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Comparative study of zooplankton scales and patterns of variability at four monitoring sites of the Northeast Atlantic Shelves in relation to latitude and trophic status

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ABSTRACT

A comparative study of zooplankton variability was carried out analysing 15-year time series (1999 – 2013) from the sites of Stonehaven (SH: northwest North Sea), Plymouth L4 (L4: English Channel), Urdaibai 35 (U35: southeast Bay of Biscay, oligotrophic) and Bilbao 35 (B35: southeast Bay of Biscay, mesotrophic), with the aim of assessing the effect of latitude and trophic status on the scales of variability, the interannual variations and the seasonal patterns of zooplankton. The variables analysed were total zooplankton, chlorophyll *a*, temperature and 25 zooplankton taxa distinguished to group and genera levels. From the three components of zooplankton variability (interannual, seasonal and residual) the residual was the highest and the interannual the lowest at all sites, but none of theset could be clearly related to latitude or trophic status. The three components of variability were the lowest at L4, the interannual was highest at U35 due to a local event that occurred in 2012, the seasonal was highest at the northernmost site of SH, and the residual at U35 and B35, the latter likely related to lower sampling frequency and higher natural and anthropogenic stress at U35 and B35. Interannual zooplankton variations were not coherent across sites, suggesting that they were driven by forces acting locally rather than by wider scale climatic drivers. The most recurrent phenological trend was the delay of the early seasonal peak with increasing latitude. For taxa with bimodal peaks, progressively later peaks with increasing latitude were also observed. With some exceptions, the annual maxima was delayed and shortened with increasing latitude. In the Bay of Biscay sites, under oligotrophic conditions (U35) most taxa peaked in spring at the time of the early spring phytoplankton bloom, while under mesotrophic conditions (B35) most taxa peaked in summer during the post spring period of phytoplankton growth.

INTRODUCTION

The abundance of zooplankton may be highly variable at time scales that span from

minutes to decades in response to environmental drivers and stressors operating across a wide range of temporal scales (Haury et al., 1978). Relevant time scales of variance, spanning days to years involve changes in growth, production, mortality and community function (Marine Zooplankton Colloquium 1, 1989). The annual seasonal cycle is a key scale because of the great magnitude of physical and biotic variation at this scale (Mackas et al. 2012), and the importance of phenological timing for the predator and prey For example fish larvae survival and recruitment success is highly dependent on the availability of suitable zooplankton preys in synchrony with the seasonal spawning and development of larvae, and according to the match-mismatch hypothesis (Cushing, 1990), there is the potential for differential phenology shifts of predator and prey, in response to environmental changes (Edwards and Richardson 2004, Durant et al, 2007).

In addition to phenological shifts, interannual variations in overall abundance of zooplanktonare driven by year-to–year variations of the physical and nutritional environments. These also help to modulate the recruitment of fish populations (Liu et al., 2014).Therefore it is important to determine the extent to which the seasonal and interannual variations differ from site to site in order to build an ecological classification of pelagic ecosystems on a geographical basis. (Longhurst, 1998). At a large spatial scale, latitude-dependent differences in light and temperature are the main factors responsible for the most remarkable changes in the plankton annual cycles. The general pattern for oceanic zooplankton is for a large amplitude single summer peak at high-latitudes, biomodal cycles with a spring bloom and a secondary peak in autumn at middle latitudes and no clear seasonal patterns in low latitude tropical waters (Heinrich, 1962). In shallow shelf seas, however, local natural (e.g. river discharge, coastal upwelling) and anthropogenic (wastewater inputs) stressors may modify substantially the standard plankton cycles (e.g. Cloern, 1996; Jamet et al., 2001: Ribera d´Alcalà et al., 2004).

In the ICES area a large number of time series are available using comparable method (O'Brien et al. 2013), but there have been few attempts to synthesise across multiple time series (Mackas et al. 2012, Castellani et al. 2016). Policy directives such as the Marine Strategy Framework Directive (ref) need to assess baseline envelopes of variability and its causes, and to provide a broad scale geographical context for this variability. We have selected four of these ICES sites to assess the relative effects of latitude and anthropogenic nutrient enrichment on the seasonal and interannual patterns

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94   of variability of mesozooplankton in coastal ecosystems across the Northeast Atlantic

95   Shelves Province (Longhurst, 1998). We compared mesozooplankton dynamics from

96   coastal sites located in the northernmost and the southernmost limits, and in the middle

97   of the geographic province, as well as from sites located at the same latitude but with

98   different trophic status.

99   **MATERIAL AND METHODS**

100   **Study area and data acquisition**

101   This study was carried out with data from four selected sites with ongoing zooplankton

102   monitoring programs, which allowed us to make robust comparisons of the zooplankton

103   temporal variations because the same mesh size (200 μm) was used for zooplankton

104   collection and simultaneous fifteen-year data series were available. The selection of the

105   sites was made mainly on a latitudinal (Figure 1) and trophic status basis. The selected

106   sites were Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven

107   (SH). B35 and U35 are located nearby in the Basque coast, inner Bay of Biscay, but

108   they differ substantially regarding their trophic status. L4 is located off the southwest

109   coast of England, in the western English Channel (Smyth et al. 2015), and Stonehaven

110   is off the eastern Scottish coast, in the northwest North Sea, and both show a trophic

111   status more similar to that of U35 than to that B35. These sites lie in a latitudinal

112   gradient, from B35 and U35, at the southern limit of the Northeast Atlantic Shelves

113   Province (Longhurst, 1998), to SH, at the northern limit, with L4 in an intermediate

114   position (Fig. 1).

115   Data of zooplankton abundance and relevant environmental parameters that were

116   regularly measured at the four sites, i.e. temperature and chlorophyll *a*, for a fifteen-year

117   period running from1999 to 2013 (both included) were used in the present study.

118   *Bilbao 35 and Urdaibai 35*

119   The B35 site (43° 24.15'N, 3º 5.25'W), with a mean water depth of 13 m, is in the

120   coastal embayment of the marine zone (around 35 salinity below the halocline) of the

121   estuary of Bilbao, a once highly polluted system which is now in a rehabilitation phase

122   (REF:). This is a partially mixed site influenced by the estuarine plume. In contrast, U35

123   (43° 27.7'N, 2° 45.3'W) is a well-mixed site with a mean water depth of 4.5 m and high

124   rate of tidal flushing located at the mouth of the shallow estuary of Urdaibai, a marine-

125   dominated system with much lower human pressure than the estuary of Bilbao. The

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126 trophic status of the U35 and B35 sites during the study period may be classified as

127 oligotrophic and mesotrophic respectively, on the basis of the chlorophyll concentration

128 criteria (Zaldivar et al. 2008). Both coastal areas are meso-macrotidal and subject to

129 semidiurnal tides.

130 Data from the B35 and U35 sites were obtained in monthly samplings conducted at high

131 tide during neap tides. Vertical profiles of temperature were obtained *in situ* using

132 WTW and YSI Water Quality Meters, but only data from the depth of zooplankton

133 sampling were used in this study. Zooplankton samples were taken by horizontal tows

134 at a mid depth, below the halocline when this was present, with 200 μm mesh size nets

135 (mouth diameter of 0.25 m) equipped with a flowmeter. Water samples for chlorophyll

136 *a* analysis were obtained at the same depth that zooplankton samples with Oceanic

137 Niskin bottles, and chlorophyll *a* concentration was determined spectrophotometrically

138 according to the monochromatic method with acidification (Jeffrey and Mantoura,

139 1997).

