

1 **Dear Editor and Referees,**
2 **Attached is a new version of the Ms, all new/significantly corrected parts are in**
3 **blue/red. See detailed comments below.**
4

5 Yamaguchi (Referee) a-yama@fish.hokudai.ac.jp Received and published: 18 June 2016
6 This manuscript provides biomass and taxonomic compositions of meso- and
7 macrozooplankton down to greater depths. Correlation analyses between surface chlorophyll
8 a and standing stocks of various large-sized zooplankton are quite interesting and including
9 important issues. Dominance of shrimp in deep-layer is not fully documented previously.
10 This study showed their importance clearly. The message of this study is clear, robust and
11 easy to understand. Following my comment is very minor.
12

13 My only concern is at Discussion on net avoidance. For me, mentioning that vertical tow is
14 more robust for net avoidance than that of the horizontal tow is anomalous. While discussion
15 on this subject (net avoidance of shrimp) is not at main focus of this study, their effect may
16 have large impact for implication of this study.
17

18 **Authors' comment 1:** We thank Dr. Yamaguchi for his comments and for a high evaluation
19 of our work. Concerning the net avoidance, we just try to explain why vertical hauls give
20 evidence for higher SHRIMP (only shrimp) biomass values (respective to the horizontal
21 hauls). We feel that our explanations based on visual observations may make sense. As a
22 possible compromise, we have removed the last sentence "We propose the use of vertically,
23 not horizontally, towed large nets for more representative assessments of deep-pelagic
24 shrimp abundance". We have also added the following paragraph: "In contrast to decapods,
25 pelagic fishes escape in horizontal direction, as has been observed from submersibles many
26 times by the authors. This reaction is successful when vertical hauls are used and our results
27 are thus not representative for assessment of the pelagic fish biomass. This biomass may
28 occur to be finally correlated with Chl but horizontally towed gears are necessary to prove
29 that".
30

31 Interactive comment on "A novel approach reveals high zooplankton standing stock deep in
32 the sea" by A. Vereshchaka et al. Anonymous Referee #2 Received and published: 28 July
33 2016.

34 This manuscript presents an interesting attempt trying to explain deep sea zooplankton
35 biomass with surface chlorophyll concentrations. The importance of the conclusion is clear
36 as the ability to predict deep-sea zooplankton biomass from satellite-derived proxies would
37 be very useful. However, the results are not fully presented and cast doubt on the overall
38 conclusion.
39

40 In particular: - what is the actual data coverage? - how many nets were deployed in total? -
41 how many organisms were counted? - what seasons have been sampled? - what are the
42 uncertainties on your estimates? A detailed list and some metadata analysis (beyond Fig 1
43 and 2) would be useful here. Maybe a table in the supplementary material (e.g. with sampling
44 date, time and location, temperature, surface Chl, volume samples, number of individuals
45 counted)?
46

47 **Authors' comment 2:** A new Table 1 including additional information about samples is now
48 included.
49

50 Also, a figure similar to Fig 2 but with biomass instead would be useful.
51

52 **Authors' comment 3:** This figure may be given for a certain transect only, not for the whole
53 dataset discussed. Part of data along a submeridional transect (36th and 37th Cruises of the
54 R/V " Akademik Sergey Vavilov ") has been analyzed in detail and published with transect
55 in a more specialized journal; **see also comment 5.**
56

57 A scatter plot of the raw data (biomass vs Chl) is needed to properly evaluate the correlations
58 summarized in Table 2.

59
60 **Authors' comment 4:** Done as a new figure 5. In addition, Table 3 is redone to represent
61 more information about regressions (coefficients of determination (R^2), equations, and levels
62 of significance).

63
64 Over 300 taxa were identified but the data was then combined to three vaguely defined
65 groups. I am surprised that community composition is not presented, and I think it would
66 greatly enhance the manuscript.

67
68 **Authors' comment 5:** In fact, the whole database of this work contains two different
69 datasets: (1) data of 2012-2013 (R/V "Akademik Sergey Vavilov", mainly Central and South
70 Atlantic) and (2) data of 1994-2005 (R/V "Akademik Mstislav Keldysh", mainly North
71 Atlantic). Samples have been taken with the same protocol, but identification was much more
72 precise for the first dataset. The community composition, diversity, and other community
73 patterns have been analyzed in detail for the first dataset and presented in a recent paper (A
74 Vereshchaka, G Abyzova, A Lunina, E Musaeva, 2016. The deep-sea zooplankton of the
75 North, Central, and South Atlantic: Biomass, abundance, diversity. Deep Sea Research Part
76 II: Topical Studies in Oceanography. DOI: 10.1016/j.dsr2.2016.06.017). The second dataset
77 contains representative biomass values and significantly contributes to the metadata
78 concerning deep zooplankton; here we combine both datasets for a more comprehensive
79 analysis. Now we clarify the situation in the Methods section.

80
81 Throughout the manuscript, Chl concentrations and primary production are used
82 synonymously. They are not the same and should therefore be discussed more carefully (e.g.
83 L53).

84
85 **Authors' comment 6:** Corrected

86
87 L120ff: Is this contribution normalized for the depth horizons? Otherwise it is not surprising
88 that the integrated biomass in the bathypelagic (1500 to 3000 m depth) is larger than in the
89 mesopelagic (200 to ~600 m depth). Indeed Table 1 shows that biomass per m^3 was highest
90 in the upper bathy-pelagic. This difference and the implications are worthwhile discussing.

91
92 **Authors' comment 7:** No, contribution is not normalized for the depth horizons, as we
93 clearly consider standing stocks. The contribution of different depth layers is not obvious:
94 could the anonymous reviewer foresee that the standing stock in the upper bathypelagic (ca.
95 700 m thick) is much higher than in the more rich mesopelagic (ca. 400 m thick) and even
96 more productive epipelagic (200 m thick)? By the way, Table 1 shows that biomass per m^3
97 was highest in the epipelagic followed by the upper bathypelagic (NOT mesopelagic) for the
98 total plankton and most groups.

99
100 Potential time lags between surface chlorophyll concentrations and biomass in the deep sea
101 have not been discussed. You do not explain why you excluded data from temperate waters
102 (L74). A justification is needed.

103
104 **Authors' comment 8:**

105 We have added in the "Method" chapter the following sentence: "We excluded data from
106 temperate waters where the major spring peaks in primary production are being exported
107 from the euphotic zone (0–200 m depth) and reaching abyssal depths (4000 m) with a
108 significant time lag (e.g., 42 days: Smith et al., 2002); this lag differs for different depth
109 zones that may corrupt possible correlations".

110

111 The introduction should give a fairer representation of the literature. It is, for example, not
112 true that information about deep-sea zooplankton is available for the North Atlantic only
113 (L37).

114
115 **Authors' comment 9:** L37 is an awkward construction, which is now corrected and a
116 greater reference list across all Oceans is provided in the Introduction; for example, the
117 following sentence is included: "Studies on the deep-sea plankton biomass at selected sites
118 include those in the North Pacific (e.g., Vinogradov, 1968; Murano et al., 1976; Yamaguchi
119 et al., 2002a, b; Yamaguchi, 2004) and Eastern Tropical Pacific (Sameoto, 1986), North
120 Atlantic (Koppelman and Weikert, 1992; 1999; Gislason, 2003; Vinogradov, 2005) and
121 Mediterranean Sea (Scotto di Carlo et al., 1984; Weikert and Trinkaus, 1990), Indian Ocean
122 (Vinogradov, 1968) and Arabian Sea (Koppelman and Weikert, 1992; Böttger-Schnack,
123 1996)".

124
125 Minor comments: Throughout the manuscript, it would be useful if the type of biomass that
126 is referred to would be made clear (e.g. Table referring to wet weight?).

127
128 **Authors' comment 10:** Corrected throughout the text, in tables, and figure captions.

129
130 You used a 500- μ m net (L82) but only present data on zooplankton >1 mm (L60). Why is
131 this?

132
133 **Authors' comment 11:** Now we have added in Methods: "We used a closing Bogorov-Rass
134 (BR) plankton net (1-m² opening, 500- μ m mesh size, towed at a speed of 1 m sec⁻¹), which
135 was proven to successfully sample deep-sea plankton ≥ 1.0 mm long (Vinogradov *et al.*,
136 1996; 2000); smaller animals may pass through the sieve during filtration."

137
138 Overall, this study is very interesting and the results could be important. However, the data
139 presentation and discussion need work to give the overall conclusion credibility.

140
141 **ADDITIONAL CONTRIBUTION 1:** Now we used Canonical Correspondence Analysis (CCA:
142 Ter Braak, 1986) to quantify the following environmental variables: month and year as possible
143 temporal explanatory variables, latitude, longitude, and depth as possible spatial explanatory
144 variables, and chlorophyll. As the sampling was associated with distinct water masses, such
145 environmental parameters as temperature, salinity, and depth were correlated; only one and
146 simplest of them, the depth, was included in CCAs. CCAs have shown that depth and averaged
147 surface chlorophyll have major effect on the group biomass and predict plankton biomass better.
148 It is only after CCA that we use further correlation analyses.

149
150 **ADDITIONAL CONTRIBUTION 2:** We have also provided six actual biomass profiles from
151 the surface to the bathypelagic zone for several distant sites (Fig. 2).

