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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, zooplankton biomass in the upper bathypelagic domain is higher than expected,
representing an inverted biomass pyramid. Second, 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.

keywords: zooplankton communities, biological resources, shrimps, vertical zones, plankton

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1 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 quantitatively estimated yet. These ecosystems are and will continue to be impacted by climate

30   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 to estimate the biomass of the deep-sea biota for inventory purposes and for

monitoring its changes in the future.

35   In contrast to intensively documented knowledge about zooplankton distribution and diversity in the

upper water layers of the Atlantic (Hays et al., 2001; Gallienne et al., 2001; Stupnikova and

Vereshchaka, 2013), information about deep-sea zooplankton is much more scant and available for the

North Atlantic only (Williams, 1988; Gislason, 2003; Vinogradov, 2005). Fewer results concern deep-

sea zooplankton distribution over larger areas (Longhurst, Williams, 1979; Gaard et al., 2008). The data

40   about 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 (Gaard et al., 2008; Burghart et al., 2007)), functional groups (e.g. gelatinous zooplankton (Lindsay, Hunt, 2005)), or selected vertical zones (e.g. mesopelagial (Robison et al., 2010; Sutton T.T. et al., in press)). Attempts to assess an entire

45   deep-sea community have been rare and local (Vinogradov et al., 1996; Vinogradov et al., 2000; Vereshchaka, Vinogradov, 1999). 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

50   large areas. As any field data of the deep-sea zooplankton are inevitably local, we should find an indicator, which is correlated with elements of the deep-sea zooplankton and can be assessed over large water areas/volumes. Here we offer and test a hypothesis that the zooplankton biomass in the deep-pelagial is correlated with surface primary productivity. This hypothesis has been corroborated for the epipelagic (0-200 m) layer, where correlations have been obtained (Vereshchaka, Vinogradov, 1999). It

55   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 the 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

60   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

65 depth zones: epipelagic, mesopelagic, and upper- and lower-bathypelagic zones (Fig. 2). 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.

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2 Methods

Field data were taken in the deep Central, South, and North Atlantic between 1996-2012 from ultraoligotrophic to mesotrophic areas roughly between 40º S and 40º N. These areas include the two main Atlantic Gyres (North and the South) and the Equatorial Atlantic between them. Temperate waters

75 beyond the subtropical frontal zones were excluded from our analysis. 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: the epipelagic zone (0-200 m), the main pycnocline within the mesopelagic zone (from 200 m to the depth of the 7ºC isotherm, within 550-800 m), the

80 upper bathypelagic zone (from the lower boundary of the mesopelagic zone to 1500 m, mainly Antarctic Transitional Waters), and the lower bathypelagic zone (1500-3000 m, mainly North Atlantic Deep Waters) (Fig. 2). We used a closing 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 (Vinogradov et al., 1996; 2000).

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We divided the net plankton into three 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) and macroplankton (mainly shrimps; over 30 mm length). Identification was done according to literature (Rose, 1933; Brodsky, 1950; Mauchline and

90 Fisher, 1969; Brodsky et al., 1983; Markhasheva, 1996). Synonymy of species was corrected according to www.marinespecies.org. Wet weight of the two mesoplanktonic groups was estimated according to adopted procedures (Gaard, E., et al., 2008; Vinogradov et al., 1996; 2000), while macrozooplankton was weighed with a scale with a precision of 0.1 g.

95 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). Statistical procedures and regression analysis were made with the use of

100 Excel and STATISTICA. We considered correlations significant if $p < 0.01$.

3 Results

Over 300 taxa were identified, counted, measured, and their weight calculated. The main contribution to total zooplankton standing stock was made by decapod shrimps, followed by non-gelatinous and gelatinous mesoplankton (Table 1). The epipelagic zone was dominated by the two groups of mesozooplankton, the mesopelagic zone was dominated by non-gelatinous mesozooplankton and shrimps, the upper bathypelagic zone was dominated by shrimps, and the lower bathypelagic zone was dominated by gelatinous zooplankton (Table 1).

The total zooplankton biomass and the biomass of each of major faunal group in the whole water column was highly correlated with the averaged Chl ($p < 0.001$; Table 2). Moreover, in most cases the standing stock of the major groups in each of the vertical zones was also correlated with Chl; the dependence was more robust for upper vertical zones and weakened with depth (Table 2). Having the correlation between the total zooplankton standing stock and Chl, we calculated the zooplankton standing stock over selected areas. We did that for three rectangular areas roughly corresponding to the North and South Atlantic Gyres and the Equatorial Atlantic (Fig. 3). 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. 3). The contribution of the mesopelagic 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 mesoplankton accounted for nearly one-quarter of the total zooplankton

stock, while the shrimps composed approximately half. Various species of the shrimp genera

125 *Acanthephyra* A. Milne-Edwards, 1881, *Gennadas* Spence Bate, 1881, *Notostomus* A. Milne-Edwards,

1881, and *Systellaspis* Spence Bate, 1888 were dominant.