140 ***Plymouth L4***

141 The L4 site (4° 13'W, 50° 15'N) is located 13 km southwest of Plymouth. It is a

142 transitionally mixed site (Southward et al., 2005) with a mean water depth of 54 m, and

143 its hydrography is influenced both by inputs of riverine freshwater from the rivers Plym

144 and Tamar outflowing at Plymouth (Rees et al., 2009) and by oceanic water during

145 periods of strong south west winds. Samplings were carried out weekly and surface

146 temperature was measured with a thermometer placed inside a stainless steel bucket.

147 Since 2000 temperature was also measured with a CTD (Atkinson et al., 2015). CTD

148 data have been used whenever both measurements were available. Chlorophyll *a* was

149 measured by using reversed-phase HPLC as described in Atkinson et al. (2015).

150 Zooplankton samples were collected by vertical net hauls (WP2 net, 200 μm mesh size,

151 0.57 m diameter) from 50 to the surface.

152 ***Stonehaven***

153 The SH site (56° 57.8′ N, 02° 06.2′ W), with a mean depth of ~50 m, is located 5 km

154 offshore from Stonehaven. This placement was selected with the aim of reducing the

155 impact of freshwater input produced by rivers Dee and Don, which both outflow at

156 Aberdeen, fifteen miles to the north of Stonehaven. This is a dynamic site, well mixed

157 for most of the year. Thermal stratification of the water column is weak, and usually

158 confined to neap tides during the summer months due to strong tidal currents and

Comment [AA9]: Fig. 1 is good but can you show an insert for each of the areas (three maps showing how far offshore they were, how close to rivers and the water depth

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159 southerly flow. This site fulfils the requirements of the EU Water Framework Directive,

160 acting as a reference site with a "Good Environmental Status". Samplings were carried

161 out approximately weekly, weather conditions permitting. Salinity and temperature

162 were measured for the water column using a CTD. Water samples were taken with a 10

163 m integrated tube sampler for chlorophyll, which is measured fluorometrically as

164 described in Bresnan et al (2015). Vertical bongo nets (40 cm diameter and 200 µm

165 mesh) were used to collect zooplankton samples from the bottom to the surface.

166 Because of the use of 200 µm meshes to capture zooplankton at the four sites, the

167 results obtained in this study on total zooplankton and zooplankton taxa abundances

168 refer to the mesozooplankton fraction.

169 **Data pretreatment**

170 Occasional missing values (less than 5%) in the monthly data sets of the time series

171 were filled by data interpolation using the mean values of the previous month and the

172 following month of the selected variable.

173 For the purpose of the present study and to ensure data consistency, taxonomic

174 homogenization was undertaken. Zooplankton data were analysed for total zooplankton

175 and for selected zooplankton taxa belonging to two different resolution levels: (i) a

176 broad level (main groups routinely identified), consisting of six holoplankton categories

177 (copepods, cladocerans, appendicularians, chaetognaths, siphonophores and doliolids)

178 and nine meroplankton categories (cirripede larvae, decapod larvae, gastropod larvae,

179 bivalve larvae, polychaete larvae, fish eggs and larvae, bryozoan larvae, echinoderm

180 larvae and hydromedusae, which also included the far less abundant holoplanktonic

181 forms of the Hydrozoa class, such as *Liriope tetraphylla*), and (ii) a finer level, where

182 the herein termed "key" genera, consisting of genera or genera-assemblages of

183 cladocerans and copepods, were distinguished.

184 Ten "key" genera were considered. For the cladoceras the genera *Evadne* and

185 *Podon* were considered. For the copepods, *Acartia*, *Calanus*, *Centropages*, *Temora*,

186 *Oithona*, *Oncaea* and *Corycaeus* genera and the "PCPCalanus" (*Paracalanus*,

187 *Clausocalanus*, *Pseudocalanus* and *Ctenocalanus*) genera assemblage were considered.

188 Some of the above mentioned genera include recently separated new genera that were

189 not originally considered in the series like the genera *Mesocalanus* and *Calanoides*

190 within *Calanus*, the genus *Monothula* within *Oncaea*, the genus *Ditrichocorycaeus*

191 within *Corycaeus*, the genus *Pseudevadne* within *Evadne* and the genus *Pleopis* within

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192   *Podon*. The summary of the identified components and their contribution to the total

193   mesozooplankton for each selected taxon are shown in Tables 1, 2 and 3 for

194   holoplankton groups, meroplankton groups and cladoceran-copepod genera,

195   respectively. In gastropod larvae and polychaete larvae categories holoplanktonic

196   gastropods like *Limacina retroversa* and Gymnosomata and holoplanktonic polychaetes

197   like *Tomopteris helgolandica* were included, because they were not always

198   distinguished from meroplanktonic species on routine identifications.

199   As the samplings in B35 and U35 were performed on a monthly scale and most of them

200   were carried out during the last week of the month and occasionally in the third week of

201   the month or in the first week of the following one, whereas samplings in L4 and SH

202   were generally conducted weekly, the number of data per year was adjusted to twelve,

203   one per month, in all cases. For that purpose for L4 and SH the mean of all the values

204   obtained within each month was calculated. These monthly mean values were plotted

205   using in the time scale the mean Julian day value of the Julian days of all sampling

206   conducted each month.

207   To describe seasonal patterns of variability on the basis of Julian days, the astronomical

208   calendar was used. Therefore, winter refers to the time between 22 December and 20

209   March, spring to the time between 20 March and 21 June, summer to the time between

210   21 June and 23 September and autumn to the time between 23 September and 22

211   December.

212   **Data treatment**

213   The scales and patterns of variability for temperature, chlorophyll *a* (Chl *a*), total

214   zooplankton and selected zooplankton taxa, both at broad group and "key" genera

215   levels, were extracted for each monitoring site by using the multiplicative model

216   described by Cloern and Jassby (2010). This method decomposes time series into three

217   different components of variability associated to different scales: (i) an annual

218   component, herein named "interannual variability", where increasing or decreasing

219   trends, shifts and annual events can be detected, (ii) a seasonal component or "seasonal

220   variability", where a standard seasonal pattern can be identified, and (iii) a residual

221   component, or "residual variability", associated to the event scale, which includes the

222   variability that cannot be attributed to the average seasonal pattern or to fluctuations in

223   the annual mean. (Cloern and Jassby, 2010).

224   Unfortunately the data for *Centropages* in 1999 at L4 were not available. We have filled

225   this gap for calculations of interannual and seasonal variability by assuming the same

226   abundance data as in 2000. To make possible the calculations of interannual and

227   seasonal variability of doliolids at SH, where doliolids were not recorded in some years,

228   we added in such years a value of 0.01 in the month of the annual maximum obtained

229   from the years with presence of doliolids. In addition, an unusual high value of fish eggs

230   at L4 in March 2000 was considered an outlier due to a counting error, sothis was

231   replaced by the mean value of the month obtained from the rest of years of the series.

232   Paired t-tests were performed using SPSS Statistics for Windows, Version 23.0 (IBM

233   Corp., Armonk, NY) to test for differences between sites in the interannual, seasonal

234   and residual components of variability of zooplankton taxa, and to test for differences

235   between the three components of variability within each site.

