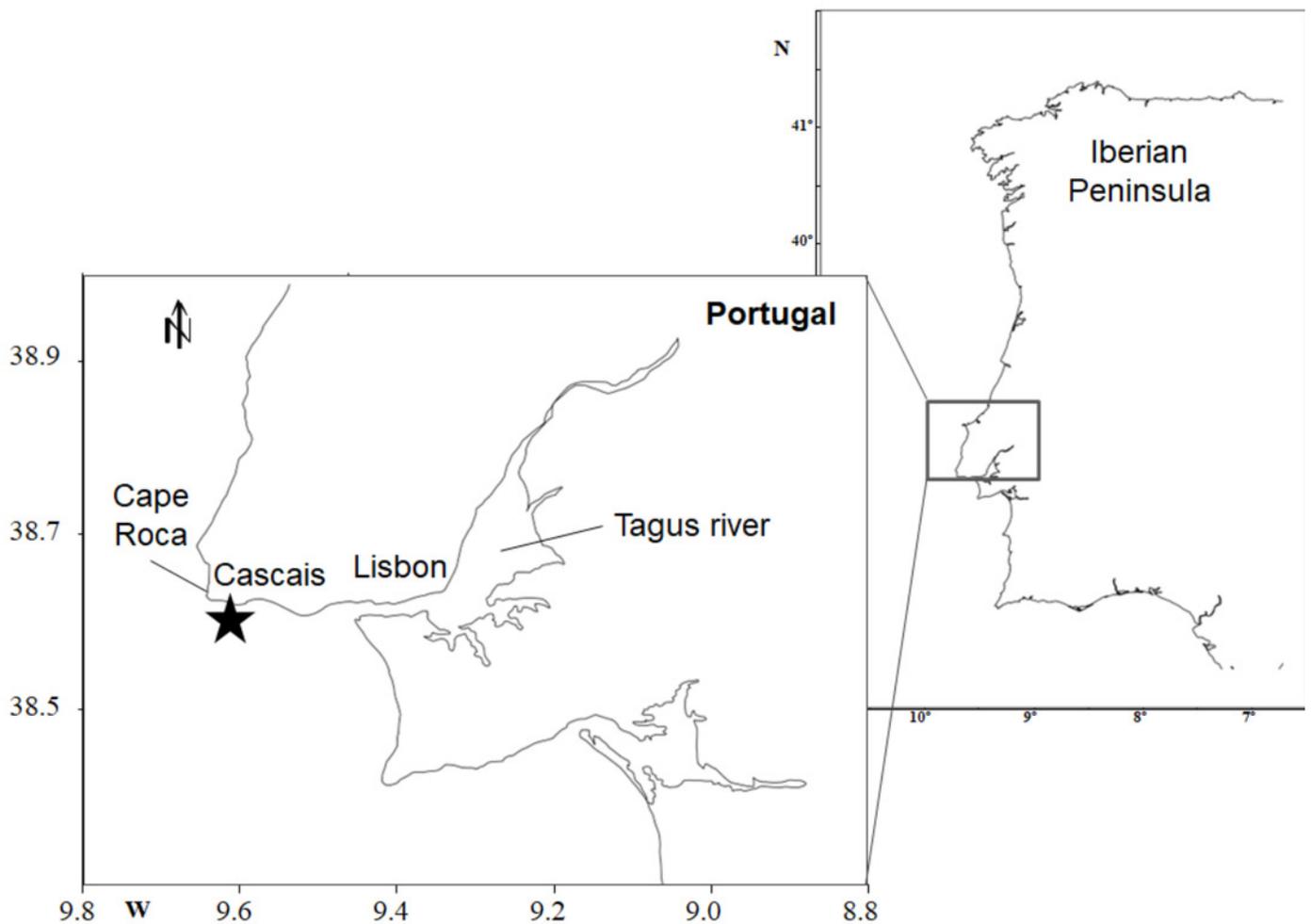
Figure 2

Environmental variables

Interannual monthly mean variation of the environmental parameters: a) chlorophyll *a* concentration (Chl a) and Sea Surface