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Diversity and abundance of pteropods and heteropods along a latitudinal gradient across the Atlantic Ocean

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ABSTRACT

Shelled pteropods and heteropods are two independent groups of holoplanktonic gastropods that are potentially good indicators of the effects of ocean acidification. Although insight into their ecology and biogeography is important for predicting species-specific sensitivities to ocean change, the species abundances and biogeographical distributions of pteropods and heteropods are still poorly known. Here, we examined abundance and distribution patterns of pteropods (euthecosomes, pseudothecosomes, gymnosomes) and heteropods at 31 stations along a transect from 46°N to 46°S across the open waters of the Atlantic Ocean (Atlantic Meridional Transect cruise AMT24). We collected a total of 7312 pteropod specimens belonging to at least 31 species. Pteropod abundances were low north of 40°N with <15 individuals per 1000 m³, varied between 100 and 2000 ind./1000 m³ between 30°N and 40°S, and reached >4000 ind./1000 m³ just south of 40°S. This accounted for an estimated biomass of 3.2 mg m⁻³ south of 40°S and an average of 0.49 mg m⁻³ along the entire transect. Species richness of pteropods was highest in the stratified (sub)tropical waters between 30°N and 30°S, with a maximum of 15 species per station. The biogeographical distribution of pteropod assemblages inferred by cluster analysis was largely congruent with the distribution of Longhurst's biogeochemical provinces. Some pteropod species distributions were limited to particular oceanographic provinces, for example, subtropical gyres (e.g. *Styliola subula*) or warm equatorial waters (e.g. *Creseis virgula*). Other species showed much broader distributions between ~35°N and ~35°S (e.g. *Limacina bulimoides* and *Heliconoides inflatus*). We collected 1812 heteropod specimens belonging to 18 species. Highest heteropod abundances and species richness were found between 30°N and 20°S, with up to ~700 ind./1000 m³ and a maximum of 14 species per station. Heteropods were not restricted to tropical and subtropical waters, however, as some taxa were also relatively abundant in subantarctic waters. Given the variation in distribution patterns among pteropod and heteropod species, it is likely that species will differ in their response to ocean changes.

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1. Introduction

Shelled pteropods and heteropods are holoplanktonic gastropods with aragonite shells that are vulnerable to the effects of ocean acidification (e.g., Bednaršek and Ohman, 2015; Gattuso et al., 2015; Wall-Palmer et al., 2016a). They are common components of the marine zooplankton and have highly diverse evolutionary histories, life strategies and morphologies. Through

production of aragonitic shells, they are involved in biogenic carbon export from the surface to the deep ocean (Bednaršek et al., 2012a). However, especially in the open Atlantic Ocean, their species diversity and abundance are still poorly understood (e.g., Bé and Gilmer, 1977; Van der Spoel and Heyman, 1983; Richter and Seapy, 1999; Van der Spoel and Dadon, 1999; Bednaršek et al., 2012a). The pteropod distribution maps from Bé and Gilmer (1977) and Van der Spoel and Heyman (1983) are based on manual estimations of distributions based on synthesized presence-only data, precluding any quantitative comparisons within and between ocean basins. Gaining more insight into the current diversity and distribution of planktonic gastropods is important for measuring future changes in diversity and distribution, and for predicting

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species-specific sensitivities to ocean changes. New data on abundance will help estimate the biomass of holoplanktonic gastropods, about which little is known for many regions, including the open Atlantic Ocean. This is important for their incorporation as a plankton functional type in ecosystem models and to estimate their contribution to ocean carbon export in biogeochemical models (Bednaršek et al., 2012a).

The oceans appear to have more biodiversity and less homogeneous species communities than has long been assumed or expected (Angel, 1993; Norris, 2000). Biogeochemical provinces of the Atlantic Ocean provide a diverse range of ecological niches as well as barriers to dispersal for zooplankton taxa (e.g., Peijnenburg and Goetze, 2013; Andrews et al., 2014; Goetze et al., 2016). For example, in *Cuvierina* pteropods, *C. cancapae* is endemic to the equatorial Atlantic and *C. atlantica* is restricted to the northern and southern subtropical gyres (Janssen, 2005; Burridge et al., 2015). Endemism of evolutionary lineages in the equatorial Atlantic is a pattern also observed in other plankton groups (e.g., Hirai et al., 2015; Goetze et al., 2016). The species composition of planktonic ostracod assemblages also is more similar within ocean provinces (e.g., northern temperate, northern subtropical gyre and equatorial regions) than between provinces (Angel et al., 2007). Ocean warming and acidification may cause shifting species distributions in the plankton (e.g., Beaugrand et al., 2009; Provan et al., 2009), as well as (local) extinctions or adaptation to new conditions (e.g., Collins, 2012; Lohbeck et al., 2012, 2014).

Pteropods are a group of heterobranch gastropods (Jörger et al., 2010), a superorder comprised of the orders Thecosomata, also referred to as “sea butterflies”, and Gymnosomata, or “sea angels” that play an important role in marine food webs (Lalli and Gilmer, 1989; Pierrot-Bults and Peijnenburg, 2015). According to the World Register of Marine Species (WoRMS, www.marinespecies.org), a total of 83 extant thecosome species and 43 gymnosome species occur worldwide, and many fossil species also have been described (Janssen and Peijnenburg, 2013). Most taxa are between 0.05 and 2 cm in size and occur in the upper 300 m of the global ocean, although some species occur at bathypelagic depths (Bé and Gilmer, 1977; Van der Spoel and Dadon, 1999). Many species are known to be vertical migrators that move to shallower depths at night (Bé and Gilmer, 1977). Most thecosomes have aragonite shells, which they maintain as adults. They include the cavoliniid euthecosomes with uncoiled, bilaterally symmetrical shells (52 species), limaciniid euthecosomes with coiled shells (8 species), and pseudothecosomes, with coiled shells or a semi-soft pseudocoil without an aragonitic shell (23 species; Van der Spoel and Dadon, 1999). All thecosomes produce and deploy mucus webs to feed on microplankton (Gilmer and Harbison, 1986). Gymnosomes have larval shells, but shed them as they grow into adults. They are predators that feed exclusively or primarily on thecosomes (Lalli and Gilmer, 1989).