236   Correlation analyses were performed to test the relationship of the year-to-year

237   variations of total zooplankton abundance, Chl *a* concentration, surface water

238   temperature and zooplankton taxa abundance at each site, and the interannual

239   relationships of each zooplankton taxa between sites using SPSS Statistics for

240   Windows, Version 23.0 (IBM Corp., Armonk, NY).

241   Resemblance analyses were carried out by means of the Bray Curtis similarity index

242   (Bray and Curtis, 1957), using the group average method, to measure the similarity (or

243   dissimilarity) between all the selected zooplankton taxa, according to their patterns of

244   variability (pooled for the four monitoring sites). Similarity (or dissimilarity) was tested

245   both for the interannual and the seasonal scales. These analyses were performed using

246   the PRIMER 6 software package (Clarke and Warwick, 2006). Results of the analyses

247   were displayed in dendrograms for each of the two scales of variability considered.

248   Contour plots of variability values for each zooplankton taxa were created with Surfer

249   software, version 10 (Golden Software, Inc, Golden, Colorado) using the kriging

250   gridding method, in order to visualize differences between sites in the year-to-year

251   changes and the seasonal patterns of variability of mesozooplankton taxa and infer the

252   relationship with latitude and trophic status.

253   **RESULTS**

254   **Scales of variability**

255   The results on the three components of variability (interannual, seasonal and residual)

256   extracted from the time series of the selected zooplankton taxa at the four sites are

257 shown in Figure 2. Overall, interannual variability was the lowest and residual
258 variability the highest at all sites, but the within site comparison of the three
259 components indicated that such differences were not statistically significant between
260 seasonal and interannual variability at U35, and between residual and seasonal
261 variability at SH (Table 4). Comparison between sites showed that the lowest
262 interannual, seasonal and residual variability were obtained at L4, while the highest
263 interannual and residual variability were found at U35 and the highest seasonal
264 variability at SH. The paired t-test for differences between sites (Table 5) showed that
265 interannual variability mainly differed between U35 and the other three sites because it
266 was significantly higher at U35 than at B35, L4 and SH. Seasonal variability was
267 significantly higher at SH than at L4, while differences between SH and the sites of the
268 Bay of Biscay (U35 and B35) approached the significance level ($p \approx 0.06$). However if
269 doliolids, which only occurred at SH in low numbers in the last years of the series, are
270 excluded from the analysis, seasonal variability of zooplankton taxa at SH was found to
271 be significantly higher than at the other three sites ($p < 0.05$). The residual variability
272 was significantly higher at U35 and B35 than at L4 and SH.

273 **Interannual variations**

274 *Total zooplankton, chlorophyll a and temperature*

275 The annual mean values and the interannual variability (dimensionless) of total
276 zooplankton abundance, chl *a* concentration and temperature at the four sites for the
277 period 1999-2013 are shown in Figure 3. Zooplankton abundance fluctuated between
278 972 and 5097 ind. m^{-3} until 2011 in all the sites under study. However, in 2012 the
279 annual means reached 9116 and 12866 ind. m^{-3} in B35 and U35, respectively, while in
280 2013 they decreased to values similar to those observed prior to 2012. The mean
281 abundance of zooplankton was significantly lower in SH (2022±464 ind. m^{-3}) than in
282 the other three sites (L4 $p = 0.003$, U35 $p = 0.009$ and U35 $p < 0.001$), and no
283 significant differences were observed between L4 (3563±936 ind. m^{-3}), U35
284 (3403±2806 ind. m^{-3}) and B35 (4195±1515 ind. m^{-3}). Interannual variations of
285 zooplankton abundance were not correlated between sites in any case.
286 Chl *a* concentrations were on average significantly higher in B35 (2.19±0.97 μg L^{-1})
287 than in the other three sites ($p < 0.001$) and did not differ statistically between U35
288 (0.82±0.23 μg L^{-1}), L4 (1.24±0.21 μg L^{-1}) and SH (1.29±0.26 μg L^{-1}). Interannual
289 variations of Chl *a* showed clear differences between sites both in terms of

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290 concentrations and dimensionless variability. The annual mean values at U35, L4 and

291 SH were similar and ranged between 0.49 and 1.81 µg L^{-1}, whereas at B35 annual mean

292 chl *a* concentrations were higher than at the other sites most of the years, reaching a

293 maximum mean annual value of 4.76 µg L^{-1} in 2000. In contrast, U35 showed the

294 lowest concentrations of Chl *a* during the study period (except in 2002). No correlation

295 of interannual variation of Chl *a* was found between sites, nor between interanual

296 variations of Chl *a* and zooplankton at each site, except at B35 , where a significant

297 negative correlation (p = 0.026) was found between Chl *a* concentration and

298 zooplankton abundance.

299 Annual mean values of water temperature clearly differed between sites in relation to

300 latitude, and, on average, they were highest at B35 (16.0±0.37°C) and U35

301 (16.2±0.34°C), the only sites without significant differences in temperature between

302 them. L4 water showed intermediate temperatures (12.6±0.36°C), and SH the lowest

303 ones (9.5±0.31°C). The warmest and the coldest years in the temperature series differed

304 between sites, although in all of them the warmest ones were recorded during an

305 intermediate period of the series comprised from 2003 to 2007 (2003 at SH, 2003 and

306 2006 with similar values at U35, 2006 at B35 and 2007 at L4) and the coldest ones in

307 the second half of the series (2007 at B35 and U35, 2010 at L4 and 2013 at SH).

308 Interannual variations in water temperature were positively correlated between B35 and

309 U35 (p<0.001), and between L4 and SH (p=0.001). In addition, a significant positive

310 correlation (p = 0.024) was found between the interannual variations of water

311 temperature and Chl *a* at L4.

312 ***Zooplankton taxa***

313 The clustering of zooplankton taxa according to their interannual variations (in

314 dimensionless units of variability) obtained from data pooled for the four sites (Figure

315 4) showed a stair-step appearance, with a lack of defined clusters. The most consistent

316 similarities were found for copepods and some of their main genera (PCPCalanus,

317 *Oithona*, *Acartia*) together with decapod larvae and appendicularians, and for

318 cladocerans and their genus *Evadne*,

319 Contour plots evidenced a general low coherence in the interannual variations of most

320 taxa along the latitudinal gradient and between the mesotrophic site B35 and the other

321 three sites (Figure 5). Cladocerans and their dominant genus at B35, U35 and L4, i.e.

