

1 A NOVEL APPROACH REVEALS HIGH ZOOPLANKTON STANDING STOCK DEEP IN
2 THE SEA

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17 **ABSTRACT**

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

33 INTRODUCTION

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

41

42 Studies on the deep-sea plankton biomass at selected sites include those in the North Pacific
43 (e.g., Vinogradov, 1968; Murano *et al.*, 1976; Yamaguchi *et al.*, 2002ab; Yamaguchi, 2004) and
44 Eastern Tropical Pacific (Sameoto, 1986), North Atlantic (Koppelman and Weikert, 1992;
45 1999; Gislason, 2003; Vinogradov, 2005) and Mediterranean Sea (Scotto di Carlo *et al.*, 1984;
46 Weikert and Trinkaus, 1990), Indian Ocean (Vinogradov, 1968) and Arabian Sea (Koppelman
47 and Weikert, 1992; Böttger-Schnack, 1996). Fewer results concern deep-sea zooplankton
48 distribution over larger areas (Longhurst & Williams, 1979; Gaard *et al.*, 2008). The data
49 regarding quantitative distribution of the deep-sea zooplankton for the Equatorial Atlantic and
50 the South Atlantic Gyre are lacking. In addition to geographic restrictions, most deep-sea
51 research has been concentrated on specific taxonomic groups (e.g. crustacean zooplankton;
52 Burghart *et al.*, 2007; Gaard *et al.*, 2008), functional groups (e.g. gelatinous zooplankton;
53 Lindsay & Hunt, 2005), or selected vertical zones (e.g. mesopelagic; Robison *et al.*, 2010; Sutton
54 *et al.*, in press). Attempts to assess an entire deep-sea community have been rare and local
55 (Vinogradov *et al.*, 1996; Vereshchaka & Vinogradov, 1999; Vinogradov *et al.*, 2000).
56 Comparative assessments of entire water column plankton over large areas are absent.
57 Thus, it is timely to provide estimates of the zooplankton biomass throughout the water column
58 over large areas. As any field data of the deep-sea zooplankton are inevitably local, we should
59 find an indicator that is correlated with elements of the deep-sea zooplankton and that can be

60 assessed over large water areas/volumes. Here we offer and test a hypothesis that the
61 zooplankton wet biomass in the deep-pelagic is correlated with surface chlorophyll
62 concentration. This hypothesis has been corroborated for the epipelagic (0-200 m) layer, where
63 correlations have been obtained (Vinogradov et al., 1999). It remains completely unknown,
64 however, if this dependence is valid for the deep sea below 200 m. In theory, the standing stock
65 of zooplankton should remain correlated with surface productivity and the correlation should
66 decrease with depth. No large-scale data, however, are available on this subject. Here we attempt
67 to fill that void by examining the relationship between remotely sensed sea surface data and *in*
68 *situ*, discrete depth sampling data across the majority of the Atlantic Ocean (Fig. 1). In order to
69 start this process, we will focus on the deep-sea meso- and macroplankton (1-10 cm length). This
70 size fraction links primary and higher levels of oceanic production and is representatively
71 sampled by the largest spectrum of plankton nets. As an indicator of surface productivity, surface
72 chlorophyll concentration (Chl hereafter) derived from satellite information has been chosen as
73 our indicator metric. We will check the presence of correlation for major groups of the
74 zooplankton and for the different depth zones: epipelagic, main thermocline, upper- and lower-
75 bathypelagic zones. If correlations exist, we will assess the standing stock of the plankton over
76 vertical zones and over geographical areas. Where possible, we will estimate the role of major
77 plankton groups and different depth zones in the total standing stock of the zooplankton. If
78 successful, this attempt will provide a new expedient method for evaluation of deep-sea
79 resources.

80 Zooplankton distribution is strongly affected by the presence of land (islands, continents,
81 seamounts) and the sea-floor (Vereshchaka, 1995). The effect is prominent at a distance of tens
82 of kilometer in the horizontal direction (Vereshchaka, 1990ab, 1994; Melo et al., 2014) and
83 hundreds of meter in the vertical direction (Vereshchaka; 1995; Vereshchaka & Vinogradov,
84 1999; Cartes et al., 2010). In order to minimize the land and the sea-floor effects, this survey of
85 the pelagic zooplankton in the open ocean will be made as far as possible from the bottom in the
86 vertical direction and from the land in the horizontal direction.

89 **METHODS**

90 Field data were taken in the deep Central, South, and North Atlantic between 1996-2012 from
91 ultraoligotrophic to mesotrophic areas roughly between 40° S and 40° N during 36th and 37th
92 cruises of the R/V “Akademik Sergey Vavilov” (ASV), and 34th, 37th, 39th, 42nd, 46th, 47th, 49th,
93 50th cruises of the R/V “Akademik Mstislav Keldysh” (AMK - Table 1, Fig. 1). These areas
94 include the two main Atlantic Gyres (North and the South) and the Equatorial Atlantic between
95 them.

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

108 Samples were taken between one hour after sunset and one hour before sunrise in order to make
109 a unified nighttime picture of the vertical distribution of animals. This method was adopted to
110 avoid the confounding effects of diel vertical migration. We sampled four discrete depth strata:
111 (1) the epipelagic zone (0-200 m), (2) the main thermocline (from 200 m to the depth of the 7°C
112 isotherm, within 550-800 m), (3) the zone from the lower boundary of the main thermocline to
113 1500 m, mainly Antarctic Transitional Waters, which we define here as the upper bathypelagic,
114 and (4) the layer 1500-3000 m, mainly North Atlantic Deep Waters, which we define here as the
115 lower bathypelagic (Fig. 2). The upper boundary of the bathypelagic zone as defined here did not

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

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

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

139 Surface chlorophyll-a concentration (Chl) derived from satellite images was used as a measure of
140 the surface productivity. Chl data were taken from Aqua MODIS (level 3, 4-km resolution) from
141 2003 to 2015. Before this period Chl data were taken from SeaWiFS (level 3, 9-km resolution)
142 from 1997 to 2002. Chl data were averaged over one year preceding the sampling date and over
143 a $5^\circ \times 5^\circ$ square (with the sampling site in the center).

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

159

160 **RESULTS**

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

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

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

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

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

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

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

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

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

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

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

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

219 Contribution of various vertical zones to the total plankton standing stock was similar in the
220 three selected areas (Fig. 6). The contribution of the main thermocline zone was the smallest
221 portion of the total plankton stock (13-16 %), the epipelagic and lower bathypelagic zones were
222 intermediate (15-25 %), and the upper bathypelagic zone contributed the highest portion (41-48
223 %). In terms of faunal contributions, gelatinous and non-gelatinous mesozooplankton accounted
224 for nearly one-quarter of the total zooplankton stock, while the decapods composed
225 approximately half. Various species of the decapod genera *Acanthephyra* A. Milne-Edwards,

226 1881 and *Gennadas* Spence Bate, 1881 were dominant throughout the studied area, *Notostomus*
227 *A. Milne-Edwards*, 1881 and *Systellaspis* Spence Bate, 1888 were dominant in the Equatorial
228 area and South Atlantic Gyre. Fishes (represented by Gonostomatidae Cocco, 1838 and
229 Myctophidae Gill, 1893) were not included in this analyses, since their biomass was not
230 correlated with studied environmental parameters.