Temperature (SST); b) Precipitation and upwelling index (UI). The filled symbols correspond to months when at least one sampling was performed.
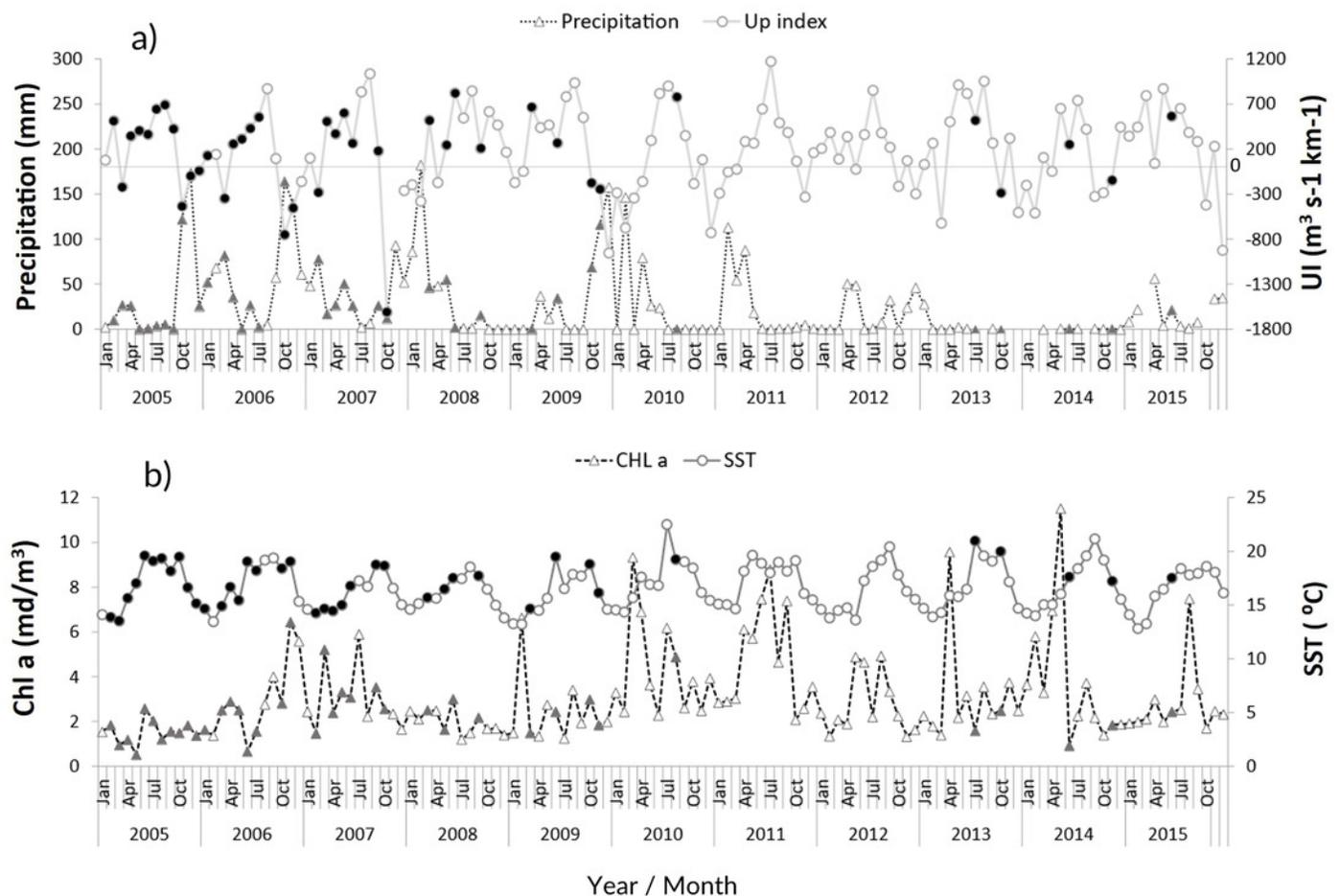
Figure 3