322 *Evadne*, showed more or less recurrent high frequency(one-two yr period) peaks along

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323 the time series at all sites, but they were not synchronised in the year-to-year scale. For
324 copepods, PCPCalanus, *Oithona*, *Acartia*, and appendicularians the most remarkable
325 feature of the time series was the prominent peak that occurred in 2012 at B35 and U35.
326 The sudden increase of abundance in 2012 at B35 and U35 was also observed for
327 meroplanktonic groups such as bivalve larvae and echinoderm larvae. Nevertheless,
328 irregular fluctuations that were unsynchronised between sites were the main features of
329 the interannual variability for most zooplankton taxa.
330 Correlation analysis further showed that few taxa had similar interannual variations at
331 different sites. In fact, there was not any taxon showing interannual synchrony between
332 the four sites. The number of taxa that showed interannual synchrony was highest
333 between the nearby sites of B35 and U35, with 8 taxa (cladocerans, siphonophores,
334 doliolids, bivalve larvae, bryozoan larvae, decapod larvae, *Evadne* and *Corycaeus*) from
335 25 selected taxa showing significant positive correlations ($p < 0.05$). The lowest
336 synchrony was found between B35 and SH and between U35 and L4, with only one
337 taxon that correlated positively in each case (gastropod larvae and chaetognaths,
338 respectively). Between B35 and L4 two taxa correlated positively (cladocerans and
339 appendicularians) and another one negatively (bivalve larvae); between U35 and SH
340 cirripede larvae correlated positively and bryozoan larvae negatively, and between L4
341 and SH cladocerans, bivalve larvae and echinoderm larvae correlated positively.
342 Significant correlations between zooplankton taxa and environmental variables, i.e.
343 water temperature and Chl *a*, at an interannual scale were very scant and unrelated
344 between sites. At SH, *Oncaea* and decapod larvae correlated positively with
345 temperature (p= .030 and p =.019, respectively), and bryozoan larvae and PCPCalanus
346 correlated negatively with Chl *a* (p= .001 and p =.019, respectively). At L4, *Calanus*
347 correlated positively with temperature (p=.039) and PPCalanus correlated negatively
348 with temperature and Chl *a* (p= .047 and p=.011, respectively). At U35 no taxa
349 correlated with temperature nor Chl *a*, and at B35 only bryozoan larva correlated
350 positibely with Chl *a* (P=.034).

351 **Seasonal patterns**

352 *Total zooplankton, chlorophyll a and temperature*

353 The monthly mean values and the seasonal variability (dimensionless) of total
354 zooplankton abundance, Chl *a* concentration and temperature at the four sites, for the
355 period 1999-2013 are shown in Figure 6. Zooplankton seasonal patterns of abundance

356 showed differences between sites, although in all of them total zooplankton reached the
357 minimum value during late autumn-early winter. At U35 the main peak of zooplankton
358 abundance was observed in early spring, with a maximum mean value of 10494±15159
359 ind. m^{-3} in late March. Thereafter the density decreased progressively in a stair-step
360 manner until January. At this site the average pattern of seasonal variability
361 (dimensionless), however, evidenced a bimodal cycle with a secondary peak in late
362 summer. At the other three sites the seasonal pattern of abundances matched that of the
363 dimensionless seasonal variability values. At B35 three peaks were observed, i.e. in
364 early spring (late March), early summer (late June) and early autumn (late September).
365 The annual maximum was in early summer, when zooplankton mean density increased
366 up to 9657±7132 ind. m^{-3}. At L4 a clear bimodal pattern with two similar peaks in
367 spring (April) and summer (August) were observed, although the highest mean value
368 (5519±2672 ind. m^{-3}) was obtained for the spring peak. In SH the seasonal pattern was
369 characterized by a unimodal cycle with an annual maximum of 5237±2337 ind. m^{-3} in
370 summer (July-August), although the stair-step form suggests two consecutive periods
371 for zooplankton increase in spring and summer.
372 The monthly mean values and the dimensionless variability of Chl *a* showed very
373 similar seasonal patterns at each site, but clear differences between sites. Two Chl *a*
374 peaks were distinguished at B35 (a small one in early spring and the highest in
375 summer), U35 (the major one in early spring and a secondary one in late summer) and
376 L4 (in April and August with similar magnitudes). An extended single peak in late
377 spring (in May-June) was observed at SH, but the stair-step shape of the decrease in
378 August suggests the masking of a secondary peak in summer. Overall, B35 was the site
379 that showed the highest maximun monthly mean value of Chl *a* (4.95±4.58 μg L^{-1}) and
380 U35 the lowest. Maximum monthly mean values of Chl *a* showed a small increase from
381 U35 (1.944±2.05 μg L^{-1}), to L4 (2.26±1.42 μg L^{-1}) and to SH (2.70±1.29 μg L^{-1}).
382 Monthly mean values of water temperature showed the expected decrease with latitude.
383 B35 and U35 were the warmest sites, with very similar values that ranged from around
384 12.4 ℃ in January-February to around 21.0 ℃ in August. L4 showed intermediate
385 values of temperature, ranging from 8.9 ℃ in March to 15.6 ℃ in August, and SH was
386 the coldest with the minimum (6.0 ℃) in March and the annual maximum (13.1 ℃) in
387 September. The standard dimensionless variability of temperature evidenced that
388 warming and cooling timings differed between sites according to latitude, both warming
389 and cooling being earliest at B35 and U35 and latest at SH.

Zooplankton taxa

The clustering of zooplankton taxa according to their patterns of seasonal variability
obtained from data pooled for the four sites (Figure 7) showed five different taxa
assemblages with similarity levels between 60% and 80%. The highest resemblance
levels were found in the assemblage constituted by cladocerans, *Evadne*, *Podon*,
appendicularians and *Acartia*. The contour plots of the dimensionless seasonal
variability of these taxa at different sites (Figure 8), showed a seasonal progression
related to latitude, with annual maxima in early spring (late March) at U35, in late
spring-early summer (May-July) at L4 and in summer (July-August) at SH. At B35 the
components of this assemblage showed the annual maxima in late spring-early summer
(late May-late June), except for *Acartia* with maximum values in early spring (late
March). Echinoderm larvae were related to this assemblage because their highest annual
values also showed a delay with latitude from U35 and B35 in spring to L4 and SH in
summer. Later in the year, the assemblage constituted by bivalve larvae, gastropod
larvae and *Centropages* also showed a seasonal delay of the annual maximum value
along the latitudinal gradient, from U35 in spring-summer (late March or late June) to
L4 and SH in summer-autumn (June-September). At B35 they reached maxima in
summer (late June-July). The group composed by *Calanus*, *Temora*, decapod larvae,
PCPCalanus, copepods and *Oithona* were characterised in most cases by bimodal
patterns, (or trimodal patterns at B35), in which the time lag between the earliest and the
latest peaks of abundance decreased with increasing latitude. The first peak tended to
occur progressively later from U35 and B35 (late February-April) to SH (May) while
the last one generally was delayed from SH (July-September) to U35 and B35 (late
August to late October) in most cases. In the components of this assemblage, however,
no clear relationship of the major annual peak with latitude was observed. The annual
maximum was found in the earliest peak or in the latest one, and even in the
intermediate peak at B35, depending on the taxon and the site. Cases with no clear
differences between the two seasonal peaks were also observed, mainly at L4. Overall,
the last peak was clearly the major one in more cases at SH (*Calanus*, *Temora*, decapod
larvae, copepods and *Oithona*) and B35 (*Temora*, decapod larvae, PCPCalanus and
Oithona) than at U35 (*Temora*, PCPCalanus). Conversely, the first peak was clearly the
major one for some taxa at U35 (copepods and *Oithona*). In PCPCalanus the importance
of the first peak decreased from SH to B35. The annual maximum of polychaete larvae
occurred earlier than in the above mentioned taxa at U35 and B35 (late February) and it

13

424 was delayed to June at L4 and July at SH. Siphonophores and hydromedusae showed

425 bimodal cycles with the annual maxima in spring (late Abril-May) at U35 and B35, and

426 unimodal cycles at L4, with the annual maximum of siphonophores in September and

427 that of medusae in July. However, at SH the annual maximum was in September for

428 siphonophores and in April for medusae. In contrast, bryozoan larvae and fish eggs and

429 larvae showed annual maxima earlier at L4 and SH (in March and April, respectively)

430 than at U35 and B35 (late April-late June), and cirripede larvae reached annual maxima

431 in March-April at SH, L4 and U35, while they occurred markedly later at B35 (late

432 June). Finally, doliolids, *Oncaea*, chaetognaths and *Corycaeus* were differentiated from

433 the other taxa because they reached annual maxima at all the sites in the second half of

434 the year, with the exception of *Oncaea* at SH. Doliolids and chaetognaths showed a

435 marked seasonality with maxima in the August-September period at all sites, while

436 *Oncaea* and *Corycaeus* peaked from late July to September at the different sites but

437 showed a second large peak in winter at SH.