231

232 **DISCUSSION**

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

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

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

254 conditions for downward energy transfer and accumulation of organic matter in the zooplankton
255 wet biomass. It is all the more interesting that our data do show statistically significant
256 correlation between Chl and the deep zooplankton biomass. The use of Chl averaged over 5° x 5°
257 area and one-year period provide a new and productive approach to assess the deep pelagic
258 biomass. The use of different temporal and spatial scaling may improve this approach in the
259 future.

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

- 263 • Correlations may be different outside the tropical/subtropical region of the
264 Atlantic Ocean. Studies in the epipelagic zone show that such correlations are
265 better in warm waters than in the cold waters (Vinogradov *et al.*, 1999).
- 266 • Correlations may be different in different oceans. Our data show better correlation
267 between the Chl concentration and the zooplankton wet biomass in the epipelagic
268 zone than in Vinogradov *et al.* (1999) - 0.67 versus 0.53. We used field data from
269 the Atlantic Ocean only, while Vinogradov *et al.* (1999) based their studies on a
270 set of data from the Atlantic, Indian, and Pacific Oceans. Each ocean probably
271 requires an individual approach until conversion factors can be obtained to link
272 geographically distant deep-sea assemblages.
- 273 • Actual wet biomass of gelatinous mesozooplankton is underestimated by our gear.
274 A significant part of ctenophores and medusae are destroyed in the mesh during
275 retrieval. Fragile gelatinous animals may dominate in the deep sea (Robison *et al.*,
276 2010) and plankton nets are suboptimal for estimating their actual abundance
277 (Vereshchaka & Vinogradov, 1999).
- 278 • Actual wet biomass of the decapods is also underestimated, as these animals
279 likely avoid plankton nets and trawls to some extent (Vereshchaka, 1990).

280

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

294 In contrast to decapods, pelagic fishes escape in horizontal direction, as has been observed from
295 submersibles many times by the authors. This reaction is successful when vertical hauls are used
296 and our results are thus not representative for assessment of the pelagic fish biomass. This
297 biomass may occur to be finally correlated with Chl but horizontally towed gears are necessary
298 to prove that.

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

306

307 The most significant contribution to the total zooplankton standing stock unexpectedly came
308 from the upper bathypelagic zone, not the epipelagic zone or the main thermocline (Fig. 6). The

309 upper bathypelagic zone was dominated by macroplanktonic decapods, which accounted for over
310 half of the standing stock wet biomass. Most decapods undertake diel vertical migration (Foxton,
311 1970a,b), feeding on mesozooplankton in the upper layers at night and hiding from predators in
312 the dark upper bathypelagic zone by day. This behaviour appears effective and provides good
313 prospects for biomass accumulation below the main thermocline in the ocean. The finding of
314 higher than expected biomass deep in the water column mirrors recent findings that suggest
315 deep-pelagic fish biomass has been underestimated by up to an order of magnitude (Kaartvedt *et*
316 *al.*, 2012; Irigoien *et al.*, 2014). The global ramifications of these findings, coupled with ours, are
317 that energy transfer efficiency from phytoplankton to intermediate and higher trophic levels in
318 oceanic ecosystems has been underestimated, and that both zooplankton and fishes are likely
319 respiring a large portion of the primary production in the deep-pelagic realm.

320

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326 **REFERENCES**

- 327 1. Böttger-Schnack, R. Vertical structure of small metazoan plankton, especially non-
328 calanoid copepods. I. Deep Arabian Sea. *J Plankton Res*, 18, 1073–1101, 1996.
- 329 2. Brodsky, K.A. Calanoida of the Far East and the Polar Basin. Leningrad Academy of
330 Science Public House, 342 pp. (in Russian), 1950.
- 331 3. Brodsky, K. A., Vyshkvartzeva, N. V., Kos, M. S., and Markhaseva, E. L. Copepoda
332 Calanoida of the seas of the USSR and adjacent seas. *Opredeliteli po faune SSSR, Izdavaemye*
333 *135(1)*, 1-358, 1983.
- 334 4. Burghart, S. E., Hopkins, T. L., and Torres J. J. (2007) The bathypelagic Decapoda,
335 Lophogastrida, and Mysida of the eastern Gulf of Mexico. *Mar. Biol* 152, 315–327.
- 336 5. Chace F. A. The Caridean decapods (Crustacea: Decapoda) of the Albatross Philippine
337 Expedition, 1907-1910, part 4: families Oplophoridae and Nematocarcinidae. Smithsonian
338 Institution Press, Washington DC, 1986.
- 339 6. Dawson M. N. Species richness, habitable volume, and species densities in freshwater,
340 the sea, and on land. *Front. Biogeogr.* 4, 105-116, 2012.
- 341 7. Foxtan P. The Vertical Distribution of Pelagic Decapods [Crustacea: Natantia] Collected
342 on the SOND Cruise 1965 I. The Caridea. *J. Mar. Biol. Ass. U.K.* 50(4), 939-960, 1970.
- 343 8. Foxtan P. The Vertical Distribution of Pelagic Decapods [Crustacea: Natantia] Collected
344 on the SOND Cruise 1965 II. The Penaeidea and General Discussion *J. Mar. Biol. Ass. U.K.*
345 *50(4)*, 961-1000, 1970
- 346 9. Gaard, E., Gislason, A., Falkenhuug, T., Søliland, H., Musaeva, E., Vereshchaka, A., and
347 Vinogradov, G. Horizontal and vertical copepod distribution and abundance on the Mid-Atlantic
348 Ridge in June 2004. *Deep-Sea Res. II* 55(1), 59-71, 2008
- 349 10. Gasol J. M., del Giorgio, P. A., and Duarte C. M. Biomass distribution in marine
350 planktonic communities. *Limnol. Oceanogr.*, 42(6), 1353-1363, 1997.
- 351 11. Gislason, A. Life-cycle strategies and seasonal migrations of oceanic copepods in the
352 Irminger Sea. *Hydrobiologia*, 503, 195–209, 2003.

