1   **Title page**

2

3   Title of article: **Density-dependent modulation of copepod body size and temperature-size**

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Running head (max 40 characters): **Density-dependent controls of copepod body size**

Keywords (between 5-12): zooplankton; temperature-size response; density dependence; competition for food; climate change; Western Channel Observatory; *Acartia clausi; Calanus helgolandicus; Centropages typicus; Oithona similis; Paracalanus parvus; Pseudocalanus elongatus; Temora longicornis.*

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Statement of significance

Dear Editor,

We hereby submit our manuscript entitled "**Density-dependent modulation of copepod body size and temperature-size responses in a shelf sea**" for consideration in *Limnology and Oceanography*.

54   Body size is a master trait, strongly influencing many biological rates (feeding, growth,

55   metabolism, reproduction, mortality), and ecological interactions. Body size reduction has also

56   been termed "the third universal response to climatic warming". The prevailing paradigm is that

57   body size responses of ectotherms to warming are governed largely by temperature and size

58   interactions with "bottom up" environmental factors (oxygen or food). Our field study - of 7098

59   adult female copepods across 13 different seasons spanning a 27-year period of warming at a

60   single shelf sea site - challenges this paradigm. We reveal the importance of density-dependent

61   factors

62   (most likely via competition) in modulating body size. Our study, based on the wellcharacterised

63   Plymouth L4 time series site, allows a far more robust and comprehensive interspecies

64   comparison than is possible, for example, by many meta-analyses which collate patchy

65   heterogeneous data on different species, sites and time periods.

66   For all these reasons, we believe that our study is of wide interest to aquatic ecologists

67   who study ectotherm life-history or population responses to environmental change, including

68   climate warming, as well as to those with special interest in impacts on marine zooplankton. This

69   is why we believe Limnology & Oceanography is the best journal for the publication of our

70   paper. We look forward to hearing your response in due course.

71   **Abstract**

72

73   Body size is a fundamental trait in ecology, and body size reduction with increasing temperature

74   has been termed the third universal response to climate warming. Whereas effects of temperature

75   and food on phenotypic plasticity of zooplankton adult body size have been investigated,

76   density-dependent effects have been neglected. We measured seasonal changes in the prosome

77   length of 7098 adult females of seven dominant copepod species in 13 years spanning a 27-year

78   period of warming at the L4 time series off Plymouth, UK. The seasonal Temperature-Size (T-S)

79   response varied greatly among species, from reductions of 2.93% of carbon mass $°C^{-1}$ for

80   *Paracalanus parvus* to 10.15% of carbon mass $°C^{-1}$ for *Temora longicornis*. Evidence for a

81   longterm T-S response was detected in at least two species, supporting the hypothesis that

82   climatic warming leads to smaller adult sizes. April was a crucial month for determining the

83   strength of the T-S response. During this month, body size related negatively to total

84   zooplankton abundance. We suggest that the mechanism for this density-dependence is via

85   competition for food and/or intraguild predation, since spring was also the period when the ratio

86   of food biomass to zooplankton biomass was at its lowest. Our study is among the first *in situ*

87   demonstrations of density-dependent effects on the body size of marine zooplankton and shows

88   the need to consider the effect of top-down as well as bottom-up factors on body size in a

89   warming climate.

90

91   **Introduction**

92   Body size is a 'master trait', influencing a multitude of physiological and ecological processes

93   and rates (Kleiber, 1947; Hirst et al., 2014; Andersen et al., 2016). Understanding how body size

94   is influenced by environmental conditions, including warming, is particularly important, given

95   that trophic interactions and vital rates are highly size-dependent in many pelagic ecosystems

96   (Hansen et al., 1994; Cuthbert et al., 2020). The commonly observed plastic phenotypic

97   response, in which body size at maturity of an ectothermic species declines with increasing

98   developmental temperature, is called the Temperature-Size Rule (Atkinson, 1994). Indeed,

99   smaller adult body size following growth in warmer conditions (a negative TemperatureSize (T-

100   S) response) is evident in many multivoltine aquatic invertebrates in laboratory experiments and

101   across thermally varying seasons and latitudes (Lock and McLaren, 1970; Forster et al., 2012;

102   Horne et al., 2017). More broadly, a warming-induced reduction in body size within a

103   community is regarded as one of the three universal responses to climate change, along with

104   responses of phenology (seasonal timing of life cycles) and geographical redistribution (Gardner

105   et al., 2011).

106

107   Body size reductions with warming are not only observed under controlled experimental

108   temperatures with food satiation (Lock and McLaren 1970; Lee et al., 2003; Forster et al., 2012),

109   but have been widely documented in thermally variable seasonal environments, often at

110   temperate latitudes (Horne et al., 2016, 2017) and with latitude (Horne et al., 2015). Such

111   correlations between seasonally-varying temperature and the body size of adults is largely

112   dependent upon periods in which adult recruitment is significant, and therefore the measured

113   environmental conditions relate closely to those experienced during the juvenile growth phase of

114   the recruiting adults. In many copepod species, in temperate and high latitude environments,

115   recruitment of adults is especially marked between spring and late summer, which has been

116   termed the 'Temperature Dependent Phase' (TDP) (followed by a 'Resting Phase' (RP) in

117   autumn-winter, Hirche et al., 2019).

118

119   Shifts in copepod body size have the potential to impact upon both their prey and their predators.

120   Besides temperature, food concentration and predation pressure can also impact growth and

121   development rates, and the body size achieved by copepod adults (Hall et al., 1976; Abrams and

122   Rowe, 1996; Bonecker et al., 2011). Indeed, seasonal body size variation is influenced by food

123   availability not only in copepods (Durbin et al., 1983) but other invertebrates too (Berrigan and

124   Charnov, 1994). Other factors that relate to the strength of T-S response in copepods include the

125   feeding mode and taxonomic affiliation of the species (Horne et al., 2016).