4 Discussion

Although scant on the global scale, our deep-sea samples collected during the last 20 years using

130 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

135 column meso/macrozooplankton standing stock.

Obtained regressions were not perfect due to 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

140 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 biomass. It is all the more interesting that our data do show statistically

significant correlation between Chl and the deep zooplankton biomass.

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145   Although our results provide a means for calculating global zooplankton 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 M. E. et al., 1999).

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- Correlations may be different in different oceans. Our data show better correlation between the Chl concentration and the zooplankton 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

155   approach until conversion factors can be obtained to link geographically distant deep-sea assemblages.

- Actual 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

160   plankton nets are suboptimal for estimating their actual abundance (Vereshchaka, Vinogradov, 1999).

- Actual biomass of the shrimps is also underestimated, as these animals likely avoid plankton nets and trawls to some extent (Vereshchaka, 1990).

165 Probably the most striking result we found was the unexpectedly high shrimp biomass. Macroplanktonic shrimp 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, 1970ab), 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

170 shrimps. Our observations from submersibles show that deep-sea shrimps are generally stationary in the water column with abdomens oriented slightly upward. When disturbed, shrimps 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 shrimps possess downward-oriented photophores for counter-illumination (Widder, 1999). Upward jumps are also effective to escape from a

175 net or a trawl that is traditionally towed in the horizontal direction. The BR net, however, is towed vertically and the shrimps may have less chance to avoid the gear. We propose the use of vertically, not horizontally, towed large nets for more representative assessments of deep-pelagic shrimp abundance.

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5 Conclusions

180   The dominance of macroplanktonic shrimp in the deep sea illustrates an inverted biomass pyramid, as their biomass is larger than that of their prey (non-gelatinous mesoplankton). This happens because the shrimp (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 shrimp distribution offers additional example

185   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 epi- or mesopelagic zones. The upper bathypelagic zone was dominated by macroplanktonic shrimp, which accounted for over half of the standing stock biomass.

190   The shrimp 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 of 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

195   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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Table 1. Average values (B) and standard deviation (d) of biomass the major plankton groups in the whole water column (g m^{-2}) and vertical zones (mg m^{-3}) of the Atlantic Ocean (N = number of samples)

Vertical zones	N	Non-gelatinous mesoplankton		Gelatinous mesoplankton		Shrimp		Total plankton	
		B	**d**	**B**	**d**	**B**	**d**	**B**	**d**
Whole water column	37	13.38	24.08	8.07	17.33	15.63	31.04	37.08	58.49
Epipelagic zone	36	28.32	54.86	20.16	53.96	0.58	2.16	49.07	78.19
Mesopelagic zone	34	5.68	12.34	1.86	4.03	5.40	9.26	12.93	18.53
Upper bathy-pelagic zone	34	4.30	9.20	4.12	11.14	12.07	25.73	20.49	36.28
Lower bathy-pelagic zone	26	0.19	0.16	1.79	4.40	0.04	0.16	2.02	9.71

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Table 2. Correlation between surface chlorophyll-a concentration (mg m^{-2}) and biomass (g m^{-2} for the whole water column and g m^{-3} for vertical zones): coefficients of correlation of (R) and levels of significance (p; significant [< 0.01] correlations shaded)

Vertical zones	Non-gelatinous mesoplankton		Gelatinous mesoplankton		Shrimp		Total plankton	
	R	p	R	p	R	p	R	p
Whole water column	0.71	<0.001	0.44	<0.01	0.40	0.01	0.65	<0.001
Epipelagic zone	0.67	<0.001	0.42	<0.01	0.17	0.17	0.76	<0.001
Mesopelagic zone	0.56	<0.001	0.62	<0.001	0.23	0.21	0.57	<0.001
Upper bathy-pelagic zone	0.63	<0.001	0.28	0.11	0.46	<0.01	0.56	<0.001
Lower bathy-pelagic zone	0.52	<0.01	0.44	0.03	0.36	<0.01	0.45	0.02

Figure Legends

Figure 1. Deep-sea plankton stations (yellow circles) sampled between 1996 -2012 in the Atlantic

Ocean. Background: surface chlorophyll-a concentration averaged over 2013, scale (mg m^{-2}) on right.

