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

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ABSTRACT

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

INTRODUCTION

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

Studies on the deep-sea plankton biomass at selected sites include those in the North Pacific (e.g., Vinogradov, 1968; Murano et al., 1976; Yamaguchi et al., 2002ab; Yamaguchi, 2004) and Eastern Tropical Pacific (Sameoto, 1986), North Atlantic (Koppelmann and Weikert, 1992; 1999; Gislason, 2003; Vinogradov, 2005) and Mediterranean Sea (Scotto di Carlo et al., 1984; Weikert and Trinkaus, 1990), Indian Ocean (Vinogradov, 1968) and Arabian Sea (Koppelmann and Weikert, 1992; Böttger-Schnack, 1996). Fewer results concern deep-sea zooplankton distribution over larger areas (Longhurst & Williams, 1979; Gaard *et al*., 2008). The data regarding quantitative distribution of the deep-sea zooplankton for the Equatorial Atlantic and the South Atlantic Gyre are lacking. In addition to geographic restrictions, most deep-sea research has been concentrated on specific taxonomic groups (e.g. crustacean zooplankton; Burghart *et al*., 2007; Gaard *et al*., 2008), functional groups (e.g. gelatinous zooplankton; Lindsay & Hunt, 2005), or selected vertical zones (e.g. mesopelagic; Robison *et al*., 2010; Sutton *et al*., in press). Attempts to assess an entire deep-sea community have been rare and local (Vinogradov *et al*., 1996; Vereshchaka & Vinogradov, 1999; Vinogradov *et al*., 2000). Comparative assessments of entire water column plankton over large areas are absent.

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

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

METHODS

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

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

Samples were taken between one hour after sunset and one hour before sunrise in order to make a unified nighttime picture of the vertical distribution of animals. This method was adopted to avoid the confounding effects of diel vertical migration. We sampled four discrete depth strata: (1) the epipelagic zone (0-200 m), (2) the main thermocline (from 200 m to the depth of the 7°C isotherm, within 550-800 m), (3) the zone from the lower boundary of the main thermocline to 1500 m, mainly Antarctic Transitional Waters, which we define here as the upper bathypelagic, and (4) the layer 1500-3000 m, mainly North Atlantic Deep Waters, which we define here as the lower bathypelagic (Fig. 2). The upper boundary of the bathypelagic zone as defined here did not coincide with the traditional one (1000 m), because our sampling was associated with water masses. The lower boundary of the bathypelagic was 3000 m instead of usually adopted 4000 m, as we had to avoid sampling of the benthopelagic zone.

We used a closing Bogorov-Rass (BR) plankton net (1-m^2 opening, 500-µm mesh size, towed at a speed of 1 m sec^{-1}), which was proven to successfully sample deep-sea plankton $\geq$ 1.0 mm long (Vinogradov *et al.*, 1996; 2000); smaller animals may pass through the sieve during filtration. The net was deployed at the maximal depth of haul, then opened and towed vertically upwards, and finally closed at the minimal depth of haul with a mechanical device. The minimal horizontal distance between station and the land was 400 km and the minimal vertical distance the lower boundary of the deepest haul and the sea-floor was 750 m (Table 1), so that the land/sea-floor effect could be ignored.

We divided the net plankton into four major groups: non-gelatinous mesozooplankton (mainly copepods and chaetognaths; 1-30 mm length), gelatinous mesozooplankton (mainly siphonophorans and medusae; individual or zooid; 1-30 mm length), decapods and small (macroplanktonic) fishes (both groups over 30 mm length). Identification was done according to literature (e.g., Rose, 1933; Brodsky, 1950; Mauchline & Fisher, 1969; Brodsky *et al.*, 1983; Markhasheva, 1996). Synonymy of species was corrected according to www.marinespecies.org.

Decapods, fishes, and gelatinous species were weighed with a precision of 0.1 g before fixation. Wet weight of mesoplanktonic groups was estimated according to adopted procedures (Vinogradov *et al.*, 1996; 2000; Gaard, E., *et al.*, 2008). In brief, wet weight w_{tot} of the non-gelatinous mesozooplankton (mainly copepods) was estimated as $w_{\mathrm{tot}} = \Sigma\ (k * l_i^3)$, where l_i is length of an individual specimen, k is a species-dependent coefficient; tables of these coefficients have been published elsewhere (e.g., Vinogradov & Shushkina, 1987).

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

In order to establish relationships between the major plankton group wet biomass and possible environmental factors, Canonical Correspondence Analysis (CCA: Ter Braak, 1986) was performed on major group biomass using an assortment of environmental variables: temporal (month and year), spatial (latitude, longitude, and depth), and surface chlorophyll concentration (Chl). As the sampling was associated with distinct water masses, such environmental parameters as temperature, salinity, and depth were correlated and only one of them, the depth, was included in CCAs. CCA is a powerful multivariate technique to extract synthetic environmental gradients from ecological data (Ter Braak and Verdonschot, 1995). Ordination axes are based on the measured environmental variables and represent linear combinations of the variables. Arrows showing variables in the ordination plots are proportional in length to the importance of each variable (Ter Braak, 1986), and therefore community variation can be directly related to environmental variation. CCAs included either all hauls, or hauls from separate strata and made possible to assess the contribution of all analyzed factors.

Calculations, statistical procedures, regression analysis, an ANOVA tests were carried out with the use of Excel and STATISTICA, CCAs with PAST 3.04 (Hammer et al., 2001).

RESULTS

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

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

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

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

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

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

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

Multivariative CCA with lower bathypelagic hauls (Fig. 4E) showed aggregation of hauls in two groups: one was mainly related to the share of decapods (the left of OY axis), another was linked to plankton groups (the right of OY axis). The first factor (F1) was mainly linked to longitude and year, the second factor (F2) was primarily associated with Chl (Fig. 4E).