126

127   Pelagic copepod species play a pivotal role as grazers of microplankton, and as conduits of

128   energy and material to higher trophic levels, including fish and predatory invertebrates (Banse,

129   1995; Beaugrand et al., 2003). It is still unclear how their seasonal body size distribution varies

130   from year to year, and among species, and how this may change with respect to climate

131   warming. Sea surface temperature has increased significantly worldwide in the last 100 years

132   (IPCC report, 2014). However, climate warming occurs with great inter-annual fluctuations, yet

133   few previous studies have investigated the effects of copepod body size over multiple years

134   (although see e.g. Evans, 1981) and no study has simultaneously considered the T-S response of

135   many species over several years at a single location. To achieve such multi-year, within-site

136   synthesis of species body size responses across a copepod community we investigated seven

137   contrasting copepod species (*Acartia clausi, Oithona similis, Paracalanus parvus,*

138   *Pseudocalanus elongatus, Calanus helgolandicus, Centropages typicus, Temora longicornis*) in

139   13 years sampled from a 27-year record at the Plymouth L4 site, an inshore site in the Western

140   English Channel. To have several species measured over so many years allows us to explore both

141   inter-annual changes in body size and whether such patterns could be related to drivers related to

142   climate change.

143

144   Previous interpretations of size responses of different species based on meta-analyses across

145   different geographical locations and different decades (e.g. Horne et al., 2016) are potentially

146   complicated by the confounding effects of location-specific environmental factors. These

147   confounding effects make it hard to tease out the various biotic and abiotic factors that shape the

148   T-S response. For example, in addition to bottom-up factors, zooplankton community density has

149   already been shown to be related to increased mortality of copepod early-stages and to decreased

150   population growth, egg production and hatching success rate (Ohman and Hirche, 2001; Franco

151   et al., 2017). However, very little is known about the influence of community abundance *in situ*

152   on individual copepod body size. We used, for the first time, an extensive dataset from a single

153   location across multiple years to address the following questions: 1) To what degree do the

154   seasonal temperature-size responses of the seven copepod species differ? 2) Do food

155   concentration, long-term temperature anomalies, or both, regulate copepod size changes across

156   years? 3) Are copepod body size and strength of T-S response also governed by factors that

157   depend on zooplankton community density?

158

159

160   **Methods**

161   All the samples used for this study were taken from the zooplankton time series at Plymouth

162   Station L4 (50°15'N 4°13'W), 13 km SSW of Plymouth, which has been sampled at weekly

163   resolution, weather permitting, since March 1988 by Plymouth Marine Laboratory (Harris, 2010;

164   http://www.westernchannelobservatory.org.uk/). The water is ~54 m deep, which stratifies

165   seasonally, with a thermocline forming typically from about May to September. Surface water

166   temperature typically ranges from about 9°C in winter to 17°C in summer. The study location is

167   affected periodically by freshwater outflow from the rivers Plym and Tamar at Plymouth (Rees

168   et al., 2009). Further details about the Plymouth L4 station and microplankton and zooplankton

169   sampling are reported respectively in Widdicombe et al., (2010) and Atkinson et al.

170   (2015).

171

172   **Environmental data**

173   An electronic probe for conductivity, temperature and depth analysis (CTD) is currently used at

174   L4, but sea surface temperature (SST) has been measured consistently throughout the whole time

175   series using a mercury-in-glass thermometer inside a stainless steel bucket of water collected at

176   the surface. For consistency across all our sampling years, we used these latter measurements,

177   which showed close agreements with surface values from the CTD (Atkinson et al. 2015).

178

179   **Food data**

180   Microplankton, which are used to represent the copepod food variable in our study, have been

181   routinely collected and identified on a near-weekly basis since October 1992. Paired water

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182   samples collected from 10m depth were preserved at sea with acid Lugol's iodine and neutral

183   formaldehyde. Samples were analysed at Plymouth Marine Laboratory following the British and

184   European Standard EN 15204:2006 "Water quality - Guidance standard on the enumeration of

185   phytoplankton using inverted microscopy" (Utermöhl technique, more microplankton sampling

186   details in Widdicombe et al., 2010). For this study we used the carbon mass density values

187   (measured as mg C m^{-3}) of diatoms, dinoflagellates, coccolithophorids and *Phaeocystis*, as well

188   as ciliates and flagellates, from the following copepod data years that had microplankton data

189   availability: 1993, 1997, 2000, 2003, 2005, 2008, 2010, 2012, 2013 and 2014. The flagellate

190   group includes taxa that are nanoplanktonic in size, although only the larger nanoflagellates were

191   counted using the above method. However for simplicity we term our copepod food variable

192   "microplankton" since this group encompasses the size range which the copepods can eat.

193

194   **Zooplankton data**

195   Zooplankton have been sampled since 1988. Each sample consisted of two replicate tows made

196   with a WP-2 net (56 cm diameter, 200 µm mesh) towed vertically from a depth of 50 m to the

197   surface. Each plankton sample was fixed in 4% buffered formalin. Laboratory analysis involved

198   counting and identifying large and/or rare taxa in a fraction of the original sample (a half, a

199   quarter or an eighth, depending on the abundance of the original), sub-sampled using a Folsom

200   plankton splitter (Atkinson et al., 2015; Highfield et al., 2010). Each replicate was given an

201   estimated abundance average, measured as individuals m^{-3} (John et al., 2001). The source of the

202   dataset used here can be found in Atkinson et al. (2019).

203

204   For this study, one sample per month from April to October was considered from each of the

205   years 1989, 1991, 1993, 1995, 1997, 2000, 2003, 2005, 2008, 2010, 2013, 2014, 2016. These

206   years were chosen to cover a wide range of temperature conditions between years at L4, with

207   1991 being the coldest, and 2014 the warmest year. Other years, with intermediate temperature,

208   were chosen in order to provide a wide range of coverage and conditions.

