

Changes in zooplankton communities from epipelagic to lower mesopelagic waters

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ABSTRACT

Zooplankton form a trophic link between primary producers and higher trophic levels, and exert significant influence on the vertical transport of carbon through the water column ('biological carbon pump'). Using a MultiNet we sampled and studied mesozooplankton communities (i.e. > 0.2 mm) from six locations around Bermuda targeting four depth zones: ~0–200 m, ~200–400 m, ~400–600 m (deep-scattering layer), and ~600–800 m. Copepoda, our focal taxonomic group, consistently dominated samples (~80% relative abundance). We report declines in zooplankton and copepod abundance with depth, concurrent with decreases in food availability. Taxonomic richness was lowest at depth and below the deep-scattering layer. In contrast, copepod diversity peaked at these depths, suggesting lower competitive displacement in these more food-limited waters. Finally, omnivory and carnivory, were the dominant trophic traits, each one affecting the biological carbon pump in a different way. This highlights the importance of incorporating data on zooplankton food web structure in future modelling of global ocean carbon cycling.

1. Introduction

The mesopelagic zone, also known as dysphotic or twilight zone, is the part of the ocean where solar illumination is enough to enable visual predation but insufficient for photosynthesis (Sutton, 2013). Typically considered to occur between 200 and 1000 m water depth (Proud et al., 2017; Sutton, 2013; Sutton et al., 2017), recent evidence suggests that the mesopelagic vertical range is not static but varies significantly by latitude and across ocean basins, and can be attributed to the quantity of available light, the mixed layer depth and the flux of particulate organic carbon (Reygondeau et al., 2018). This makes the mesopelagic biome one of the largest habitats in the marine realm comprising a third (31%) of the global ocean volume (Reygondeau et al., 2018). The mesopelagic hosts a rich and diverse animal community and may contain the largest fish stocks on Earth (Anderson et al., 2018; Irigoien et al., 2014; Jennings and Collingridge, 2015). It also plays a critical role in carbon cycling (Robinson et al., 2010), and is important for food security and aquaculture (St John et al., 2016). One of the largest diel migrations on Earth occurs in this zone (Hays, 2003). Dense accumulations of organisms comprising zooplankton, shrimp,

squid, fish, and jellyfish, are known as the deep-scattering layers (DSLs), ascend from ~300 to 850 m during daytime to depths < 200 m at night to feed when detection probability by predators is lowest (Klevjer et al., 2016). However, due to logistical constraints and sampling difficulties, this oceanic zone remains still vastly underexplored (Sutton et al., 2017; Webb et al., 2010), resulting in a paucity of biodiversity and ecology knowledge (Rowden et al., 2010). Because of the interconnected nature of the oceans, growing anthropogenic pressures on the world's largest ecosystem (e.g. climate warming, directly and overfishing) (Danovaro et al., 2017b; Levin and Le Bris, 2015; Rogers, 2015) are very likely to impact mesopelagic communities as well (Boerger et al., 2010; Clarke et al., 2015; Proud et al., 2017). Consequently, enhancing our understanding of this oceanic zone is crucial.

One ubiquitous component of marine pelagic food webs are zooplankton. Zooplankton play a central role in marine ecosystems being a trophic link between primary producers and higher trophic levels (e.g. fish) (Kruse et al., 2010). They are also substantial contributors to the biological carbon pump (BCP), which encompasses all biological processes that mediate transport of carbon from the upper ocean to the deep sea, by ingesting, consuming and fragmenting surface-derived

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particulate organic carbon (Giering et al., 2014; Mayor et al., 2014). Through their vertical migrations, mucous feeding webs, molts, carcasses and faecal pellets they further affect carbon export to greater depths, thus profoundly influencing deeper planktonic and benthic communities alike (Guidi et al., 2016; Longhurst, 1991).

Despite their importance in marine ecosystem functioning, current knowledge of zooplankton communities from mesopelagic or greater depths is rather poor (Bucklin et al., 2010). With that in mind, we explored the community structure of mesozooplankton (i.e. retained on meshes of 0.2 mm) assemblages over a wide depth range, spanning from the euphotic (=epipelagic) up to the lower mesopelagic zone (800 m depth), with an emphasis on copepods, the dominant component in this size spectrum. Our study area centred around the waters off Bermuda, where zooplankton have been collected and studied since the mid-20th century (Deevey, 1971; Deevey and Brooks, 1971, 1977; Menzel and Ryther, 1961; Moore, 1949; Roman et al., 1993, 1995) including the more recent long-term sampling programmes at the Bermuda Atlantic Time Series Study (BATS) site (Dam et al., 1995; Madin et al., 2001; Steinberg et al., 2012). However, but for a few exceptions (Deevey, 1971; Deevey and Brooks, 1971, 1977; Moore, 1949), most of the previous work has focused on bulk abundance and/or biomass of zooplankton communities from waters < 200 m deep, leaving deeper mesopelagic communities comparatively understudied.

Considering the above, our objectives were to: i) conduct a quantitative survey of mesozooplankton community characteristics (abundance, diversity, composition) across a wide depth range spanning from the surface down to 800 m, ii) elucidate the interaction between the environment and zooplankton community structure, and iii) infer the implications of zooplankton community structure on carbon cycling (i.e. BCP) and energy transfer in mesopelagic food webs. We expect the findings of the present study to be of interest to marine biologists, biogeographers, conservationists and policy-makers alike, since zooplankton taxonomic data are central in several existing marine biodiversity management and conservation programmes (McQuatters-Gollop et al., 2017), and have been incorporated in recent global assessments of the state of the seas (Malone et al., 2016; Pörtner et al., 2014).

2. Methods

2.1. Data collection

Samples were taken onboard the *CCGS Hudson* (17th July–14th August 2016) at six locations northeast and southwest of Bermuda (Fig. 1, Appendix A). Following an adaptive sampling strategy we used the depth of the DSL (~350–600 m) as identified from the Acoustic Doppler Current Profiler (ADCP) (Teledyne Ocean Surveyor II, frequency 75 kHz, minimum particle size identification: > 10 mm) and targeted the following depths with a Multi Plankton Sampler MultiNet system (HYDRO-BIOS, mouth opening: 0.25 m²; net mesh size: 200 µm, winch speed: 0.5 m/s, towed vertically) corresponding to four depth zones: 10–100, 10–150 and 100–200 m (epipelagic layer); 150–250, 200–300, 200–400 and 300–400 m (above the DSL); 350–550 and 400–600 m (DSL); 550–750 and 600–800 m (below the DSL). Sample collection occurred during day light hours (i.e. 10 a.m. to 6 p.m.) and not within 2 h of sunrise or sunset in order to avoid the effect of diurnal migration. Onboard the ship, samples were immediately bulk preserved in absolute (100%) ethanol until later analysis in the lab.