Zooplankton biomass and abundance

Average variation of the zooplankton abundance and biomass at CCW by month (a) and season (b).
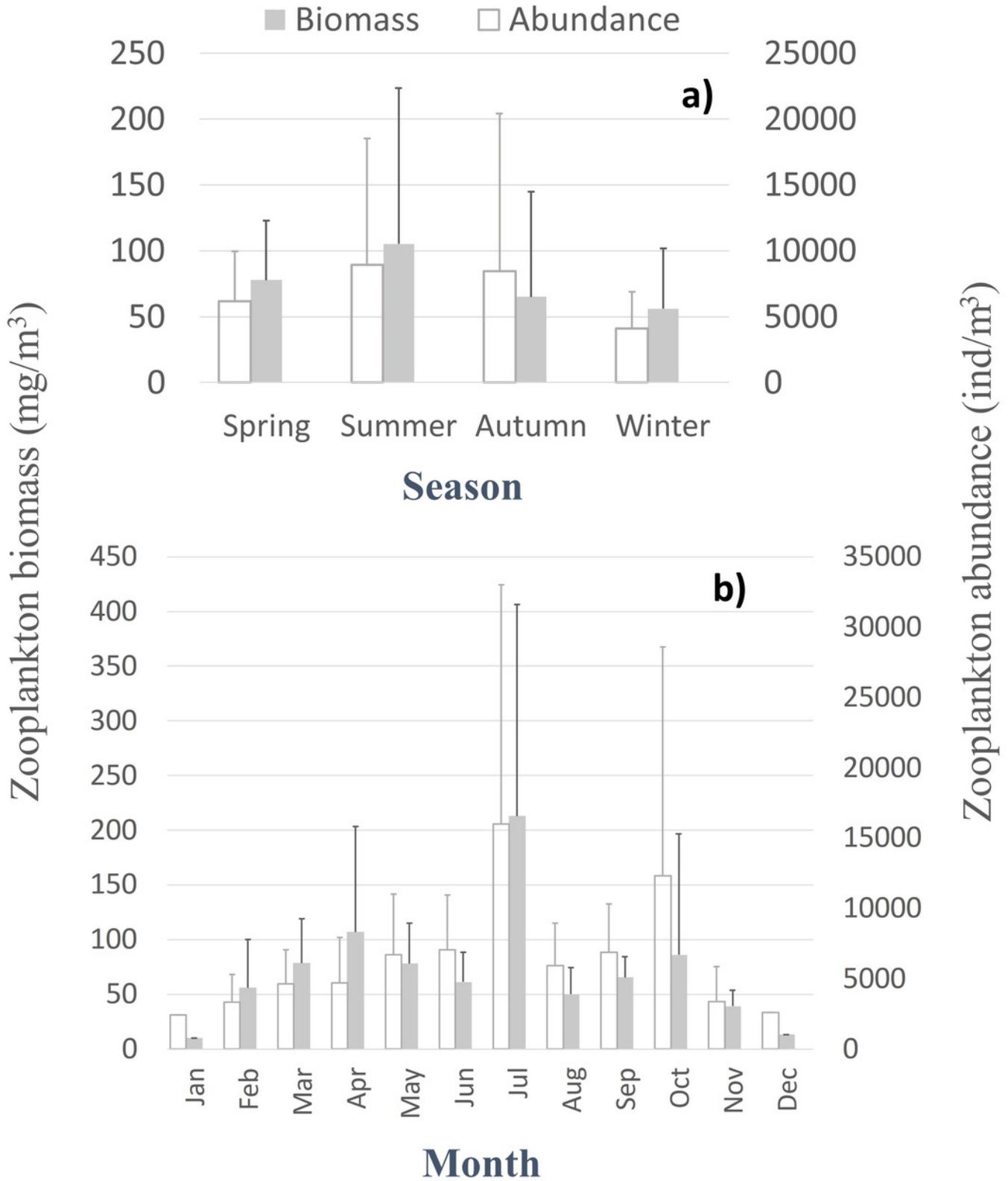
Figure 4