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

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

Having the correlation between the total zooplankton standing stock and Chl, we calculated the total zooplankton standing stock (wet biomass under 1 m^{-2} in the whole water column) and standing stocks within each strata (wet biomass under 1 m^{-2} integrated over whole layer) over selected areas. We did that for three rectangular areas roughly corresponding to the North and South Atlantic Gyres and the Equatorial Atlantic (Fig. 6). The maximum plankton stock was found in the Equatorial Atlantic (3.8×10^7 t wet weight), with the South and North Gyres being approximately half (2.2×10^7 t) and one-quarter (1.0×10^7 t) of this amount, respectively. Contribution of various vertical zones to the total plankton standing stock was similar in the three selected areas (Fig. 6). The contribution of the main thermocline zone was the smallest portion of the total plankton stock (13-16 %), the epipelagic and lower bathypelagic zones were intermediate (15-25 %), and the upper bathypelagic zone contributed the highest portion (41-48 %). In terms of faunal contributions, gelatinous and non-gelatinous mesozooplankton accounted for nearly one-quarter of the total zooplankton stock, while the decapods composed approximately half. Various species of the decapod genera *Acanthephyra* A. Milne-Edwards, 1881 and *Gennadas* Spence Bate, 1881 were dominant throughout the studied area, *Notostomus* A. Milne-Edwards, 1881 and *Systellaspis* Spence Bate, 1888 were dominant in the Equatorial area and South Atlantic Gyre. Fishes (represented by Gonostomatidae Cocco, 1838 and Myctophidae Gill, 1893) were not included in this analyses, since their biomass was not correlated with studied environmental parameters.

DISCUSSION

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

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

Multivariative analysis showed that depth and Chl were the main general factors affecting the wet biomass of main plankton groups (Fig. 4A). Obtained regressions between Chl and biomass of the major plankton groups are obfuscated by several factors. First, algorithms for conversion of satellite images to Chl data are not perfect (Watson *et al*., 2009). Second, Chl data, even if estimated unerringly, do not reflect surface productivity thoroughly: autotrophic organisms may live far below the surface and even create deep maxima with significant chlorophyll concentration not detectable via satellites (Uitz *et al*., 2006). Third, the trophic structure of deep-pelagic communities and deep-water circulation locally differ, thus providing different conditions for downward energy transfer and accumulation of organic matter in the zooplankton wet biomass. It is all the more interesting that our data do show statistically significant correlation between Chl and the deep zooplankton biomass. The use of Chl averaged over 5^o x 5^o area and one-year period provide a new and productive approach to assess the deep pelagic biomass. The use of different temporal and spatial scaling may improve this approach in the future.

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

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

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

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

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

The most significant contribution to the total zooplankton standing stock unexpectedly came from the upper bathypelagic zone, not the epipelagic zone or the main thermocline (Fig. 6). The upper bathypelagic zone was dominated by macroplanktonic decapods, which accounted for over half of the standing stock wet biomass. Most decapods undertake diel vertical migration (Foxton, 1970a,b), feeding on mesozooplankton in the upper layers at night and hiding from predators in the dark upper bathypelagic zone by day. This behaviour appears effective and provides good prospects for biomass accumulation below the main thermocline in the ocean. The finding of higher than expected biomass deep in the water column mirrors recent findings that suggest deep-pelagic fish biomass has been underestimated by up to an order of magnitude (Kaartvedt *et al*., 2012; Irigoien *et al*., 2014). The global ramifications of these findings, coupled with ours, are that energy transfer efficiency from phytoplankton to intermediate and higher trophic levels in oceanic ecosystems has been underestimated, and that both zooplankton and fishes are likely respiring a large portion of the primary production in the deep-pelagic realm.

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REFERENCES

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

12. Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., Acuña, J. L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J. I., Hernandez-Leon, S., Agusti, S., Aksnes, D. L., Duarte, C. M., and S. Kaartvedt . Large mesopelagic fishes biomass and trophic efficiency in the open ocean. Nature Communications 5, doi: 10.1038/ncomms4271, 2014.

13. Kaartvedt, S., Staby, D., and Aksnes, D. Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. Mar. Ecol. Progr. Ser. 456, 1-6, 2012

14. Koltermann K. P., Gouretski V., and Jancke, K. Hydrographic Atlas of the World Ocean Circulation Experiment (WOCE): Volume 3: Atlantic Ocean. National Oceanography Centre, Southampton, U.K., 2011.

15. Koppelmann, R. and Weikert, H. Full-depth zooplankton profiles over the deep bathyal of the NE Atlantic. Mar Ecol-Prog Ser, 82, 263–272, 1992.

16. Koppelmann, R., and Weikert, H. Deep Arabian Sea mesozooplankton distribution. Intermonsoon, October 1995. Mar Biol, 129, 549–560, 1997.

17. Koppelmann, R., and Weikert, H. Temporal changes of deep-sea mesozooplankton abundance in the temperate NE Atlantic and estimates of the carbon budget. Mar Ecol-Prog Ser, 179, 27–40, 1999.

18. Lindsay, D. J., and Hunt J. C. Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and northwestern Pacific. J. Mar. Biol. Ass. U.K. 85, 503–517, 2005.

19. Longhurst, A., and Williams, R. Materials for plankton modelling: vertical distribution of Atlantic zooplankton in summer. J. Plank. Res. 1, 1–28, 1979.

20. Markhasheva, E. L. Calanoid copepods of the family Aedideidae of the World Ocean. In: Proceedings of the Zoological Institute in St. Petersburg. St. Petersburg, 331pp. 1996.

21. Mauchline, J., and Fisher, L. R. The Biology of Euphausiids. Advances in Marine Biology, 85, 1969.

22. Murano, M., Marumo, R., Nemoto, T., Aizawa, Y. Vertical distribution of biomass of plankton and micronekton in the Kuroshio Water off central Japan. Bulletin of Plankton Society of Japan 23, 1–12, 1976.

23. Okey, T. A., Alidina, H. M., Lo, V., Montenegro, A., and Jessen, S. Climate change impacts and vulnerabilities in Canada's Pacific marine ecosystems. World Wildlife Fund/Canadian Parks and Wilderness Society, Vancouver, Vancouver, 157 pp. 2012.

24. Robison, B. H., Sherlock, R. E., and Reisenbichler, K. The bathypelagic community of Monterey Canyon. Deep-Sea Res. II 57 1551–1556. 2010.

25. Rose, M. Faune de France. 26. Copepods Pelagiques. Typographie Firmin-Didot et cie, Paris, 374 pp. 1933.

26. Sameoto, D.D. Influence of the biological and physical environment on the vertical distribution of mesozooplankton and micronekton in the eastern tropical Pacific. Mar Biol 93, 263–279, 1986.

27. Smith, K. L., Baldwin, R. J., Karl, D. M. and Boetius, A. Benthic community responses to pulses in pelagic food supply: North Pacific Subtropical Gyre. Deep-Sea Res I: Oceanographic Research Papers, 49(6), 971-990, 2002.

28. Sutton T.T. et al. PERSPECTIVES - A global biogeographic classification of the mesopelagic zone: An aid for marine conservation planning. J. Biogeogr. (in press). 2016.

29. Uitz, J., Claustre, H., Morel, A., and Hooker, S. B. Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll, J. Geophys. Res. 111, C08005, doi:10.1029/2005JC003207, 2006.