For each sampling event, additional environmental data (temperature and salinity, dissolved oxygen, fluorescence – the latter used as a proxy for chlorophyll-phytoplankton biomass) were also measured using a Sea-Bird Electronics SBE 9/11 CTD system in dual-sensor confirmation (i.e., all key physical properties and dissolved oxygen concentrations were measured in two independent sensor lines pumped by individual SBE pumps), and their average values were then used for subsequent statistical analysis.

2.2. Sample processing

Zooplankton enumeration and identification was based on entire samples or where specimens were numerous within a sample, subsamples (1/2, 1/4, 1/8), obtained using a Folsom plankton sample divider (HYDRO-BIOS), were used instead. Where a subsample was used, it was ensured that it contained at least 100 individuals of the most abundant taxonomic group (in all cases copepods), otherwise additional subsamples were processed until that goal was reached (Postel et al., 2000). Preservation state of sample HUD16-19_0022 was poor, hence, it was removed from the statistical analysis. Zooplankton were initially sorted into broad taxonomic groupings following Castellani and Edwards (2017) with the use of a stereomicroscope (Motic SMZ 171) and a transmission light microscope (Motic BA 210). These were: (1) Amphipoda, (2) Appendicularia, (3) Bryozoa larvae, (4) Cephalopoda larvae, (5) Chaetognatha, (6) Cladocera, (7) Colonial hydrozoa (= siphonophores, ctenophores and pelagic tunicates-salps; these were grouped together since most of the specimens were damaged and could not be reliably set apart), (8) Copepoda, (9) Crustacea larvae (= larvae of Decapoda, Euphausiacea, Mysida and Stomatopoda), (10) Echinodermata larvae, (11) Euphausiacea (adults), (12) Fish larvae, (13) Foraminifera, (14) Gastropoda, (15) Isopoda, (16) Mysida, (17) Porifera, (18) Ostracoda, (19) Polychaeta, (20) Radiolaria, and (21) Scyphozoa and non-colonial hydrozoa (e.g. medusa) larvae. Subsequently, Copepoda were identified to family level. A total of 100 adult copepods were picked randomly from each (sub)sample and identified following the taxonomic schemes of Boxshall and Halsey (2004), and Wootton and Castellani (2017), except in two occasions where the total number of adults in the whole sample was less (82 and 95, respectively). Only six out of 2877 adult copepods could not be placed in a known family, hence, they were omitted from subsequent diversity and community composition analyses.

2.3. Statistical analysis

For our statistical analysis we followed the traditional definition of the mesopelagic zone and considered samples from 100 to 200 m depth to be part of the epipelagic zone. Nevertheless, recent evidence by Reygondeau et al. (2018) places the epipelagic/mesopelagic boundary in Bermuda at potentially < 100 m depth, thus the 100–200 m samples could also be considered part of the above the DSL as well. Nevertheless, re-running all of our analysis using this alternative mesopelagic classification produced identical results, hence, these will not be discussed further.

Changes in abundance with depth was tested with Kruskal-Wallis (non-normal data distribution, Shapiro-Wilk Test: $p < 0.05$) followed by Mann-Whitney pairwise comparisons applied with Bonferroni corrections on raw abundance (individuals m⁻³) data for the whole zooplankton community or individual higher groupings, and on raw count data for copepod families (standardised to or close to 100). Alpha diversity for zooplankton (at the higher level) and copepods (at the family level) was estimated using the following indexes: richness of taxa (i.e. number of higher zooplankton groupings or copepod families in a sample), the exponential Shannon index ($\exp(-\sum p_i \log p_i)$), and the inverse Simpson index ($1/\sum p_i^2$) (Gotelli and Chao, 2013). Evenness was also measured as $J = H'/\log(S)$ (Pielou, 1975). These indexes were then compared against depth zone using Kruskal-Wallis followed by Mann-Whitney pairwise comparisons applied with Bonferroni corrections.

Changes in zooplankton community and copepod assemblage structure with depth was visualised using Principal Coordinates Analysis (PCO) and further explored with permutational analysis of variance (PERMANOVA) on Bray-Curtis similarity matrices of $\log(x + 1)$ -transformed abundance (zooplankton) and count (copepod) data, respectively. All PERMANOVAs were run for 9999 permutations selecting Type III (partial) sums of squares and unrestricted permutation

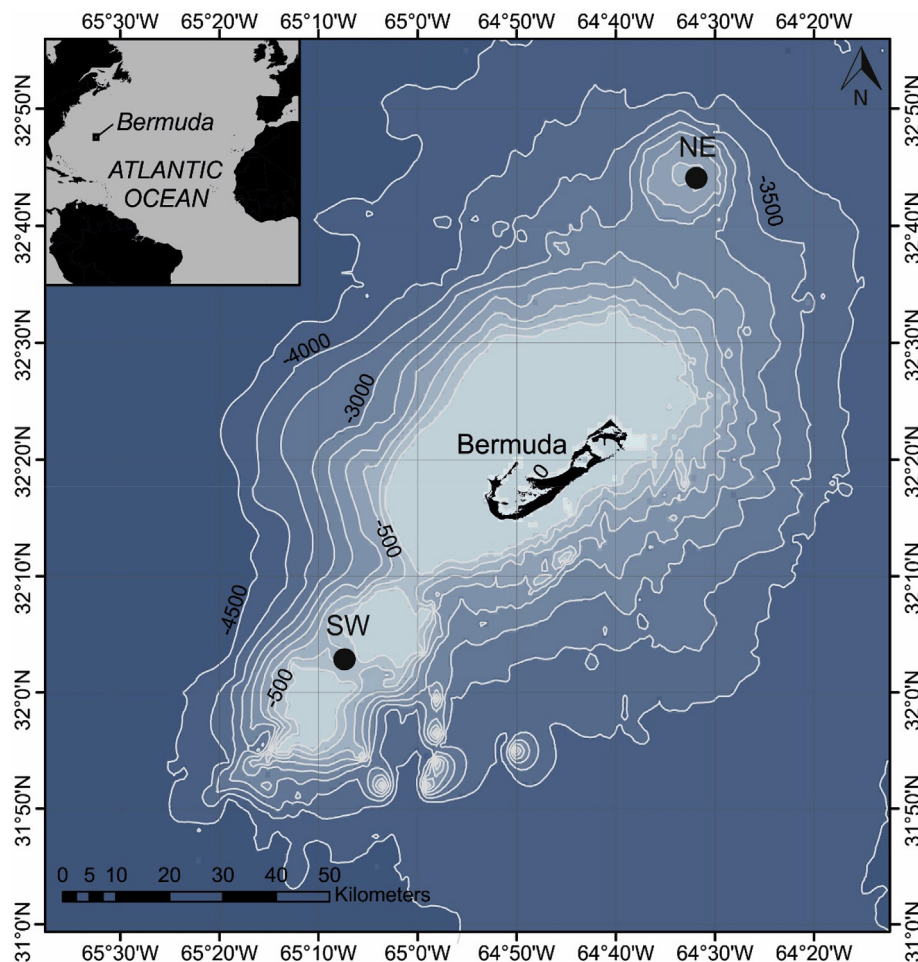


Fig. 1. Map showing the two sampling areas (NE: northeast, SW: southwest) around Bermuda. Three sampling events occurred in each area, however, due to their similar coordinates only two points are depicted in the map. Data overlay GEBCO_2014 Grid which provides 30 arc-second global grid of elevations.