Zooplankton relative abundance

Average a) monthly and b) interannual seasonal variation of the taxa composition (relative abundance to the total of the samples for each period) of zooplankton at CCW. The group "Other Crustacea" includes Ostracoda, Mysida, Amphipoda, Isopoda and Cumacea, and "Other taxa" includes Ctenophora, Phronida, Foraminifera and Radiozoa.
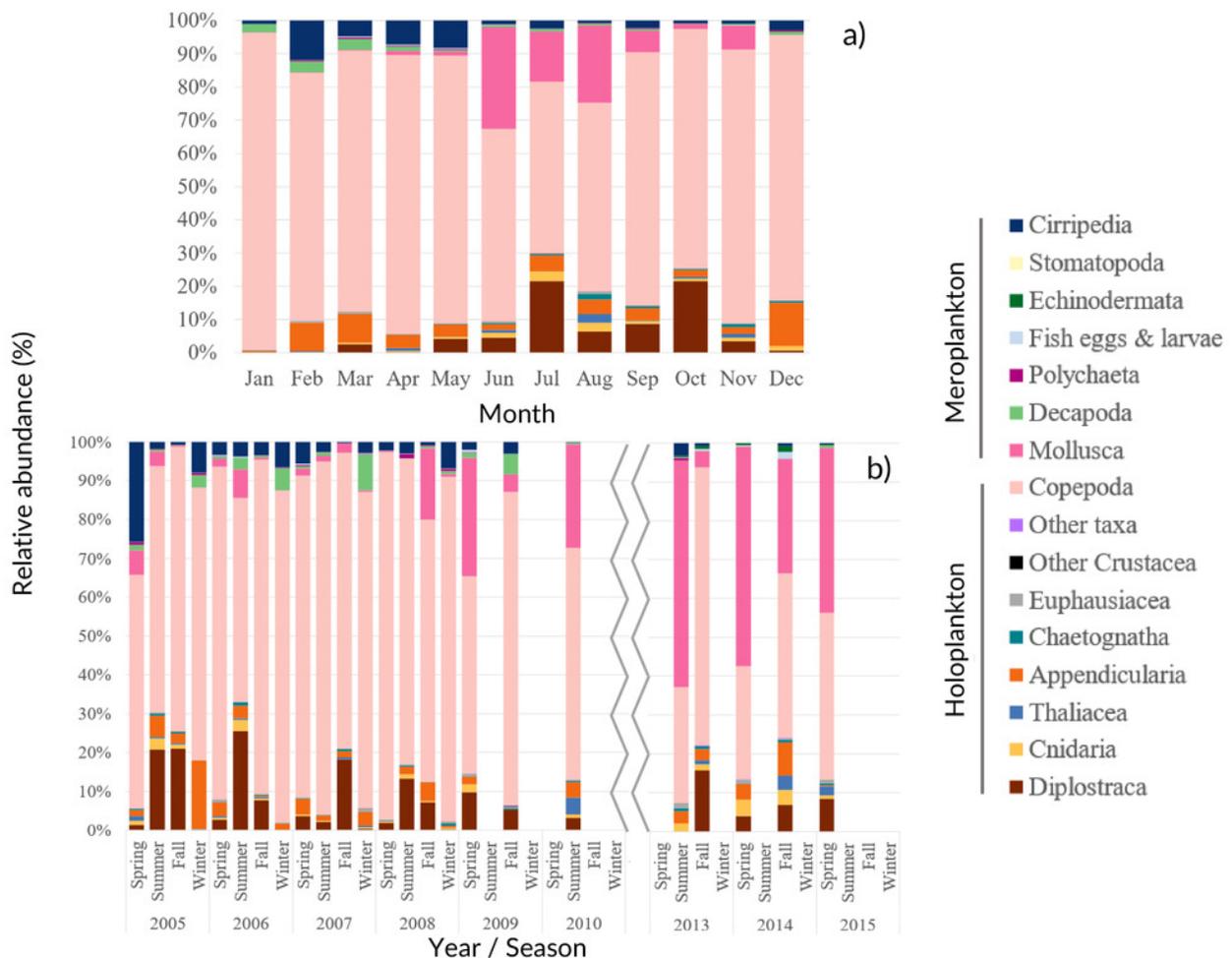
Figure 5