- 353 12. Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., Acuña, J. L., Bode, A.,
354 Echevarria, F., Gonzalez-Gordillo, J. I., Hernandez-Leon, S., Agusti, S., Aksnes, D. L.,
355 Duarte, C. M., and S. Kaartvedt . Large mesopelagic fishes biomass and trophic efficiency in the
356 open ocean. *Nature Communications* 5, doi: 10.1038/ncomms4271, 2014.
- 357 13. Kaartvedt, S., Staby, D., and Aksnes, D. Efficient trawl avoidance by mesopelagic fishes
358 causes large underestimation of their biomass. *Mar. Ecol. Progr. Ser.* 456, 1-6, 2012
- 359 14. Koltermann K. P., Gouretski V., and Jancke, K. Hydrographic Atlas of the World Ocean
360 Circulation Experiment (WOCE): Volume 3: Atlantic Ocean. National Oceanography Centre,
361 Southampton, U.K., 2011.
- 362 15. Koppelman, R. and Weikert, H. Full-depth zooplankton profiles over the deep bathyal
363 of the NE Atlantic. *Mar Ecol-Prog Ser*, 82, 263–272, 1992.
- 364 16. Koppelman, R., and Weikert, H. Deep Arabian Sea mesozooplankton distribution.
365 Intermonsoon, October 1995. *Mar Biol*, 129, 549–560, 1997.
- 366 17. Koppelman, R., and Weikert, H. Temporal changes of deep-sea mesozooplankton
367 abundance in the temperate NE Atlantic and estimates of the carbon budget. *Mar Ecol-Prog Ser*,
368 179, 27–40, 1999.
- 369 18. Lindsay, D. J., and Hunt J. C. Biodiversity in midwater cnidarians and ctenophores:
370 submersible-based results from deep-water bays in the Japan Sea and northwestern Pacific. *J.*
371 *Mar. Biol. Ass. U.K.* 85, 503–517, 2005.
- 372 19. Longhurst, A., and Williams, R. Materials for plankton modelling: vertical distribution of
373 Atlantic zooplankton in summer. *J. Plank. Res.* 1, 1–28, 1979.
- 374 20. Markhasheva, E. L. Calanoid copepods of the family Aedideidae of the World Ocean. In:
375 *Proceedings of the Zoological Institute in St. Petersburg. St. Petersburg*, 331pp. 1996.
- 376 21. Mauchline, J., and Fisher, L. R. The Biology of Euphausiids. *Advances in Marine*
377 *Biology*, 85, 1969.
- 378 22. Murano, M., Marumo, R., Nemoto, T., Aizawa, Y. Vertical distribution of biomass of
379 plankton and micronekton in the Kuroshio Water off central Japan. *Bulletin of Plankton Society*
380 *of Japan* 23, 1–12, 1976.

- 381 23. Okey, T. A., Alidina, H. M., Lo, V., Montenegro, A., and Jessen, S. Climate change
382 impacts and vulnerabilities in Canada's Pacific marine ecosystems. World Wildlife
383 Fund/Canadian Parks and Wilderness Society, Vancouver, Vancouver, 157 pp. 2012.
- 384 24. Robison, B. H., Sherlock, R. E., and Reisenbichler, K. The bathypelagic community of
385 Monterey Canyon. *Deep-Sea Res. II* 57 1551–1556. 2010.
- 386 25. Rose, M. Faune de France. 26. Copepods Pelagiques. Typographie Firmin-Didot et cie,
387 Paris, 374 pp. 1933.
- 388 26. Sameoto, D.D. Influence of the biological and physical environment on the vertical
389 distribution of mesozooplankton and micronekton in the eastern tropical Pacific. *Mar Biol* 93,
390 263–279, 1986.
- 391 27. Smith, K. L., Baldwin, R. J., Karl, D. M. and Boetius, A. Benthic community responses
392 to pulses in pelagic food supply: North Pacific Subtropical Gyre. *Deep-Sea Res I:*
393 *Oceanographic Research Papers*, 49(6), 971-990, 2002.
- 394 28. Sutton T.T. et al. PERSPECTIVES - A global biogeographic classification of the
395 mesopelagic zone: An aid for marine conservation planning. *J. Biogeogr.* (in press). 2016.
- 396 29. Uitz, J., Claustre, H., Morel, A., and Hooker, S. B. Vertical distribution of phytoplankton
397 communities in open ocean: An assessment based on surface chlorophyll, *J. Geophys. Res.* 111,
398 C08005, doi:10.1029/2005JC003207, 2006.
- 399 30. Vereshchaka, A. L. Pelagic decapods from seamounts of the Nazca and Sala-y-Gomez
400 ridges. Plankton and benthos from the Nazca and Sala-y-Gomez submarine ridges. *Trud. Inst.*
401 *Okeanol, Acad. Sci., Moscow* 124: 129-155, 1990.
- 402 31. Vereshchaka, A. L. Revision of the genus *Sergestes* (Decapoda: Dendrobranchiata:
403 *Sergestidae*): taxonomy and distribution. *Galathea Report* 22, 7-104, 2009.
- 404 32. Vereshchaka, A. L. Revision of the genus *Sergia* (Decapoda: Dendrobranchiata:
405 *Sergestidae*): taxonomy and distribution. *Galathea Report*, 18, 69-207, 2000.
- 406 33. Vereshchaka, A. L. The distribution of pelagic macroplankton (mysids, euphausiids, and
407 decapods) over the continental slopes and seamounts of the western Indian Ocean. *Oceanology*,
408 34 (1), 81-86, 1994.

- 409 34. Vereshchaka, A. L., and Vinogradov, G. M. Visual observations of vertical distribution of
410 plankton through the water column above Broken Spur vent field, Mid-Atlantic Ridge. *Deep-Sea*
411 *Res. I* 46, 1615–1632, 1999.
- 412 35. Vereshchaka, A., Abyzova, G., Lunina, A., and Musaeva, E. The deep-sea zooplankton
413 of the North, Central, and South Atlantic: Biomass, abundance, diversity. *Deep-Sea Res Part II:*
414 *Topical Studies in Oceanography*. 2016
- 415 36. Vinogradov, G.M. Vertical distribution of macroplankton at the Charlie-Gibbs Fracture
416 Zone (North Atlantic), as observed from the manned submersible ‘‘Mir-1’’. *Mar. Biol.* 146, 325–
417 331, 2005.
- 418 37. Vinogradov, M.E. Vertical Distribution of the Oceanic Zooplankton. Institute of
419 Oceanography Academy Science USSR, Moscow, 339pp. (English translation, I.P.S.T.,
420 Jerusalem, 1970). 1968.
- 421 38. Vinogradov, M. E., Vereshchaka, A. L., and Shushkina, E. A. Vertical structure of the
422 zooplankton communities in the oligotrophic areas of the Northern Atlantic, and influence of the
423 hydrothermal vent. *Okeanologiya* 36(1): 71-79, 1996.
- 424 39. Vinogradov, M. E., Shushkina, E. A., Nezhlin, N. P., Vedernikov, V. I., and Gagarin, V. I.
425 Correlation between different parameters of the ecosystem of the epipelagic zone of the World
426 Ocean. *Oceanology*, 39(1), 54-63, 1999.
- 427 40. Vinogradov, M. E., Vereshchaka, A. L., and Vinogradov, G. M. Vertical distribution of
428 zooplankton at the periphery of the North Atlantic subtropical gyre. *Izvestiya Akademii Nauk*
429 *Seriya Biologicheskaya* 4: 496-510, 2000.
- 430 41. Weikert, H., and Trinkaus, S. Vertical mesozooplankton abundance and distribution in
431 the deep Eastern Mediterranean Sea SE of Crete. *J Plankton Res*, 12, 601–628, 1990.
- 432 42. Widder E. A. Bioluminescence. In: *Adaptive Mechanisms in the Ecology of Vision*.
433 Springer Netherlands p. 555-581, 1999.
- 434 43. Wiebe, P.H.. Functional regression equations for zooplankton displacement volume, wet
435 weight, dry weight, and carbon: a correction. *Fish B-NOAA*, 86, 833–835, 1988.