209

210   **Body size measurements**

211   One quarter of each plankton sample was removed and observed under the stereomicroscope in

212   order to identify the first 30 (when possible) adult females of each of the species: *Acartia clausi,*

213   *Oithona similis, Paracalanus parvus, Pseudocalanus elongatus, Calanus helgolandicus,*

214   *Centropages typicus and Temora longicornis*. In the case of *C. helgolandicus* a small number of

215   the congener *Calanus finmarchicus* may have been inadvertently included, as these occur rarely

216   at the site (a median composition of 4% of *C. finmarchicus*, according to Maud et al., 2015).

217   Each individual was photographed with a stereomicroscope digital camera and then processed

218   using the software ImageJ to determine prosome lengths, by measuring from the tip of the

219   cephalothorax to the end of the last pedigerous somite. To avoid erroneous size estimations of *C.*

220   *typicus* resulting from broken spines, the end of the prosome was considered not as the tips of its

221   two most posterior lateral spines, but as the mid-point where the prosome articulates with the

222   urosome. In *O. similis* the end of the prosome is very hard to identify because of its complex

223   structure and reduced size, so, instead, we measured to the connection between the first and the

224   second segment of the urosome, as this is more visible (as done in Sabatini and Kiørboe 1994).

11

225　Prosome lengths were converted into estimated carbon mass (µg) using appropriate species-

226　specific equations from the published literature (See Table S1). These equations were obtained

227　from copepods commonly sampled in the North Sea. However, for all analyses we tested both

228　estimated carbon mass and prosome length, in order to see if different patterns would emerge.

229

230　**Determination of temperature-dependence of body size reduction**

231　We defined the TDP for each species as between the month with the largest average size (1st

232　generation of copepods of the year) and the month with the smallest average size (last generation

233　of the year). To quantify the relationship within the TDP between mean adult body size in each

234　month and temperature in the previous 30 days, the mean carbon mass values for each species in

235　each month in each year was regressed against mean temperature recorded in the 30 days prior to

236　and including the sample day. We chose 30 days partly to correspond broadly with previous

237　studies on the generation times of the same seven species (Sabatini and Kiørboe, 1994; Irigoien

238　and Harris, 2003; Leandro et al., 2006; Carlotti et al., 2007; Stegert et al., 2007; Dzierzbicka-

239　Głowacka et al., 2011). For fitting the body size-temperature regressions (µg C individual^{-1} vs.

240　°C) we used exponential models as in Horne et al. (2016). The slopes from these exponential

241　regressions were transformed into percentage change in carbon mass per °C as: $(exp^{slope} -1) \times 100$

242　(Forster et al., 2012). These values have a negative value when mass decreases with warming,

243　and a positive value when body mass increases with increasing temperature.

244

245 To assess interannual change in body mass, carbon mass values were transformed into anomaly

246 values i.e., the observed value for a specific month in a given year, minus the mean value for that

247 month across all 13 years. Anomalies of temperature and food biomass concentrations were also

248 determined, but to ascribe these values to the copepod juvenile developmental period they were

249 calculated as mean values over the 30 days prior to the date at which the copepod body sizes

250 were determined. To assess the seasonal effect of food (estimated as the sum of diatoms,

251 dinoflagellates, coccolithophorids, *Phaeocystis*, flagellates and ciliates biomass (mg C m^{-3})) on

252 body size, the body mass values (μg C) were plotted against the average concentration of food in

253 the 30 days prior to the sample day. A multiple linear regression model was used to test the

254 effect of food and temperature together ($\log_{10}$(Carbon mass) ~ Temperature + Food). Food data

255 were derived from fewer years (nine years), so the relationships among food, temperature and

256 copepod body size were examined using the same nine sample years across all months.

257

258 To test the relationship between zooplankton density and adult female copepod body size, we

259 first tested for each month the effect of total zooplankton density on carbon mass values of all

260 the 7 copepod species (scaled, centred and pooled together with the z-score method: (value –

261 mean) / standard deviation). The only significant size-density correlation was in April, which had

262 the strongest beta coefficient ($\beta = -0.52$, $p < 0.01$, n = 81). We therefore regressed body mass

263 values of all copepod species in April against the density (ind m^{-3}) of the different groups of

264 zooplankton: 1) gelatinous zooplankton (i.e. cnidarians and ctenophores), 2) holoplanktonic

265 crustaceans, 3) fish larvae, 4) non-gelatinous/non-crustacean holoplankton, and 5) meroplankton.

266 These were all estimated as the mean density in the 30 days prior to the date on which body size

267   was determined. The second variable (holoplanktonic crustacean density) was the strongest and

268   only significant one. We therefore performed species-specific linear regression between carbon

269   mass and holoplanktonic crustacean density, for each month. Another multiple regression was

270   performed to assess the effect of holoplanktonic crustacean density, temperature and food on

271   copepod body size in April. In all multiple regressions we checked the collinearity of each

272   independent variable (those with a Variance Inflation Factor greater than 5 were discarded, as

273   suggested in James et al., 2017).

274

275   **Results**

276   **Seasonal variation in adult body size**

277   A total of 7098 adult females were measured from the seven copepod species studied. The

278   duration of the Temperature Dependent Phase (TDP) differed slightly among the species: this

279   period was from April to October for *Acartia clausi, Oithona similis, Paracalanus parvus,*

280   *Pseudocalanus elongatus,* and from May to October for *Calanus helgolandicus, Centropages*

281   *typicus, Temora longicornis* (Figure 1). In each species, body mass showed a strong significant

282   negative correlation with temperature, being weakest in *Paracalanus parvus* ($R^2 = 0.25$,

283   compared to 0.48-0.82 for the other species; Figure 2). Copepod carbon mass variation was

284   always better explained by temperature than by food biomass (as judged by the outcomes of the

285   models in Table 1).