438 Figure 9 shows for each month of the year the number of taxa with annual maxima at

439 that month. The highest number of zooplankton taxa maxima occurred in early spring at

440 U35, in early summer at B35, in mid summer at L4 and in late summer at SH. In

441 addition, the distribution of annual maxima occurrences was skewed towards spring at

442 U35 and L4 and towards autumn at B35 and SH. In holoplankton groups, a clear

443 reduction of the peaking period along the year with increasing latitude was observed

444 from U35 (6 months, from March to August) to L4 (5 months, from May to September)

445 and to SH (3 months, from July to September). However, no clear latitudinal patterns

446 were observed for the seasonal span of annual maxima of meroplankton groups and

447 cladoceran-copepod genera. At B35 the seasonal span of holoplankton group maxima

448 was longest (7 months, from March to September), and holoplankton groups,

449 meroplankton groups and cladoceran-copepod genera showed the highest similarity in

450 their seasonal spans of annual maxima.. Overall, annual maxima of meroplankton

451 groups tended to occur earlier than those of holoplankton groups at all sites. However,

452 the largest difference was observed at SH where most meroplankton groups showed

453 annual maxima in April-June and most holoplankton groups in August-September, and

454 the smaller difference at U35 and B35 where most of meroplankton and holoplankton

455 groups showed annual maxima in the same season. A latitudinal progression in the

456 distribution of annual maxima of cladoceran-copepod genera was also observed from

457 U35 (highest number of maxima in spring) to SH (highest number of maxima in

14

458 summer) with L4 at a middle position (similar number of maxima in spring and

459 summer). At B35, the highest number of annual maxima occurred in early summer and

460 early autumn for key genera.

461 **DISCUSSION**

462 **Scales of variability**

463 Between-site differences of the interannual, seasonal and residual components of

464 zooplankton taxa variability were not related to latitude, since all three components of

465 zooplankton variability showed the lowest values at the intermediate latitude site (L4),

466 and the ones from the mesotrophic site (B35) did not differ from those of the other three

467 sites, except the interannual differences with U35.

468 Overall, the residual component was the highest at all sites, as it has also been found for

469 many coastal phytoplankton series across the world (Cloern and Jassby, 2010). This

470 suggests that the main component of variability in plankton series can be attributed

471 either to events occurring at scales shorter than the seasonal and/or to strong year to

472 year changes of the seasonal pattern, as observed in the annual cycles of total

473 zooplankton in the four sites studied (Figure 10). The greater residual component of

474 zooplankton taxa variability at B35 and U35 than at L4 and SH might be attributable to

475 some extent to differences in sampling frequency (monthly at B35 and U35 and weekly

476 at L4 and SH), because single measurements as estimators of monthly mean values can

477 contribute to increase the residual component of variability in plankton time series

478 (Cloern and Jassby, 2010). However, the effect of natural (tides, river discharge) and

479 anthropogenic stressors that act at shorter time scales than the seasonal cycle on

480 zooplankton dynamics may have had a stronger effect in coastal sites associated to

481 estuaries (B35 and U35) than in further offshore sites (L4 and SH). In fact, U35 is

482 subject to strong tidal mixing and transport and B35 to the effect of the nutrient-rich

483 estuarine plume from the estuary of Bilbao, factors which have been found to determine

484 phytoplankton and dissolved oxygen dynamics at these sites (Villate et al., 2008; 2013,

485 Iriarte et al, 2010; 2014). Zooplankton time series with a temporal resolution shorter

486 than the monthly scale are required to resolve clearly these event-scale variations (Jiang

487 et al., 2007).

488 In general, the seasonal component of variability of zooplankton was higher than the

489 interannual in the present study. And this seems to be the most common pattern reported

490 for coastal plankton, since it has been found both for phytoplankton biomass from many

15

491 different coastal sites (Cloern and Jassby, 2010; Zingone et al., 2010) and for

492 zooplankton taxa abundance (Bode et al., 2013). However, the predominance of

493 seasonal/interannual variations of coastal/estuarine phytoplankton biomass has been

494 shown to vary geographically (Cloern and Jassby, 2010) and for zooplankton

495 abundance, in agreement with our findings, it has been shown to vary among taxa from

496 the same site (Licandro et al., 2001). When comparing the sites, interannual variability

497 was higher in the zooplankton of the southern sites of the Bay of Biscay (U35 and B35)

498 than in the English Channel (L4) and the North Sea (SH) sites. However, year-to-year

499 fluctuations of total and most zooplankton taxa were not higher at the sites located in

500 the Bay of Biscay than at the other sites if we exclude the atypically high values

501 obtained in 2012 at the sites of the Bay of Biscay, especially at the U35 site. Abrupt

502 increases in one year can result in large interannual variability (Cloern and Jassby,

503 2010), so this isolated event seems responsible for the higher values of the interannual

504 component of the zooplankton taxa series of the Bay of Biscay. Marked fluctuations of

505 mean zooplankton abundance between years have also been found at high latitude

506 around Iceland (Gislason et al., 2009), so there seems to be no evidence that the

507 magnitude of interannual variations is linked to latitude.

508 The seasonal component of zooplankton taxa variability was higher at the

509 northernmost site (SH) than at the other ones. However, the expected decrease of the

510 seasonal component with decreasing latitude was not observed because the lowest

511 varaiability was at the intermediate latitude site (L4). Latitude appears as a determinant

512 factor of the seasonal component of phytoplankton biomass when a wide latitudinal

513 range and many cases are considered (Cloern and Jassby, 2010), but in our case the

514 lowest seasonal component at L4 is in agreement with the most equitable distribution of

515 zooplankton taxa maxima along the year and the bimodal cycle with less pronounced

516 changes of total zooplankton and many zooplankton taxa at this site.

517 **Interannual variations**

518 Strong atmospheric forcing can lead to population fluctuations that have synrchoncity

519 across wide areas (Atkinson et al. 2004, Kang and Ohman 2014). The fact that we did

520 not observe this reflects a prevalence of local-scale effects.. The number of zooplankton

521 taxa with synchronous interannual variation across sites was very low in general, and

522 did not differ clearly from pairs of sites with similar interannual variability of

523 temperature (B35-U35, and L4-SH), to pairs of sites with uncorrelated year-to-year

Comment [AA11]: Is this what you mean?

Comment [AA12]: I dont know what you mean with this sentence. Can you re-word it?