- 436 44. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S.,
437 Ishizaka, J., Ikeda, T. and Takahashi, M.M. Community and trophic structures of pelagic
438 copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep-Sea*
439 *Res I* 49, 1007–1025, 2002a.
- 440 45. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S.,
441 Ishizaka, J., Ikeda, T., Takahashi, M.M. Structure and size distribution of plankton communities
442 down to the greater depths in the western North Pacific Ocean. *Deep-Sea Res II* 49, 5513–5529,
443 2002b.
- 444 46. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S.,
445 Ishizaka, J., Ikeda, T., Takahashi, M.M. Latitudinal differences in the planktonic biomass and
446 community structure down to the greater depths in the western North Pacific. *J Oceanogr*, 60,
447 773–787, 2004.
- 448 47. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Maeda, M., Ishizaka, J., Ikeda T,
449 and Mac Takahashi, M. Biomass and chemical composition of net-plankton down to greater
450 depths (0–5800m) in the western North Pacific ocean. *Deep-Sea Res Part I: Oceanographic*
451 *Research Papers*, 52(2), 341-353, 2005.
- 452
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454 **Table 1. List of stations, cruises of R/V “Akademik Sergey Vavilov” (ASV) and R/V**
 455 **“Akademik Mstislav Keldysh” (AMK). Sampling zones: E - epipelagic, M - main**
 456 **thermocline, U- upper bathypelagic, L - lower bathypelagic; T - total haul (0-3000 m, net**
 457 **was not closed).**
 458

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

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.

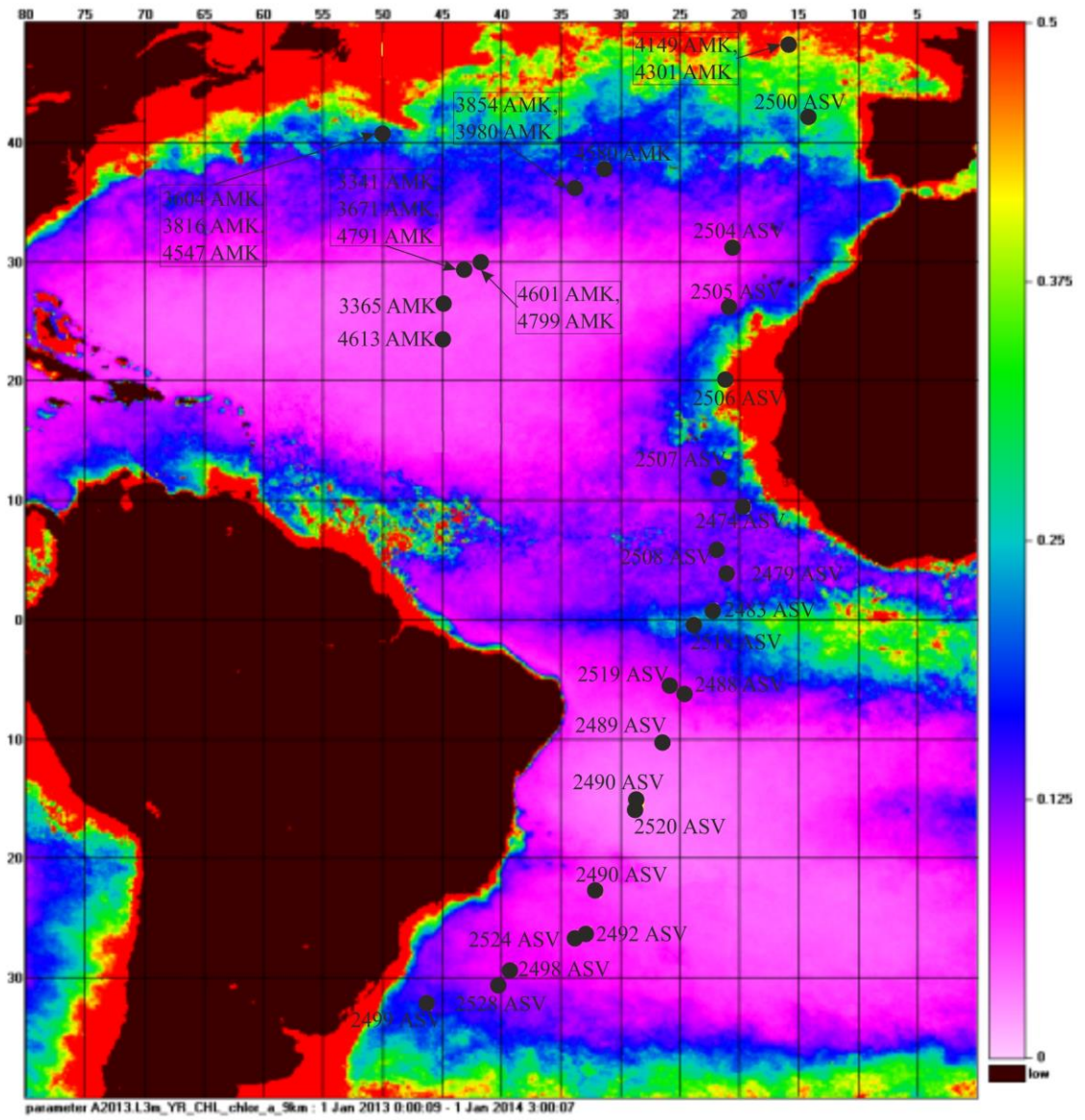


Figure 1.