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156 A NOVEL APPROACH REVEALS HIGH ZOOPLANKTON STANDING STOCK DEEP IN
157 THE SEA

158

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165

166

167 **keywords:** zooplankton communities, biological resources, decapods, vertical zones, plankton
168 groups, vertical distribution

169

170

171

172 **ABSTRACT**

173 In a changing ocean there is a critical need to understand global biogeochemical cycling,
174 particularly regarding carbon. We have made strides in understanding upper ocean dynamics, but
175 the deep ocean interior (> 1000 m) is still largely unknown, despite representing the
176 overwhelming majority of Earth's biosphere. Here we present a method for estimating deep-
177 pelagic zooplankton biomass on an ocean-basin scale. In so doing we have made several new
178 discoveries about the Atlantic, which likely apply to the World Ocean. **First, multivariate**
179 **analysis showed that depth and Chl were the main factors affecting the wet biomass of the main**
180 **plankton groups. Wet biomass of all major groups except fishes was significantly correlated with**
181 **Chl. Second**, zooplankton biomass in the upper bathypelagic domain is higher than expected,
182 representing an inverted biomass pyramid. Third, the majority of this biomass comprises
183 macroplanktonic shrimps, which have been historically underestimated. These findings, coupled
184 with recent findings of increased global deep-pelagic fish biomass, revise our perspective on the
185 role of the deep-pelagic fauna in oceanic biogeochemical cycling.

186

188 **INTRODUCTION**

189 The deep sea accounts for nearly 99% of the habitable volume of the planet (Dawson, 2012).
190 Waters below 200 m are highly heterogeneous in space and time, harbouring diverse biological
191 resources which are not yet quantitatively estimated. These ecosystems are and will continue to
192 be impacted by climate change due to the cumulative effect of different stressors on their biota,
193 including expanding oxygen minimum zones, shoaling of aragonite saturation horizons,
194 acidification and warming (Okey *et al.*, 2012). It is urgent that we estimate the biomass of the
195 deep-sea biota for inventory purposes and for monitoring its changes in the future.

196

197 [Studies on the deep-sea plankton biomass at selected sites include those in the North Pacific](#)
198 [\(e.g., Vinogradov, 1968; Murano et al., 1976; Yamaguchi et al., 2002ab; Yamaguchi, 2004\) and](#)
199 [Eastern Tropical Pacific \(Sameoto, 1986\), North Atlantic \(Koppelman and Weikert, 1992;](#)
200 [1999; Gislason, 2003; Vinogradov, 2005\) and Mediterranean Sea \(Scotto di Carlo et al., 1984;](#)
201 [Weikert and Trinkaus, 1990\), Indian Ocean \(Vinogradov, 1968\) and Arabian Sea \(Koppelman](#)
202 [and Weikert, 1992; Böttger-Schnack, 1996\).](#) Fewer results concern deep-sea zooplankton
203 distribution over larger areas (Longhurst & Williams, 1979; Gaard *et al.*, 2008). The data
204 regarding quantitative distribution of the deep-sea zooplankton for the Equatorial Atlantic and
205 the South Atlantic Gyre are lacking. In addition to geographic restrictions, most deep-sea
206 research has been concentrated on specific taxonomic groups (e.g. crustacean zooplankton;
207 Burghart *et al.*, 2007; Gaard *et al.*, 2008), functional groups (e.g. gelatinous zooplankton;
208 Lindsay & Hunt, 2005), or selected vertical zones (e.g. mesopelagic; Robison *et al.*, 2010; Sutton
209 *et al.*, in press). Attempts to assess an entire deep-sea community have been rare and local
210 (Vinogradov *et al.*, 1996; Vereshchaka & Vinogradov, 1999; Vinogradov *et al.*, 2000).
211 Comparative assessments of entire water column plankton over large areas are absent.
212 Thus, it is timely to provide estimates of the zooplankton biomass throughout the water column
213 over large areas. As any field data of the deep-sea zooplankton are inevitably local, we should
214 find an indicator that is correlated with elements of the deep-sea zooplankton and that can be

215 assessed over large water areas/volumes. Here we offer and test a hypothesis that the
216 zooplankton wet biomass in the deep-pelagic is correlated with surface [chlorophyll](#)
217 [concentration](#). This hypothesis has been corroborated for the epipelagic (0-200 m) layer, where
218 correlations have been obtained (Vinogradov et al., 1999). It remains completely unknown,
219 however, if this dependence is valid for the deep sea below 200 m. In theory, the standing stock
220 of zooplankton should remain correlated with surface productivity and the correlation should
221 decrease with depth. No large-scale data, however, are available on this subject. Here we attempt
222 to fill that void by examining the relationship between remotely sensed sea surface data and *in*
223 *situ*, discrete depth sampling data across the majority of the Atlantic Ocean (Fig. 1). In order to
224 start this process, we will focus on the deep-sea meso- and macroplankton (1-10 cm length). This
225 size fraction links primary and higher levels of oceanic production and is representatively
226 sampled by the largest spectrum of plankton nets. As an indicator of surface productivity, surface
227 chlorophyll concentration (Chl hereafter) derived from satellite information has been chosen as
228 our indicator metric. We will check the presence of correlation for major groups of the
229 zooplankton and for the different depth zones: epipelagic, [main thermocline](#), upper- and lower-
230 bathypelagic zones. If correlations exist, we will assess the standing stock of the plankton over
231 vertical zones and over geographical areas. Where possible, we will estimate the role of major
232 plankton groups and different depth zones in the total standing stock of the zooplankton. If
233 successful, this attempt will provide a new expedient method for evaluation of deep-sea
234 resources.

235 [Zooplankton distribution is strongly affected by the presence of land \(islands, continents,](#)
236 [seamounts\) and the sea-floor \(Vereshchaka, 1995\). The effect is prominent at a distance of tens](#)
237 [of kilometer in the horizontal direction \(Vereshchaka, 1990ab, 1994; Melo et al., 2014\) and](#)
238 [hundreds of meter in the vertical direction \(Vereshchaka; 1995; Vereshchaka & Vinogradov,](#)
239 [1999; Cartes et al., 2010\). In order to minimize the land and the sea-floor effects, this survey of](#)
240 [the pelagic zooplankton in the open ocean will be made as far as possible from the bottom in the](#)
241 [vertical direction and from the land in the horizontal direction.](#)

242

244 **METHODS**

245 Field data were taken in the deep Central, South, and North Atlantic between 1996-2012 from
246 ultraoligotrophic to mesotrophic areas roughly between 40° S and 40° N during 36th and 37th
247 cruises of the R/V “Akademik Sergey Vavilov” (ASV), and 34th, 37th, 39th, 42nd, 46th, 47th, 49th,
248 50th cruises of the R/V “Akademik Mstislav Keldysh” (AMK - Table 1, Fig. 1). These areas
249 include the two main Atlantic Gyres (North and the South) and the Equatorial Atlantic between
250 them.

251 The whole database of this work contains two different datasets: (1) data of 2012-2013 (R/V
252 "Akademik Sergey Vavilov", mainly Central and South Atlantic) and (2) data of 1994-2005 (R/V
253 "Akademik Mstislav Keldysh", mainly North Atlantic). Samples have been taken with the same
254 protocol, but identification was much more precise for the first dataset. The community
255 composition, diversity, and other community patterns have been analyzed in detail for the first
256 dataset and presented in a recent paper (Vereshchaka et al., 2016). The second dataset contains
257 representative biomass values and significantly contributes to the metadata concerning deep
258 zooplankton; here we combine both datasets for a more comprehensive analysis. We excluded
259 data from temperate waters where the major spring peaks in primary production are being
260 exported from the euphotic zone (0–200 m depth) and reaching abyssal depths (4000 m) with a
261 significant time lag (e.g., 42 days: Smith et al., 2002); this lag differs for different depth zones
262 that may corrupt possible correlations.

263 Samples were taken between one hour after sunset and one hour before sunrise in order to make
264 a unified nighttime picture of the vertical distribution of animals. This method was adopted to
265 avoid the confounding effects of diel vertical migration. We sampled four discrete depth strata:
266 (1) the epipelagic zone (0-200 m), (2) the main thermocline (from 200 m to the depth of the 7°C
267 isotherm, within 550-800 m), (3) the zone from the lower boundary of the main thermocline to
268 1500 m, mainly Antarctic Transitional Waters, which we define here as the upper bathypelagic,
269 and (4) the layer 1500-3000 m, mainly North Atlantic Deep Waters, which we define here as the
270 lower bathypelagic (Fig. 2). The upper boundary of the bathypelagic zone as defined here did not

271 coincide with the traditional one (1000 m), because our sampling was associated with water
272 masses. The lower boundary of the bathypelagic was 3000 m instead of usually adopted 4000 m,
273 as we had to avoid sampling of the benthopelagic zone.

274 We used a closing Bogorov-Rass (BR) plankton net (1-m² opening, 500- μ m mesh size, towed at
275 a speed of 1 m sec⁻¹), which was proven to successfully sample deep-sea plankton \geq 1.0 mm long
276 (Vinogradov *et al.*, 1996; 2000); smaller animals may pass through the sieve during filtration.
277 The net was deployed at the maximal depth of haul, then opened and towed vertically upwards,
278 and finally closed at the minimal depth of haul with a mechanical device. The minimal
279 horizontal distance between station and the land was 400 km and the minimal vertical distance
280 the lower boundary of the deepest haul and the sea-floor was 750 m (Table 1), so that the
281 land/sea-floor effect could be ignored.