Comment [AA13]: I suggests that you look at the NE Atlantic literatura and quote some NAO relationships?

temperature variations. The finding of the highest number of taxa with synchronous year-to-year variations between U35 and B35 seems the result of the geographic proximity of these two nearby sites rather than the response to interannual variations of temperature. The low correlations observed between zooplankton components and climatic variables in other zooplankton series of nearby coastal areas also suggest that local factors play a major role accounting for interannual abundance changes (Bode et al., 2013).

As for zooplankton, no synchronous year-to-year variations of phytoplankton biomass (chlorophyll *a*) were observed between the four sites, and they were found to be related to temperature only at L4. A lack of relationship between series of phytoplankton biomass and of key environmental factors such as temperature may be expected when changes in the environmental variable are below the response threshold of phytoplankton or when other relevant factors have not been considered (Zingone et al., 2010). For instance, the lack of relationship between phytoplankton biomass and temperature at the coastal U35 site was attributed to the effect of nutrient limitation in summer, that distorts the enhancement of phytoplankton biomass by temperature, which can be observed at the non-nutrient limited lower salinity sites within the estuary of Urdaibai (Villate et al. 2008).

The unusually high abundance of total zooplankton observed at U35 and B35 in 2012 as a result of the noticeable increase of copepods such as *Acartia*, PCPCalanus and *Oithona*, appendicularians and bivalve larvae could be considered as one of the so-called "surprises" that long-term observations may provide due to the multiple stressors that may interact to cause change (Cloern et al., 2015), and corroborates the importance of local or region-specific physical processes in disturbing the range of interannual fluctuations of zooplankton abundance. The 2012 season is reported as a peculiar in the southern part of the Bay of Biscay, where the average positive values of the upwelling index for February and March were far from normal (Rodriguez et al., 2015) and climate anomalies were found to be responsible for exceptional blooms of *Dinophysis acuminata* in the southeastern area (Diaz et al., 2013). Sudden increases of similar magnitude in year-to-year zooplankton abundance have been reported for other zooplankton series like those of the mouth of the Ria de Vigo, where hydrodynamic factors driven by meteo-climatic conditions are claimed to be very important in the control of zooplankton fluctuations at the interannual scale (Buttay et al., 2015). If the local event affecting U35, and to a lesser extent B35, in 2012 is excluded, the

Comment [AA14]: Need to clarify a mechaisms, eg their sharing larger-scale populations etc

Comment [AA15]: Can you simplify this sentence?

558 asynchronous and regular interannual fluctuations of zooplankton taxa at all sites

559 suggest that there were no large-scale forcings able to produce synchronous remarkable

560 changes in the four zooplankton monitoring sites.

561 The mesotrophic site of Bilbao differed from the other sites by the clear increasing

562 trends of total zooplankton and many zooplankton taxa, in parallel to the decreasing

563 trend of phytoplankton biomass, and may be related to the rehabilitation process that

564 this anthropized system is undergoing in the last decades, after the construction of a

565 waste water treatment plant and the decline of the industrial activity in the area (Borja et

566 al., 2010). The observed decrease in nutrient loads of human origin in the system during

567 the studied period (Villate et al., 2013) could account for the decrease in phytoplankton

568 biomass. Accordingly, the B35 site illustrated during our study period a process of

569 oligotrophication similar to that reported for other phytoplankton time series in coastal

570 areas upon the implementation of nutrient load reductions (Mozetič et al. 2010;

571 Nishikawa et al. 2010; Zingone et al., 2010). Bottom-up control has been claimed to be

572 the cause of zooplankton density increase in some time-series (Steinberg et al., 2012),

573 however, the decreasing trend of Chl *a* at B35 excludes the bottom-up control as a

574 likely mechanism driving the increase in zooplankton at this site. Similarly, very few

575 cases of synchrony were found between zooplankton taxa and temperature or

576 phytoplankton biomass at each site, this reinforcing the idea that year-to-year changes in

577 zooplankton might be primarily driven by a combination of stressing forces that differ

578 locally.

579 The higher interannual coherence of cladocerans with *Evadne* and of copepods with

580 PCPCalanus, *Acartia* and *Oithona* revealed which genera had a greater contribution to

581 the broad category in which they are included, but also that the main copepod genera

582 showed a rather high interannual coherence at each site, enhanced by the sudden

583 increase of all of them in 2012 at the sites located in the southeast Bay of Biscay.

Seasonal patterns

585 Average seasonal patterns of total zooplankton abundance, phytoplankton biomass and

586 some zooplankton taxa appeared to be related to latitude in a clear way, and showed the

587 expected delay of the spring peak and the advancement of the late peak from the

588 southernmost site (U35) to the northernmost one (SH), in agreement with the principle

589 that spring processes tend to occur earlier and autumn processes later in the year with

590 increasing temperature (Richardson, 2008)

> **Comment [AA16]:** Is this the correct Word. All 4 sites have much higher chl a values tan central ocean gyres

> **Comment [AA17]:** No thats phenology shift directions with a warming climate

591 In most plankton taxa with bimodal patterns at the four sites, the lowest differences in

592 the magnitude of both peaks was observed at L4, although generally the early peak was

593 slightly higher than the late one, in agreement with previous reports (e.g. John et al.,

594 2001; Eloire et al. 2010). At this site, the April peak of zooplankton abundance has been

595 associated to the spring bloom of phytoplankton biomass dominated by diatoms and the

596 second one to the bloom of dinoflagellates occurring at the beginning of autumn

597 (Widdicombe et al., 2010). In contrast, the bimodal patterns at U35 showed clear

598 differences in magnitude from the spring maximum to the secondary peak. In both sites

599 (L4 and U35), however, the spring peak of both zooplankton abundance and

600 phytoplankton biomass occurred simultaneously, in April or late March, while the late

601 zooplankton peak occurred earlier (August) than that of phytoplankton. The decrease of

602 phytoplankton biomass between the first and the second peak is related to nutrient

603 limitation associated to the summer stratification (Atkinson et al., 2015; Villate et al.,

604 2008).

605 Five main assemblages of zooplankton taxa were distinguished in relation to their mode

606 of seasonal behaviour with latitude: (1) taxa that showed a similar seasonal pattern at all

607 latitudes, (2) taxa that showed a delay in the seasonal distribution at the southernmost

608 sites, (3) taxa that showed a delay in their seasonal distribution with increasing latitude,

609 (4) taxa with bimodal cycles that showed a delay of the early peak during the first half

610 of the year but an advance of the late peak during the second half of the year with

611 increasing latitude, or a convergence of the bimodal cycles to unimodal ones at the

612 northernmost site, and (5) taxa with bimodal cycles at the northernmost site that become

613 unimodal ones with decreasing latitude. Total zooplankton abundance and

614 phytoplankton biomass followed the first and second alternatives of mode 4 of seasonal

615 behaviour with latitude, respectively.