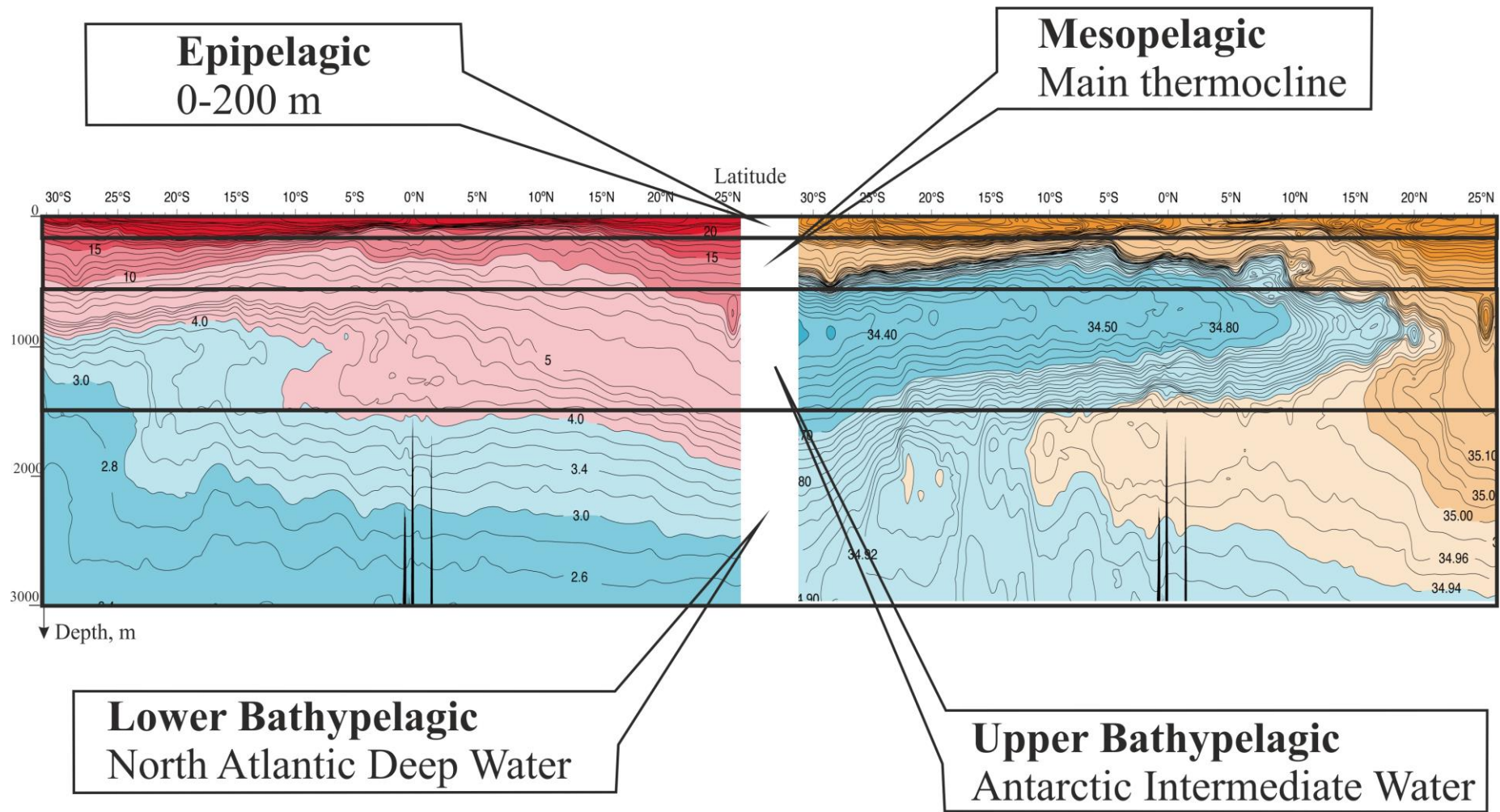


Figure 2.