Zooplankton interannual abundance

Interannual seasonal average for the abundance of the main groups of taxa collected in the Cascais-Watch site for the entire period of 2005 to 2015. In g), gelatinous zooplankton include the Cnidaria, Ctenophora and Thaliacea taxa. Only the most informative linear regressions are presented.
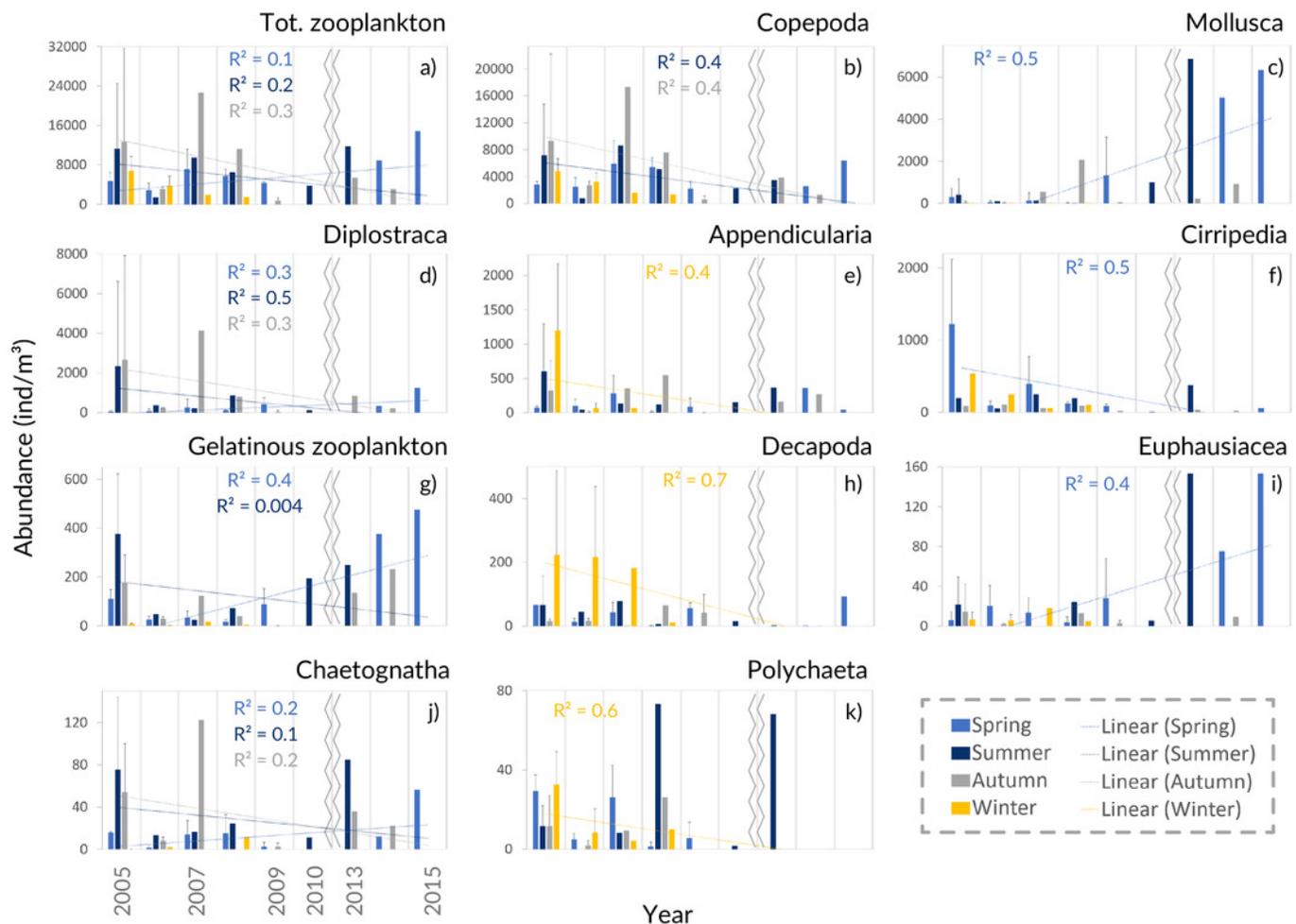
Figure 6