of raw data. With the same similarity matrices we assessed the effect measured environmental variables (depth, salinity, temperature, dissolved oxygen and fluorescence; average values per studied sample) on zooplankton and copepod structure using a distance-based linear modelling (DISTLM) approach. DISTLMs were run for 9999 permutations and the best model was identified using the BEST routine and Akaike's criterion.

Kruskal Wallis and Mann-Whitney pairwise comparisons were carried out in SPSS v24 (IBM Corp., Armonk, NY), while PERMANOVA, PCO and DISTLM in PRIMER 7 (Clarke, 2015) and the add-on package PERMANOVA+ (Anderson et al., 2008).

3. Results

3.1. Abundance and diversity

Zooplankton and copepod abundance decreased with increasing depth (Kruskal Wallis, $p < 0.001$ in both cases). In each case, abundance was significantly higher in the epipelagic layer compared to the two deepest studied depths (Mann-Whitney's, DSL: $p = 0.009$ and 0.014 for zooplankton and copepods, respectively; below the DSL $p = 0.001$ and 0.001 , respectively) (Fig. 2A–B).

Alpha diversity (expressed as richness of taxa, Shannon, Simpson and Pielou's index, respectively) was comparable between depth zones for both zooplankton (at the higher grouping) and copepod (at the family level) faunas with the exception of richness of taxa (Kruskal-Wallis, $p = 0.015$ and 0.043 for zooplankton and copepods, respectively, Fig. 2C–D). For zooplankton, higher grouping richness was

greater in the epipelagic compared to below the DSL (Mann-Whitney's, $p = 0.031$), while for copepods family richness was highest in the deepest layer (i.e. below the DSL) compared to the above the DSL (Mann-Whitney's, $p = 0.039$).

3.2. Taxonomic composition

Some representative examples of the 21 diverse taxonomic groups that were identified in our samples are shown in Fig. 3. Copepods were by far the most abundant group making up 78–84% of all sampled individuals in each depth zone, followed by ostracods (5–9%) and chaetognaths (2–7%) (Fig. 4). We identified 32 copepod families, from which nine made significant contributions to the copepod abundance (i.e. $> 5\%$ relative abundance) in at least one studied depth zone (Fig. 4). Oithonidae and Oncaeididae were the two most commonly encountered families making up 35–47% of copepods at each depth zone. Detailed abundance data for each major taxonomic group and copepod family per sample can be found in Appendix B.

Kruskal-Wallis analysis revealed that for more than half (11 out of 21) of higher taxonomic groups there were significant depth-related differences in their abundance. In all cases, abundances were significantly higher in the epipelagic layer compared to the deeper zones (see Table 1). For copepods respectively, eight families showed significant differences with depth: Corycaeididae and Lucicutiidae were more abundant in the epipelagic layer, Clausocalanidae was more common above the DSL, while Euchaetidae, Metridinidae, Mornonillidae, Nullosetigeridae and Scolecitrichidae were more frequently observed in one of the two deepest layers (Table 1).

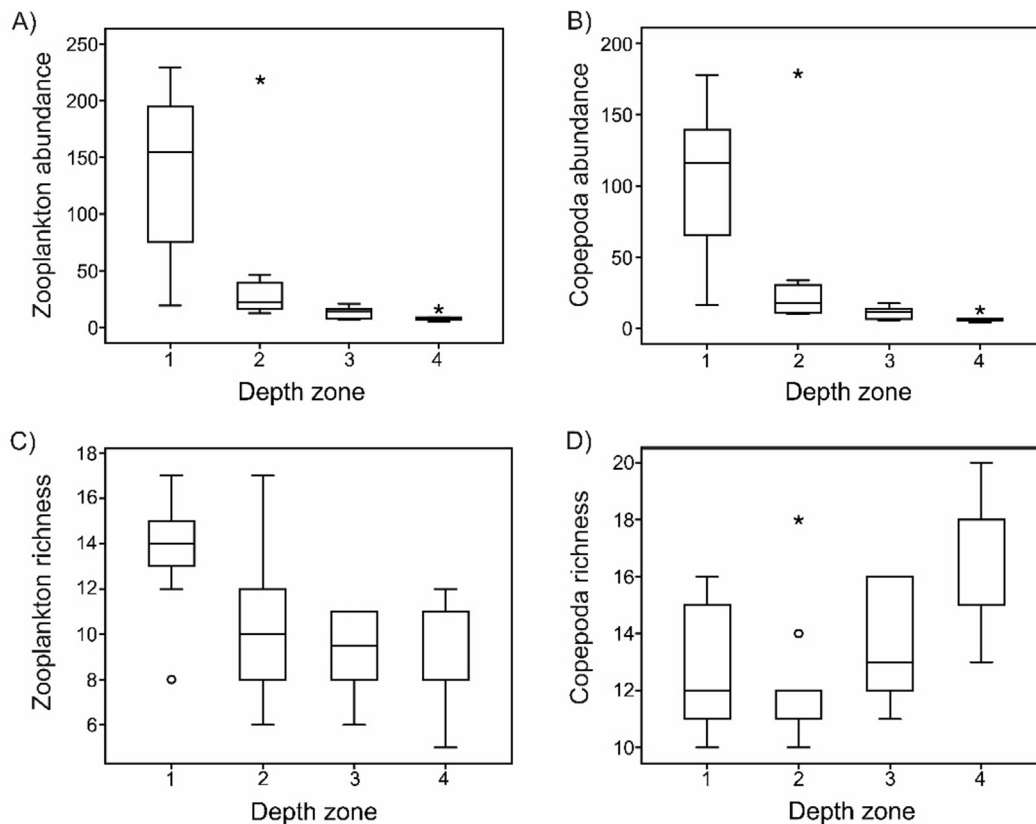


Fig. 2. Results of Kruskal-Wallis tests showing dependence of biological parameters with depth. A) Total zooplankton abundance (indiv. m^{-3}), B) Copepoda abundance (indiv. m^{-3}), C) Zooplankton (higher grouping) richness, D) Copepoda (family) richness. On the x-axis: 1: Epipelagic layer, 2: Above the DSL, 3: DSL, 4: Below the DSL. Boxes indicate the 25th and 75th quartiles, line is median, whiskers are 1.5 the interquartile, circles are outliers, and asterisks extreme outliers.