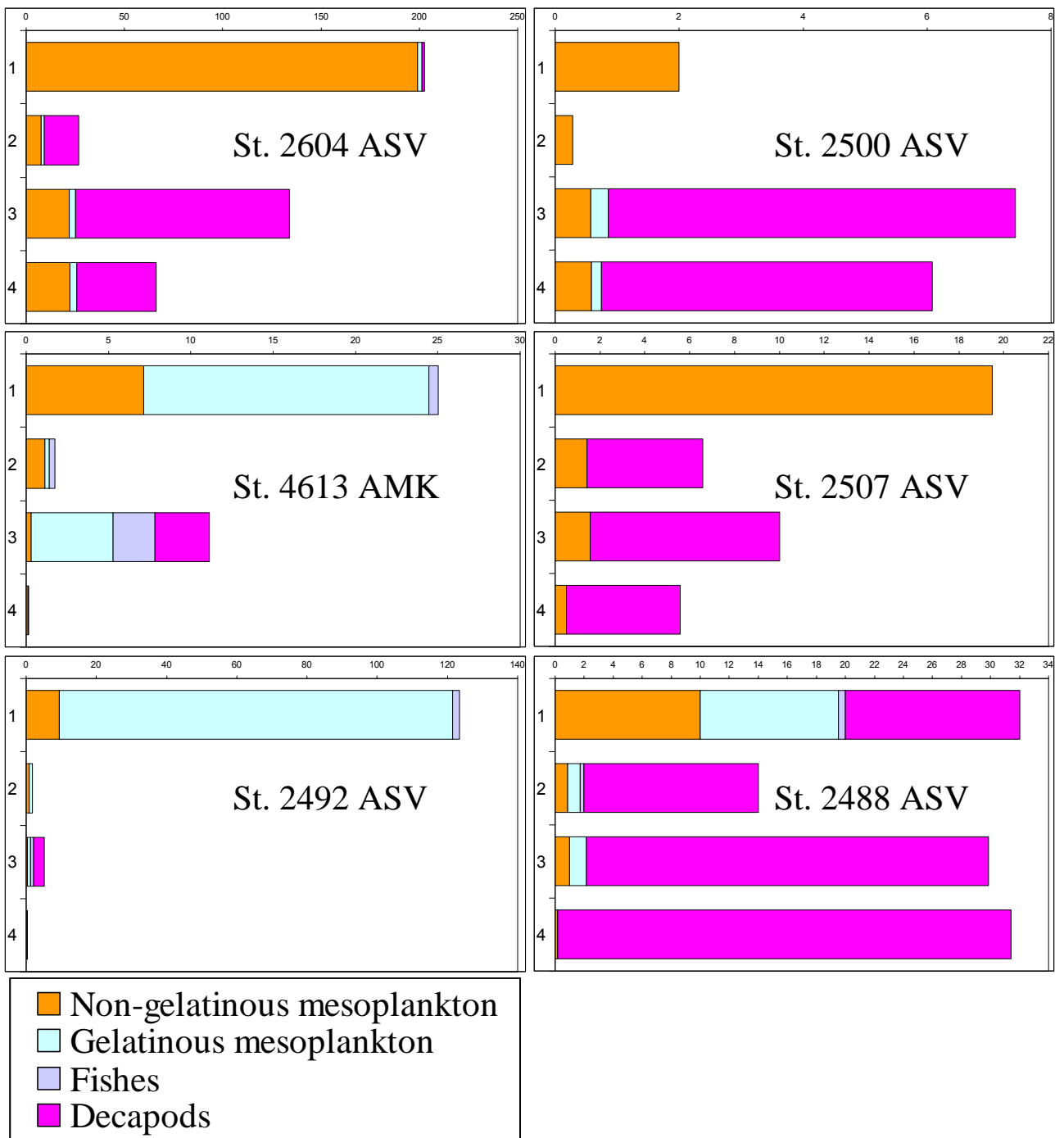
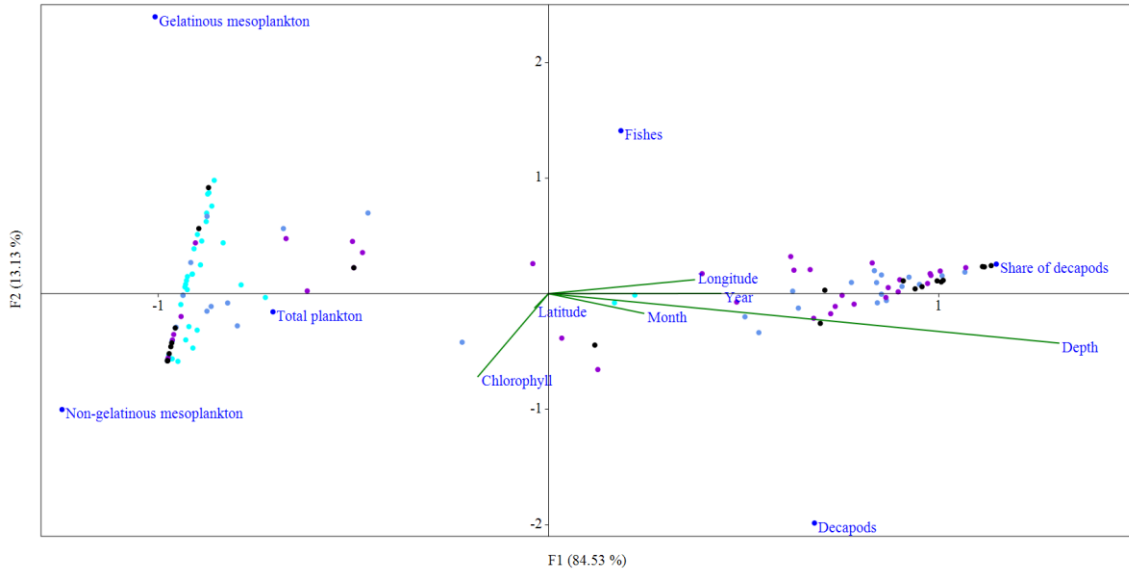
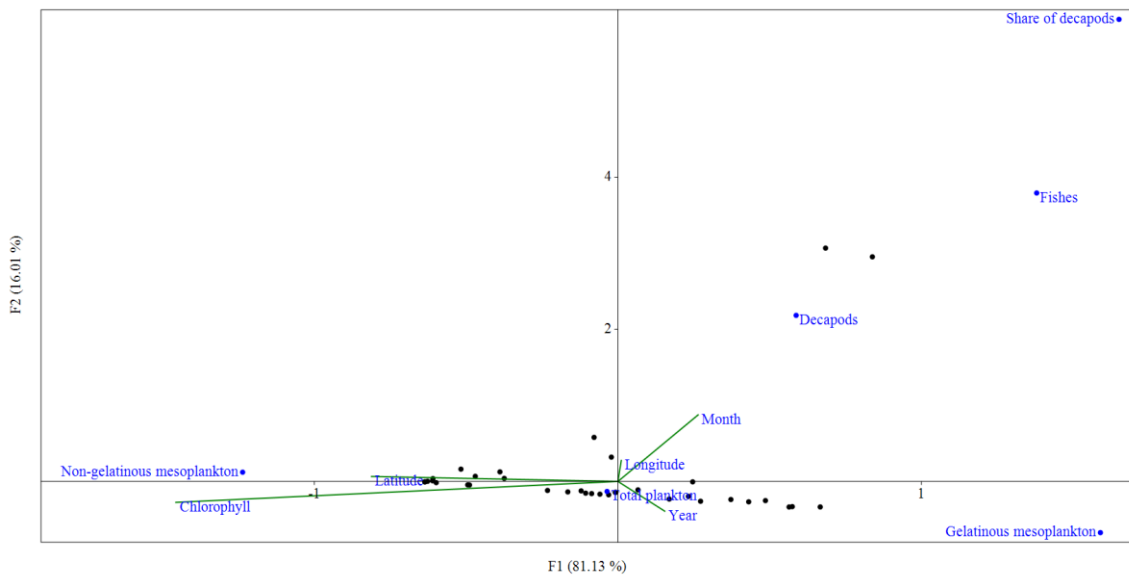


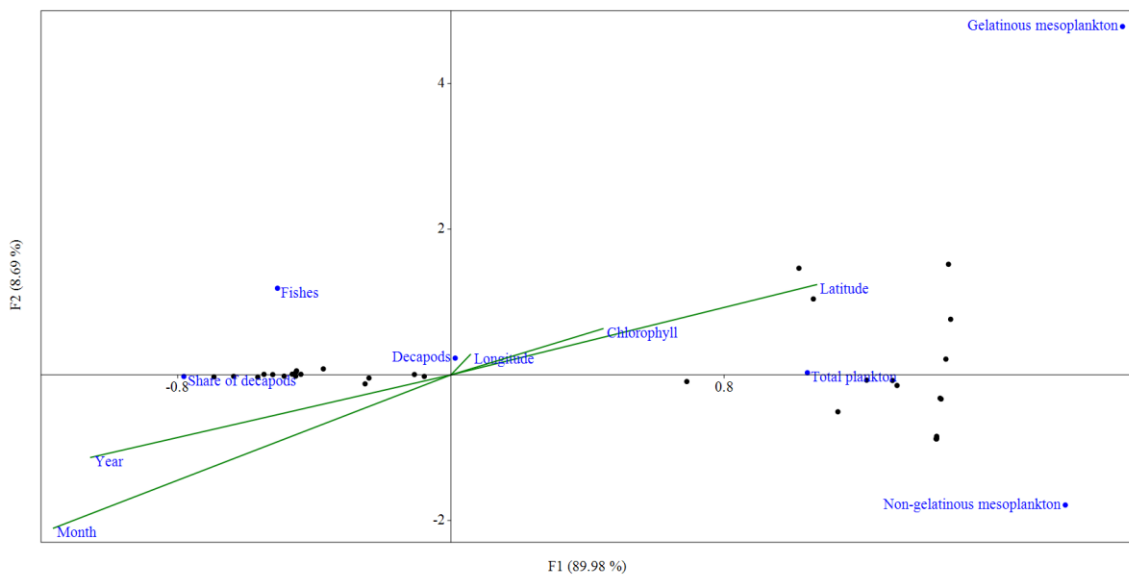
Figure 3.