Heteropods or “sea elephants”, formally known as Pterotracheoidea, are a group of Caenogastropoda. According to WoRMS, this group consists of 35 extant species that occur in moderately low abundance in the global ocean, primarily at tropical and subtropical latitudes (Richter and Seapy, 1999). However, there is evidence that some taxa thrive in cold waters, e.g., south of Australia and during glacial periods in the geological past (Howard et al., 2011; Wall-Palmer et al., 2014). The vertical distribution of heteropods is not well understood, but they have been found to live at epipelagic and upper mesopelagic depths (e.g., Lalli and Gilmer, 1989; Richter and Seapy, 1999; Ossenbrügger, 2010). Heteropods are visual predators with well-developed eyes. To the extent that it is known, adults feed on other zooplankton and small fishes, and juveniles feed on phytoplankton and small zooplankton (Lalli and Gilmer, 1989; Seapy et al., 2003). The three heteropod families,

Atlantidae, Carinariidae and Pterotracheidae, are highly diverse in size and body form. The Atlantidae have the highest species diversity (21 species; one additional species described by Wall-Palmer et al., 2016b), are generally less than 1 cm in size, are the least efficient swimmers of all heteropods, and can retract their bodies entirely into their keeled, dextrally coiled aragonite shells (Seapy et al., 2003). They are the most thoroughly sampled heteropod group in the southern subtropical Atlantic, with species densities of 410–1710 individuals per 1000 m³ accounting for 80–99% of the total sampled heteropod community (Richter and Seapy, 1999). The Carinariidae (9 species) have a cylindrical body that is very large in relation to their shells, and can be as long as 50 cm (Lalli and Gilmer, 1989). The Pterotracheidae (5 species) only have larval shells, and have an elongated body that can reach a length of 33 cm in the Atlantic Ocean (Richter and Seapy, 1999). The Carinariidae and Pterotracheidae are thought to be more efficient swimmers than Atlantidae because of the relatively small body size and large shell of the latter group (Lalli and Gilmer, 1989).

In this study, we quantitatively sampled pteropods and heteropods from 46°N to 46°S along a transect of >12,000 km across the Atlantic Ocean, during Atlantic Meridional Transect (AMT) cruise 24. The AMT is a multidisciplinary programme aimed at understanding biological, chemical, and physical oceanographic processes, with annual transect sampling across the Atlantic Ocean (Rees et al., 2015). Here we (1) assess species distributions, abundances and biomass of pteropods and heteropods at 31 sampling stations along the transect, (2) estimate biogeographical trends in species diversity, and (3) compare inter-station similarities in community structure with Longhurst's (1998) biogeochemical provinces. To our knowledge, this is the first paper to report quantitative abundance data of pteropods and heteropods across a large-scale latitudinal gradient in the Atlantic.

2. Methods

2.1. Sampling and sorting

Holoplanktonic gastropods were collected during the AMT24 expedition (United Kingdom to Falkland Islands) between 46°23'N and 46°05'S from September 28th to October 30th, 2014 (Table 1). We conducted oblique tows at night from the upper 311 (216–401) m at 31 stations, representing the epipelagic and upper mesopelagic zones. The stations were assigned to biogeochemical provinces according to Longhurst (1998) and Reygondeau et al. (2013) (Table 1). We used a bongo net of 0.71 m diameter and 200 µm mesh size with a General Oceanics flowmeter (2030RC) mounted in the mouth of the net to measure the volume of seawater filtered during the tow. The flowmeter was calibrated both pre- and post-cruise. Bulk zooplankton samples were quantitatively split using a Folsom plankton splitter and one or more quantitative fractions were immediately preserved in 96% ethanol. The alcohol was replaced within 24 h of collection, and samples were stored at –20 °C. Pteropods and heteropods were sorted from 25% or 50% of the quantitative zooplankton samples, depending on the bulk sample volume (Table 1).

Pteropod and heteropod material was sorted by species and counted after the expedition. The majority of taxa could be identified to species morphologically. However, we counted individuals in larval or juvenile growth stages separately if they could not be assigned to species because they lacked the morphological characters to distinguish between closely related species. This ambiguity occurred for juvenile *Cuvierina* euthecosomes (Bé et al., 1972), larval stages of *Diacria* and *Cavolinia* euthecosomes, *Peracle* pseudothecosomes, as well as larval stages of some atlantid heteropods. Some other taxa were registered only at the genus

Table 1

Overview of sampling locations and tow information along AMT24 and corresponding CTD stations, surface temperatures and maximum chlorophyll *a* concentrations from the upper 300 m. The biogeochemical provinces of the sampling stations are based on Longhurst (1998) and Reygondeau et al. (2013): NADR (North Atlantic drift), NAST E (Northeast Atlantic subtropical gyre), NAST W (Northwest Atlantic subtropical gyre), NATR (North Atlantic tropical gyre), WTRA (Western tropical Atlantic), SATL (South Atlantic gyre), SSTC (Southern subtropical convergence), SANT (Subantarctic water ring), FKLD (Southwest Atlantic shelves).

Station	Sampling date	Latitude	Longitude	Max. depth (m)	Sorted water volume (m ³), (% of total volume)	Surface temperature (–10 m) (°C)	Maximum Chlorophyll <i>a</i> (mg m ⁻³)	Longhurst province
1	2014-09-28	46°23'N	10°58'W	NR	483 (50%)	19.3	0.748	NADR
2	2014-09-29	44°05'N	14°54'W	297	567 (50%)	20.4	0.583	NAST E
3	2014-09-30	41°46'N	18°44'W	382	491 (50%)	19.8	0.518	NAST E
4	2014-10-01	39°25'N	22°29'W	274	669 (50%)	21.0	0.584	NAST E
5	2014-10-03	34°45'N	26°37'W	364	538 (50%)	23.7	0.262	NAST W
6	2014-10-04	31°18'N	27°44'W	319	621 (50%)	24.5	0.126	NATR
7	2014-10-05	27°30'N	28°53'W	328	611 (50%)	26.7	0.123	NATR
8	2014-10-06	24°03'N	29°54'W	258	693 (50%)	26.7	0.147	NATR
9	2014-10-07	20°27'N	29°16'W	274	754 (50%)	26.6	0.154	NATR
10	2014-10-08	17°49'N	28°42'W	294	320 (25%)	26.8	0.240	NATR-WTRA
11	2014-10-09	14°12'N	27°56'W	305	342 (25%)	28.1	0.381	WTRA
12	2014-10-10	10°47'N	27°12'W	323	569 (50%)	28.3	0.192	WTRA
13	2014-10-11	7°17'N	26°30'W	329	686 (50%)	28.9	0.292	WTRA
14	2014-10-12	3°48'N	25°47'W	364	596 (50%)	28.0	0.262	WTRA
15	2014-10-13	0°05'N	25°01'W	341	637 (50%)	26.0	0.435	WTRA
16	2014-10-14	3°53'S	25°02'W	339	328 (25%)	26.0	0.329	WTRA
17	2014-10-15	7°28'S	25°07'W	266	353 (25%)	25.6	0.258	WTRA-SATL
18	2014-10-16	11°02'S	25°03'W	292	358 (25%)	25.4	0.175	SATL
19	2014-10-17	14°40'S	25°04'W	311	345 (25%)	24.7	0.249	SATL
20	2014-10-18	18°19'S	25°05'W	283	368 (25%)	23.4	0.176	SATL
21	2014-10-20	20°51'S	25°05'W	309	352 (25%)	22.9	0.165	SATL
22	2014-10-21	24°27'S	25°03'W	323	335 (25%)	22.0	0.143	SATL
23	2014-10-22	27°46'S	25°01'W	260	370 (25%)	20.5	0.172	SATL
24	2014-10-23	31°20'S	26°06'W	330	334 (25%)	18.5	0.500	SATL
25	2014-10-24	34°11'S	27°13'W	NR	227 (25%)	16.7	0.342	SATL
26	2014-10-25	37°54'S	28°44'W	372	308 (25%)	14.0	0.377	SSTC
27	2014-10-26	40°07'S	30°55'W	216	438 (25%)	13.2	0.321	SSTC
28	2014-10-27	41°29'S	33°52'W	228	422 (25%)	12.0	0.449	SSTC
29	2014-10-28	43°01'S	37°08'W	253	372 (25%)	11.6	0.406	SSTC
30	2014-10-29	44°37'S	40°42'W	350	301 (25%)	8.8	0.485	SANT-FKLD
31	2014-10-30	46°05'S	44°12'W	401	277 (25%)	9.3	0.528	SANT-FKLD