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Inter-annual variation in copepod adult body size

Simple linear regressions between monthly adult carbon mass and year were never significant (no evident increase or decrease overall over years) for any species. However, any potential body size reduction driven by climate change is likely to be obscured by great inter-annual fluctuations in warming at the L4 site over time (Atkinson et al., 2015), including a lack of correlation between warming anomalies in one season versus another season. For instance, temperature during summer at L4 is not significantly correlated with the temperature in the preceding spring ($R^2 = 0.09$; $p = 0.08$, n = 31). Therefore, relatively colder summers may sometimes follow relatively warmer springs and *vice versa*. For this reason, monthly anomaly values of carbon mass, temperature and food biomass across years were used to assess long-term changes in these variables and their co-dependence in each of the copepod species. Monthly carbon mass anomalies were negatively related to monthly temperature anomalies for: *Acartia clausi* and *Centropages typicus* as shown in Figure S1 (Suppl. Information), revealing the existence of an inter-annual T-S response along with the seasonal one. No species showed significant regressions between their body mass anomaly and food biomass anomaly.

In April, the only month that showed a significant relationship between body size of all species pooled and total zooplankton density, effects of densities of different groups of zooplankton on the overall copepod carbon mass (z-scores) showed that holoplanktonic crustacean density was the strongest and only significant explanatory variable ($\beta = -0.69$, $p < 0.05$). Across the seven copepod species and seven months (49 combinations) examined, significant correlations were found between $\log_{10}$ of adult body carbon mass of a given copepod species and $\log_{10}$ crustacean

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309 holoplankton density in eight cases: six were confined to April (all species except *A. clausi*) and

310 one in October (*Calanus helgolandicus*). All these seven body mass-holoplankton density

311 relationships were negative (Figure 3), accounting for between 47 and 80% of the variance in log

312 adult copepod body carbon mass in April, and 38% in October (Figure 3).

313

314

315 **Discussion**

316 **Seasonal T-S response and taxonomic differences**

317

318 This study represents one of the most comprehensive comparisons of seasonal and inter-annual

319 shifts in body size of multiple copepod species at a single site, based on 7098 individuals

320 measured. Indeed, this work allows the assessment of pelagic copepod body sizes from a single

321 location and hence with similar environmental conditions and annual temperature range (~ 10

322 °C), which makes the comparison across species much easier than in previous meta-analyses, in

323 which different species had experienced different environments (Horne et al., 2016). Firstly, we

324 assessed that the TDP of our species started around April or May (depending on the species) and

325 generally terminated around October, similar to what was shown in previous *in situ* analyses

326 (Hirst et al., 1999; Horne et al., 2016; Cornwell et al., 2018). During the rest of the year (the so-

327 called 'Resting Phase', set roughly between November and March) there appears to be little or

328 no recruitment to the adult stage (Djeghri et al., 2018), hence, adult size in the resting phase is a

329 legacy of conditions at the end of the previous TDP, possibly coupled with any size-dependent

330 adult mortality during the resting phase. The 'Transition Phase' then follows, usually in the first

months of Spring (March, April, May), when a mix of older but smaller individuals (from the

resting phase), and newly recruited, larger, individuals are found (Hirche et al., 2019).

Among our seven species, the range in T-S strength (based on monthly size and temperature

values, across the TDP over 13 years) was wide: strongest values were ~-8% to ~-10% change in

C mass $^{\circ}C^{-1}$ for *Acartia clausi, Centropages typicus, Pseudocalanus elongatus* and *Temora*

longicornis. This last species had the most intense T-S response (-10.15% change in C mass $^{\circ}C^{1}$),

with body size in October roughly half that at the start of the TDP. This reduction of body mass

may be associated with a change in copepod fitness, feeding rates and food web connectivity

(Hansen et al., 1994; Rice et al., 2014). The weakest T-S response (-2.93% change in C mass $^{\circ}C^{-1}$

), demonstrated in *Paracalanus parvus* (Order Calanoida), was considerably weaker than that of

the other Calanoida, while *Oithona similis,* the only non-calanoid, had the second weakest T-S

response (-3.33% change in C mass $^{\circ}C^{-1}$). These marked differences concur with the weak T-S

response in both *O. similis* and *P. parvus* observed by Horne et al., (2016). This latter species

also showed the most inconsistent T-S relationship, with the lowest R^2 (0.25, see Table 1).

However, the seasonal body length distribution of *P. parvus* observed by Riccardi and Mariotto

(2000) and Hirche et al. (2019) was similar to the one we have found. A difference in the T-S

response strengths between Cyclopoida and Calanoida species, although not statistically

supported here (possibly because of limited number of taxa), has previously been observed by

Horne et al. (2016), who suggested this may relate to their different feeding strategies (active

filtering in calanoids vs. ambush-feeding in cyclopoids) and the difference in body mass scaling

of physiological rates between these different feeding types.

Effects of food concentration on copepod body size

The models showed that, seasonally, temperature was always a stronger predictor of copepod body size than was food biomass (Table 2). It is possible, however, that our use of measured body lengths rather than actual masses or biovolumes may have led to our overlooking effects of food concentration on changes in body condition, hence actual carbon mass values. As Klein Breteler and Gonzalez (1988) found in laboratory experiments, food is likely to affect more the "fatness" of a copepod than its prosome length. However, the direct C mass determinations made from L4 (Fig. 6 in Pond et al. 1996) show that even for the larger lipid-storing species *Calanus helgolandicus* females have a -8.9% change in µg C $°C^{-1}$ (95% C.I.: -11, -6.8) during the TDP. This does not differ significantly from the estimates in our study based on prosome length-mass conversion (-6.2%; 95% C.I.: -7.5, -4.9).

Inter-annual body mass variation

We tested species-specific size anomaly against temperature anomaly from each individual month and year, to see how the copepod body size would react in the same month of another year with anomalous temperature (Figure S1). Only two species (*Acartia clausi* and *Centropages typicus*) showed a significant negative correlation between carbon mass anomaly and temperature anomaly. This shows the existence of a long-term T-S response in at least these two species. Although R^2 values were ≤ 0.2, in evolutionary terms, even low effect size values may still be relevant and significant. High scatter may also have been caused by the low number of years (13), lag effects, food seasonality, and the high scatter of the SST - time relationship at L4

18

375   itself (R^2 = 0.17, Atkinson et al., 2015). Temperature increases are apparent in the English

376   Channel, although with a shallow slope (0.02° C increase per year, Atkinson et al., 2015) and

377   great inter-annual variability, making climate-change impacts on the plankton community more

378   challenging to detect. Moreover, body size in April was not modulated by temperature or food,

379   and as described in the next section, density-dependent effects became more important then.