282 We divided the net plankton into four major groups: non-gelatinous mesozooplankton (mainly
283 copepods and chaetognaths; 1-30 mm length), gelatinous mesozooplankton (mainly
284 siphonophorans and medusae; individual or zooid; 1-30 mm length), decapods and small
285 (macroplanktonic) fishes (both groups over 30 mm length). Identification was done according to
286 literature (e.g., Rose, 1933; Brodsky, 1950; Mauchline & Fisher, 1969; Brodsky *et al.*, 1983;
287 Markhasheva, 1996). Synonymy of species was corrected according to www.marinespecies.org.
288 Decapods, fishes, and gelatinous species were weighed with a precision of 0.1 g before fixation.
289 Wet weight of mesoplanktonic groups was estimated according to adopted procedures
290 (Vinogradov *et al.*, 1996; 2000; Gaard, E., *et al.*, 2008). In brief, wet weight w_{tot} of the non-
291 gelatinous mesozooplankton (mainly copepods) was estimated as $w_{\text{tot}} = \Sigma (k * l_i^3)$, where l_i is
292 length of an individual specimen, k is a species-dependent coefficient; tables of these coefficients
293 have been published elsewhere (e.g., Vinogradov & Shushkina, 1987).

294 Surface chlorophyll-a concentration (Chl) derived from satellite images was used as a measure of
295 the surface productivity. Chl data were taken from Aqua MODIS (level 3, 4-km resolution) from
296 2003 to 2015. Before this period Chl data were taken from SeaWiFS (level 3, 9-km resolution)
297 from 1997 to 2002. Chl data were averaged over one year preceding the sampling date and over
298 a $5^\circ \times 5^\circ$ square (with the sampling site in the center).

299 In order to establish relationships between the major plankton group wet biomass and possible
300 environmental factors, Canonical Correspondence Analysis (CCA: Ter Braak, 1986) was
301 performed on major group biomass using an assortment of environmental variables: temporal
302 (month and year), spatial (latitude, longitude, and depth), and surface chlorophyll concentration
303 (Chl). As the sampling was associated with distinct water masses, such environmental
304 parameters as temperature, salinity, and depth were correlated and only one of them, the depth,
305 was included in CCAs. CCA is a powerful multivariate technique to extract synthetic
306 environmental gradients from ecological data (Ter Braak and Verdonschot, 1995). Ordination
307 axes are based on the measured environmental variables and represent linear combinations of the
308 variables. Arrows showing variables in the ordination plots are proportional in length to the
309 importance of each variable (Ter Braak, 1986), and therefore community variation can be
310 directly related to environmental variation. CCAs included either all hauls, or hauls from
311 separate strata and made possible to assess the contribution of all analyzed factors.
312 Calculations, statistical procedures, regression analysis, an ANOVA tests were carried out with
313 the use of Excel and STATISTICA, CCAs with PAST 3.04 (Hammer et al., 2001).

314

315 **RESULTS**

316 Over 300 taxa were identified, counted, measured, and their weight calculated to estimate
317 standing stocks (the plankton assemblages are considered in detail elsewhere - Vereshchaka et
318 al., 2016). The main contribution to the total zooplankton standing stock was made by decapod
319 decapods, followed by non-gelatinous mesozooplankton, gelatinous mesozooplankton, and fishes
320 (Table 2).

321 The epipelagic zone was dominated by the two groups of mesozooplankton, the main
322 thermocline was dominated by non-gelatinous mesozooplankton and decapods, the upper
323 bathypelagic zone was dominated by decapods, and the lower bathypelagic zone was dominated
324 by gelatinous zooplankton (Table 2). The dominant role of decapods will be further quantified as
325 a separate parameter, the share of decapods in the total plankton wet biomass (%).

326 Actual vertical distribution of major groups varied, but typical profiles are represented for the
327 northwest and northeast corners of studied area (Fig. 3 AB), for the central part and the eastern
328 periphery of the North Atlantic Gyre (Fig. 3 CD), and for the Equatorial area and southwestern
329 periphery of the South Atlantic Gyre (Fig. 3 EF).

330 Multivariate CCA with all hauls included (Fig. 4A) showed aggregation of hauls in two
331 groups. The first group (the left of OY axis) was mainly represented by the epi- and lower
332 bathypelagic hauls and related to non-gelatinous, gelatinous, and total plankton. The second
333 group (the right of OY axis) was represented by the and upper/lower bathypelagic hauls and
334 related to the share of decapods. The first factor (F1) was mainly linked to depth, the second
335 factor (F2) was primarily associated with Chl (Fig. 4A). Contribution of other factors was less
336 significant. Such variables as Chl and depth had the largest effect on wet biomass of all major
337 groups, the share of decapods was mostly linked to depth.

338 Multivariate CCA with only epipelagic hauls (Fig. 4B) showed one group of samples. The first
339 factor (F1) was mainly linked to Chl, the second factor (F2) was primarily associated with month
340 (Fig. 4B). Chl had the largest effect on biomass of both mesoplanktonic groups and total
341 plankton, decapods and fish were also linked to month.

342 Multivariate CCA with hauls from the main thermocline (Fig. 4C) showed aggregation of
343 hauls in two groups: one was mainly related to fishes and the share of decapods (the left of OY
344 axis), another was linked to both groups of mesoplankton and total plankton (the right of OY
345 axis). The first factor (F1) was mainly linked to year and latitude, the second factor (F2) was
346 primarily associated with longitude (Fig. 4C).

347 Multivariate CCA with upper bathypelagic hauls (Fig. 4D) showed aggregation of hauls in two
348 groups: one was mainly related to the share of decapods (the left of OY axis), another was linked
349 to main plankton groups (the right of OY axis). The first factor (F1) was mainly linked to Chl,
350 the second factor (F2) was primarily associated with month and year (Fig. 4D).

351 Multivariate CCA with lower bathypelagic hauls (Fig. 4E) showed aggregation of hauls in two
352 groups: one was mainly related to the share of decapods (the left of OY axis), another was linked

353 to plankton groups (the right of OY axis). The first factor (F1) was mainly linked to longitude
354 and year, the second factor (F2) was primarily associated with Chl (Fig. 4E).

355 Multivariate CCA with wet biomass values integrated over whole water column (Fig. 4F)
356 showed aggregation of hauls in two groups: one was mainly related to the share of decapods (the
357 right of OY axis), another was linked to plankton groups (the left of OY axis). The first factor
358 (F1) was mainly linked to Chl, month, and year, the second factor (F2) was primarily associated
359 with geographical coordinates (Fig. 4F).

360 Results of multivariate analyses allow search for possible correlations between wet biomass of
361 the major plankton groups and the most important environmental factor, Chl. The total
362 zooplankton wet biomass in the whole water column and the biomass of all major faunal groups
363 **except fishes** were highly correlated with the averaged Chl (Fig. 5, Table 3). Moreover, in most
364 cases the standing stock of the major groups **except fishes** in each of the vertical zones was also
365 correlated with Chl; the dependence was more robust for upper vertical zones and weakened
366 with depth. **Fish wet biomass was never robustly correlated with Chl.**

367 Having the correlation between the total zooplankton standing stock and Chl, **we calculated the**
368 **total zooplankton standing stock (wet biomass under 1 m⁻² in the whole water column) and**
369 **standing stocks within each strata (wet biomass under 1 m⁻² integrated over whole layer) over**
370 **selected areas.** We did that for three rectangular areas roughly corresponding to the North and
371 South Atlantic Gyres and the Equatorial Atlantic (Fig. 6). The maximum plankton stock was
372 found in the Equatorial Atlantic (3.8×10^7 t wet weight), with the South and North Gyres being
373 approximately half (2.2×10^7 t) and one-quarter (1.0×10^7 t) of this amount, respectively.

374 Contribution of various vertical zones to the total plankton standing stock was similar in the
375 three selected areas (Fig. 6). The contribution of **the main thermocline** zone was the smallest
376 portion of the total plankton stock (13-16 %), the epipelagic and lower bathypelagic zones were
377 intermediate (15-25 %), and the upper bathypelagic zone contributed the highest portion (41-48
378 %). In terms of faunal contributions, gelatinous and non-gelatinous mesozooplankton accounted
379 for nearly one-quarter of the total zooplankton stock, while the decapods composed
380 approximately half. Various species of the decapod genera *Acanthephyra* A. Milne-Edwards,

381 1881 and *Gennadas* Spence Bate, 1881 were dominant throughout the studied area, *Notostomus*
382 A. Milne-Edwards, 1881 and *Systellaspis* Spence Bate, 1888 were dominant in the Equatorial
383 area and South Atlantic Gyre. Fishes (represented by Gonostomatidae Cocco, 1838 and
384 Myctophidae Gill, 1893) were not included in this analyses, since their biomass was not
385 correlated with studied environmental parameters.

386

387 **DISCUSSION**

388 Although scant on the global scale, our deep-sea samples collected during the last 20 years using
389 standardized methods throughout the whole water column provide an unprecedented opportunity
390 to investigate the distribution of zooplankton biomass at an ocean-basin scale. This is the first
391 snapshot of the biomass distribution throughout the whole water column over a significant
392 oceanic area. Further, this is a first attempt to quantitatively connect the dots related to surface
393 productivity and deep-sea zooplankton biomass, including the bathypelagic zone, which
394 contained the highest portion of water column meso/macrozooplankton standing stock.