level because of their complex and unresolved taxonomies, including *Diacavolinia* euthecosomes, *Corolla* and *Gleba* pseudothecosomes, and *Pterotrachea* heteropods (Van der Spoel et al., 1993; Richter and Seapy, 1999; Van der Spoel and Dadon, 1999). Two forms of the euthecosome *Clio pyramidata*, forma *lanceolata* and forma *pyramidata*, were recorded together as *C. pyramidata* because these varieties were not found to be genetically distinct (Jennings et al., 2010), and likely represent a single species. We identified gymnosomes to order because we could not identify them to species following fixation in ethanol, and excluded them from many subsequent analyses. The ratio between the abundances of gymnosomes, if present, and thecosomes was calculated to estimate the potential predation intensity by gymnosomes on thecosomes across the AMT24 transect. This ratio was calculated only for stations with more than 10 pteropod specimens.

2.2. Species diversity, abundance and biomass

To summarize the diversity of thecosomes and heteropods along AMT24, we calculated species richness *R*, Shannon-Wiener's diversity index *H'* and Pielou's evenness index *J'* at each station. Shannon-Wiener's *H'* is commonly used as a measure for species diversity in a community and accounts for abundance and evenness of the species present (Shannon and Weaver, 1949; Spellerberg and Fedor, 2003):

$$H' = - \sum_{i=1}^R (p_i \ln p_i)$$

In this formula, *R* is the species richness or total number of species, and *p_i* is the fraction of individuals belonging to species *i* relative to the total number of specimens. Pielou's evenness *J'* is

derived from *H'* and quantifies how close in numbers or abundance each species is in an environment, given that there are at least two species present per location (Pielou, 1967):

$$J' = \frac{H'}{\ln R}$$

To assess trends in species diversity and abundance of thecosomes and heteropods, we analyzed our gastropod diversity and abundance data in relation to oceanographic data obtained during AMT24. Abundances of pteropods and heteropods were quantified in terms of individuals per 1000 m³ of seawater filtered. Ocean temperature and chlorophyll *a* concentrations along AMT24 were obtained using a Sea-Bird Electronics 3P Temperature Sensor and a CTG Aquatracka MKIII Fluorometer. Oceanographic data were calibrated and archived by the British Oceanographic Data Centre (BODC, www.bodc.ac.uk). Sea surface temperature was measured at 10 m depth. Contour plots of temperature and chlorophyll *a* concentration in the upper 300 m were prepared in Ocean Data View 4 (Schlitzer, 2015). This depth range represents the zooplankton tow depth as well as the depth range of most pteropod and heteropod species. We examined whether species richness *R* showed a relationship with sea surface temperature and maximum chlorophyll *a* in the upper 300 m using regression analysis in the software package PAST 2.17 (Hammer et al., 2001).

We calculated the pteropod biomass in terms of total dry weight from the abundances and shell sizes using mostly genus-specific formulae from Bednaršek et al. (2012a). The formulae are presented in Supplementary Table 1. These were only available for euthecosomes and gymnosomes, so we did not include shelled pseudothecosomes (*Peracle* species) and heteropods in our calculations. These formulae use estimated averages of shell length and width. Because some suggested size averages clearly overesti-

mated the observed sizes along AMT24, we adjusted them to represent the collected specimens along AMT24 (Supplementary Table 1). We did this for *Clio cuspidata*, *C. pyramidata*, *C. pyramidata antarctica*, *C. pyramidata sulcata*, *Cuvierina* sp., *Styliola subula*, *Hyaloclylis striata* and gymnosomes. Average sizes of *Clio recurva*, *Cavolinia gibbosa* and *Diacavolinia* were not indicated by Bednaršek et al. (2012a), so we used our own size estimates as well as their genus-level formulae to estimate their dry weight (using the *Cavolinia* formula for *Diacavolinia*). We used the formula for *Limacina helicina* (Bednaršek et al., 2012b) for all coiled euthecosomes. Bednaršek et al. (2012b) estimated that ~27% of the total carbon of *L. helicina antarctica* consisted of inorganic carbon.

2.3. Species composition

For subsequent analyses of inter-station similarities of species composition, sampling completeness and relative species dominance, we reduced our abundance dataset to exclude small sample sizes as follows. We excluded all stations with fewer than 10 thecosomes or heteropods, all larval and juvenile specimens that could be assigned to two or more species, and all identified species that only occurred at one selected station. The stations that were excluded from analyses of thecosome species composition were 1–4 and 31 because there were fewer than 10 specimens that could be identified to species or genus level. The thecosome species or genera that were excluded because they were observed at only one station were *Cavolinia gibbosa*, *Clio recurva*, *Diacria major*, *Gleba* and *Corolla*. *Cuvierina* juveniles and adults were binned into a single genus-level group because upon exclusion of the juveniles there would not be enough specimens (one adult: *Cuvierina atlantica*). For heteropods, we excluded stations 1–5, 12, 22, 24–26 and 30–31; also *Atlanta oligogyra* was excluded.