PCO suggested depth-related changes in zooplankton community structure (Fig. 5A). On the PCO plot samples were positioned across a shallow-deep axis (from left to right) with those from the epipelagic forming distinct clusters, thus indicating unique community structure in that depth range. Separation was less clear for the rest of the samples, although samples from above and below the DSL were clearly separated from each other. Similarly, copepods appeared to form distinct assemblages in the epipelagic, but also below the DSL (Fig. 5B). Representative families for each depth zone were Corycaidae and Calanidae for the epipelagic (although this is not supported by Kruskal-Wallis for the latter – Table 1), Clausocalanidae for above the DSL, Mormonillidae for the DSL, and Metridinidae and Euchaetidae for below the DSL.

PERMANOVA confirmed the PCO findings as both zooplankton and copepod assemblage structure composition were found to vary with depth (PERMANOVA, $p < 0.001$ in both cases). For zooplankton, pairwise comparisons showed the epipelagic having consistently distinct assemblages compared to the deeper layers. The layer above the DSL was distinct from the two deeper layers (Table 2). For copepods, pairwise comparisons demonstrated that both the epipelagic layer as well as the layer below the DSL contained distinct communities (Table 2).

3.3. Environmental drivers

The vertical profiles of temperature, salinity, dissolved oxygen and fluorescence at the locations of MultiNet sampling and additional CTD sites in the studied areas are shown in Fig. 6. In general, all measured environmental variables were found to decrease with increasing depth, with the exception of fluorescence that peaked at just over 100 m. DISTILM analysis indicated significant relationships between

zooplankton and copepod assemblage structure and measured environmental variables and depth (Table 3). In both cases, depth and dissolved oxygen accounted for the largest proportion of variance in composition structure, followed by temperature, fluorescence and salinity. The best models included depth and salinity or salinity and dissolved oxygen, explaining 58% and 31% of zooplankton community and copepod assemblage structure, respectively.

4. Discussion

Currently, data on deep-water zooplankton from the NW Atlantic are temporally and spatially sparse (e.g. Bucklin et al., 2010; Goldthwait and Steinberg, 2008; Vereshchaka et al., 2016). In addition, they often rely on bulk indicators such as total abundance or biomass (e.g. Madin et al., 2001; Piontkovski and Castellani, 2009), hence, lack taxonomic resolution, or alternatively are limited to a single taxonomic group (e.g. Angel, 2010; Pierrot-Bults and Nair, 2010). Although zooplankton bulk indicators are time and cost-efficient and provide information on overall productivity, they lack details on biodiversity and community structure, and their relationship with ecosystem functioning. Furthermore, the state and magnitude of ecosystem services provided by zooplankton such as sustainable fisheries or climate regulation are often taxon-dependant (McQuatters-Gollop et al., 2017). For example, crustaceans (i.e. copepods, cladocerans, euphausiids) are an integral part of the diet of some commercially important fish such as the Atlantic cod (*Gadus morhua*) (Beaugrand et al., 2003), while gelatinous zooplankton (i.e. ctenophores, medusae, salps) can be an important prey item for dogfish (*Squalus* spp.) and grenadiers (*Macrourous holotrachys*) (Diaz Briz et al., 2017). Such information is not possible to obtain using a bulk-indicator approach.