PCA analysis

Principal Component Analysis results for the main taxonomic groups of zooplankton (a, b) and Copepoda (c) that contributed most to the differentiation of the samples according to the environmental factors (a, c) – upwelling index (UI), precipitation (Pp), Sea Surface Temperature (SST) and chlorophyl *a* (Chl) – and temporal periods (b). For the temporal analyses, only the variable month was represented, considering the high correlation with season. The first two components are represented, accounting for more than 67% of the cumulative variance. Groups represented in the plots: abundances of Copepoda (Cop), Mollusca (Mol), Diplostraca (Dipl), Cnidaria (Cni), Appendicularia (App), Cirripedia (Cirri), Decapoda (Dec), Chaetognatha (Chaet), Polychaeta (Poly), Euphausiacea (Euph), fish eggs/larvae (Fish), Calanoida (Calan), Cyclopoida (Cyclo), *Acartia* spp. (Aca), *Calanus* spp. (Cal), *Oncaea* spp. (Onc), *Oithona* spp. (Oit), *Centropages* spp. (Cent), *Paracalanus* spp. (Para) and *Clausocalanus* spp. (Claus).
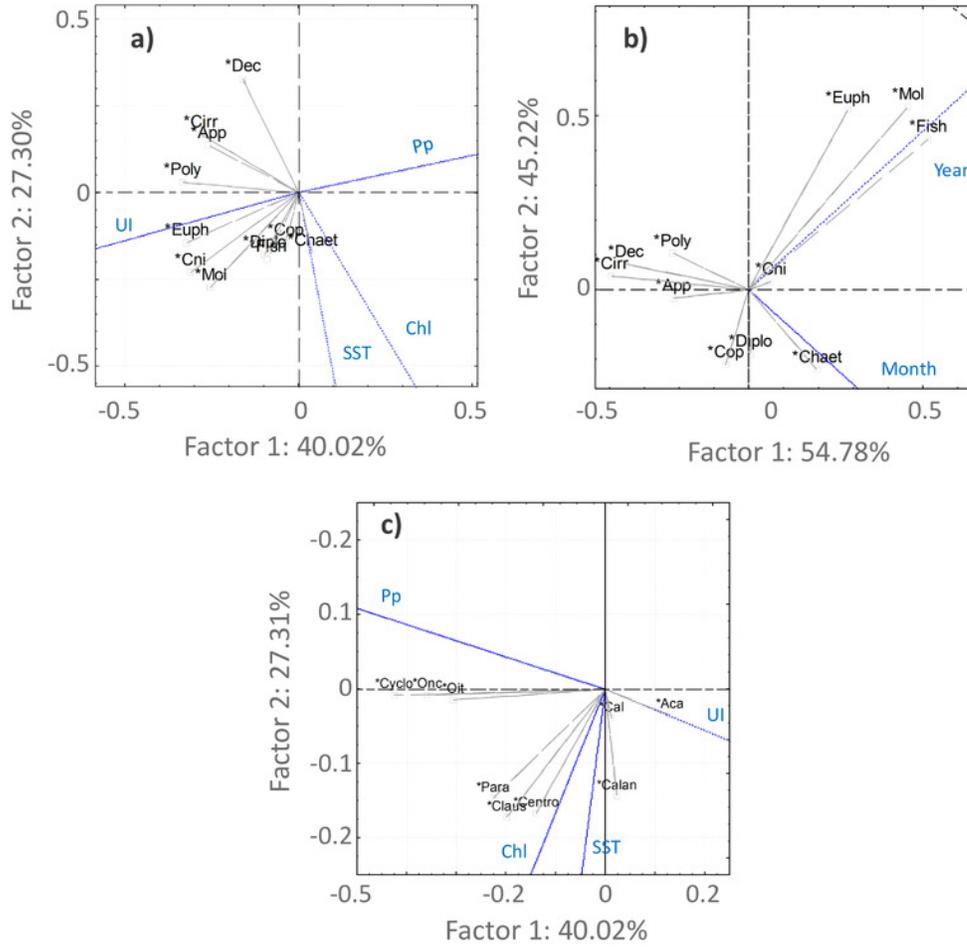
Figure 7

Copepoda interannual abundance

Average interannual seasonal variation (relative abundance to the total of the samples for each period) of the Copepoda composition at the CCW.