To examine whether the distributions of distinct species assemblages correspond with the distribution of Longhurst's (1998) biogeochemical provinces as defined by biogeochemistry and ecosystem dynamics, we quantified and visualized inter-station similarities of species composition and identified key species. For inter-station comparisons we performed a hierarchical cluster analysis, similarity profile analysis (SIMPROF), and non-metric multidimensional scaling analysis (nMDS) in PRIMER 6, without *a priori* assumptions (Clarke, 1993; Clarke and Warwick, 2001; Clarke and Gorley, 2006). To perform cluster analysis, SIMPROF and nMDS, we standardized and transformed ($\log(x + 1)$) the abundance data and then calculated a Bray-Curtis similarity matrix. For the cluster analysis we used the group average setting. The significance of the clusters was tested with SIMPROF analyses using 1000 permutations and a significance level of $p < 0.05$. The nMDS ordinations were performed with 25 restarts. Furthermore, we created rank abundance curves based on the thecosome species abundances at each station in order to assess patterns of dominance across ocean biomes.

To assess sampling completeness, we created sample-based as well as individual-based rarefaction curves for thecosomes and heteropods in Primer 6 (Clarke and Gorley, 2006) and PAST 2.17 (Hammer et al., 2001). The sample-based curves were based on the Jackknife 2 index (Gotelli and Colwell, 2010) and only included non-transitional stations that belong to distinct biogeochemical provinces.

3. Results

3.1. Species abundance, biomass and diversity

We counted and identified a total of 7312 pteropods across all stations on the transect, traversing the northern temperate zone,

the eastern side of the northern subtropical gyre, the equatorial upwelling zone, the southern subtropical gyre, the southern subtropical convergence and the northernmost part of the subantarctic (Fig. 1A; Table 1). Among the pteropod specimens, there were 1028 uncoiled and 5980 coiled euthecosomes, 230 pseudothecosomes and 74 gymnosomes. Pteropod abundances were low (<15 ind./1000 m^3) north of 40°N and they were absent from station 3. Their abundance varied between 100 and 2000 ind./1000 m^3 between 30°N and 40°S. Abundances were highest at stations 27–29, just south of 40°S, with a maximum abundance of >4000 ind./1000 m^3 at station 28 (Figs. 1B, C and 2A; Supplementary Table 2). Coiled euthecosomes were particularly abundant in this high productivity area, while pseudothecosomes were more abundant in the subtropical gyres.

Gymnosomes feed almost exclusively on thecosomes. The ratio between gymnosomes, if present, and thecosomes (euthecosomes and pseudothecosomes) ranged from 0.005 to 0.019 in (sub)tropical waters between ~28°N and ~28°S (stations 7–23) (Supplementary Table 3). Gymnosomes were always present between ~32 and ~45°S (stations 24–30), with ratios between 0.012 and 0.091, suggesting higher potential predation intensity by gymnosomes on thecosomes at these southern stations than in (sub)tropical waters.

We observed taxa with strong preferences for particular oceanographic provinces, in particular among euthecosomes and pseudothecosomes (Fig. 1C–E). In the equatorial province and in the subantarctic, the thecosome community consisted of one or two dominant species, and especially in the equatorial region a number of additional species occurred in low abundance. The relative species abundances were more equal in the subtropical gyres (Supplementary Fig. 1; abundances per species per station are listed in Supplementary Table 2). Uncoiled euthecosomes were found between 46°N and 43°S (Fig. 1D). Two *Clio* taxa, *C. pyramidata sulcata* and *C. pyramidata antarctica*, were restricted to the subantarctic, but were never dominant. *Clio pyramidata pyramidata/lanceolata* was found in all other regions along the transect. Key species that were most abundant in the subtropical gyres included *Creseis clava*, *Diacria danae* and *Styliola subula*, the latter of which was entirely absent in the equatorial upwelling region. Although *Cavolinia inflexa* was present across warm water environments, this species only occurred in high abundances in the southern gyre. *Creseis virgula* was found in the equatorial region and occurred nowhere else along the transect (Supplementary Table 2). Coiled euthecosomes were found between 35°N and 46°S (Fig. 1E). *Heliconoides inflatus* was abundant along the entire transect and did not show a clear preference for particular provinces. However, *H. inflatus* specimens in the subantarctic region were morphologically distinct from warm water *H. inflatus* specimens. Shells of the cold water form (listed as *H. inflatus* S herein) appeared to be coarser and thicker and, in contrast to the warm water form, they had a reddish hue along the whorls and aperture. *Limacina helicina antarctica* was dominant in subantarctic waters. *Limacina bulimoides* had a strong preference for the subtropical gyres, although it was also present in low numbers in the equatorial region. *Limacina lesueurii* was present throughout the warm water regions and *L. trochiformis* was only found in the southern gyre, though never in high numbers (maximum $N = 9$ at St. 20; Fig. 1E). Most *Peracle* pseudothecosome species demonstrated a strong preference for the subtropical gyres (Fig. 1C), but the large, soft-bodied genera *Corolla* and *Gleba* were only found in cooler waters north of 40°N and south of 40°S in very low numbers (never more than $N = 2$ per station).

Areas with high chlorophyll *a* concentrations had the highest estimated pteropod biomass, except the northern temperate zone, where hardly any pteropods were captured (Fig. 2B; Supplementary Table 4). A total biomass of more than 3.1 mg m^{-3} in the upper ~300 m was reached in the southern subantarctic region, mainly