The present study is one of the few to investigate the

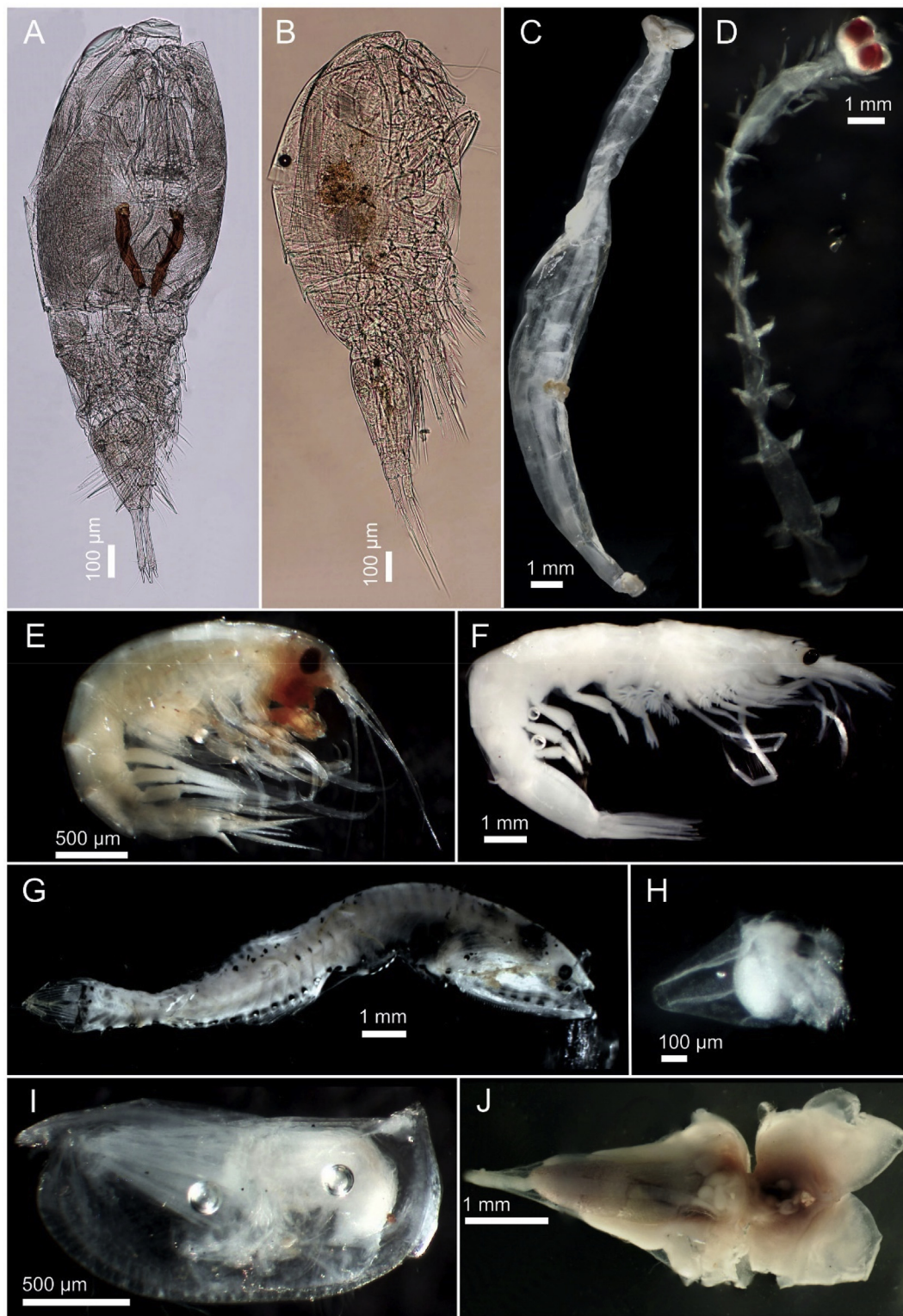


Fig. 3. Representative examples of zooplankton groups encountered in the MultiNet samples of this study. A) Copepoda (Corycaidae, HUD16-19_0059, 100–200 m), B) Copepoda (Oncaeidae, HUD16-19_0023, 350–550 m), C) Chaetognatha (*Sagitta* sp., HUD16-19_0048, 200–400 m), D) Polychaeta (Alciopidae, HUD16-19_0023, 350–550 m), E) Amphipoda (Gammaridae, HUD16-19_0027, 200–400 m), F) Euphausiacea (Euphausiidae, HUD16-19_0040, 550–750 m), G) Fish larva (*Cyclothone* sp., HUD16-19_0005, 600–800 m), H) Cladocera (Podonidae, HUD16-19_0054, 0–100 m), I) Ostracoda (Halocyprididae, HUD16-19_0025, 600–800 m), J) Gastropoda (Cavoliniidae, HUD16-19_0023, 350–550 m).

mesozooplankton community and its characteristics (abundance, diversity and composition) from Bermuda, NW Atlantic, across a wide bathymetric gradient spanning from the surface to the lower mesopelagic at 800 m depth.

4.1. Vertical zonation patterns of zooplankton abundance and diversity

We report a depth-related decrease of zooplankton abundance with depth (Fig. 2A), with the majority (67.5%) of net-caught zooplankton

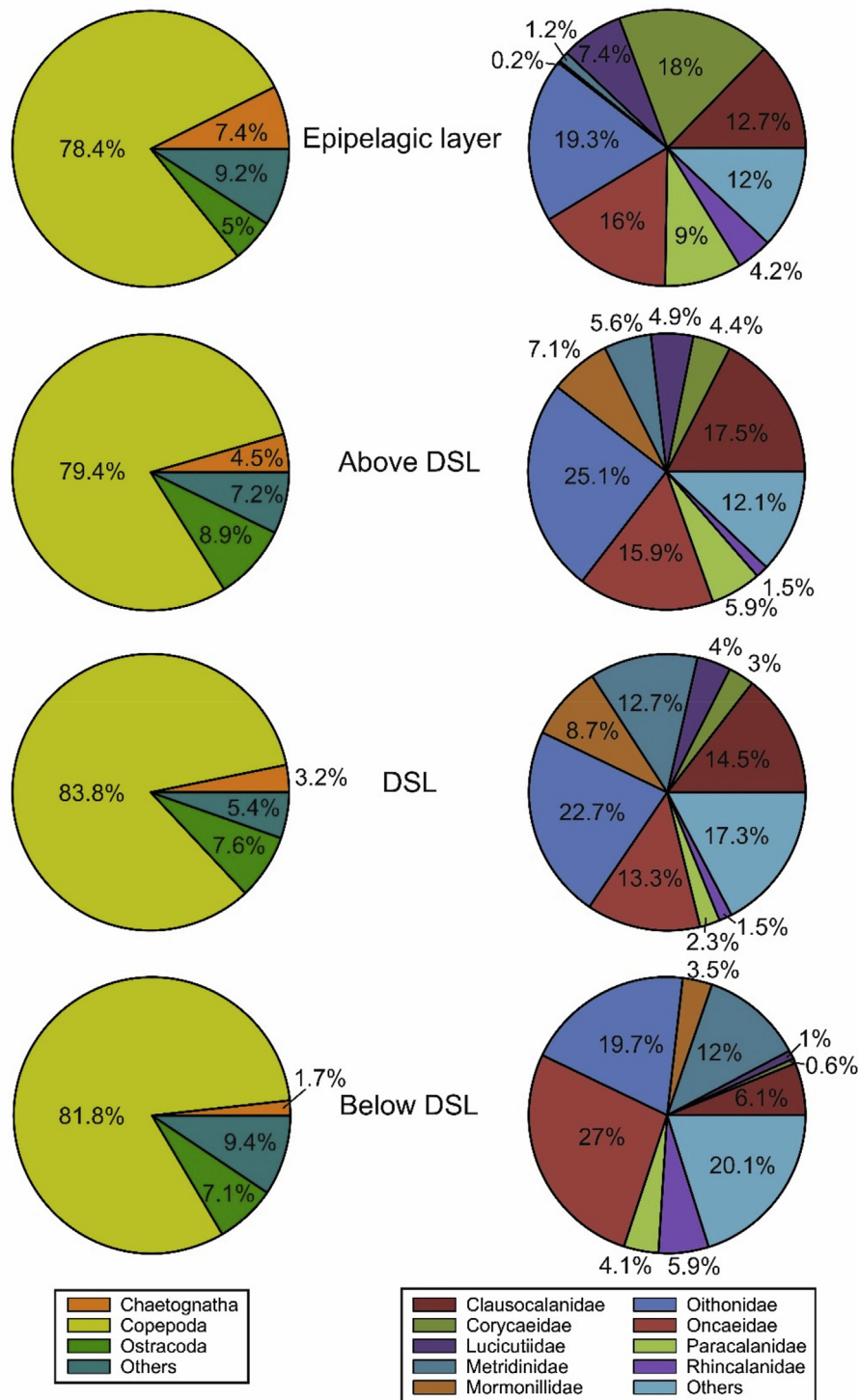


Fig. 4. Taxonomic composition of zooplankton assemblages (left) and copepod assemblages (right) averaged per depth zone across all studied locations in Bermuda. Only zooplankton taxa and copepod families with > 5% relative abundance in at least a depth zone, respectively, are depicted separately.

occurring in the epipelagic biome, compared to 22%, 6.5% and 4% that was found in the successive deeper zones, respectively. This pattern is a direct consequence of the distribution of phytoplankton abundance and primary production in the water column that typically peaks in the sunlit epipelagic zone (Chavez et al., 2010), and declines logarithmically thereafter (Angel, 1997) (see Fig. 6D for depth-related declines of fluorescence in Bermuda). It is interesting to note the fluorescence peak at just over 100 m, which contradicts the model estimates by

Reygondeau et al. (2018) of an upper mesopelagic depth limit < 100 m for Bermuda. Notably, however, we did not observe a second peak in abundance within the DSL as identified from our ADCP readings. The most likely pelagic scatterers that can be identified by a 75-kHz ADCP such as the one we used in this study are > 10 mm in size (Haus et al., 2016), hence, a large proportion of the zooplankton (including the dominant copepods) in our net samples were not detected in our ADCP readings. Other confounding factors could be spatial variation

Table 1

Output of the Kruskal-Wallis analysis on zooplankton (higher grouping) abundance and copepod (family) abundance against depth zone, followed by post hoc pairwise Mann-Whitney comparisons applied with a Bonferroni correction. Only statistically significant ($p < 0.05$) results are shown. 1: Epipelagic layer, 2: Above the DSL, 3 DSL, 4: Below the DSL.

