Dear Editor and Referees,

Attached is a new version of the Ms, all new/significantly corrected parts are in blue/red. See detailed comments below.

Yamaguchi (Referee) a-yama@fish.hokudai.ac.jp Received and published: 18 June 2016

This manuscript provides biomass and taxonomic compositions of meso- and macrozooplankton down to greater depths. Correlation analyses between surface chlorophyll a and standing stocks of various large-sized zooplankton are quite interesting and including important issues. Dominance of shrimp in deep-layer is not fully documented previously. This study showed their importance clearly. The message of this study is clear, robust and easy to understand. Following my comment is very minor.

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

Authors' comment 1: We thank Dr. Yamaguchi for his comments and for a high evaluation of our work. Concerning the net avoidance, we just try to explain why vertical hauls give evidence for higher SHRIMP (only shrimp) biomass values (respective to the horizontal hauls). We feel that our explanations based on visual observations may make sense. As a possible compromise, we have removed the last sentence "We propose the use of vertically, not horizontally, towed large nets for more representative assessments of deep-pelagic shrimp abundance". We have also added the following paragraph: "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".

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

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

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

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

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

Authors' comment 3: This figure may be given for a certain transect only, not for the whole dataset discussed. Part of data along a submeridional transect (36th and 37th Cruises of the R/V " Akademik Sergey Vavilov ") has been analyzed in detail and published with transect in a more specialized journal; see also comment 5.
A scatter plot of the raw data (biomass vs Chl) is needed to properly evaluate the correlations summarized in Table 2.

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

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

Authors' comment 5: In fact, 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 (A Vereshchaka, G Abyzova, A Lunina, E Musaeva, 2016. The deep-sea zooplankton of the North, Central, and South Atlantic: Biomass, abundance, diversity. Deep Sea Research Part II: Topical Studies in Oceanography. DOI: 10.1016/j.dsr2.2016.06.017). 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. Now we clarify the situation in the Methods section.

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

Authors' comment 6: Corrected

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

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

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

Authors' comment 8: We have added in the "Method" chapter the following sentence: "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".
The introduction should give a fairer representation of the literature. It is, for example, not true that information about deep-sea zooplankton is available for the North Atlantic only (L37).

Authors' comment 9: L37 is an awkward construction, which is now corrected and a greater reference list across all Oceans is provided in the Introduction; for example, the following sentence is included: "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., 2002a, b; 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)."

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

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

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

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

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

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

ADDITIONAL CONTRIBUTION 2: We have also provided six actual biomass profiles from the surface to the bathypelagic zone for several distant sites (Fig. 2).
A NOVEL APPROACH REVEALS HIGH ZOOPLANKTON STANDING STOCK DEEP IN THE SEA

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

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, multivariate 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; Giselson, 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-m² opening, 500-µm mesh size, towed at a speed of 1 m sec⁻¹), which was proven to successfully sample deep-sea plankton ≥ 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 $w_{tot} = \sum (k * l^3)$, where $l$ 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° × 5° 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 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).

Multivariate 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.

Multivariate 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.

Multivariate 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).

Multivariate 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).

Multivariate 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 ($3.8 \times 10^7$ t wet weight), with the South and North Gyres being approximately half ($2.2 \times 10^7$ t) and one-quarter ($1.0 \times 10^7$ 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° x 5° 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. Macropelagic 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 macropelagic 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


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).

<table>
<thead>
<tr>
<th>No of Station</th>
<th>Date</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Sampling zones</th>
<th>Depth, m</th>
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<tbody>
<tr>
<td>2474 ASV</td>
<td>24.10.2012</td>
<td>9°25' N</td>
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<td>4282</td>
</tr>
<tr>
<td>2479 ASV</td>
<td>25.10.2012</td>
<td>3°51' N</td>
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<td>5235</td>
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<td>2483 ASV</td>
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<td>0°50' N</td>
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<td>4360</td>
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<td>2488 ASV</td>
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<td>6°12' S</td>
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<td>3800</td>
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<td>2489 ASV</td>
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</tr>
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<td>2490 ASV</td>
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<td>2492 ASV</td>
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<td>33°58' W</td>
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<td>2498 ASV</td>
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<td>39°15' W</td>
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<td>4724</td>
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<td>2499 ASV</td>
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<td>3780</td>
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<tr>
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<td>2505 ASV</td>
<td>29.09.2013</td>
<td>26°14' N</td>
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<td>2506 ASV</td>
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<td>2507 ASV</td>
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<td>2518 ASV</td>
<td>10.10.2013</td>
<td>1°25' S</td>
<td>24°00' W</td>
<td>EMUL</td>
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</tr>
<tr>
<td>2519 ASV</td>
<td>11.10.2013</td>
<td>07°01' S</td>
<td>26°04' W</td>
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<td>2520 ASV</td>
<td>14.10.2013</td>
<td>5°50' N</td>
<td>22°00' W</td>
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<td>29°06' N</td>
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<td>3365 AMK</td>
<td>16.09.1994</td>
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<td>3604 AMK</td>
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<tr>
<td>3816 AMK</td>
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<td>49°54' W</td>
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<td>3854 AMK</td>
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<td>48°06' N</td>
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<td>25-26.06.2003</td>
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<td>3700</td>
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<td>4580 AMK</td>
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<td>2070</td>
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<td>4601 AMK</td>
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<td>4799 AMK</td>
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<td>2545</td>
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</table>
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.

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

<table>
<thead>
<tr>
<th>Vertical zones</th>
<th>Non-gelatinous mesoplankton</th>
<th>Gelatinous mesoplankton</th>
<th>Decapods</th>
<th>Fishes</th>
<th>Total plankton</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R(^2)</td>
<td>Regression equations</td>
<td>R(^2)</td>
<td>Regression equations</td>
<td>R(^2)</td>
</tr>
<tr>
<td>Whole water column, n=36</td>
<td>0.5129****</td>
<td>B = 121,54Chl - 6,3663</td>
<td>0.1971***</td>
<td>B = 54,22Chl - 0,7371</td>
<td>0.1609**</td>
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<tr>
<td>Epipelagic zone, n=35</td>
<td>0.4674****</td>
<td>B = 258,84Chl - 13,001</td>
<td>0.1374***</td>
<td>B = 138,03Chl - 1,8744</td>
<td>0.028</td>
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<tr>
<td>Main thermocline zone, n=35</td>
<td>0.4082****</td>
<td>B = 53,63Chl - 3,2029</td>
<td>0.2971****</td>
<td>B = 14,929Chl - 0,6162</td>
<td>0.0512</td>
</tr>
<tr>
<td>Upper bathypelagic zone, n=35</td>
<td>0.4152****</td>
<td>B = 40,335Chl - 2,3795</td>
<td>0.0569</td>
<td>B = 18,065Chl + 1,1344</td>
<td>0.2118**</td>
</tr>
<tr>
<td>Lower bathypelagic zone, n=26</td>
<td>0.284****</td>
<td>B = 14,61Chl - 0,9625</td>
<td>0.1518*</td>
<td>B = 2,6226Chl + 0,0143</td>
<td>0.1263**</td>
</tr>
</tbody>
</table>

* Levels of significance: **** indicate p <0.001, *** for p <0.01, ** for p <0.01, * for p <0.05.
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 (‰, 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.
Figure 4.
Figure 5.
Figure 6.