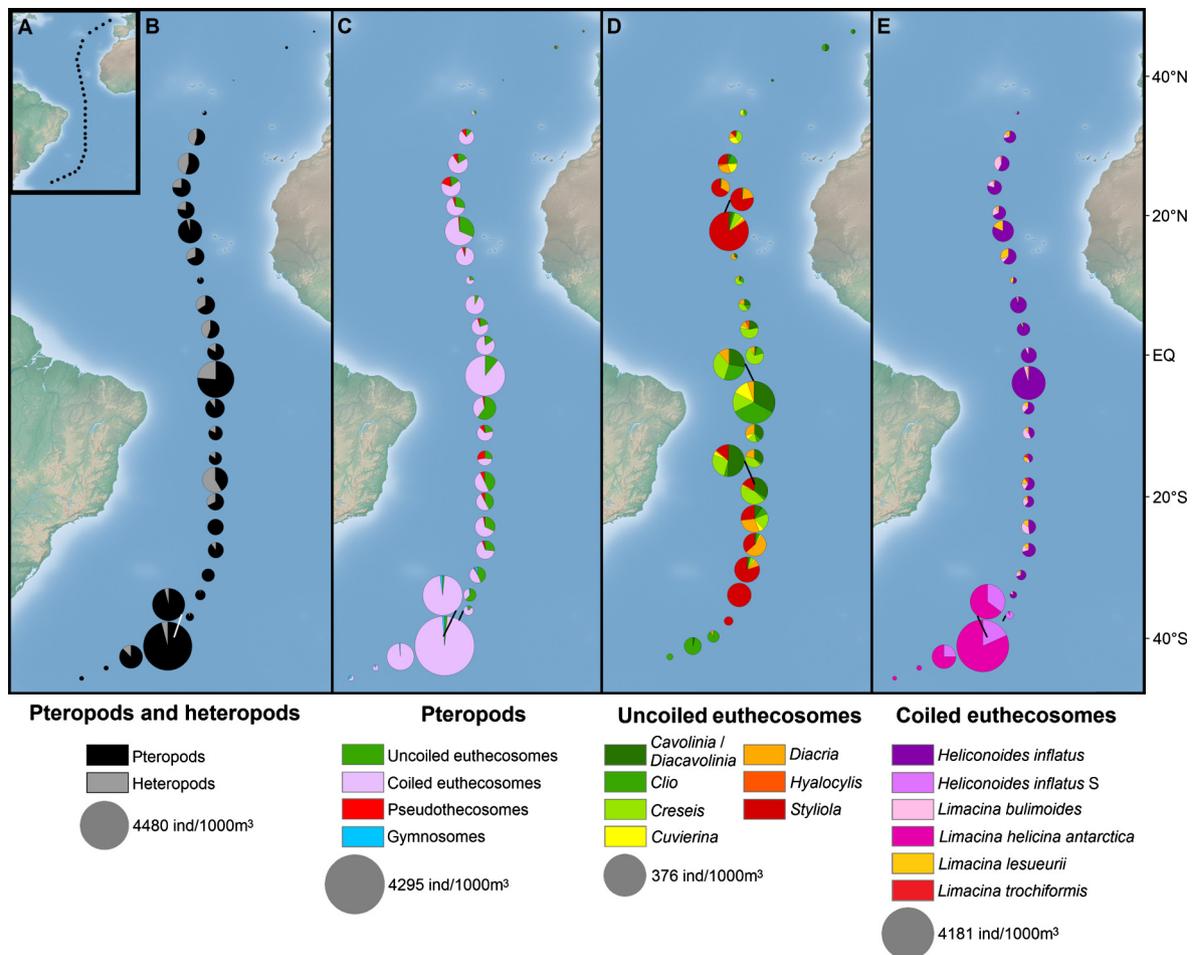


Fig. 1. (A) Overview of pteropod and heteropod sampling locations along Atlantic Meridional Transect 24. (B–E) Distribution of (B) pteropods and heteropods, (C) eutecosome, pseudothecosome and gymnosome pteropods, (D) genera of uncoiled eutecosomes and (E) species of coiled eutecosomes along Atlantic Meridional Transect 24. The size of the pie charts is scaled according to the total abundance of the examined groups (size of the maximum abundance is shown in legend for each plot). True sampling locations are indicated with a white (B) or black (C–E) line if pie sizes did not allow placement at true locations.

caused by high abundances of *Limacina helicina antarctica* and *Heliconoides inflatus S.* Just south of the equator there was an estimated biomass of more than 1.9 mg m⁻³ because of high abundances of *Cavolinia inflexa* and *Clio pyramidata*. The median and average pteropod biomass across all stations along AMT24 was 0.28 mg m⁻³ and 0.49 mg m⁻³, respectively.

The species richness of thecosomes was highest in the stratified (sub)tropical waters between ~30°N and ~30°S and was consistently high (11–13 species) in the southern gyre (Fig. 2C and D), a pattern that was also evident from the Shannon-Wiener's diversity indices H' per station (Supplementary Table 3). Uncoiled eutecosomes generally had a higher species richness than coiled eutecosomes and pseudothecosomes (Fig. 2C). Although most equatorial stations had slightly lower species richness than the gyre stations, the highest species richness (15 species) was observed close to the equator at station 14. Species richness showed a positive relationship with sea surface temperature ($R^2 = 0.55$; $N = 30$; $p < 0.001$; Fig. 3A) and a negative relationship with chlorophyll *a* concentration at the deep chlorophyll maximum ($R^2 = 0.57$; $N = 30$; $p < 0.001$; Fig. 3B). We note that sea surface temperature and chlorophyll *a* were only weakly correlated ($R^2 = 0.28$; $N = 31$; $p < 0.01$), and hence the degree of collinearity between these two explanatory variables was low. The species evenness J' was highest in the subtropical gyres, especially in the southern gyre (J' up to 0.84), when disregarding the high evenness values observed at the northern temperate stations 1, 2 and 5

because of their relatively low sample sizes. At equatorial stations 13–16 the evenness was lower (J' of 0.25–0.44) than in the gyres.

From the 1812 heteropods, a total of 1312 were atlantids, 325 were pterotracheids and 175 were carinariids. Heteropods were not found at stations 1–4 and 30–31. Highest heteropod species richness (up to 14 species) as well as abundances (maximum 704 ind./1000 m³) were found in the (sub)tropical waters between ~30°N and ~20°S (Fig. 4). A high abundance of heteropods (>100 ind./1000 m³) was also found in the subantarctic region (Supplementary Table 2). There were no clear patterns in species evenness along the transect except a lower evenness at stations 28–29 (J' of 0.10–0.37; Supplementary Table 3).

3.2. Species composition

The cluster and SIMPROF analyses of thecosome species composition of the different stations along AMT24 resulted in six significant clusters ($p < 0.05$; Fig. 5A). These results are further confirmed by the nMDS ordination, in which the six different clusters can be clearly recognized (Fig. 5B and C). The species composition in the subantarctic region (St. 26–30) demonstrated almost no overlap with species compositions in other regions. The other clusters consisted of the equatorial stations (St. 11–16), the northern and southern gyres together (St. 6–9 and 18–23), the northern gyre-equatorial transition (St. 10), the southern subtropical convergence (St. 25), and the northern temperate zone and southern gyre-