380   When April samples were removed, two further species showed significant and negative long-

381   term T-S responses: *Pseudocalanus elongatus* and *Oithona similis*. Therefore, it is reasonable to

382   hypothesize a generalized long-term T-S response in most of the copepod species, consistent

383   with similar findings in *Acartia tonsa* and *A. hudsonica* by Rice et al., (2014) and in fish by

384   Daufresne et al. (2009). A long-term decrease in body size, driven by global warming, would

385   have major implications for food web structure and function, given the strong size-structuring

386   (Webb, 2012) and importance of copepods in these food webs (Ware and Thomson, 2005).

387

388   **Copepod T-S response strength relates to zooplankton density**

389   To date, very few studies (e.g. Cyr and Pace 1993) have explored how body size of copepods

390   may be impacted by the abundance of their own species or of the whole community, and this

391   topic has been historically underexamined in the marine environment. Our analysis of large

392   numbers of individuals, sampled through multiple seasons at a single site, showed a strong

393   relationship between copepod size and holoplankton density (in April), providing new evidence

394   that density-dependent controls on copepod body size can operate *in situ*.

395

396   Are the changes in copepod body size reflecting density-dependent changes in competition or

397   predation? The timing of the strong relationship with zooplankton density, being found only in

398   April, may provide some clues to the cause. In the spring months of March and April, food levels

399   were still low and increasing, whereas their grazers had already reached fairly high biomasses

400   (Fig. 4; Atkinson et al. 2015). The period preceding and including April thus experienced a low

401   food concentration to grazer biomass ratio (Fig. 4), pointing to the potential for increased

402   competition for food at this time. The ensuing competition for food may provide one explanation

403   for the reduced copepod size with increased community density in April.

404

405   An alternative or additional explanation for the density-dependent effects observed in April may

406   relate to direct predation. Work at L4 has increasingly emphasized the role of predation in

407   regulating copepod abundance and phenology (e.g.: Bonnet et al., 2005; Atkinson et al. 2015;

408   Cornwell et al 2018). Some of the food consumed by adult copepods is in fact often early stages

409   of copepods (Irigoien and Harris, 2006; Boersma et al., 2014; Djeghri et al., 2018), as well as

410   eggs (Hirst et al., 2007; Maud, 2017; Cornwell et al., 2018). Ohman and Hirche (2001) suggested

411   that cannibalism could even be a form of population self-limitation from their study on *Calanus*

412   *finmarchicus,* and likewise Maud (2018) concluded the same for *C. helgolandicus* at L4. This

413   intraguild/cannibalistic predation on young stages would explain a reduced size at adulthood

414   according to Abrams and Rowe (1996), who affirm that high mortality rates on early stages

415   favour earlier maturity (hence smaller size at adult). The same phenomenon occurs for fish when

416   exposed to intense fishery activity (Olsen et al., 2004). However, this would imply that juvenile

417   copepods must produce an adaptive plastic response (developmental acceleration) to predation

418   cues during the Transition Phase (April), when exposed to high predation risk. Hence, the

20

419 intraguild predation hypothesis seems to need several assumptions in order to be sustained,

420 whereas the competition for food appears a simpler explanation. As is apparent in Figure 4,

421 increases in zooplankton abundance at L4 tend to occur well before the spring bloom, a

422 phenological effect seen across a suite of the component taxa including copepods (Atkinson et al.

423 2015). It is possible that the first cohorts of copepods of the TDP (around April) that are highly

424 abundant, when food is relatively scarce, will suffer from a poor diet and reach adulthood at a

425 more reduced size than usual (Durbin and Durbin, 1978; Klein Breteler and Gonzalez, 1988).

426

427 In this study we observed that the T-S response strength varies substantially among different

428 copepod species. This variation may relate to different thermal sensitivities of mechanisms

429 generating thermal reaction norms for growth and development rates (Verberk et al. 2020).

430 Intriguingly, large differences between species also exist in the two other "universal" responses

431 of copepods to climate change: the phenological response (Atkinson et al., 2015; Mackas et al.,

432 2012) and the distributional change (Chivers et al., 2017). These contrasting responses are also

433 manifested in their long-term population trajectories of the major copepod species. Most have

434 undergone substantial declines in summertime abundance across the NE Atlantic, whereas a few

435 species have increased (Schmidt et al. 2020). It is therefore an urgent priority to explore whether

436 these responses to climate change are inter-related, paying particular attention not just to bottom-

437 up controls, but also to top-down factors.