Black squares around each station: a $5° \times 5°$ area (with the sampling site in the center) over which

surface chlorophyll-a concentration was averaged.

Figure 2. Temperature ($°$C, left) and salinity (right) along the transect A16 (Vinogradov *et al*., 1996)

and defined vertical zones.

Figure 3. The standing stock (t) of the deep-sea plankton and contribution (%) of vertical zones in the

North, Equatorial, and South Atlantic. Background: surface chlorophyll-a concentration averaged over
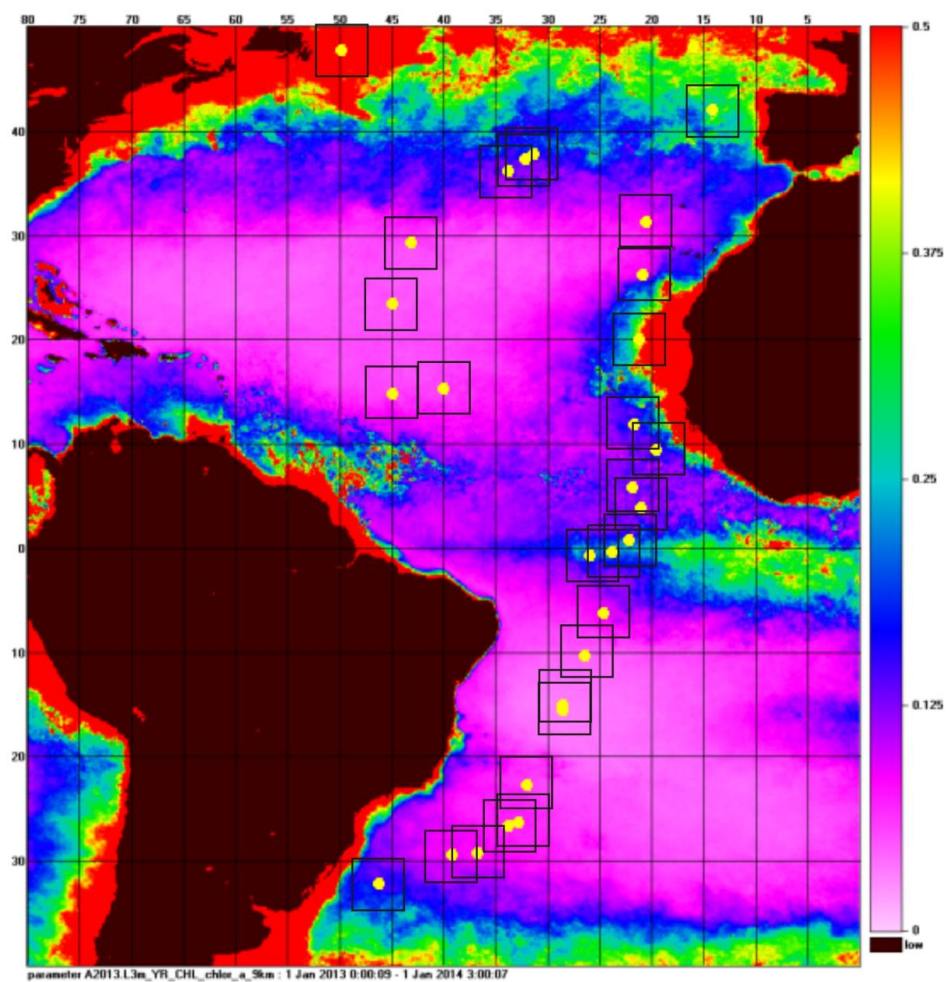
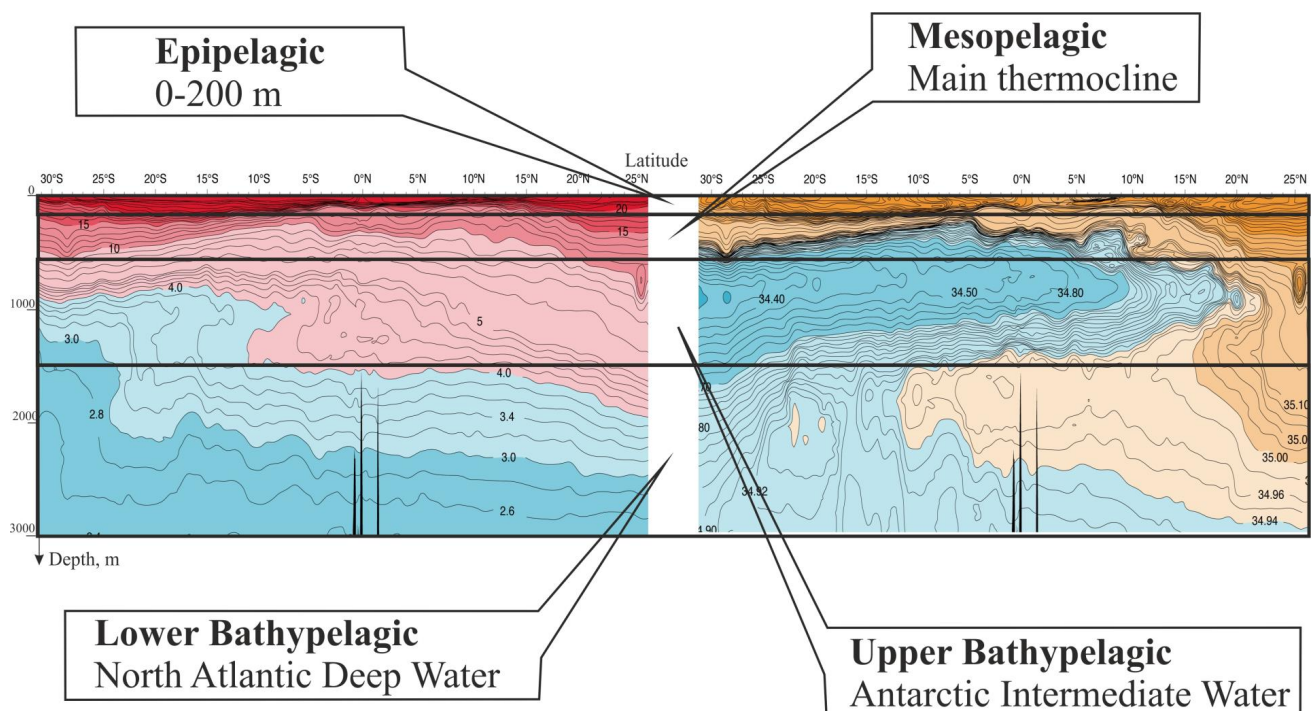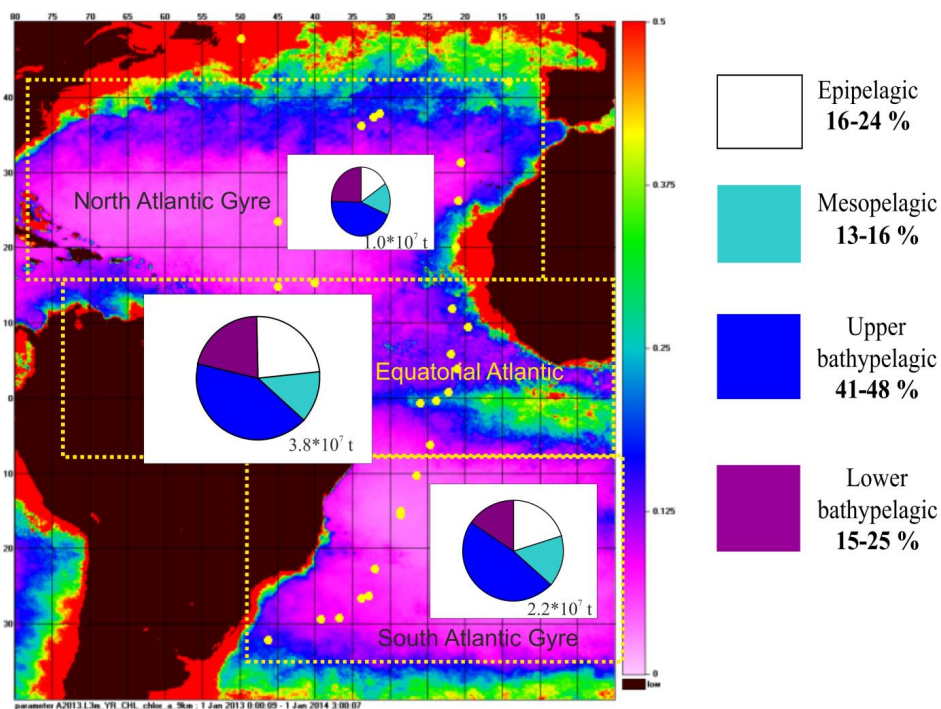2013, scale (mg m^{-2}) on right. Yellow circles: stations.

Figure 1.

Figure 2.

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Figure 3.