395 The wet biomass profiles (Fig. 3), although different at various sites, show same
396 quasiexponential decrease of the mesoplankton biomass, as has been known before (e.g.,
397 Vinogradov, 1970). As for novelty, high decapod biomasses are recorded from many sites. Since
398 these animals may avoid plankton nets, high biomass values are even more striking. Our data do
399 not allow detailed analysis of profiles, because vertical resolution of samples is lower than
400 necessary, but assessment of factors influencing biomass values is possible.

401 Multivariate analysis showed that depth and Chl were the main general factors affecting the
402 wet biomass of main plankton groups (Fig. 4A). Obtained regressions between Chl and biomass
403 of the major plankton groups are obfuscated by several factors. First, algorithms for conversion
404 of satellite images to Chl data are not perfect (Watson *et al.*, 2009). Second, Chl data, even if
405 estimated unerringly, do not reflect surface productivity thoroughly: autotrophic organisms may
406 live far below the surface and even create deep maxima with significant chlorophyll
407 concentration not detectable via satellites (Uitz *et al.*, 2006). Third, the trophic structure of deep-
408 pelagic communities and deep-water circulation locally differ, thus providing different

409 conditions for downward energy transfer and accumulation of organic matter in the zooplankton
410 wet biomass. It is all the more interesting that our data do show statistically significant
411 correlation between Chl and the deep zooplankton biomass. [The use of Chl averaged over 5° x 5°](#)
412 [area and one-year period provide a new and productive approach to assess the deep pelagic](#)
413 [biomass. The use of different temporal and spatial scaling may improve this approach in the](#)
414 [future.](#)

415 Although our results provide a means for calculating global zooplankton wet biomass by
416 integrating satellite remote sensing with *in situ* sampling, some caveats must be noticed,
417 including:

- 418 • Correlations may be different outside the tropical/subtropical region of the
419 Atlantic Ocean. Studies in the epipelagic zone show that such correlations are
420 better in warm waters than in the cold waters (Vinogradov *et al.*, 1999).
- 421 • Correlations may be different in different oceans. Our data show better correlation
422 between the Chl concentration and the zooplankton wet biomass in the epipelagic
423 zone than in Vinogradov *et al.* (1999) - 0.67 versus 0.53. We used field data from
424 the Atlantic Ocean only, while Vinogradov *et al.* . (1999) based their studies on a
425 set of data from the Atlantic, Indian, and Pacific Oceans. Each ocean probably
426 requires an individual approach until conversion factors can be obtained to link
427 geographically distant deep-sea assemblages.
- 428 • Actual wet biomass of gelatinous mesozooplankton is underestimated by our gear.
429 A significant part of ctenophores and medusae are destroyed in the mesh during
430 retrieval. Fragile gelatinous animals may dominate in the deep sea (Robison *et al.*,
431 2010) and plankton nets are suboptimal for estimating their actual abundance
432 (Vereshchaka & Vinogradov, 1999).
- 433 • Actual wet biomass of the decapods is also underestimated, as these animals
434 likely avoid plankton nets and trawls to some extent (Vereshchaka, 1990).

435

436 Probably the most striking result we found was the unexpectedly high decapod wet biomass.
437 Macroplanktonic decapod biomass, even in the maximum layers, is typically 0.05-0.5 mg m⁻³
438 and never exceeds 1.0 mg m⁻³ in the Atlantic (Foxton, 1970a, b), Indian (Vereshchaka, 1994),
439 and in the Southeast Pacific (Vereshchaka, 1990). The values presented are one order of
440 magnitude higher (Table 1), which seems paradoxical, as the nets were smaller and should have
441 ostensibly caught fewer and smaller decapods. Our observations from submersibles show that
442 deep-sea decapods are generally stationary in the water column with abdomens oriented slightly
443 upward. When disturbed, decapods try to escape and jump upward using the abdomen and tail
444 fan. This behaviour is effective in the pelagic realm where predators are thought to attack from
445 below and thus many deep-pelagic decapods possess downward-oriented photophores for
446 counter-illumination (Widder, 1999). Upward jumps are also effective to escape from a net or a
447 trawl that is traditionally towed in the horizontal direction. The BR net, however, is towed
448 vertically and the decapods may have less chance to avoid the gear.

449 [In contrast to decapods, pelagic fishes escape in horizontal direction, as has been observed from](#)
450 [submersibles many times by the authors. This reaction is successful when vertical hauls are used](#)
451 [and our results are thus not representative for assessment of the pelagic fish biomass. This](#)
452 [biomass may occur to be finally correlated with Chl but horizontally towed gears are necessary](#)
453 [to prove that.](#)

454 The dominance of macroplanktonic decapods in the deep sea illustrates an inverted biomass
455 pyramid, as their biomass is larger than that of their prey (non-gelatinous mesozooplankton).
456 This happens because decapods (typical life spans of several years) grow and reproduce much
457 slower than mesozooplankton (typical life span several months), which equates to a low
458 production rate relative to its high standing stock; ergo, the energy pyramid is not inverted. Thus,
459 the decapod distribution offers additional example of the inverted biomass pyramid described for
460 plankton communities (Gasol *et al.*, 1997).

461

462 The most significant contribution to the total zooplankton standing stock unexpectedly came
463 from the upper bathypelagic zone, not the epipelagic zone or [the main thermocline](#) (Fig. 6). The

464 upper bathypelagic zone was dominated by macroplanktonic decapods, which accounted for over
465 half of the standing stock wet biomass. Most decapods undertake diel vertical migration (Foxton,
466 1970a,b), feeding on mesozooplankton in the upper layers at night and hiding from predators in
467 the dark upper bathypelagic zone by day. This behaviour appears effective and provides good
468 prospects for biomass accumulation below the main thermocline in the ocean. The finding of
469 higher than expected biomass deep in the water column mirrors recent findings that suggest
470 deep-pelagic fish biomass has been underestimated by up to an order of magnitude (Kaartvedt *et*
471 *al.*, 2012; Irigoien *et al.*, 2014). The global ramifications of these findings, coupled with ours, are
472 that energy transfer efficiency from phytoplankton to intermediate and higher trophic levels in
473 oceanic ecosystems has been underestimated, and that both zooplankton and fishes are likely
474 respiring a large portion of the primary production in the deep-pelagic realm.

475

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479

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Table 1. List of stations, cruises of R/V “Akademik Sergey Vavilov” (ASV) and R/V “Akademik Mstislav Keldysh” (AMK). Sampling zones: E - epipelagic, M - main thermocline, U- upper bathypelagic, L - lower bathypelagic; T - total haul (0-3000 m, net was not closed).

No of Station	Date	Latitude	Longitude	Sampling zones	Depth, m
2474 ASV	24.10.2012	9°25' N	19°44' W	EMUL	4282
2479 ASV	25.10. 2012	3°51' N	21°15' W	EMUL	5235
2483 ASV	28.10. 2012	0°50' N	22°26' W	EMUL	4360
2488 ASV	29.10. 2012	6°12' S	24°05' W	EMU	3800
2489 ASV	30.10. 2012	10°18' S	26°37' W	EMUL	5500
2490 ASV	01.11. 2012	15°06' S	28°45' W	EMUL	5030
2491 ASV	03.11. 2012	22°43' S	32°05' W	EMUL	4690
2492 ASV	05.11. 2012	26°39' S	33°58' W	EMUL	4710
2498 ASV	07.11. 2012	29°27' S	39°15' W	EMUL	4724
2499 ASV	10.11. 2012	32°11' S	46°26' W	T	3780
2500 ASV	23.09. 2013	41°58' N	14°17' W	EMUL	5000
2504 ASV	27.09. 2013	31°12' N	20°48' W	EMU	3150
2505 ASV	29.09. 2013	26°14' N	21°03' W	EMUL	4700
2506 ASV	30.09. 2013	19°59' N	21°22' W	EMUL	3780
2507 ASV	03.10. 2013	11°50' N	21°47' W	EMUL	4900
2508 ASV	04.10. 2013	5°50' N	22°00' W	EMUL	3800
2518 ASV	10.10. 2013	1°25' S	24°00' W	EMUL	4700
2519 ASV	11.10. 2013	07°01' S	26°04' W	EMUL	4500
2520 ASV	14.10. 2013	15°35' S	28°41' W	EMUL	5100
2524 ASV	19.10. 2013	26°23' S	32°53' W	EMU	3000
2528 ASV	21.10. 2013	31°00' S	40°38' W	EMU	2250
3341 AMK	12.09.1994	29°06' N	43°12' W	EMUL	3205
3365 AMK	16.09. 1994	26°12' N	44°54' W	EMUL	3887
3604 AMK	08.09. 1995	41°42' N	49°54' W	EMUL	3749
3671 AMK	28.08. 1996	29°06' N	43°12' W	EMUL	5270
3816 AMK	10.09. 1998	41°42' N	49°54' W	EMUL	3750
3854 AMK	28.10. 1998	36°12' N	33°54' W	EMU	2470
3980 AMK	9-10.10. 1999	36°12' N	33°54' W	EMUL	3285
4149 AMK	10-11.06. 2001	48°06' N	16°06' W	EMUL	4700
4301 AMK	01-04.06. 2002	48°06' N	16°06' W	EMUL	4800
4547 AMK	25-26.06. 2003	41°42' N	49°54' W	EMUL	3700
4580 AMK	30.07. 2003	37°54' N	31°30' W	EMU	2070
4601 AMK	08.08. 2003	30°06' N	42°06' W	EMU	1800
4613 AMK	12-13.08. 2003	23°24' N	45° 00' W	EMUL	4700
4791 AMK	24-25.08. 2005	29°06' N	43°12' W	EMU	3070
4799 AMK	28.08. 2005	30°06' N	42°06' W	EMU	2545

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Table 2. Average values \pm standard deviation of wet biomass the major plankton groups in the whole water column (g m^{-2}) and vertical zones (mg m^{-3}) of the Atlantic Ocean.