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Acknowledgments

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703

Conflict of interest
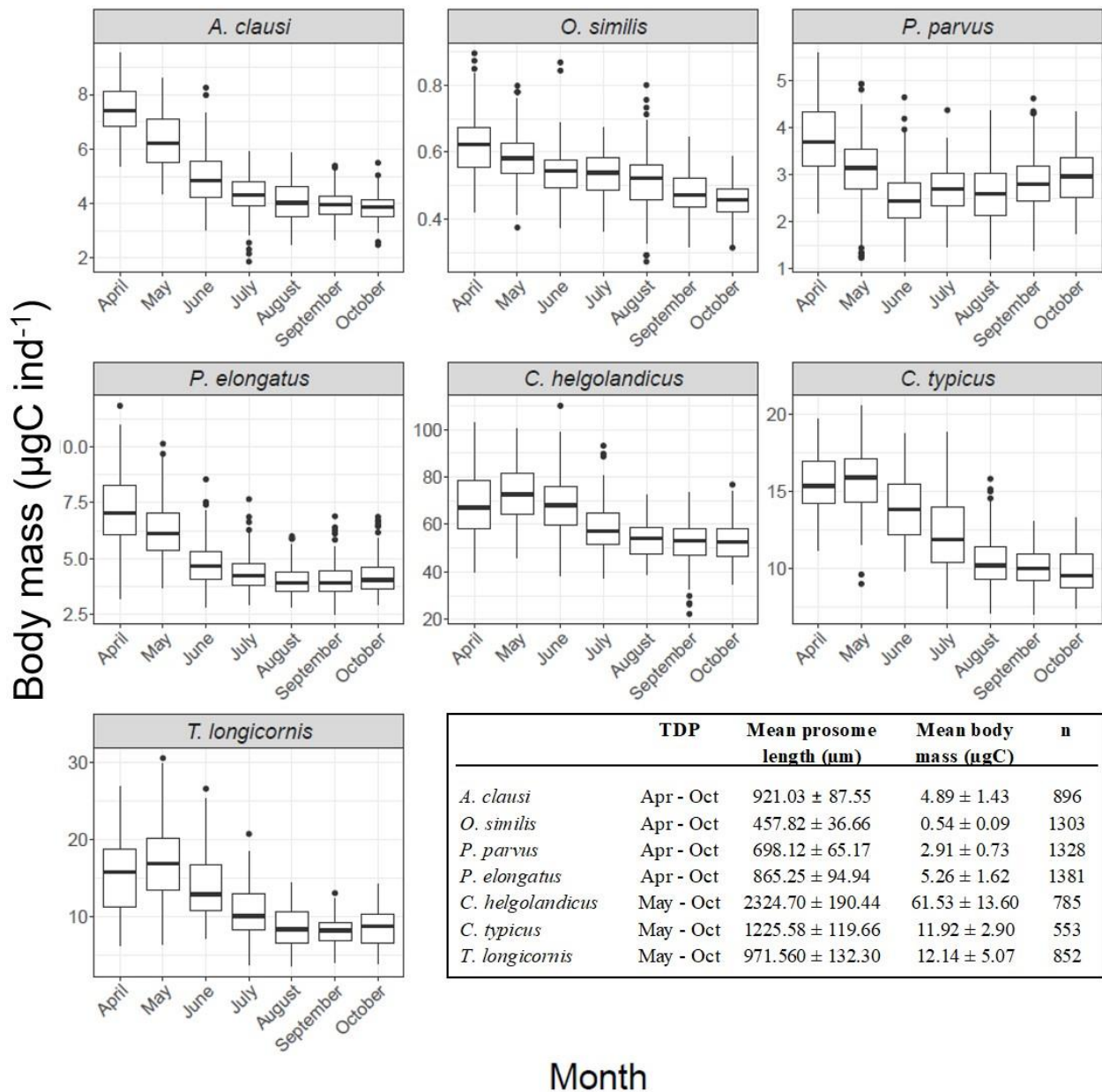
705   None declared

Tables ang Figures

707

708 Table 1: Multiple linear regressions coefficients: Standardized beta coefficients (β_T refers to

709 temperature coefficient and β_F refers to food biomass coefficient, in bold when significant) R^2

710 and p values of each model. The regression equations with actual units for each species are here

711 reported: *A. clausi:* $\log_{10}M = 2.75 - 0.08T + 3 \times 10^{-4}F$; *P. parvus:* $\log_{10}M = 1.74 - 0.02T - 0.07F$;

712 *P. elongatus:* $\log_{10}M = 2.83 - 0.07T - 0.05F$; *O. similis:* $\log_{10}M = -0.30 - 0.04T + 0.05F$; *C.*

713 *helgolandicus:* $\log_{10}M = 4.61 - 0.05T + 0.06F$; *C. typicus:* $\log_{10}M = 3.26 - 0.07T + 0.07F$; *T.*

714 *longicornis:* $\log_{10}M = 3.70 - 0.09T + 0.02F$ (note that M refers to body mass measured as µg C,

715 T refers to temperature measured as the average °C of sea surface in the 30 days before sampling

716 day, and F refers to food biomass measured as the average mg C m^{-3} in the 30 days before

717 sampling day).

718

RESPONSE	**Log$_{10}$(Body mass)**			
PREDICTOR	**Temperature + Food biomass**			
	β_T	β_F	R^2	p
Acartia clausi	**-0.90**	0.00	0.81	< 0.01
Paracalanus parvus	**-0.41**	**-0.26**	0.30	< 0.01
Pseudocalanus elongatus	**-0.79**	-0.14	0.73	< 0.01
Oithona similis	**-0.82**	**0.27**	0.54	< 0.01
Calanus helgolandicus	**-0.77**	0.18	0.48	< 0.01
Centropages typicus	**-0.90**	**0.18**	0.74	< 0.01
Temora longicornis	**-0.76**	0.04	0.54	< 0.01
Average	-0.76	0.04		