616 Coincident seasonal distribution at all latitudes was observed in a low number of taxa

617 characterized by peaks early or late in the year, e,i. cirripede larvae in March-April and

618 doliolids and chaetognaths in August-September. Cirripede larvae comprise the most

619 abundant meroplanktonic component of the mesozooplankton at all four sites studied

620 (Bresnan et al., 2015; Highfield et al., 2010; Villate, 1989-1990; 1991). Although there

621 is no information on the specific composition of cirripede larvae at the sites we studied,

622 several studies on the benthic populations and larvae settlement seasonality (Crisp et al.,

623 1981; Kendall and Bredford, 1987; O´Riordan et al., 2004) indicate the presence of

624 different barnacle species distributed along a latitudinal gradient from the north of

625   Scotland to the south of Portugal, with *Balanus balanoides* as the species restricted to

626   the northernmost area, and the dominant cogeneric species *Chthamalus montagui* and

627   *Chthamalus stellatus* showing extensive geographical overlap, but with the distribution

628   of the first one being skewed towards the south. However, no marked seasonal

629   differences in the spawning have been found, and the highest abundance of cirripede

630   larvae during March and April at all the sites seems to be the response to the same

631   external stimulus such as the timing of phytoplankton increase from late winter-early

632   spring (Starr et al., 1991; Highfield et al. 2010). The coincidence of the annual

633   maximum of doliodids in late summer agrees with the fact that doliolid development

634   occurs at the highest annual temperatures and is favoured by the stratification of the

635   water column (Menard et al., 1997), factors that may be responsible for the

636   synchronization of the seasonal pattern of doliolids, in spite of the between-site

637   differences in temperature. The coincidence of the seasonal distribution of chaetognaths,

638   despite the different composition observed at the three latitudes (dominance of

639   *Parasagitta friderici* in the southern Bay of Biscay, of *P. setosa* in the English Channel

640   and of *P. elegans* in the northern North Sea), suggests that regardless of the species

641   involved, the chaetognath seasonal distribution may be driven by trophic parameters of

642   the seasonal plankton succession. Studies on the diet of *P. friderici* (Vega-Pérez and

643   Liang, 1992; Gibbsons and Stuart, 1994), *P. setosa* (Tönnesson and Tiselius, 2005) and

644   *P. elegans* (Falkenhaug, 1991; Sullivan, 1980) reveal that their development depends on

645   the abundance of small copepods from nauplii to calanoid copepodites, with preference

646   for cyclopoids (*Oithona*, *Oncaea*, *Corycaeus*) and small calanoids (*Paracalanus*,

647   *Pseudocalanus*, early stages of *Calanus*). So, the annual cycle of chaetognaths appears

648   to be linked to the annual distribution of small copepods that peak in the warmest

649   period.

650   The annual maxima of bryozoan larvae and icthyoplankton were delayed at the

651   southernmost sites of the Bay of Biscay. No information about the composition of

652   bryozoans is available, but in the case of the ichthyoplankton latitudinal differences may

653   be related to compositional differences that involve differences in the seasonal

654   spawning behaviour. In the North Sea, where the SH site is located, sandeels

655   (Ammoditidae) are found at high concentration in the east coast of Scotland and herring

656   (Clupeidae) increase northwards (Edwards et al., 2011). In the southern areas of the Bay

657   of Biscay, however, the most numerous ichthyoplankton species are sardine (Clupeidae)

658   and anchovy (Engraulidae), this last one being a species more restricted to the Bay of

659   Biscay, and spawning together with mackerel in warmer conditions than other co-

660   occurring species (Edwards et al., 2011; Ibaibarriaga et al., 2007). This may account for

661   the delay of fish egg and larvae maxima at U35 and B35, where the high presence of

662   anchovy in the ichthyoplankton of the marine zone of the estuaries of Urdaibai and

663   Bilbao have already been reported (Villate, 1989-1990; 1991)

664   Among the zooplankton taxa showing a delay of the annual maxima with latitude, we

665   have the spring-summer assemblage constituted by cladocerans and their genera *Podon*

666   and *Evadne*, the copepod *Acartia* and appendicularians. All are major taxa at these sites

667   (Bresnan et al., 2015; Eloire et al., 2010; Villate et al., 2004) and showed a general

668   delay of the annual maxima from early spring at U35 to late summer at SH. Because

669   *Evadne nordmanni* and *Acartia clausi* are the dominant species of the respective genera

670   at all sites, the latitudinal differences in their seasonal pattern may reflect a specific

671   temperature optima. This was evident mainly for *A. clausi* which maintains the seasonal

672   maximum in late March (even at the mesotrophic B35), with temperature values near

673   the annual minimum (12.4 ºC) at the southernmost sites, and near the annual maximum

674   (13 ºC) at the northernmost site of SH. Anyway, *A. clausi* is found to present allopathic

675   populations with different temperature responses because of the different temperature

676   regimes they are subjected to (Leandro et al., 2006).

677   In the taxa assemblage characterized by bimodal annual cycles with a delay of the early

678   peak during the first half of the year and an advance of the late peak during the second

679   half, or a convergence of the bimodal cycle into a unimodal one at the northernmost

680   site, the latitudinal differences in the magnitude of early and late peaks in some cases

681   were mainly related to compositional differences. For instance, *Temora* showed peaks

682   close in time of rather similar magnitude at SH and L4, where *Temora longicornis* was

683   the only (SH) or the clearly dominant (L4) *Temora* species, but peaks widely separated

684   in time at U35 and B35, where the first peak was due to *T. longicornis* while the second

685   one was much higher than the first one and was mostly due to the more abundant *T.*

686   *stylifera*. This is a summer-autumn species that has become the dominant *Temora*

687   species in coastal waters of the southeastern Bay of Biscay since the late 1980s (Villate

688   et al., 1997). Later it experienced a northward advance, reaching the English Channel

689   (Lindley and Daykin, 2005). Similarly, the PCPCalanus is an abundant group of related

690   small calanoids dominated by *Pseudocalanus elongatus* in the northernmost site (SH)

691   but by *Paracalanus parvus* in the southernmost sites of U35 and B35. This last species

692   was responsible for the much higher magnitude of the second peak of PCPCalanus at

693 U35 and B35. *P. elongatus*, by contrast, is the dominant copepod at SH, particularly

694 during the spring period (Bresnan et al., 2015), and is slightly more abundant than *P.*

695 *parvus* at L4, where *P. elongatus* peaks in spring and *P. parvus* in autumn (Eloire et al.,

696 2010). In the case of *Oithona*, the clear bimodal cycle at U35, becomes unimodal at SH,

697 likely as a result of the delay with increasing latitude of the annual maximum of

698 *Oithona similis,* which is the dominant *Oithona* species at U35, the only one reported at

699 L4 (Castellani et al., 2016), and, therefore, the expected species also at SH. *Oithona*

700 *nana* has only been recorded at the southermost sites (U35 and B35), where it appeared

701 as the main species responsible for the second annual *Oithona* peak at these sites.

702 In contrast, *Oncaea* and *Corycaeus* showed bimodal cycles at the northernmost site

703 (SH), and unimodal at the southernmost one (U35). In agreement with previous reports

704 by Eloire et al. (2010) for *Ditrichorycaeus anglicus* and *Oncaea* spp., our results

705 showed a skewed distribution of *Corycaeus* and *Oncaea* towards autumn and winter at

706 L4 and SH in a similar way, which is likely related to the later cooling of water at the

707 latter sites as compared to U35 and B35.