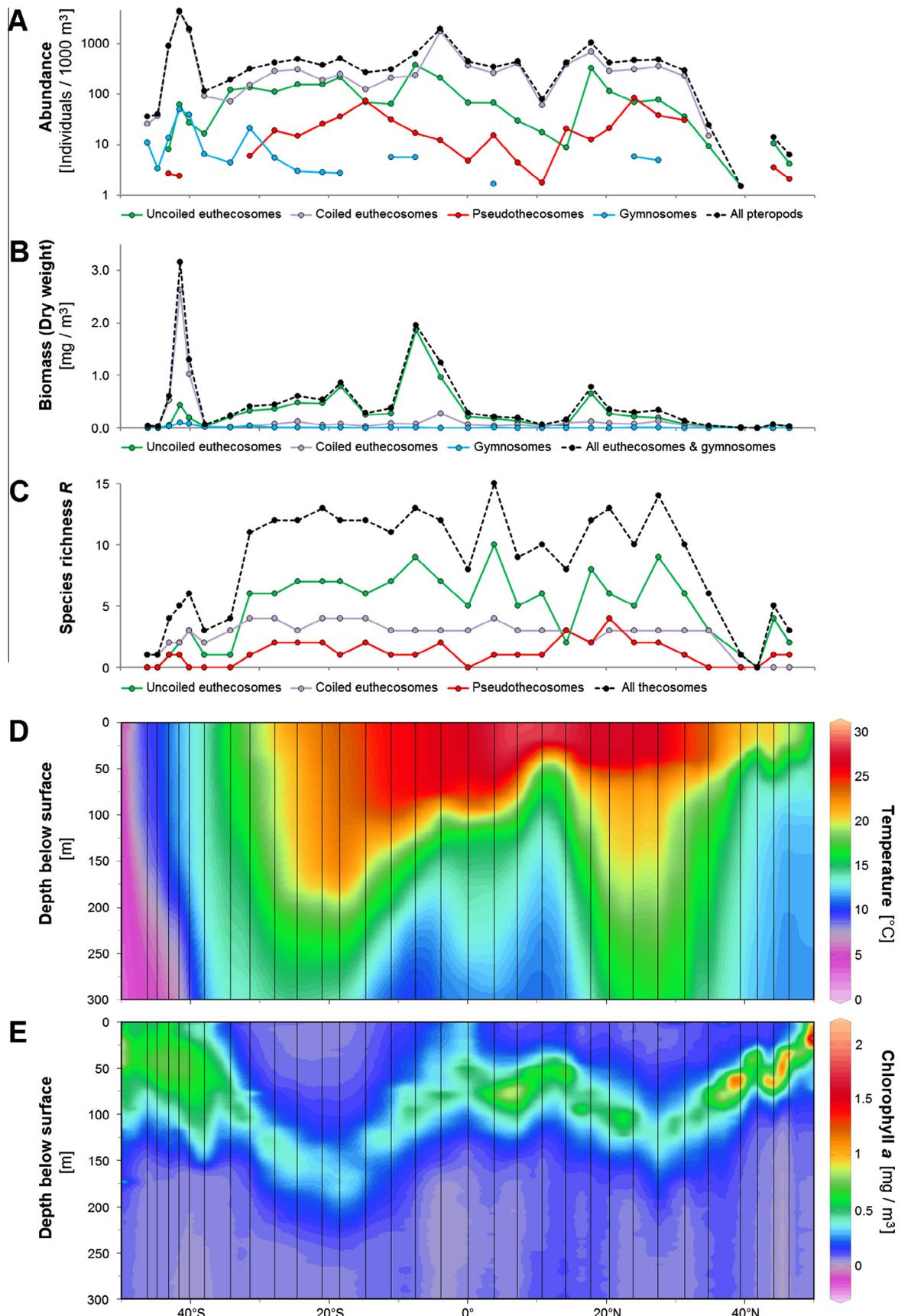


Fig. 2. Basin-scale patterns of (A) pteropod abundance (individuals/1000 m³), (B) pteropod biomass in terms of total dry weight (mg m⁻³), (C) pteropod species richness *R*, (D) seawater temperature and (E) chlorophyll *a* concentrations in the upper 300 m of the water column, measured during Atlantic Meridional Transect cruise 24. Lines in (A) are interrupted in case of zero abundances. Because gymnosomes were not identified to the species level, they were not included in the calculation of species richness *R* in (C).

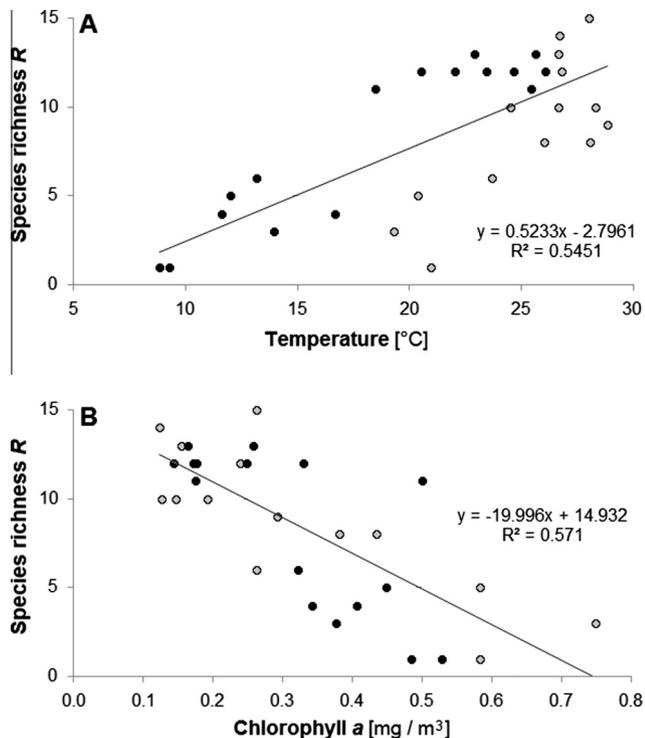


Fig. 3. Relationships of species richness R of thecosome pteropods (euthecosomes and pseudothecosomes) with (A) sea surface temperature and (B) maximum chlorophyll a concentration in the upper 300 m of the water column. Lines are based on linear regression. Grey and black dots represent locations north and south of the equator, respectively.

equatorial transition (St. 5 and 17) together. Because of the overlap between species compositions in the northern temperate and in the northern and southern gyre-equatorial transitions, the ordination of St. 5 and 17 may be an artefact of the gradual nature of the transitions between oceanographic provinces (Fig. 5). According to

the rarefaction curves of the equatorial, gyre and subantarctic stations, the major oceanographic provinces traversed during AMT24 were well-sampled for thecosomes (Supplementary Fig. 2A). Although transitions between oceanographic provinces were gradual, we were not able to thoroughly sample these areas at more than one location per transition (Supplementary Fig. 2B).

Heteropod species had a wider distribution than the subtropical gyres and equatorial regions: some of them also occurred in the subantarctic (Figs. 1B and 4). This was the case for an exclusively subantarctic and yet undescribed *Atlanta* morphotype, listed as *Atlanta* species A herein (Wall-Palmer et al., 2016b). In particular, the taxa that produce very large adults, the carinariids and pterotracheids, had patchy distributions, with high numbers at a few stations and no or a few specimens at the adjacent stations (Supplementary Table 2). It was therefore difficult to identify large-scale biogeographical distribution patterns among the heteropods. This patchy pattern was also reflected in rarefaction curves of heteropods, which were represented by fewer samples with at least 10 specimens compared to pteropods. Suboptimal sampling of the heteropods was demonstrated especially in the rarefaction curves representing the northern subtropical gyre and subantarctic stations (Supplementary Fig. 2C and D). We did not generate rarefaction curves for heteropods from northern and southern temperate stations because they contained too few (<6) specimens.