30. Vereshchaka, A. L. Pelagic decapods from seamounts of the Nazca and Sala-y-Gomez ridges. Plankton and benthos from the Nazca and Sala-y-Gomez submarine ridges. Trud. Inst. Okeanol, Acad. Sci., Moscow 124: 129-155, 1990.

31. Vereshchaka, A. L. Revision of the genus *Sergestes* (Decapoda: Dendrobranchiata: Sergestidae): taxonomy and distribution. Galathea Report 22, 7-104, 2009.

32. Vereshchaka, A. L. Revision of the genus *Sergia* (Decapoda: Dendrobranchiata: Sergestidae): taxonomy and distribution. Galathea Report, 18, 69-207, 2000.

33. Vereshchaka, A. L. The distribution of pelagic macroplankton (mysids, euphausiids, and decapods) over the continental slopes and seamounts of the western Indian Ocean. Oceanology, 34 (1), 81-86, 1994.

34. Vereshchaka, A. L., and Vinogradov, G. M. Visual observations of vertical distribution of plankton through the water column above Broken Spur vent field, Mid-Atlantic Ridge. Deep-Sea Res. I 46, 1615–1632, 1999.

35. Vereshchaka, A., Abyzova, G., Lunina, A., and Musaeva, E. The deep-sea zooplankton of the North, Central, and South Atlantic: Biomass, abundance, diversity. Deep-Sea Res Part II: Topical Studies in Oceanography. 2016

36. Vinogradov, G.M. Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible ‘‘Mir-1’’. Mar. Biol. 146, 325–331, 2005.

37. Vinogradov, M.E. Vertical Distribution of the Oceanic Zooplankton. Institute of Oceanography Academy Science USSR, Moscow, 339pp. (English translation, I.P.S.T., Jerusalem, 1970). 1968.

38. Vinogradov, M. E., Vereshchaka, A, L., and Shushkina, E. A. Vertical structure of the zooplankton communities in the oligotrophic areas of the Northern Atlantic, and influence of the hydrothermal vent. Okeanologiya 36(1): 71-79, 1996.

39. Vinogradov, M. E., Shushkina, E. A., Nezlin, N. P., Vedernikov, V. I., and Gagarin, V. I. Correlation between different parameters of the ecosystem of the epipelagic zone of the World Ocean. Oceanology, 39(1), 54-63, 1999.

40. Vinogradov, M. E., Vereshchaka, A. L., and Vinogradov, G. M. Vertical distribution of zooplankton at the periphery of the North Atlantic subtropical gyre. Izvestiya Akademii Nauk Seriya Biologicheskaya 4: 496-510, 2000.

41. Weikert, H., and Trinkaus, S. Vertical mesozooplankton abundance and distribution in the deep Eastern Mediterranean Sea SE of Crete. J Plankton Res, 12, 601–628, 1990.

42. Widder E. A. Bioluminescence. In: Adaptive Mechanisms in the Ecology of Vision. Springer Netherlands p. 555-581, 1999.

43. Wiebe, P.H.. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. Fish B-NOAA, 86, 833–835, 1988.

44. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T. and Takahashi, M.M. Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). Deep-Sea Res I 49, 1007–1025, 2002a.

45. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T., Takahashi, M.M. Structure and size distribution of plankton communities down to the greater depths in the western North Pacific Ocean. Deep-Sea Res II 49, 5513–5529, 2002b.

46. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T., Takahashi, M.M. Latitudinal differences in the planktonic biomass and community structure down to the greater depths in the western North Pacific. J Oceanogr, 60, 773–787, 2004.

47. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Maeda, M., Ishizaka, J., Ikeda T, and Mac Takahashi, M. Biomass and chemical composition of net-plankton down to greater depths (0–5800m) in the western North Pacific ocean. Deep-Sea Res Part I: Oceanographic Research Papers, 52(2), 341-353, 2005.

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

Table 2. Average values ± 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±24.08	8.07±17.33	15.63±31.04	1.25±2.32	37.08±58.49	36
Epipelagic zone	28.32±54.86	20.16±53.96	0.58±2.16	0.62±0.86	49.07±78.19	35
Main thermocline zone	5.68±12.34	1.86±4.03	5.40±9.26	0.38±0.63	12.93±18.53	35
Upper bathy-pelagic zone	4.30±9.20	4.12±11.14	12.07±25.73	0.61±0.81	20.49±36.28	35
Lower bathy-pelagic zone	0.19±0.16	1.79±4.40	0.04±0.16	0.04±0.16	2.02±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 (R^2), 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 bathy-pelagic 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 bathy-pelagic 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.