708 The seasonal distribution of the annual maxima of zooplankton taxa was related to

709 latitude in three main aspects: (1) the delay in the timing of the highest number of taxa

710 annual maxima from early spring at the southernmost oligotrophic site (U35) to late

711 summer at the northernmost site (SH), (2) the shortening of the seasonal span of

712 holoplankton taxa maxima from 6 months at the southernmost oligotrophic site (U35) to

713 3 months at the northernmost site (SH), and (3) the decrease of the overlap of periods of

714 holoplankton annual maxima and meroplankton annual maxima from the southernmost

715 oligotrophic site (U35) to the northernmost site (SH). The seasonal distribution of

716 phytoplankton biomass may be partly responsible for those three patterns. The delay in

717 the timing of the highest number of taxa annual maxima is associated to the timing of

718 the annual maximum of phytopkakton biomass. The northward shortening of the period

719 of the year in which zooplankton taxa maxima occur also seems to be linked to the

720 seasonality of phytoplankton, since such period is shortest at SH coinciding with a later

721 diatom bloom and the annual maximun of dinoflagellates in summer, which merges the

722 chlorophyll maximum of late spring-early summer (Bresnan et al., 2015) and may

723 favour the grouping of zooplankton abundance in summer. The decreasing overlap of

724 holopankton taxa maxima and meroplankton taxa maxima periods northward is mainly

725 due to the shortening of the period of holoplankton taxa maxima and might be also

726 linked to different responses to phytoplankton availability. So the occurrence of

727 meroplankton taxa maxima distributed over a wide year period suggest that the

728 spawning behaviour of different benthic populations is not only dependent on

729 phytoplankton abundance directly but also on phytoplankton composition or physical

730 factors like temperature as reported in other studies (Starr et al., 1992; 1993; Highfield

731 et al., 2010).

732 Results revealed a clear effect of the trophic status on the seasonal patterns of

733 abundance and distribution of the annual maxima of zooplankton taxa when comparing

734 the mesotrophic site of B35 and the nearby oligotrophic site located at the same latitude

735 (U35). The most evident effect was the delay of the annual maximum from early spring,

736 mid spring, late spring or early summer at the oligrotrophic site to late spring, summer

737 or early autumn at the mesotrophic site in many taxa such as cirripede larvae,

738 cladocerans and their dominant genera *Evadne* and *Podon*, appendicularians, bivalve

739 larvae, decapod larvae, PCPCalanus and *Oithona*. By contrast, only *Oncaea* showed a

740 slight advance of the annual maximum from mid autumn at the oligotrophic site to early

741 autumn at the mesotrophic one. Another remarkable effect was the transformation of

742 some bimodal cycles at the oligotrophic site into trimodal cycles at the mesotrophic site,

743 as this was observed in the dominant group of copepods and some of their main

744 components (PCPCalanus and *Oithona*). As a result of the abovementioned changes in

745 the seasonal pattern of many taxa, most of the zooplankton taxa reached annual maxima

746 in early spring at the oligotrophic site but in early summer at the mesotrophic site. The

747 seasonal variations of zooplankton in Atlantic temperate marine systems are primarily

748 linked to temperature and phytoplankton availability (e.g. Feng et al., 2014), but

749 temperature does not show differences between U35 and B35, and consequently the

750 differences in the seasonality of zooplankton taxa seem to be mainly attributable to the

751 modified annual cycle of phytoplankton biomass and composition at the mesotrophic

752 site by human eutrophication (Garmendia et al., 2012;13). The chlorophyll *a* annual

753 cycle at the oligotrophic site (U35) showed the classical bimodal cycle, with maximum

754 values during the spring bloom and the subsequent summer decrease due to nutrient-

755 limitation, as it has been generically modelled for other nearby continental shelf areas of

756 the southern Bay of Biscay (Stenseth et al., 2006), while at the mesotrophic site (B35)

757 the standard cycle of Chl *a* showed a extended period of high concentration with the

758 maximum value in summer and a lower peak corresponding to the spring bloom. The

759 specific composition of holoplanktonic taxa such as cladocerans, *Evadne*, *Podon*,

760 appendicularians and PCPCalanus and *Oncaea* does no differ between sites, so the

761 delay in their maximum abundances at B35 in relation to U35 is because their

762 populations are able to reach higher densities after the spring bloom as a result of the

763 maintenance of a nutritionally rich environment until autumn. *Oithona* was the

764 exception, since in this case the delay of the annual maximum from early spring at U35

765 to early autumn at B35 was due to the dominance of *Oithona similis* at U35 and

766 *Oithona nana* at B35. *O. similis* is a spring peaking species that may be limited at high

767 (>20°C) temperatures (Castellani et al., 2016), while *O. nana* increase is associated with

768 high temperature and chlorophyll concentration, and to eutrophized/polluted systems

769 (Arfi et al, 1981; Villate, 1991; Jamet et al., 2001).

770 SUMMARY (CONCLUSIONS)

771 None of the between-site differences in interannual, seasonal or residual components of

772 zooplankton variability related to latitude since all of them were lowest at the

773 intermediate latitude site of the English Channel (L4). The highest interannual

774 variability at the southern site of U35 was related to a local event within the Bay of

775 Biscay that promoted an abrupt increase of total zooplankton and many relevant taxa in

776 2012 at this site, and to a lesser extent at B35. The seasonal component was highest at

777 the northernmost site of Stonehaven due to the higher recurrence and amplitude of

778 seasonal variations in many taxa. The highest residual component of zooplankton taxa

779 at B35 and U35 was attributable to the lower sampling frequency and the higher level of

780 natural and anthropogenic disturbance in comparison to the offshore sites of L4 and SH.

781 The lack of coherence in the interannual variability of zooplankton between the four

782 sites suggests that local factors rather than large-scale atmosphere-ocean forcing were

783 the main drivers of the year-to-year dynamics of shelf zooplankton abundance within

784 our study area during the period under study (1999-2013). The marked increase of total

785 zooplankton and several taxa in 2012 at U35, and to a lesser extent at B35, was not

786 observed in L4 and SH, thus denoting the local nature of this event. Therefore, the main

787 interannual differences in zooplankton abundance between sites were not attributable to

788 latitude-linked effects.

789 Seasonally the latitudinal effect on zooplankton dynamics was mainly shown by the

790 delay of the annual maximum or the early peak from spring at the southernmost site to

791 summer at the northernmost site in many taxa, accompanied by the advance in the

792 timing of the later peak northwards in taxa showing bimodal cycles, this resulting in

793 some cases in a unimodal cycle at the northernmost site. However, there were some taxa

Comment [AA18]: The discussion is very long and somight lose readers. Please try to reduce this, for instance this last section reiterates the Abstract. Perhaps you coukd just condense to a shortparagraph emphasising the imporance of inshore time series for the MSFD, and for distinguishing climatic varibility and change-induced perturbations fromacute effects from man (purpose of MSFD). For example you can cite the 2012 anomalies and the fact that this paper defines envelopes of variability.

794 showing early or late annual maxima that maintained very similar seasonal patterns at

795 all latitudes. Another interesting finding was the shortening of the period within which

796 holoplankton groups peaked, and the increase in the temporal segregation of the peaking

797 periods of meroplankton groups (earlier) and holoplankton groups (later) with

798 increasing latitude.

799 The trophic status affected the seasonal pattern of many zooplankton taxa in different

800 ways, i.e. the bimodal cycle of some taxa in oligotrophic conditions became trimodal in

801 mesotrophic conditions, and most taxa reached annual maxima in spring, associated to

802 the spring phytoplankton bloom, in oligotrophic conditions, while most taxa reached

803 annual maxima in summer, which is the period of highest phytoplankton biomass in

804 anthropogenically enriched conditions.

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