Vertical zones	Non-gelatinous mesoplankton	Gelatinous mesoplankton	Decapods	Fishes	Total plankton	Number of samples
Whole water column (0-3000 m)	13.38 \pm 24.08	8.07 \pm 17.33	15.63 \pm 31.04	1.25 \pm 2.32	37.08 \pm 58.49	36
Epipelagic zone	28.32 \pm 54.86	20.16 \pm 53.96	0.58 \pm 2.16	0.62 \pm 0.86	49.07 \pm 78.19	35
Main thermocline zone	5.68 \pm 12.34	1.86 \pm 4.03	5.40 \pm 9.26	0.38 \pm 0.63	12.93 \pm 18.53	35
Upper bathy-pelagic zone	4.30 \pm 9.20	4.12 \pm 11.14	12.07 \pm 25.73	0.61 \pm 0.81	20.49 \pm 36.28	35
Lower bathy-pelagic zone	0.19 \pm 0.16	1.79 \pm 4.40	0.04 \pm 0.16	0.04 \pm 0.16	2.02 \pm 9.71	26

Table 3. Correlation between surface chlorophyll-a concentration (Chl, mg m⁻²) and wet biomass (g m⁻² for the whole water column and mg m⁻³ for vertical zones): coefficients of determination (R²), equations, and levels of significance (** indicate $p < 0.001$, *** for $p < 0.01$, ** for $p < 0.01$, * for $p < 0.05$).**

Vertical zones	Non-gelatinous mesoplankton		Gelatinous mesoplankton		Decapods		Fishes		Total plankton	
	R ²	Regression equations	R ²	Regression equations	R ²	Regression equations	R ²	Regression equations	R ²	Regression equations
Whole water column, n=36	0,5129****	B = 121,54Chl - 6,3663	0,1971***	B = 54,22Chl - 0,7371	0,1609**	B = 87,747Chl + 1,3743	0,026	B = 2,5959Chl + 0,8296	0,4235****	B = 266,1Chl - 4,8996
Epipelagic zone, n=35	0,4674****	B = 258,84Chl - 13,001	0,1374***	B = 138,03Chl - 1,8744	0,028	B = 2,6517Chl + 0,181	0,0151	B = -0,7718Chl + 0,7576	0,544****	B = 397,96Chl - 13,863
Main thermocline zone, n=35	0,4082****	B = 53,63Chl - 3,2029	0,2971****	B = 14,929Chl - 0,6162	0,0512	B = 15,151Chl + 3,0384	0,0012	B = -0,156Chl + 0,418	0,3925****	B = 78,963Chl + 0,0833
Upper bathypelagic zone, n=35	0,4152****	B = 40,335Chl - 2,3795	0,0569	B = 18,065Chl + 1,1344	0,2118**	B = 85,558Chl - 1,2733	0,0216	B = -0,8529Chl + 0,7653	0,2599****	B = 125,8Chl - 0,0726
Lower bathypelagic zone, n=26	0,284***	B = 14,61Chl - 0,9625	0,1518*	B = 2,6226Chl + 0,0143	0,1263**	B = 22,622Chl + 0,7622	0,0484	B = 0,2334Chl + 0,0038	0,1715*	B = 34,942Chl + 0,3334

Figure Legends

Figure 1. Deep-sea plankton stations (black circles) sampled during the cruises of R/V “Akademik Sergey Vavilov” (ASV) and R/V “Akademik Mstislav Keldysh” (AMK) (see also Table 1). Background: surface chlorophyll-a concentration averaged over 2013, scale (mg m^{-2}) on right.

Figure 2. Temperature ($^{\circ}\text{C}$, left) and salinity (‰ , right) along the transect A16 (Koltermann et al., 2011).

Figure 3. Wet biomass profiles (mg m^{-3}) of the main plankton groups in the epipelagic (1), main thermocline (2), upper bathypelagic (3) and lower bathypelagic obtained during the cruises of R/V “Akademik Sergey Vavilov” (ASV) and R/V “Akademik Mstislav Keldysh” (AMK) (see also Fig. 1 and Table 1).

Figure 4. CCAs of all hauls included (A), of hauls taken in the epipelagic (B), main thermocline (C), upper- (D) and lower bathypelagic (E), and of the calculated standing stocks (F). Two first axes (F1 and F2) with respective explained variance represented.

Figure 5. Wet biomass of major plankton groups (vertical axes) in the whole water column (g m^{-2}) and in different vertical zones (mg m^{-3}) versus surface chlorophyll (horizontal axes, mg m^{-2}).

Figure 6. The standing stock (wet biomass) of the deep-sea plankton and contribution (%) of vertical zones in the North, Equatorial, and South Atlantic. Background: surface chlorophyll-a concentration averaged over 2013, scale (mg m^{-2}) on right. Yellow circles: stations.

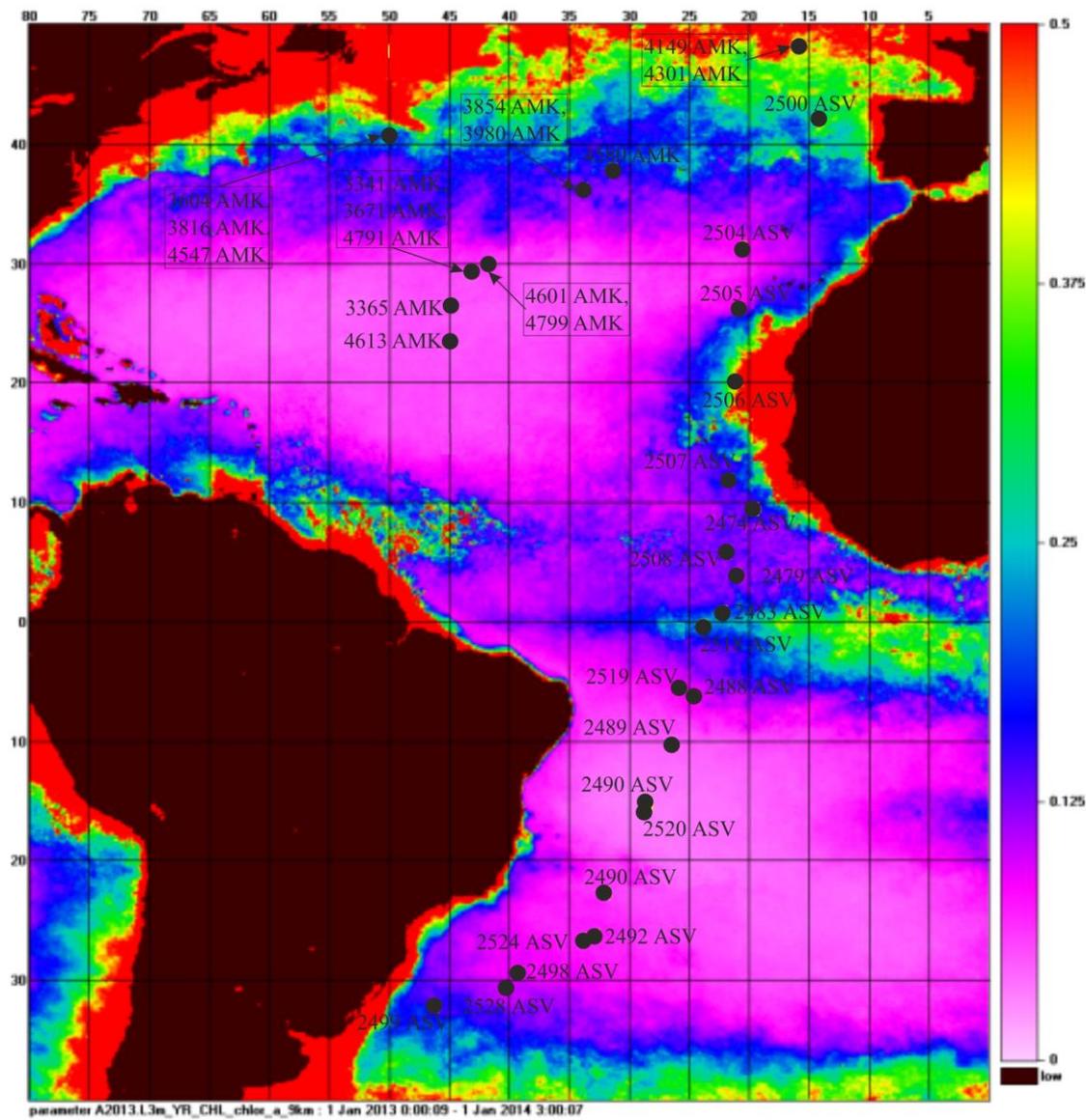


Figure 1.