Taxonomic group		Kruskal-Wallis	Mann-Whitney
Zooplankton	Amphipoda	0.002	1 > 3
	Appendicularia	0.001	1 > 3, 4
	Chaetognatha	< 0.001	1 > 3, 4
	Cladocera	0.024	1 > 4
	Colonial hydrozoa, ctenophora and thaliacea	0.002	1 > 3
	Copepoda	< 0.001	1 > 3, 4
	Crustacea larvae	0.003	1 > 2, 3
	Fish larvae	0.047	1 > 2
	Gastropoda	0.017	1 > 4
	Ostracoda	0.002	1 > 3, 4
	Polychaeta	0.001	1 > 3, 4
Copepoda	Clausocalanidae	0.026	2 > 4
	Corycaeiidae	< 0.001	1 > 2, 3, 4
	Euchaetidae	0.008	4 > 1, 2
	Lucicutiidae	0.024	1 > 4
	Metridinidae	0.04	3, 4 > 1
	Mormonillidae	0.015	3 > 1
	Nullotetigeridae	0.001	4 > 1, 2, 3
	Scolecitrichidae	0.002	4 > 1, 2

(patchiness) of pelagic communities, and/or undersampling of fast-swimming organisms such as fish, euphausiids and siphonophores by our nets (Ashjian et al., 2002), which may be substantial contributors to acoustic backscatter measurements (Stanton et al., 1994; Wiebe and Greene, 1994). Our findings, on decreased abundance with depth, are concordant with previous studies on deep-water zooplankton conducted in Bermuda (Deevey and Brooks, 1971, 1977), the wider Atlantic basin (Vereshchaka et al., 2017), the Mediterranean (Danovaro et al., 2017a), the western tropical North Pacific (Dai et al., 2017) and the western subarctic Pacific (Yamaguchi et al., 2002). Copepod assemblages, closely followed the abundance pattern of the whole zooplankton community (Fig. 2B), which was expected considering they were numerically the dominant faunal component in all of our studied samples (Fig. 4). Notably, the consistently high relative abundance of copepods recorded throughout the water column off Bermuda (Fig. 4), concurs with previous surveys conducted across the globe (Cartes et al., 2013; Dai et al., 2017; Kosobokova and Hirche, 2000; Turner, 2004).

Regarding diversity, most estimated indices (Shannon, Simpson and Pielou's index) remained comparable with depth, with the exception of the zooplankton (higher grouping) richness that decreased below the epipelagic zone and was significantly lower below the DSL (Fig. 2C). Similar depth-related decreases in zooplankton diversity, including richness, have been recorded elsewhere and linked to decreases of organic matter and temperature (Danovaro et al., 2017a; Vereshchaka et al., 2017). We too found food availability (i.e., represented by fluorescence measurements, as well as by zooplankton abundance for heterotrophic plankton) and temperature - both negatively correlated with depth - to be important in shaping zooplankton communities, in addition to salinity and dissolved oxygen (Table 3). We therefore suggest that the lower temperatures and oxygen levels in combination with dwindling food resources in deeper waters likely led to lower taxon diversity. In contrast, copepod family richness peaked below the DSL (Fig. 2D). This is in line with previous studies reporting depth-related increases in copepod diversity with peaks occurring in lower mesopelagic to bathypelagic waters (Bucklin et al., 2010; Deevey and Brooks, 1971). In Bermuda, copepod families such as Nullotetigeridae, Parapontellidae and Tharybidae were uniquely encountered in the lower mesophotic (below the DSL, Table 1). These families are known to

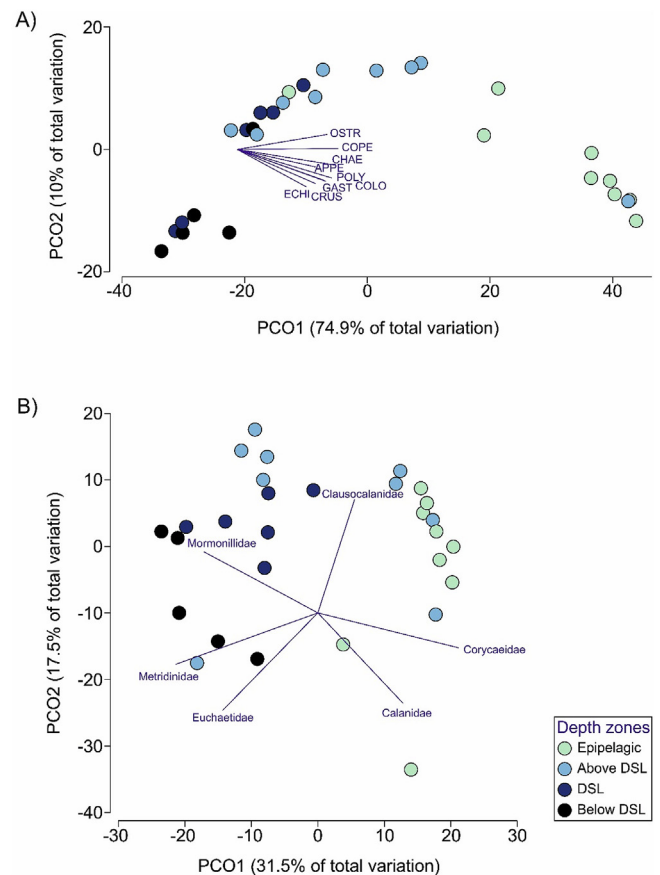


Fig. 5. Principal coordinates analysis ordination on log(x+1)-transformed zooplankton (A) and copepod (B) abundance data using Bray-Curtis dissimilarity matrices. Superimposed are vectors of taxa highly correlated with the two PCO axes (Pearson's correlation coefficient, $\rho > |0.7|$). The length and direction of each vector indicates the strength and sign, respectively, of the relationship between each taxonomic group and the PCO axes. OSTR = Ostracoda, COPE = Copepoda, CHAE = Chaetognatha, APPE = Appendicularia, POLY = Polychaeta, GAST = Gastropoda, CRUS = Crustacea larvae, ECHI = Echinodermata larvae, COLO = Colonial hydrozoa, ctenophora and thaliacea.

occur across wide depth ranges spanning from epipelagic to bathypelagic waters (Boxshall and Halsey, 2004), however, since very little is known about their ecology and biology we cannot speculate as to why they were restricted below the DSL in Bermuda.