719

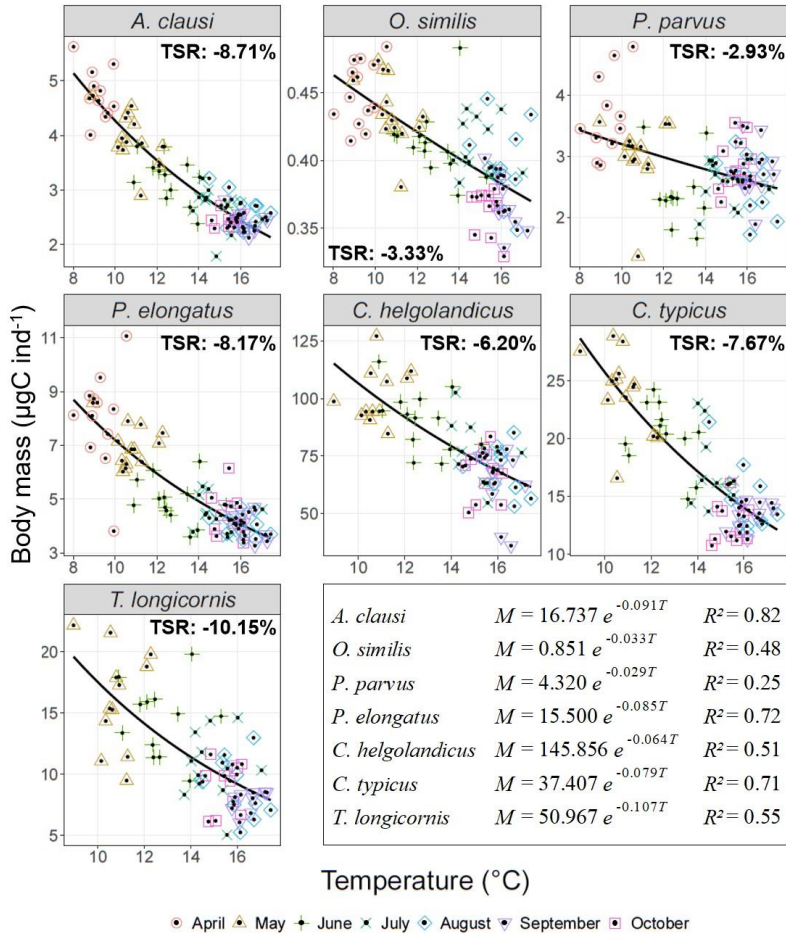|	TDP	Mean prosome length (µm)	Mean body mass (µgC)	n
A. clausi	Apr - Oct	921.03 ± 87.55	4.89 ± 1.43	896
O. similis	Apr - Oct	457.82 ± 36.66	0.54 ± 0.09	1303
P. parvus	Apr - Oct	698.12 ± 65.17	2.91 ± 0.73	1328
P. elongatus	Apr - Oct	865.25 ± 94.94	5.26 ± 1.62	1381
C. helgolandicus	May - Oct	2324.70 ± 190.44	61.53 ± 13.60	785
C. typicus	May - Oct	1225.58 ± 119.66	11.92 ± 2.90	553
T. longicornis	May - Oct	971.560 ± 132.30	12.14 ± 5.07	852

720

Figure 1: Seasonal body mass distribution (µg C ind^{-1}) of adult females for each of the seven pelagic copepod species at the L4 site. The TDP of each species is reported in the box on the bottom-right, along with species-specific mean prosome length and mean body mass values (both with corresponding ± standard deviations) across all samples.

725

A. clausi   TSR: -8.71%

O. similis   TSR: -3.33%

P. parvus   TSR: -2.93%

P. elongatus   TSR: -8.17%

C. helgolandicus   TSR: -6.20%

C. typicus   TSR: -7.67%

T. longicornis   TSR: -10.15%

Body mass (µgC ind^{-1})

A. clausi	$M = 16.737\,e^{-0.091T}$	$R^2 = 0.82$
O. similis	$M = 0.851\,e^{-0.033T}$	$R^2 = 0.48$
P. parvus	$M = 4.320\,e^{-0.029T}$	$R^2 = 0.25$
P. elongatus	$M = 15.500\,e^{-0.085T}$	$R^2 = 0.72$
C. helgolandicus	$M = 145.856\,e^{-0.064T}$	$R^2 = 0.51$
C. typicus	$M = 37.407\,e^{-0.079T}$	$R^2 = 0.71$
T. longicornis	$M = 50.967\,e^{-0.107T}$	$R^2 = 0.55$

Temperature (°C)

⊙ April   △ May   + June   × July   ⊙ August   ▽ September   ☐ October

726

727 Figure 2: Exponential regressions (solid lines) between monthly average body mass (µg C ind^{-1})
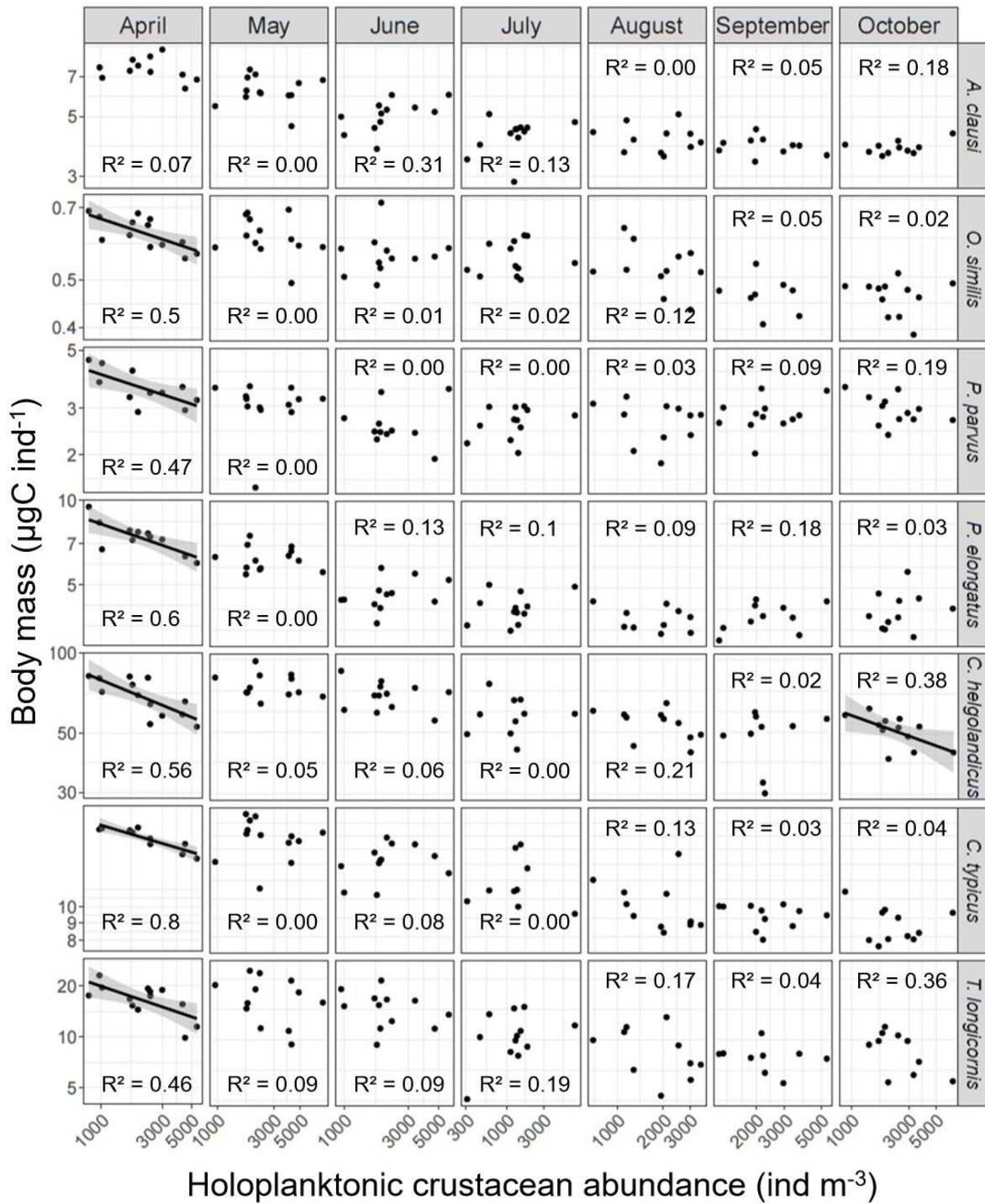
728 values and temperature (°C), across all 13 years studies. On each plot the TSR is also reported