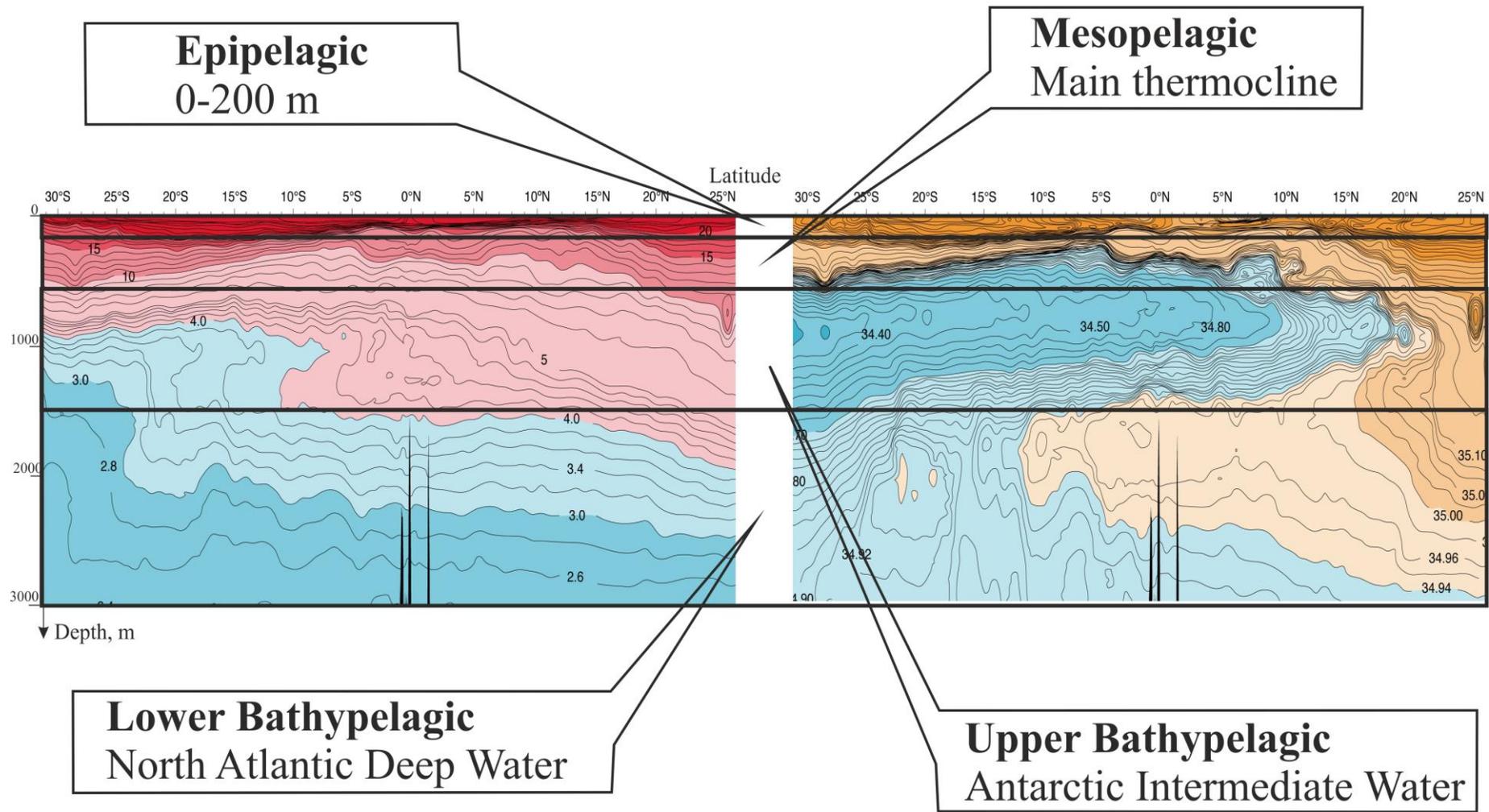


Figure 2.

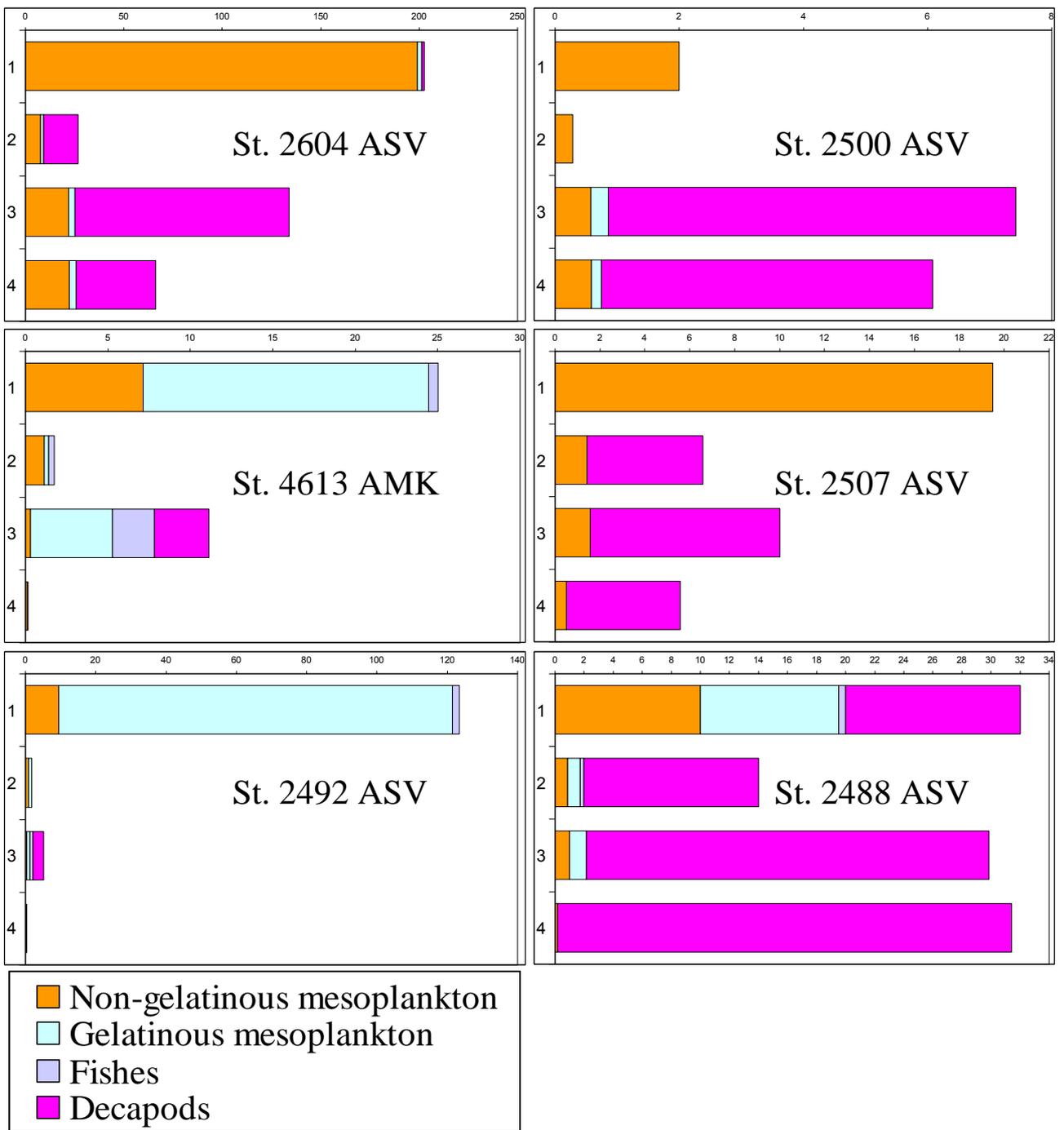
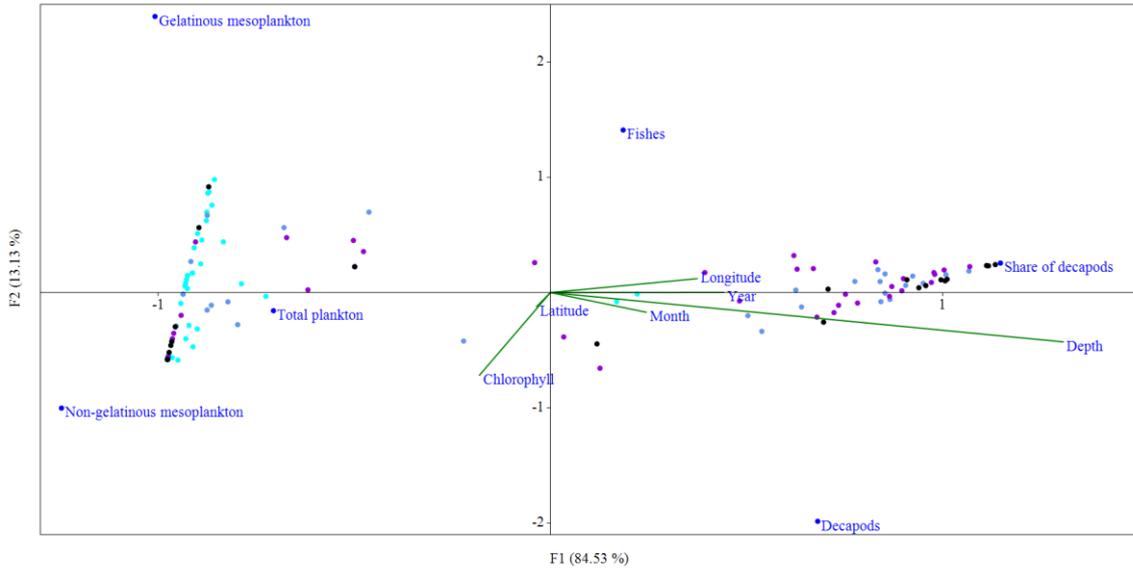
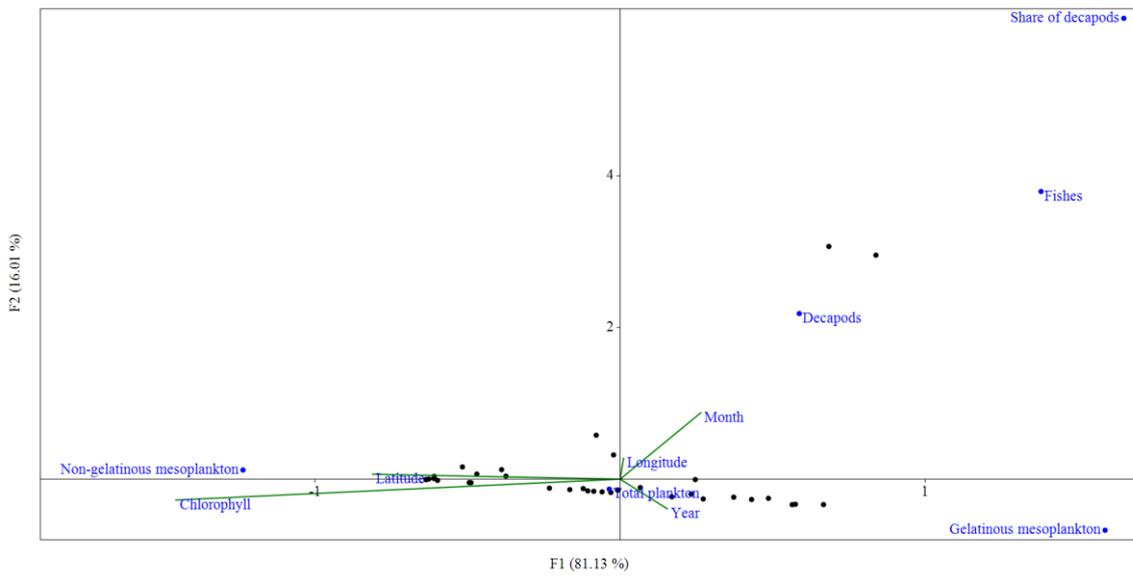