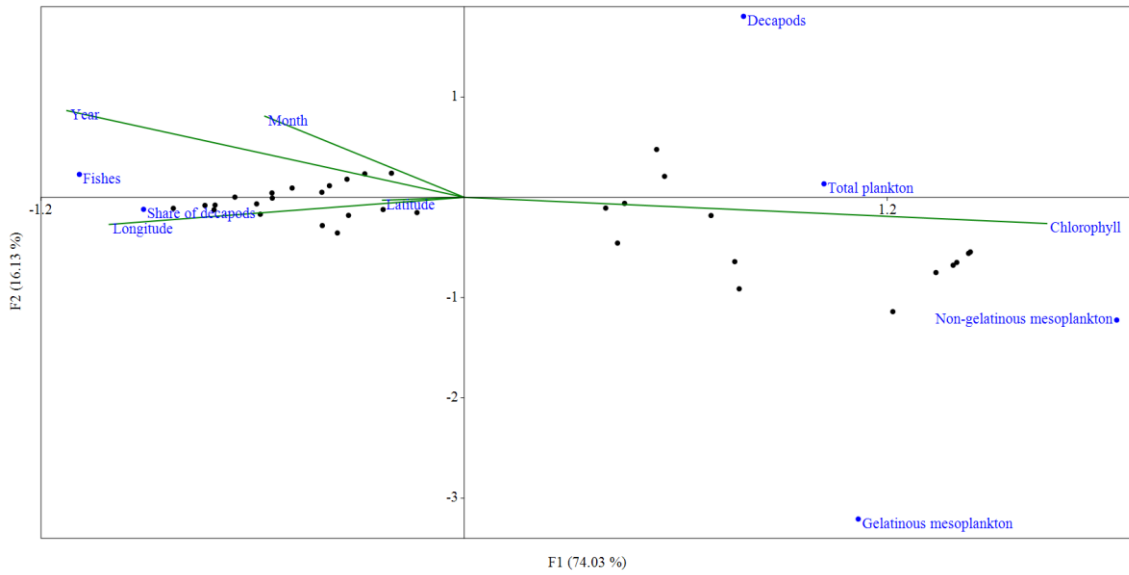
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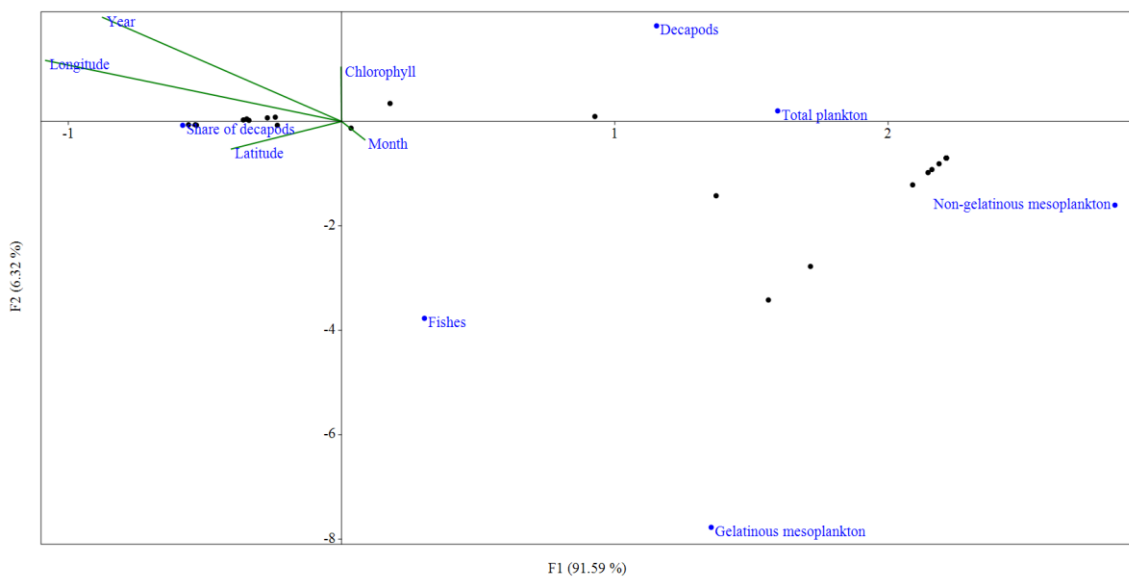
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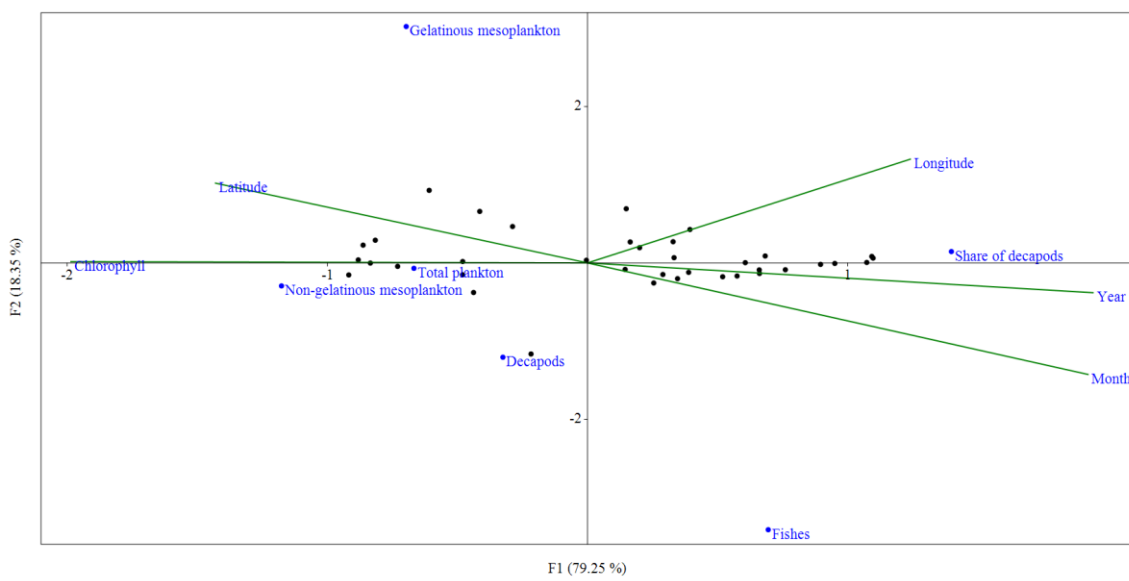
C



D



E



F

Figure 4.