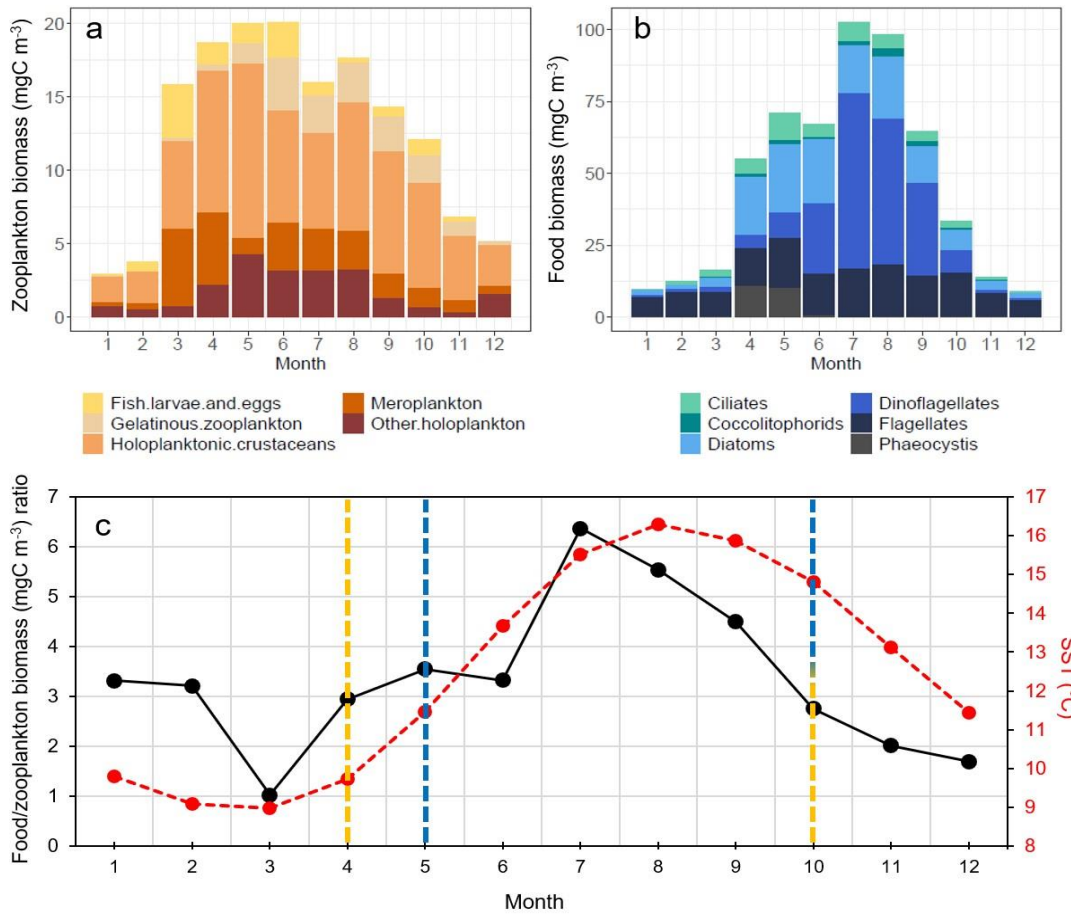729 (expressed as % change in µg C °C^{-1}). Values for each month are indicated by the different

730 symbols, see key in the lowest part of the figure. In the box on the bottom-right, each exponential

731 TSR regression is reported along with its corresponding R^2 value (note: M = body mass, T =

732 temperature.

Figure 3: Monthly mean body mass of the adult females of the 7 copepod species ($\mu g\ C\ ind^{-1}$) plotted against holoplanktonic crustacean abundance (ind m^{-3}). Associated R^2 values are reported, solid black lines represent significant regressions. Note that both the x and y scales are on a log_{10} scale.

37

737

Figure 4: a) Zooplankton biomass (mg C m^{-3}) distribution across months for five major functional

groups (see key; note that "holoplanktonic crustaceans" is the group whose density in April is

inversely correlated with copepod body mass in April (Figure 3); "other holoplankton" refers to non-

crustacean and non-gelatinous holoplankton); b) food (microplankton) biomass (mg C m^{-3}) across

months for six major functional groups (see key); c) food/zooplankton biomass ratio (black solid

lines) and sea surface temperature (red dashed lines) across months, vertical dashed lines indicate the

boundaries of the TDP April- October (yellow vertical line) and the TDP May-October (blue vertical

line). Plots are based on the whole L4 time-series (1988-2019).