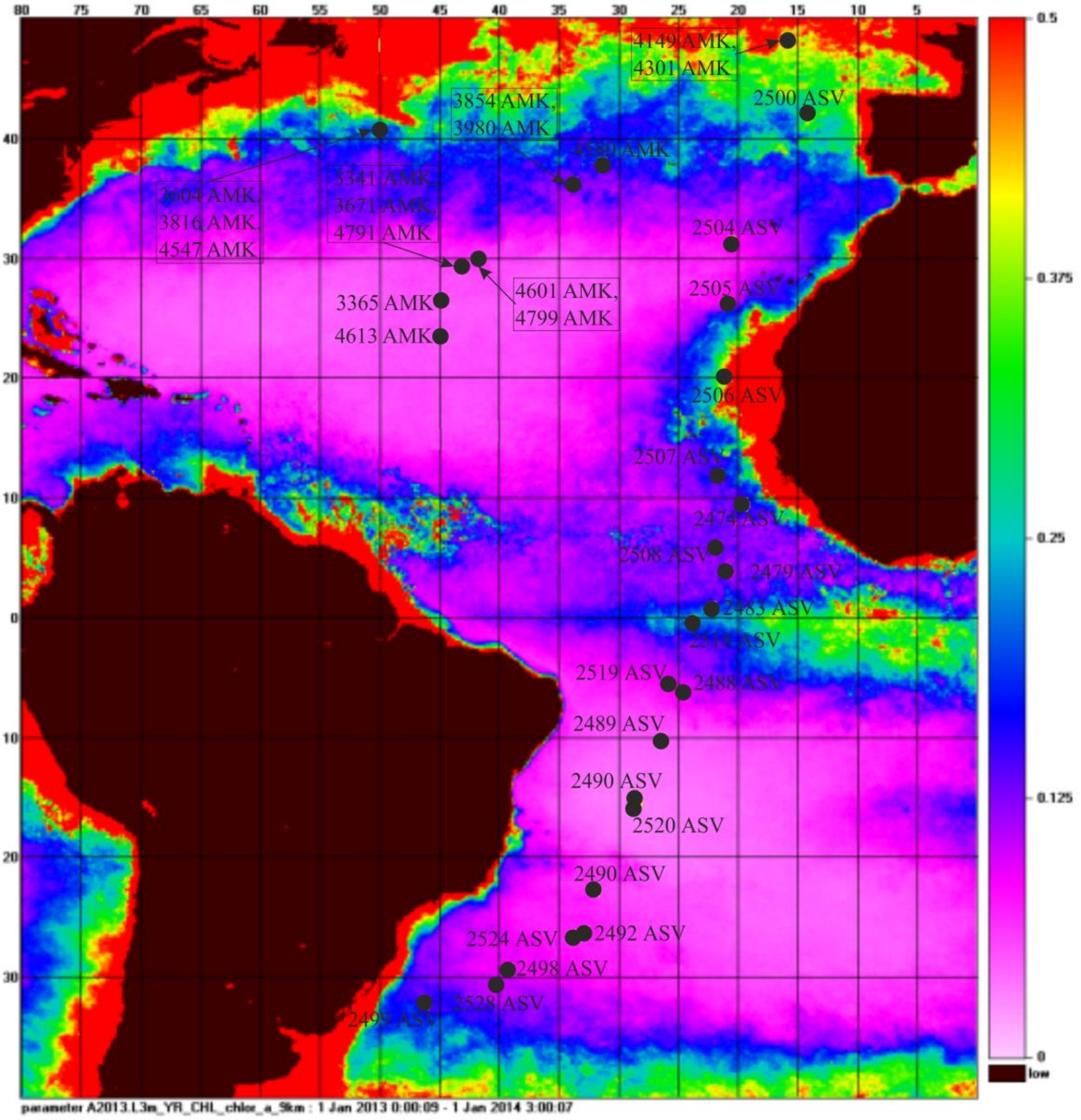
Figure 2. Temperature (°C, left) and salinity (%o, right) along the transect A16 (Koltermann et al., 2011).

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.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20
10
0
10
20
30
4149 AMK,
4301 AMK
3854 AMK,
3980 AMK
2500 ASV
4580 AMK
3604 AMK,
3816 AMK,
4547 AMK
3341 AMK,
3671 AMK,
4791 AMK
2504 ASV
4601 AMK,
4799 AMK
3365 AMK
4613 AMK
2505 ASV
2506 ASV
2507 ASV
2474 ASV
2508 ASV
2479 ASV
2483 ASV
2518 ASV
2519 ASV
2488 ASV
2489 ASV
2490 ASV
2520 ASV
2490 ASV
2524 ASV
2492 ASV
2498 ASV
2528 ASV
2499 ASV
0.5
0.375
0.25
0.125
0
low
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Figure 1.

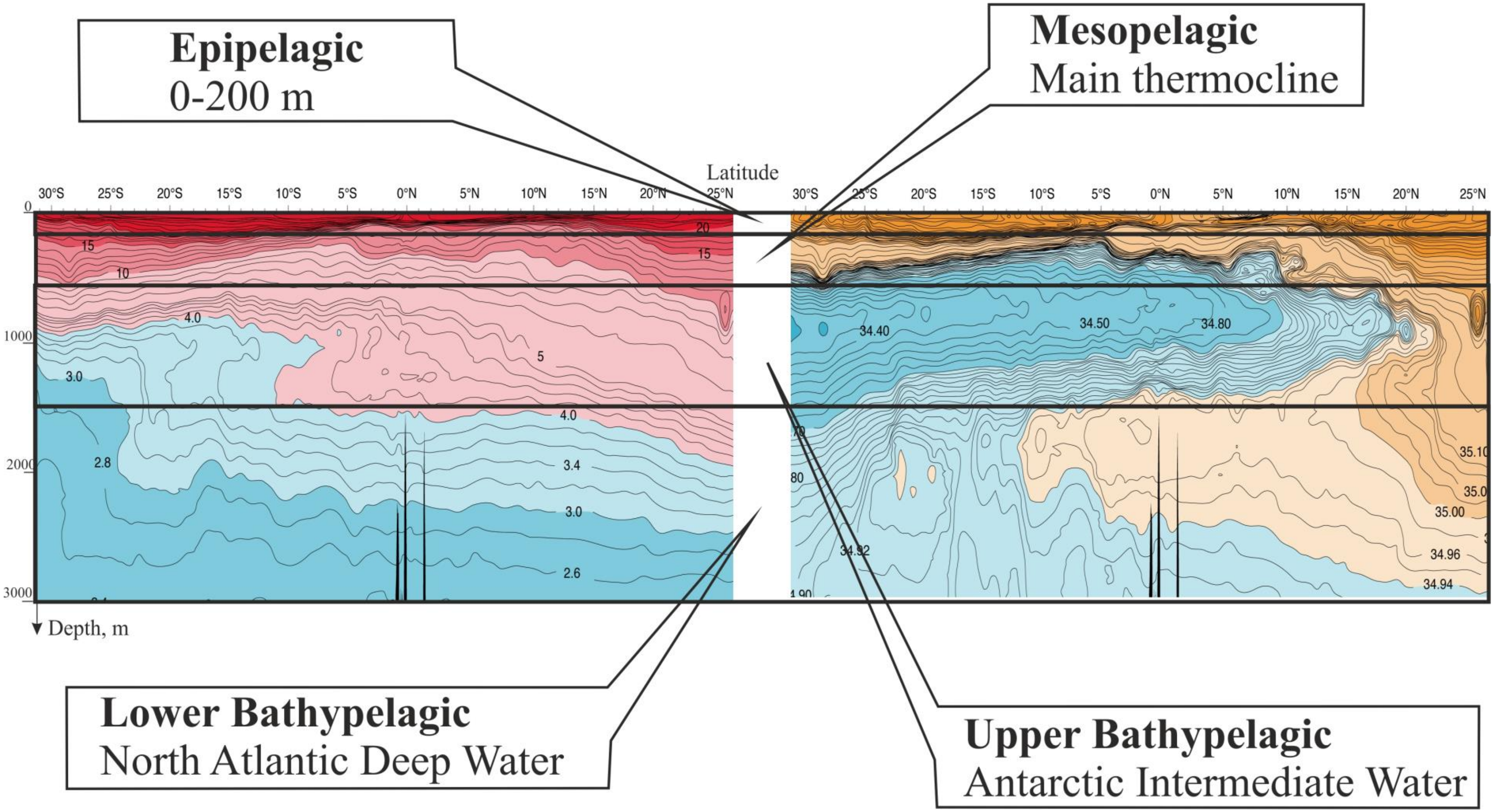

Epipelagic
0-200 m
Mesopelagic
Main thermocline
Latitude
30°S
25°S
20°S
15°S
10°S
5°S
0°N
5°N
10°N
15°N
20°N
25°N
0
1000
2000
3000
Depth, m
20
15
15
10
4.0
5
3.0
4.0
2.8
3.4
3.0
2.6
34.40
34.50
34.80
35.10
35.00
34.96
34.94
34.92
Lower Bathypelagic
North Atlantic Deep Water
Upper Bathypelagic
Antarctic Intermediate Water

Figure 2.