4.2. Drivers of zooplankton community composition

A number of factors could drive distribution and composition of zooplankton communities including trophic conditions (primary production, macronutrients), temperature, salinity, oxygen or mesoscale physical perturbations (e.g. eddies) (Cartes et al., 2013; Danovaro et al., 2017a; Eden et al., 2009; Gaard et al., 2008; Goldthwait and Steinberg, 2008; Steinberg et al., 2012). Most of these environmental gradients covary with depth, hence, strong vertical zonation patterns of marine zooplankton structure have been in general well-documented (Ortner et al., 1981; Sameoto, 1986; Steinberg et al., 2008; Tsuda et al., 2006; Wishner et al., 1998). Our analysis demonstrated that mesozooplankton distribution in Bermuda was also depth-stratified, with distinct communities occupying the epipelagic zone, the above the DSL zone, and finally the DSL and below the DSL zones combined (Fig. 5; Table 2). Salinity, dissolved oxygen, temperature and fluorescence, all of which were negatively correlated with depth, were identified as being important predictors of zooplankton community structure, with salinity

Table 2

Changes of zooplankton and copepod structure in relation to depth zone using PERMANOVA on Bray-Curtis similarity matrices of $\log(x + 1)$ -transformed abundance data. The Pseudo- F statistic and $P(\text{perm})$ are analogous to the F statistic and P -value for multi-factorial univariate ANOVA models. Unique perms, indicates how many unique values of the pseudo- F statistic were obtained under permutation.

Factor	Zooplankton			Copepods		
	Pseudo- F	$P(\text{perm})$	Unique Perms	Pseudo- F	$P(\text{perm})$	Unique Perms
Depth zone	10.107	< 0.001	9941	3.6689	< 0.001	9911
Pairwise tests	t	$P(\text{perm})$	Unique Perms	t	$P(\text{perm})$	Unique Perms
Epipelagic, Above DSL	2.912	0.004	8162	1.722	0.005	8102
Epipelagic, DSL	4.534	0.001	4274	2.338	< 0.001	4335
Epipelagic, Below DSL	4.735	0.001	1983	2.778	< 0.001	1992
Above DSL, DSL	2.015	0.018	4337	1.019	0.425	4318
Above DSL, Below DSL	2.64	0.003	1985	1.849	0.005	1981
DSL, Below DSL	1.603	0.068	462	1.498	0.005	462

and dissolved oxygen included in the best models for zooplankton and copepods, respectively (Table 3).

The three most abundant taxonomic groups throughout the water column were copepods, ostracods and chaetognaths, which is consistent

with previous studies from Bermuda and the Sargasso Sea (Deevey and Brooks, 1971; Eden et al., 2009) and elsewhere (e.g. Boston Harbor, Massachusetts Bay, and Cape Cod Bay, Turner, 2004; subtropical and subarctic North Pacific Ocean, Steinberg et al., 2008). The

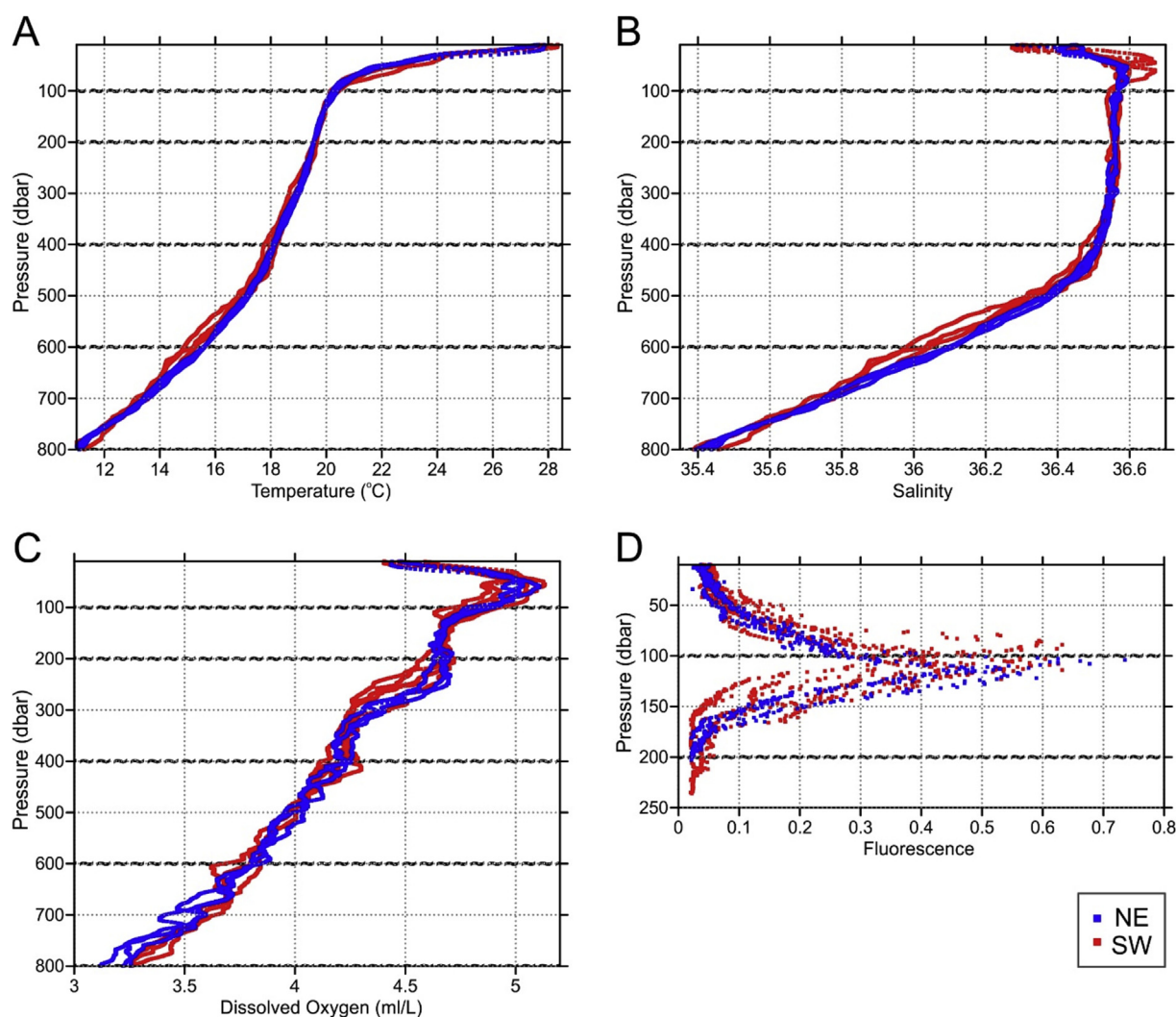


Fig. 6. Vertical profiles of (A) temperature (°C), (B) salinity, (C) dissolved oxygen (ml/L), and (D) fluorescence obtained from the CTD casts conducted in the study area during the survey. The profiles northwest (NW) and southeast (SE) of Bermuda have been grouped together as indicated in the colour of the dots since the environmental conditions in these locations are spatially uniform. 1 dbar \approx 1 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Percentage of variation explained by environmental variables in a distance-based multilinear model for zooplankton communities and copepod assemblages using abundance and count data, respectively. The Pseudo-*F* statistic is analogous to the *F* statistic for multi-factorial univariate ANOVA models.