4. Discussion

4.1. General observations

We assessed pteropod and heteropod abundances, diversity and distributions in the Atlantic Ocean based on quantitative sampling along a basin-scale transect from 46°N to 46°S, crossing seven biogeochemical provinces. The AMT programme allowed us to combine zooplankton diversity and abundance data with ocean metadata from the same expedition, providing a rich oceanographic context to explain the observed patterns (e.g., Rees et al., 2015). Our results show that the species richness of both pteropods

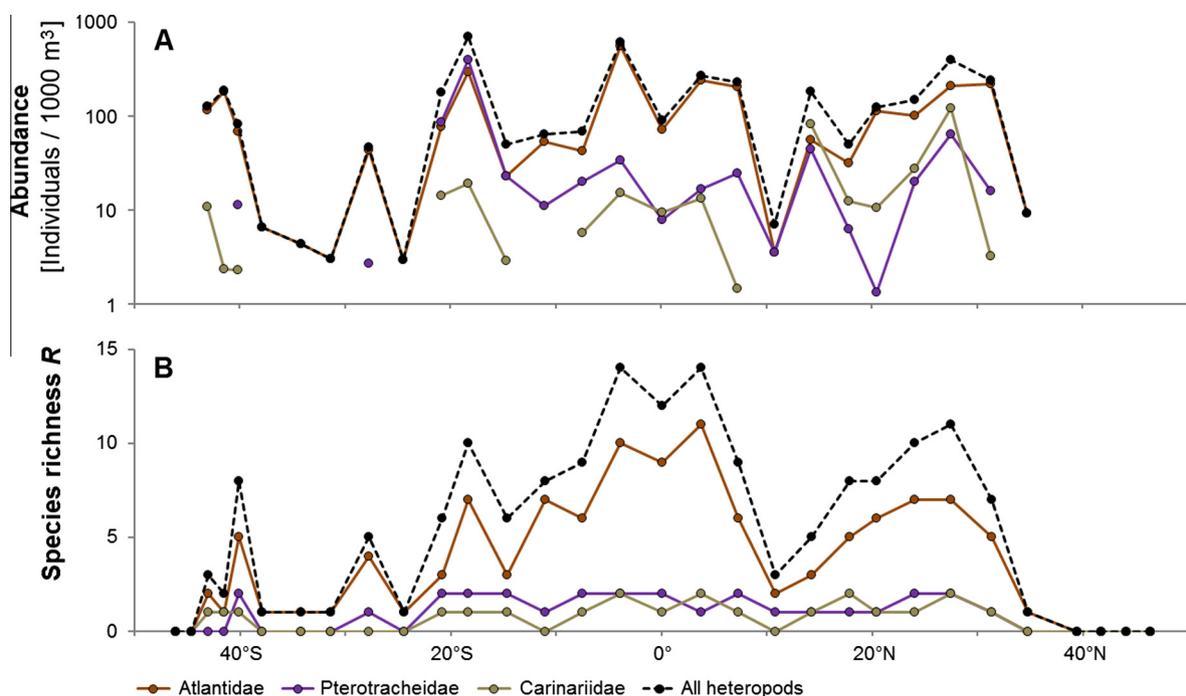


Fig. 4. Basin-scale patterns of (A) heteropod abundance (individuals/1000 m³), and (B) heteropod species richness R . Lines in (A) are interrupted in case of zero abundances.