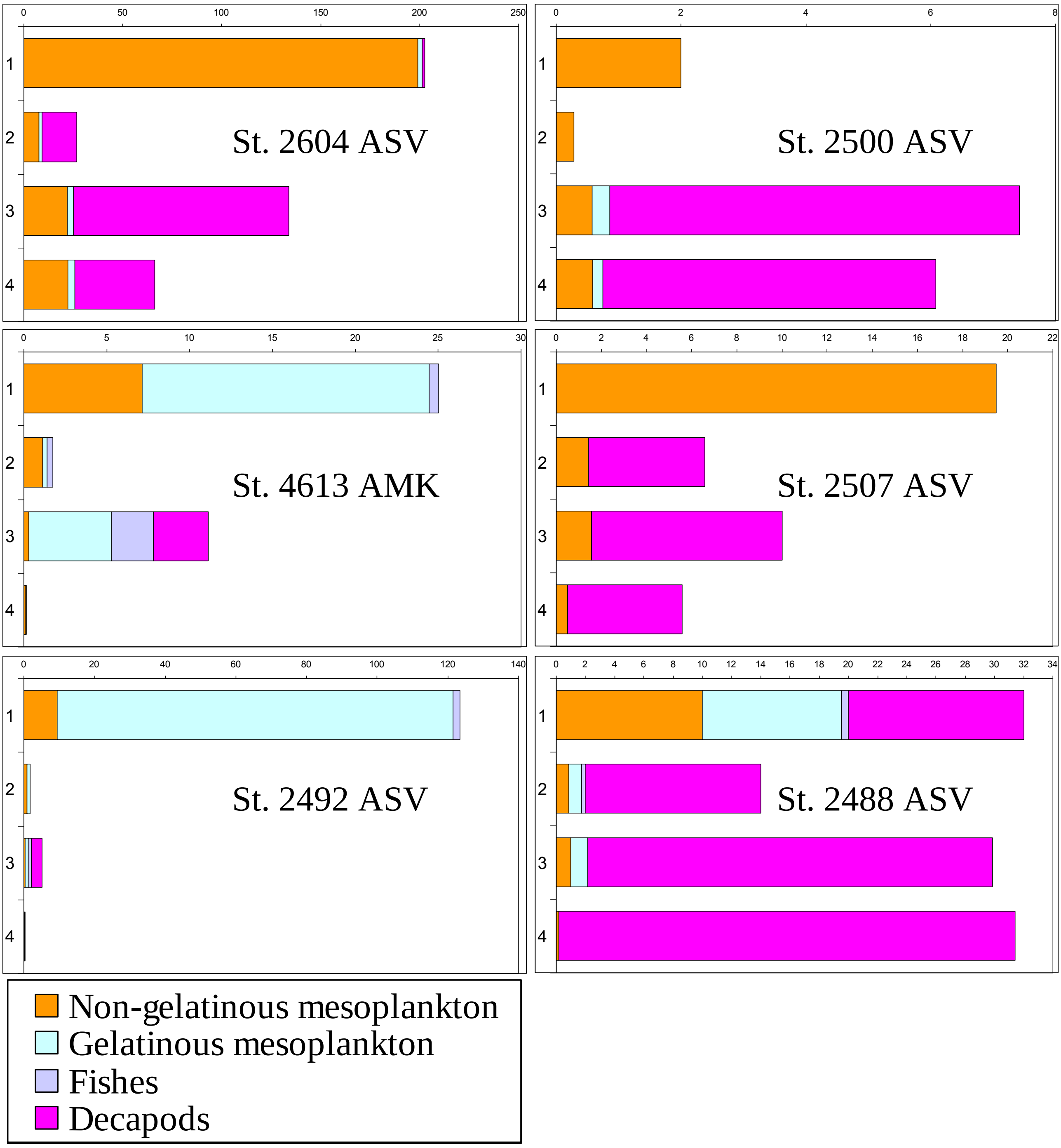
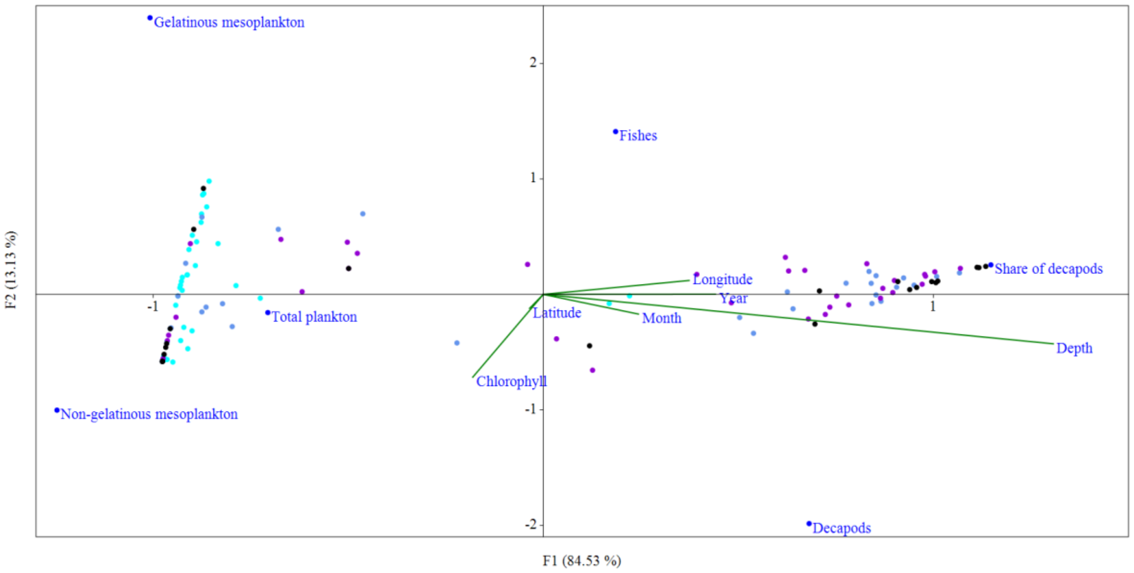
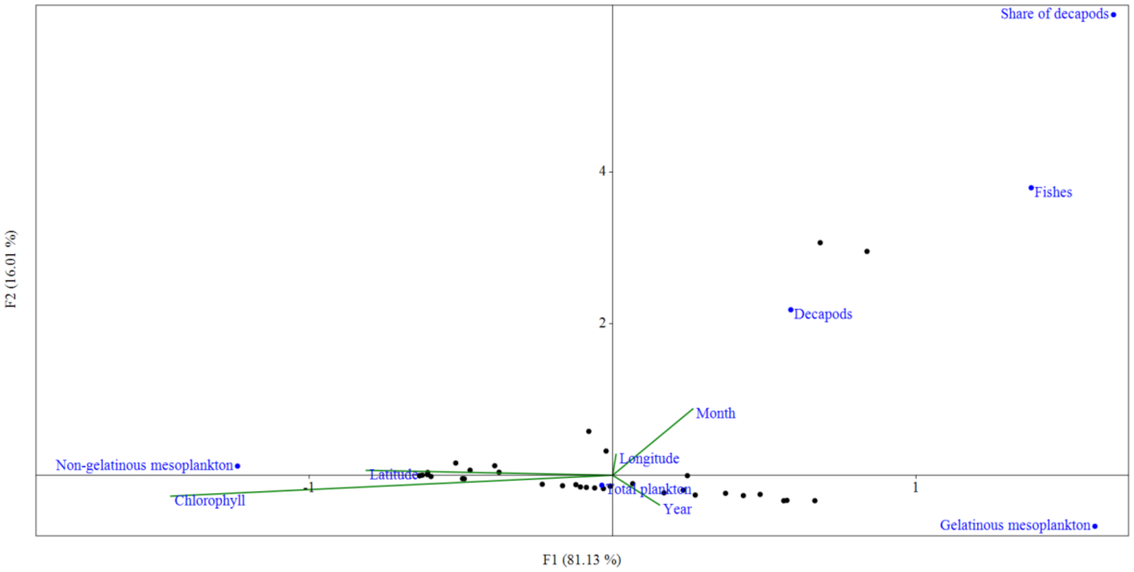