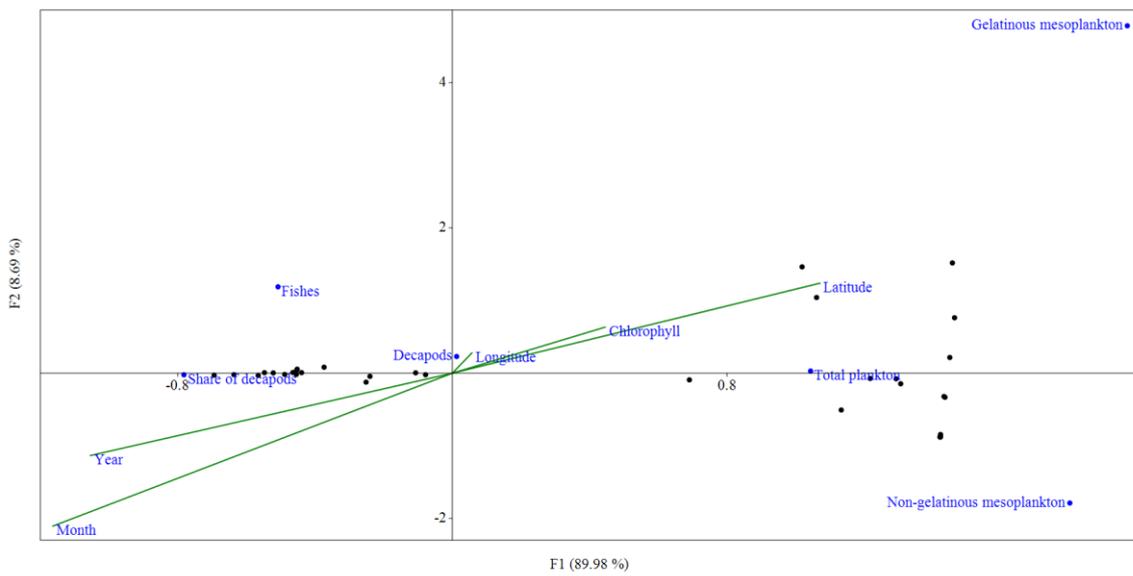
Figure 3.