Explanatory variable	Zooplankton			Copepods		
	Pseudo- <i>F</i>	<i>P</i>	% of variation explained	Pseudo- <i>F</i>	<i>P</i>	% of variation explained
Depth	27.081	< 0.001	50.08	7.7241	< 0.001	22.24
Salinity	10.118	0.0015	27.26	5.1236	< 0.001	15.95
Temperature	22.906	< 0.001	45.90	6.4039	< 0.001	19.17
Dissolved Oxygen	25.018	< 0.001	48.10	8.0902	< 0.001	23.06
Fluorescence	19.704	< 0.001	42.19	6.4476	< 0.001	19.28
Best Model (Depth + Salinity)			57.65			
Best Model (Salinity + Dissolved Oxygen)						30.63

distinctiveness of the epipelagic was both a result of the greater higher taxon richness and the enhanced abundances it harboured for more than half of the 21 groups identified in this study (Table 1). Of note, larvae of fish and crustacea were more abundant in epipelagic than mesopelagic waters (Table 1) benefiting from the enhanced food supply (i.e. fluorescence levels; Fig. 6d) in the former. It is expected that with age and increasing size, adult specimens of these groups will descend during the day into meso- and bathypelagic waters in order to avoid epipelagic predators (Sutton, 2013).

Copepods were found to form distinct assemblages in epipelagic waters, above and within the DSL, and finally below the DSL (Tables 1 and 2, Fig. 5). Epipelagic communities were characterised by Corycaidae, a family comprising small carnivorous species that feed on microzooplankton (< 200 µm) and juvenile copepods common in surface waters, as well as Calanidae and Lucicutiidae, which contain filter-feeding species with a tendency towards herbivory (Benedetti et al., 2015; Boxshall and Halsey, 2004; Brun et al., 2017). Herbivorous families such as Clausocalanidae and Mormonillidae were also typical for waters above and within the DSL, while the carnivorous Euchaetidae, Metridinidae, Nullosetigeridae and the omnivorous-detritivorous Scolecitrichidae (Benedetti et al., 2015; Boxshall and Halsey, 2004) were more common below the DSL. Omnivory was nevertheless the dominant copepod trophic trait across all depths. This is largely because of the widespread presence of Oithonidae (in particular *Oithona*) and Oncaeidae (*Oncaea*) in all samples (Fig. 4), despite the fact that our choice of net mesh size (200 µm) is known to undersample members of the former (Gallienne and Robins, 2001). Our results, confirm Oithonidae's status as a major constituent of the world's ocean plankton independent of depth and abiotic conditions (Gallienne and Robins, 2001). They also confirm the increasing importance of Oncaeidae with depth (Böttger-Schnack, 1990; Yamaguchi et al., 2002), as it accounted for a quarter of all copepods present in the lower mesopelagic (i.e. below the DSL, Fig. 4).

4.3. Implications for the biological pump

Mesozooplankton play a critical role in regulating carbon flows through the mesopelagic zone via their grazing on microzooplankton, diel vertical migration, metabolism, production of sinking faecal pellets, mucous feeding webs, molts and carcasses (Steinberg, 2017). Because of the sheer diversity of life histories, functional traits, feeding behaviours, and physiologies encountered in different zooplankton taxa, community structure exerts significant control on the magnitude of each of these carbon processing mechanisms (Steinberg and Landry, 2017). This has important implications for the functioning of mesopelagic food webs and the transport of particulate organic matter to depth, ultimately affecting the efficiency of carbon storage in the deep ocean.

Even though we lack species-level information that would better take into account the variability of body sizes, food sources and life histories of different zooplankton taxa, we can use the higher grouping

and copepod family-level data which indicate that omnivorous taxa feeding largely on sinking and suspended particles (e.g. ostracods, copepods: Oithonidae, Oncaeidae) was the dominant trophic trait throughout the water column. By intercepting particulate organic matter and repackaging particles into new classes of faecal pellets (Cavan et al., 2017; Goldthwait et al., 2004; Wilson et al., 2008), these zooplankton exert control on mesopelagic carbon flux, and ultimately on the deeper, food-deprived bathypelagic communities. For example, high abundances of small-sized species such as *Oithona* spp. have been inversely correlated with fluxes of faecal pellet flux (Svensen and Nejstgaard, 2003), thus reducing the efficiency of the BCP, especially in oligotrophic ecosystems (Wilson et al., 2008). It is likely that is the case for the oligotrophic waters off Bermuda as well.

To a lesser degree, carnivory was also an important feeding behaviour, with Corycaidae copepods peaking in the epipelagic, and chaetognaths constituting the third most abundant group across the water column (Fig. 4). As with diel vertical migration, carnivory represents an alternative source of nutrition that can partially meet carbon demand of mesopelagic zooplankton communities (Steinberg et al., 2008) and can be occasionally the dominant trait (Stone and Steinberg, 2016). Carnivorous feeders produce new faecal pellets which can feed detritivores in deeper waters, hence, enhancing the efficiency of the BCP (Wilson et al., 2008; Yamaguchi et al., 2002).

The above highlight the need of studying zooplankton trophic traits when investigating carbon flux in the deep ocean. While bottom-up control of vertical carbon flux (i.e. nutrients fuelling phytoplankton primary production, which form aggregate sinking particles after their death) is undoubtedly crucial, we suggest that future experimental or modelling studies of ocean carbon export should incorporate information on zooplankton food web structure as well (Giering et al., 2014; Siegel et al., 2016).

Author contributions

LCW and ADR conceived the study. Zooplankton sample collection was conducted by LCW, and environmental data collection by IMY. PVS, MR and HF processed the net samples, counted and identified the zooplankton taxa described in this paper. IY processed and interpreted the environmental data. PVS analysed the results. All authors provided advice on the data analysis and interpretation. PVS, LCW and ADR prepared the main manuscript text. PVS and IMY prepared the tables and figures. All authors provided comments and reviewed the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2019.02.014>.

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