St. 2604 ASV
0
50
100
150
200
250
1
2
3
4
St. 2500 ASV
0
2
4
6
8
1
2
3
4
St. 4613 AMK
0
5
10
15
20
25
30
1
2
3
4
St. 2507 ASV
0
2
4
6
8
10
12
14
16
18
20
22
1
2
3
4
St. 2492 ASV
0
20
40
60
80
100
120
140
1
2
3
4
St. 2488 ASV
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
1
2
3
4
Non-gelatinous mesoplankton
Gelatinous mesoplankton
Fishes
Decapods

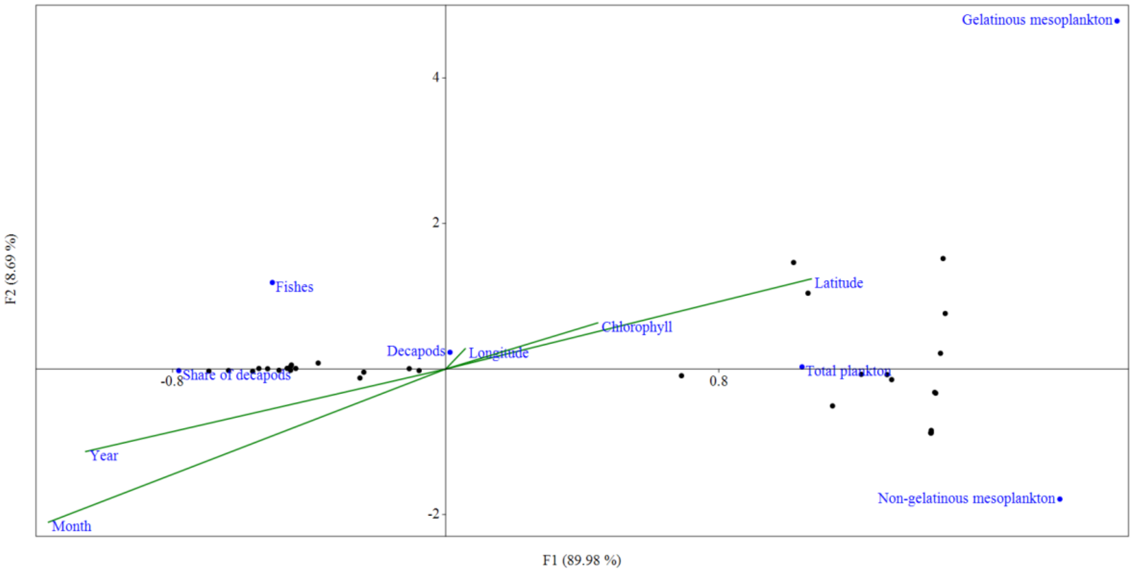
Figure 3.


Gelatinous mesoplankton
Fishes
Share of decapods
Longitude
Year
Month
Latitude
Depth
Total plankton
Chlorophyll
Non-gelatinous mesoplankton
Decapods
2
1
-1
-2
-1
1
F2 (13.13 %)
F1 (84.53 %)

A


Share of decapods
4
Fishes
Decapods
2
Month
Longitude
Non-gelatinous mesoplankton
Latitude
Total plankton
Chlorophyll
Year
Gelatinous mesoplankton
-1
1
F2 (16.01 %)
F1 (81.13 %)

B


Gelatinous mesoplankton
4
2
Fishes
Latitude
Chlorophyll
Decapods
Longitude
Share of decapods
-0.8
0.8
Total plankton
Year
Month
Non-gelatinous mesoplankton
-2
F2 (8.69 %)
F1 (89.98 %)