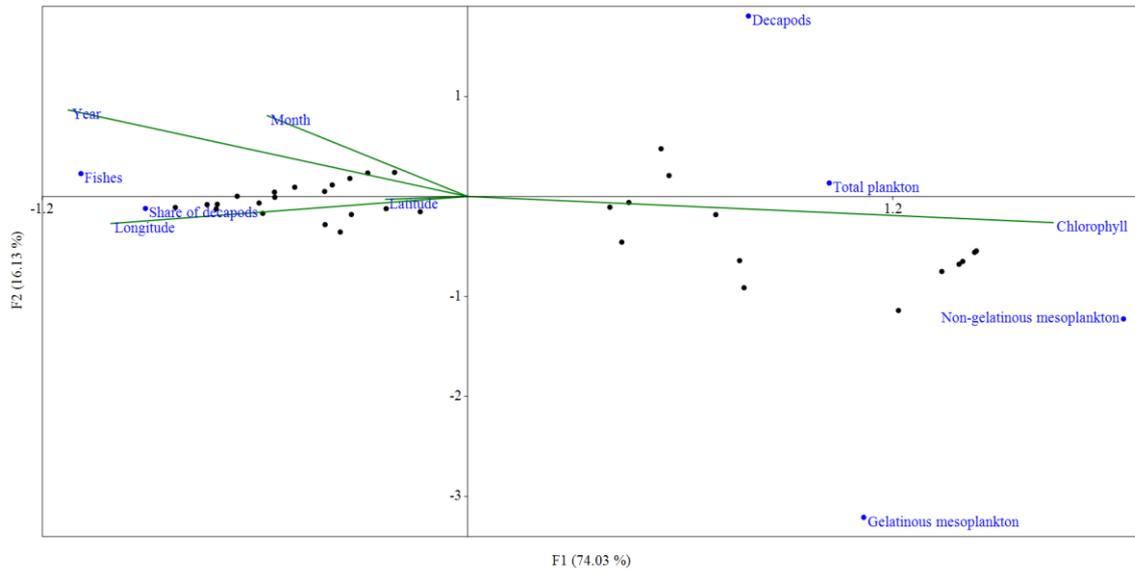
A



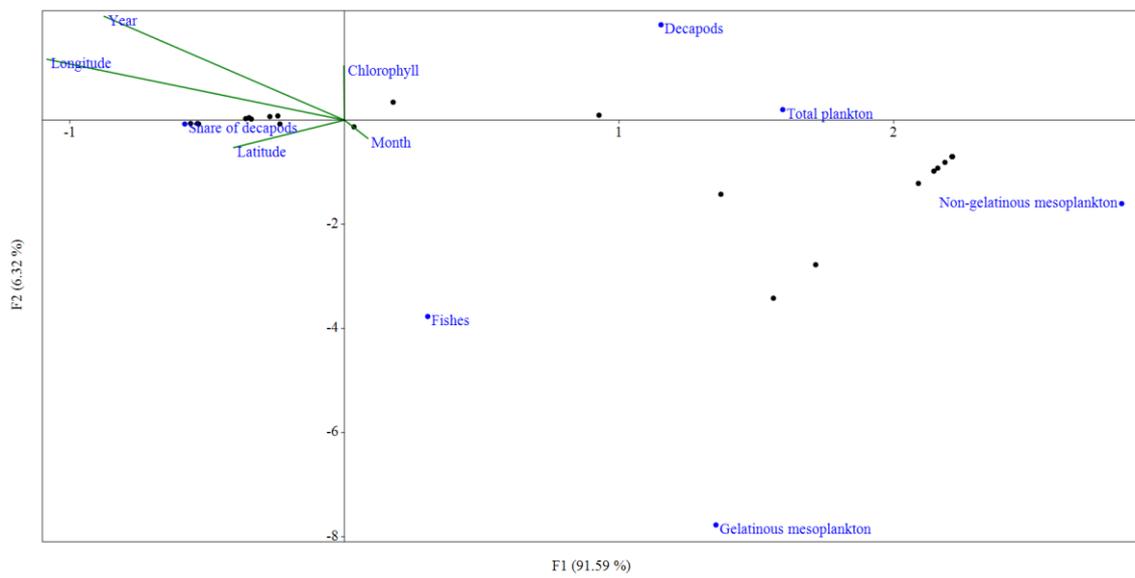
B



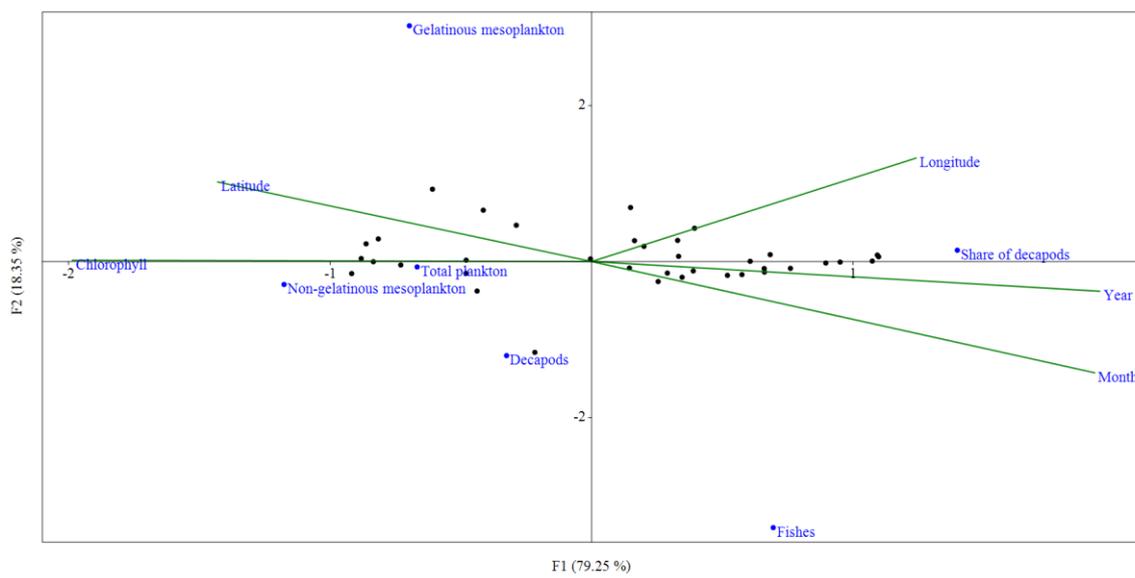
C



D



E



F

Figure 4.

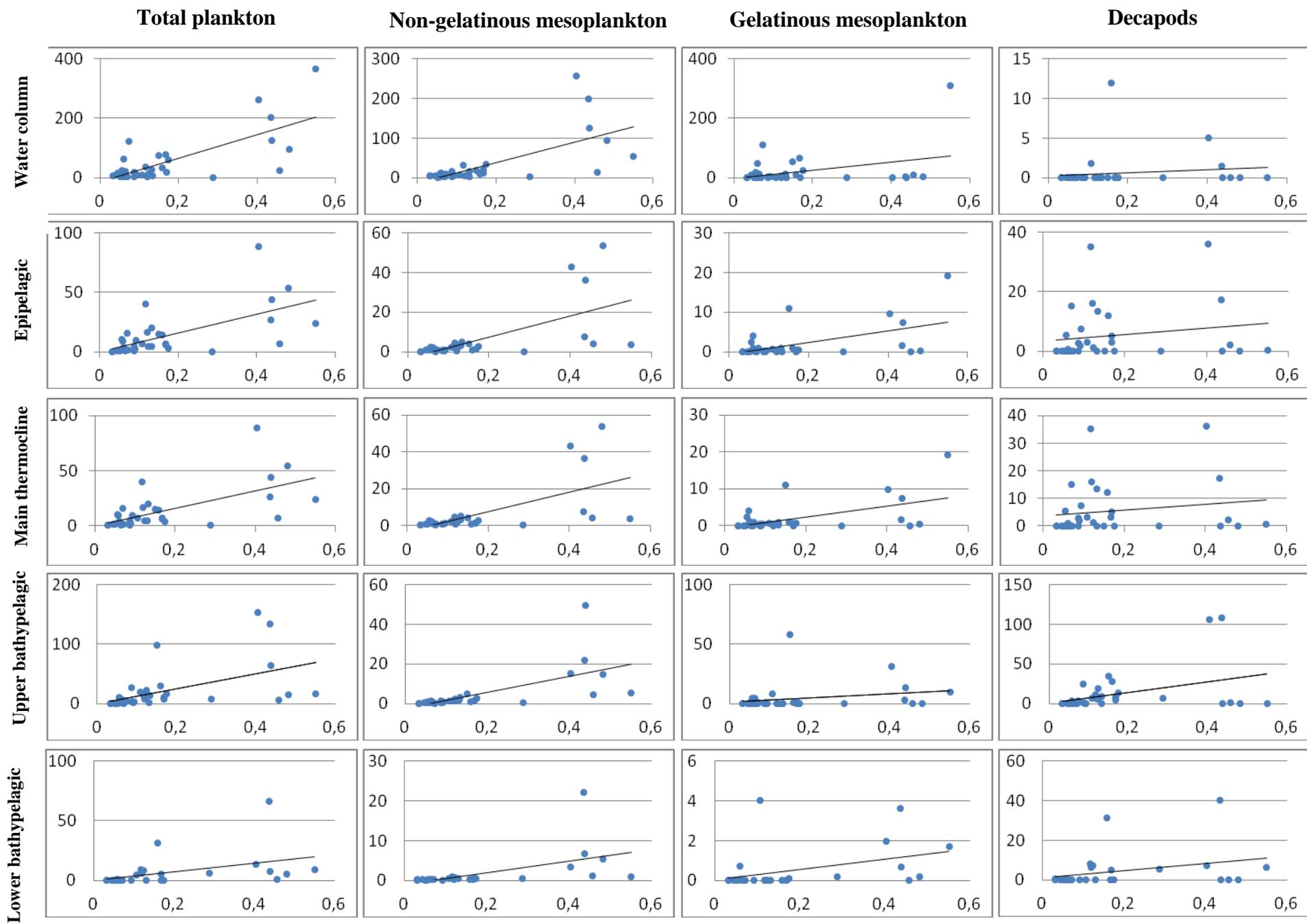


Figure 5.

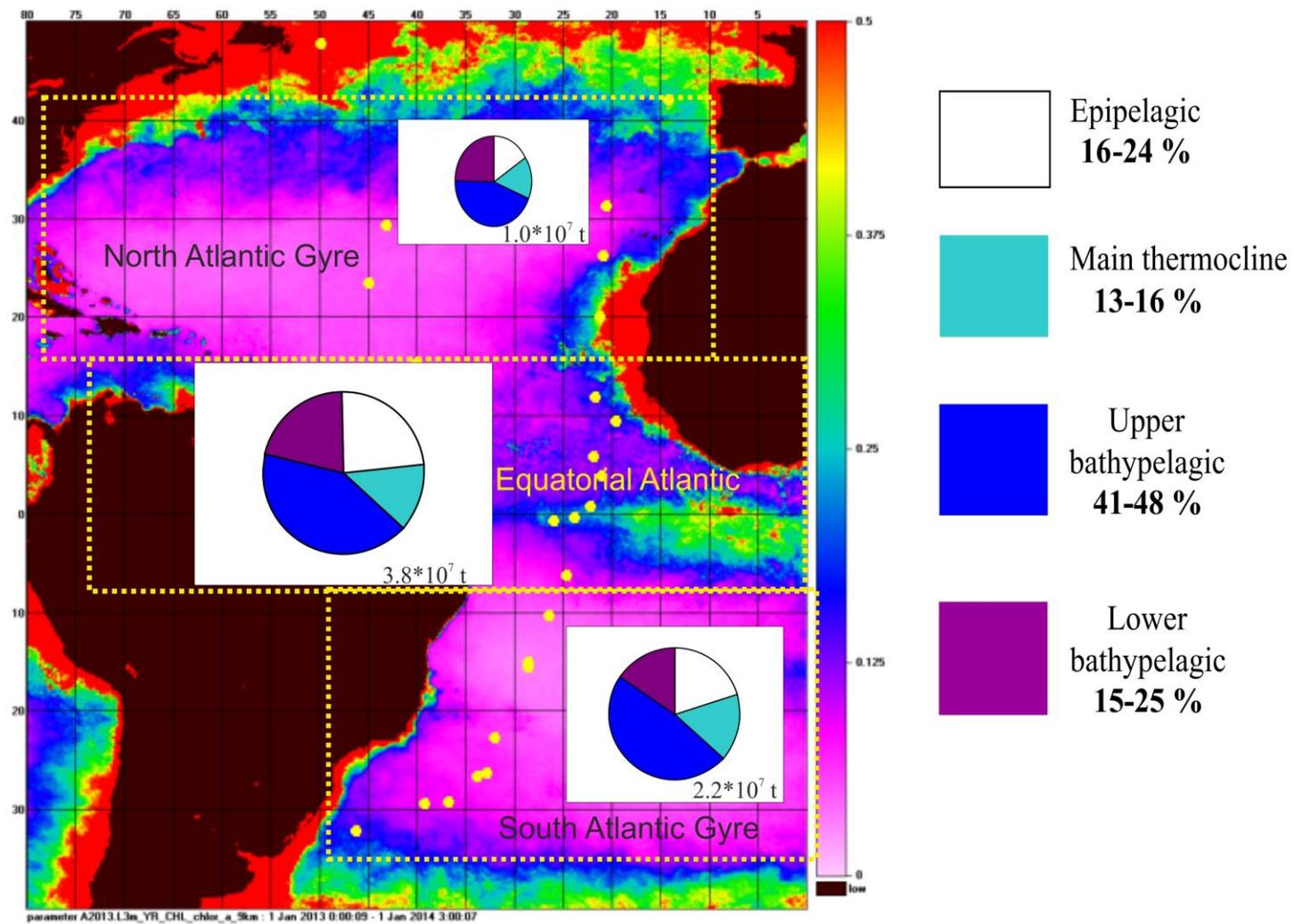


Figure 6.