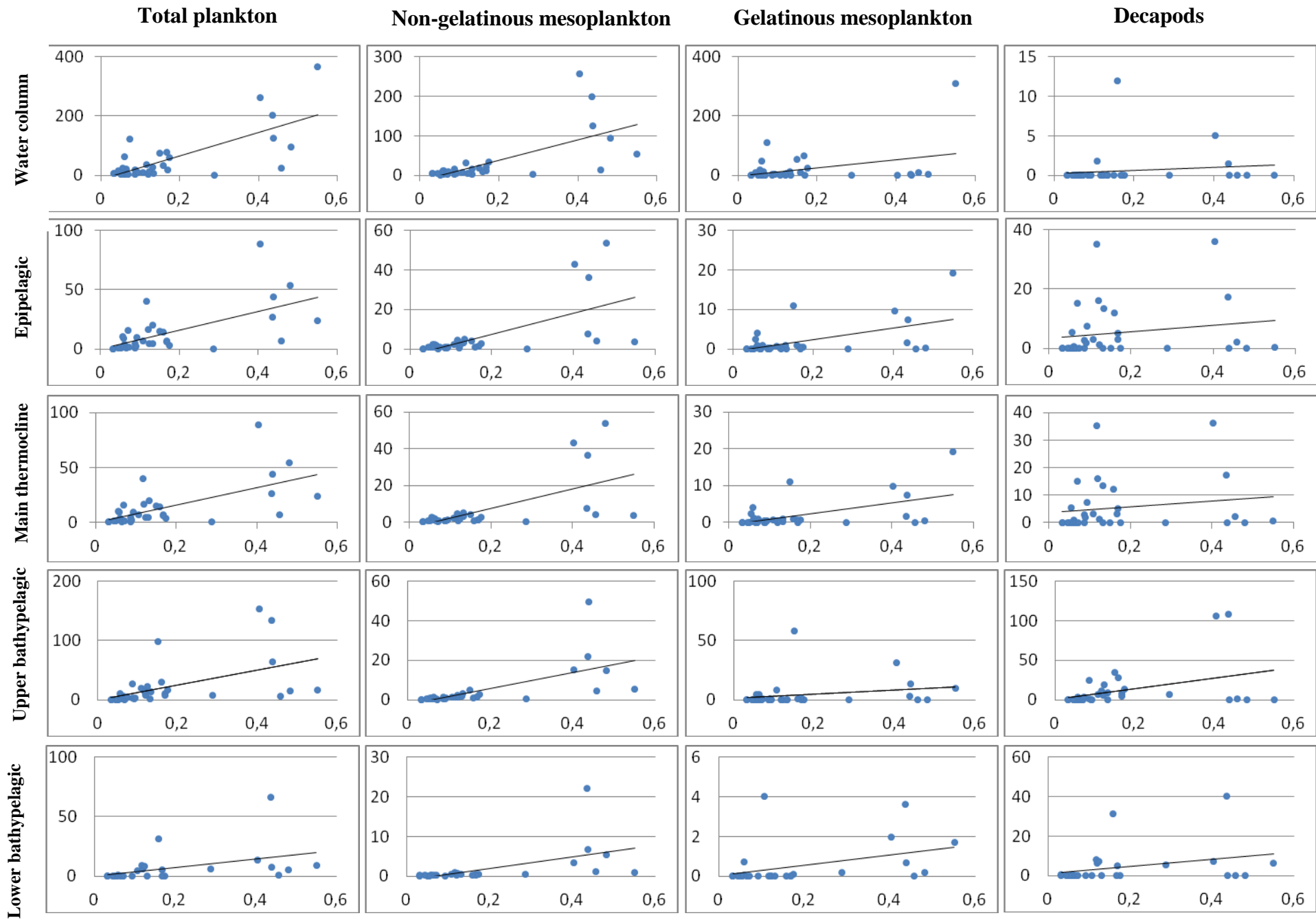


Figure 5.

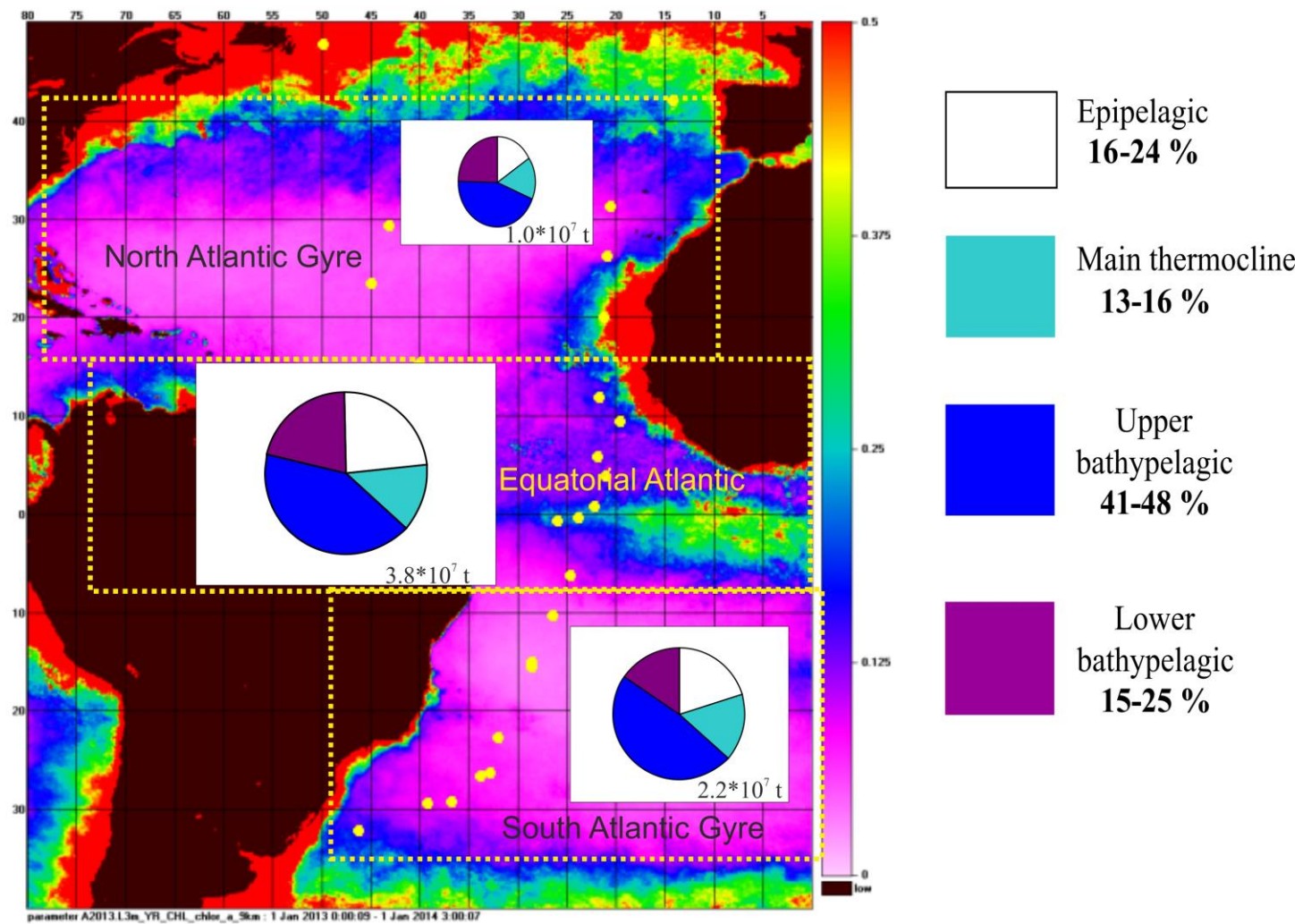


Figure 6.