C

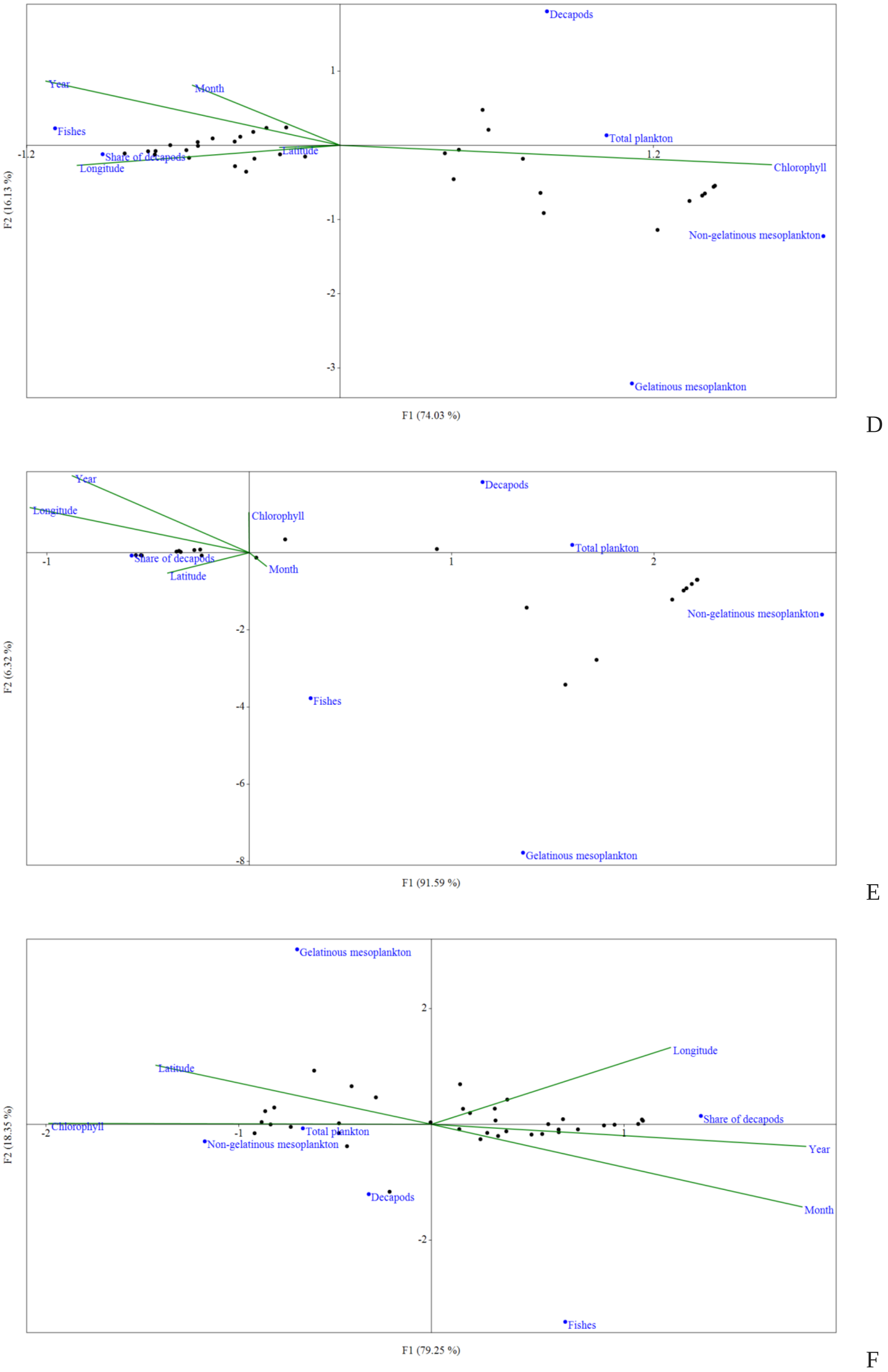
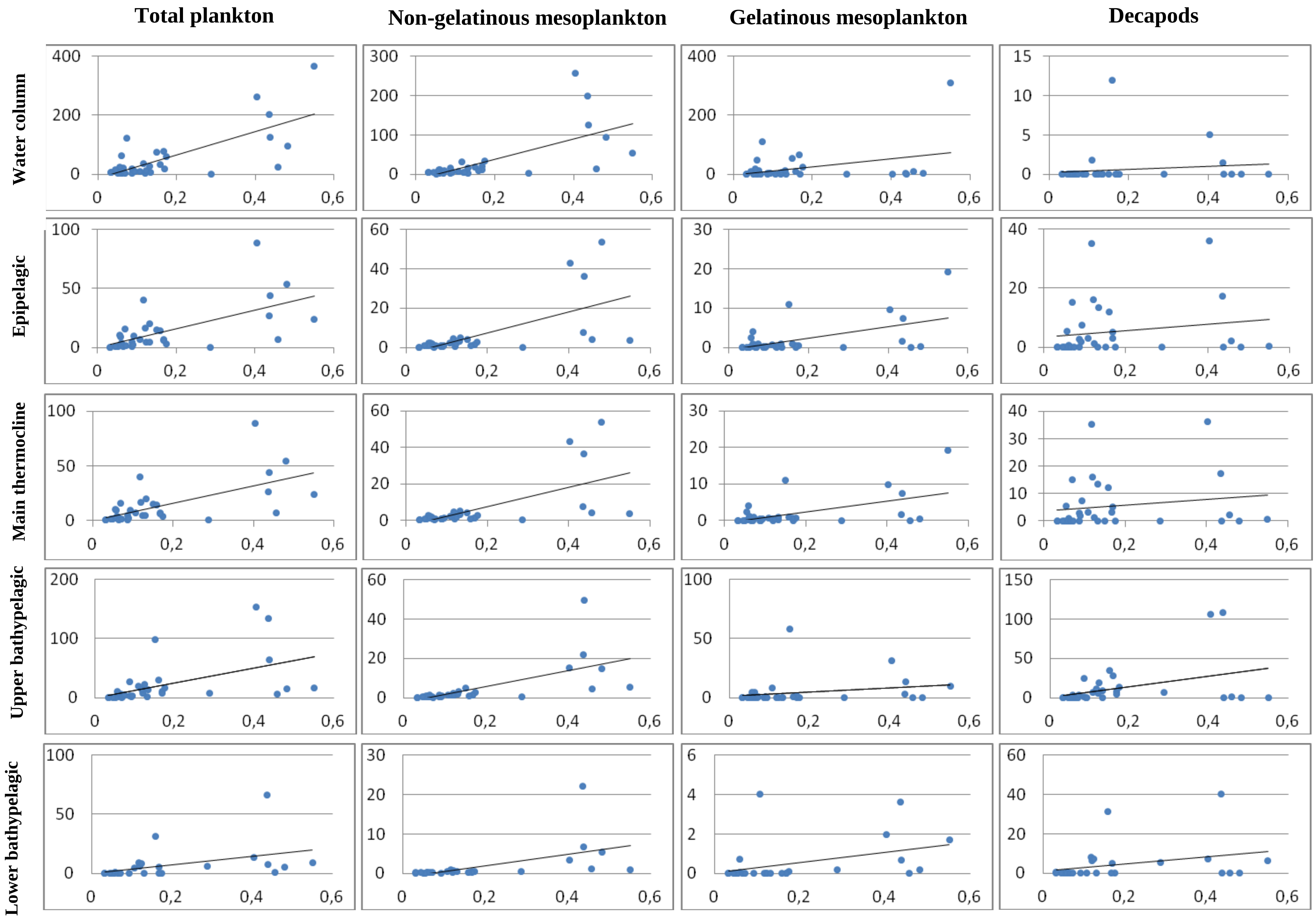

Decapods
1
Year
Month
Fishes
Total plankton
-1.2
1.2
Share of decapods
Latitude
Longitude
Chlorophyll
-1
Non-gelatinous mesoplankton
-2
-3
Gelatinous mesoplankton
F2 (16.13 %)
F1 (74.03 %)
D
Year
Decapods
Longitude
Chlorophyll
Total plankton
-1
1
2
Share of decapods
Month
Latitude
Non-gelatinous mesoplankton
-2
-4
Fishes
-6
-8
Gelatinous mesoplankton
F2 (6.32 %)
F1 (91.59 %)
E
Gelatinous mesoplankton
2
Longitude
Latitude
Share of decapods
-2
Chlorophyll
-1
Total plankton
1
Year
Non-gelatinous mesoplankton
Decapods
Month
-2
Fishes
F2 (18.35 %)
F1 (79.25 %)
F

Figure 4.


Total plankton
Non-gelatinous mesoplankton
Gelatinous mesoplankton
Decapods
Water column
Epipelagic
Main thermocline
Upper bathypelagic
Lower bathypelagic
0
200
400
0
100
200
300
0
200
400
0
5
10
15
0
50
100
0
20
40
60
0
10
20
30
0
20
40
0
50
100
0
20
40
60
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40
60
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50
100
0
50
100
150
0
50
100
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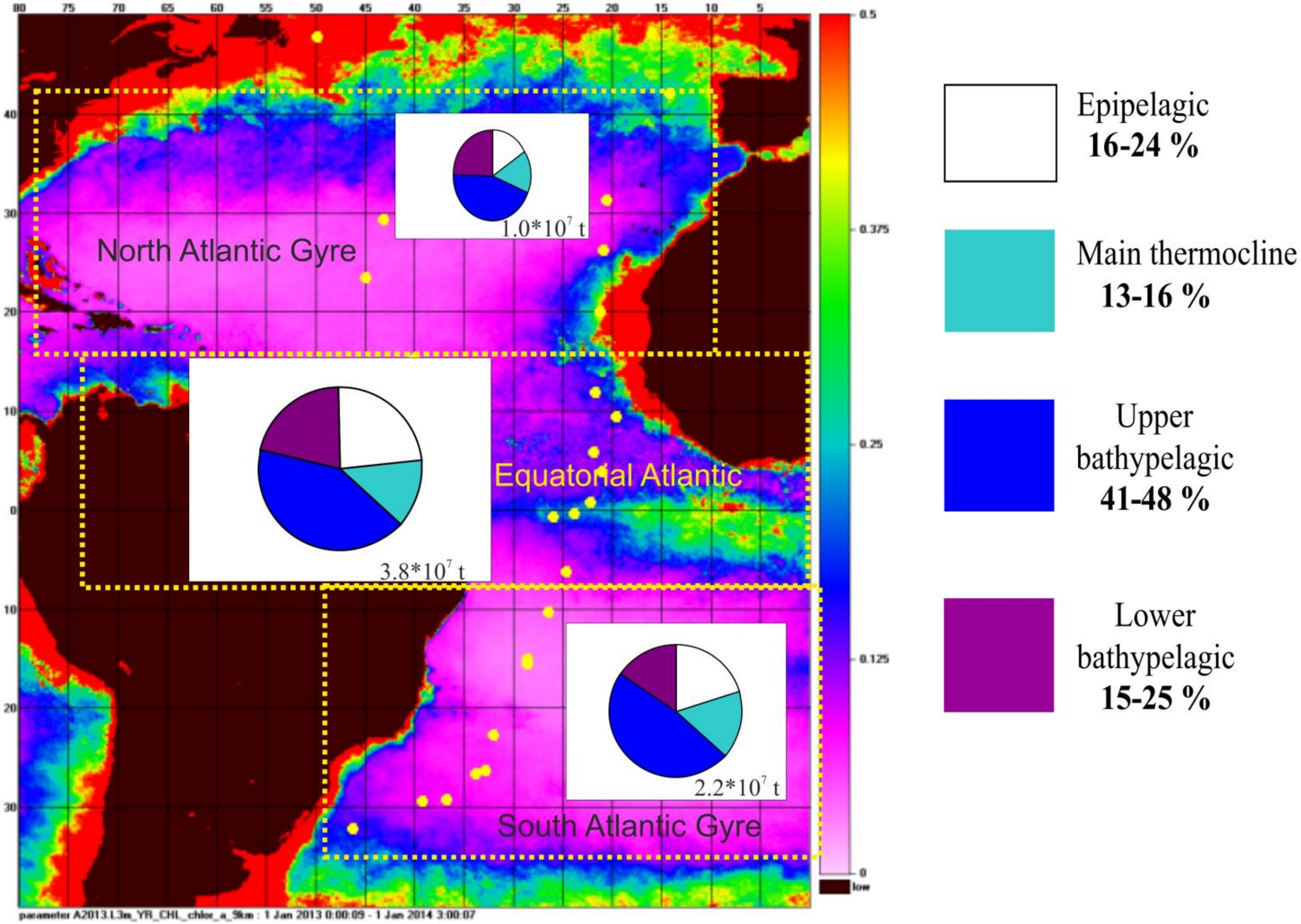
40
60
0
0,2
0,4
0,6

Figure 5.


80
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35
30
25
20
15
10
5
40
30
20
10
0
10
20
30
North Atlantic Gyre
1.0*10^7 t
Equatorial Atlantic
3.8*10^7 t
South Atlantic Gyre
2.2*10^7 t
0.5
0.375
0.25
0.125
0
low
parameter A2013.L3m_YR_CHL_chlor_a_9km : 1 Jan 2013 0:00:09 - 1 Jan 2014 3:00:07
Epipelagic
16-24 %
Main thermocline
13-16 %
Upper bathypelagic
41-48 %
Lower bathypelagic
15-25 %

Figure 6.