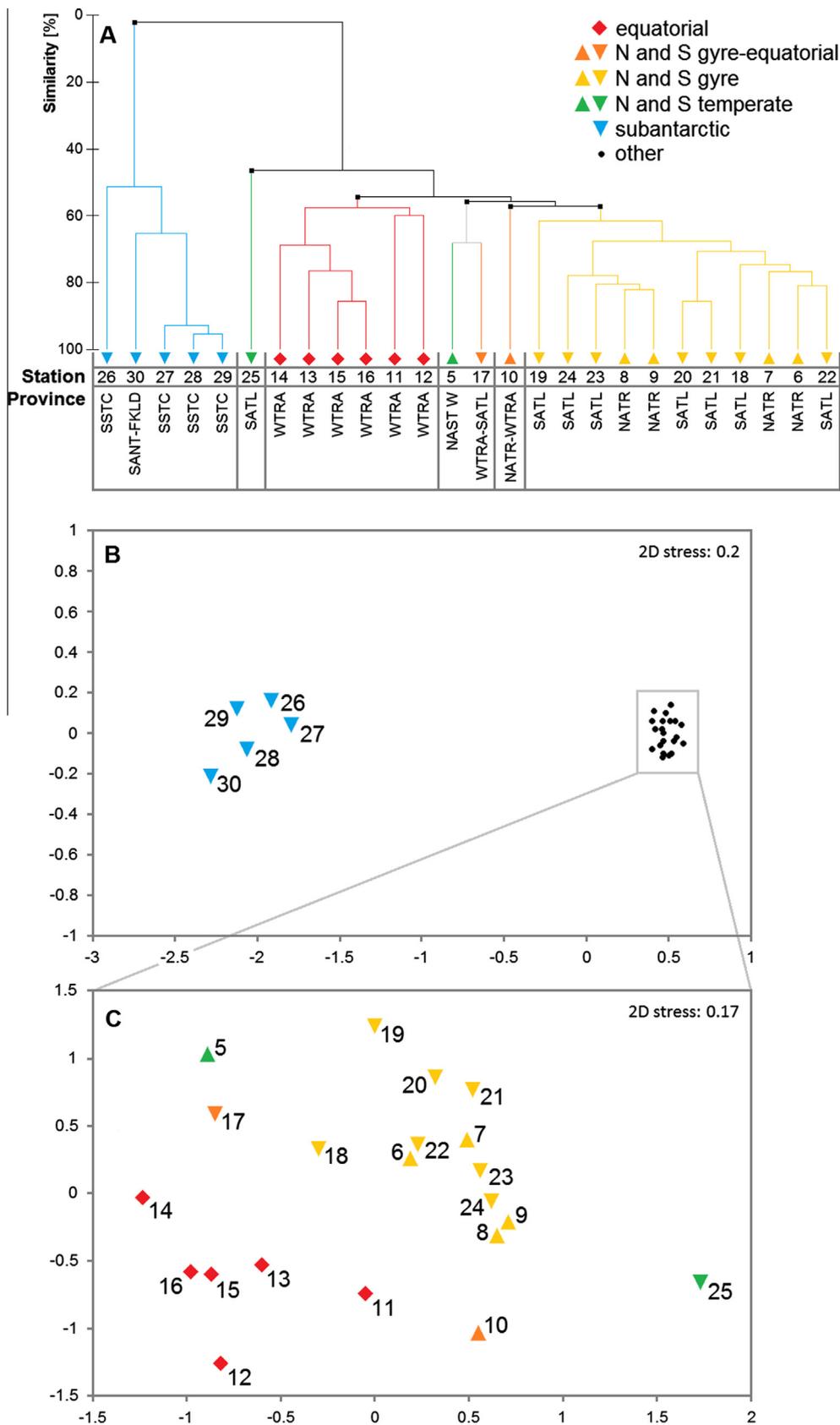


Fig. 5. (A) Hierarchical cluster analysis of the stations according to their community composition of theosoma pteropods (euthecosomes and pseudotheosomes). The analysis is based on all stations with at least 10 specimens, and resulted in the indicated six significant clusters (SIMPROF $p < 0.05$). (B and C) nMDS ordination based on the community composition of theosoma pteropods, (B) using all stations with at least 10 specimens, and (C) excluding the subantarctic stations 26–30. Symbols are colored according to their geographical location, with upward pyramids for the northern hemisphere, downward pyramids for the southern hemisphere and diamonds for equatorial locations. The Longhurst provinces (Longhurst, 1998; Reygondeau et al., 2013) of the sampling stations are indicated in (A): NAST E (Northeast Atlantic subtropical gyral), NAST W (Northwest Atlantic subtropical gyral), NATR (North Atlantic tropical gyral), WTRA (Western tropical Atlantic), SATL (South Atlantic gyral), SSTC (South subtropical convergence), SANT (Subantarctic water ring), FKLD (Southwest Atlantic shelves).

and heteropods was highest in the tropical and subtropical Atlantic. Pteropod abundance and biomass were highest just south of 40°S, and also reached high values near the equator (Figs. 1 and 2; Supplementary Tables 2 and 4). Some pteropod taxa showed strong preferences for particular oceanographic provinces, for example for warm equatorial waters (e.g. *Creseis virgula*), subtropical gyres (e.g. *Styliola subula*), or in and south of the southern subtropical convergence zone (e.g. *Limacina helicina antarctica*). Other species occurred across a broad range of provinces (e.g. *Heliconoides inflatus* and *Limacina lesueurii*; Supplementary Table 2). Most heteropods were restricted to warm waters, but some taxa also occurred in the subantarctic region.

We found no unexpected extremes in pteropod abundance along AMT24 (Fig. 2A) and the rarefaction curves flattened with an increasing number of samples or individuals (Supplementary Fig. 2A and B), indicating that the pteropods in this study have been representatively sampled. However, it is likely that our net aperture (0.71 m) and mesh size (200 μm) are responsible for highly variable heteropod species counts, diversities and abundances across stations, and quantitative sampling of these larger taxa requires nets with larger apertures and mesh sizes (McGowan and Fraundorf, 1966; Wells, 1973; Wall-Palmer et al., 2016a). Hence, we will focus most of our discussion on pteropods.

4.2. Distribution and abundance

The biogeographical distributions of pteropod assemblages inferred by cluster analysis were largely congruent with the distribution of Longhurst's (1998) biogeochemical provinces for the period from September to November (Fig. 5; Reygondeau et al., 2013). Our pteropod species distributions in the Atlantic Ocean also were comparable with those from the qualitative biogeographical synthesis of Bé and Gilmer (1977), however, there were some exceptions. According to Bé and Gilmer, *Limacina trochiformis* was most abundant in the equatorial province (WTRA). By contrast, we observed *L. trochiformis* only at station 14 (N = 3) in the equatorial province, but found much higher abundances throughout the south subtropical gyre. Exact localities upon which the distribution maps of Bé and Gilmer (1977) were based were not given, so we could not deduce if and where in the South Atlantic their samples were collected. We found a cold water variant of *Heliconoides inflatus* (*H. inflatus* S herein) in the subantarctic, but the distribution map from Bé and Gilmer (1977) most likely shows the broad equatorial and subtropical distribution of the warm water *H. inflatus* (listed as *Limacina inflata*) with a southern limit at ~40°S. The distribution of *Creseis virgula* was limited to the equatorial Atlantic in our study, but also occurred in the subtropical gyres according to Bé and Gilmer (1977). They also listed some species that were not found in our quantitative samples: the warm water species *Cavolinia tridentata* and the cold water species *Limacina retroversa*.

Because previous quantitative abundance data in provinces traversed by AMT24 are limited, our abundance data could only be compared to a few other pteropod studies. In October, St. 30 and 31 are within a transition zone between the Subantarctic water ring (SANT) and Southwest Atlantic shelves (FKLD) provinces (Reygondeau et al., 2013). Hunt et al. (2008) synthesized pteropod abundances in the Southern Ocean from tow data (1982–2006). In the mesozooplankton samples, they found low densities of *Limacina helicina antarctica* of only a few tens of ind./1000 m³ in October, both near the Antarctic Peninsula and south of Australia, which is comparable to the low densities of 25.3–36.5 ind./1000 m³ of *L. helicina antarctica* that we found at St. 30 and 31 (45–46°S) in October. Much higher population densities of this species were found in the mid austral summer (January–February), with 10³ to 10⁴ ind./1000 m³ at the Antarctic Peninsula and south of Australia, and even 10⁵ ind./1000 m³ near South Geor-

gia (Hunt et al., 2008). Bednaršek et al. (2012b) report similar seasonal dynamics from the Antarctic Peninsula to South Georgia, with higher numbers of *L. helicina antarctica* in the austral summer and autumn than in the spring. We did find high densities of *L. helicina antarctica*, exceeding 10³ to 10⁴ ind./1000 m³ in October, further up north at St. 27 and 28 (40–41°S), which may indicate that the growing season for this species started earlier at lower latitudes.

The total zooplankton abundance in the upper 200 m of the northeast Atlantic Ocean during July 1996 was characterized by Gallienne et al. (2001) by vertical hauls of 200 μm mesh size nets (aperture 0.57 m). They found low pteropod abundances of 0–75 ind./1000 m³ between 39 and 47°N, comparable to 0–24.2 ind./1000 m³ between 35 and 46°N in our study in late September/early October (St. 1–5). Gallienne et al. (2001) found higher summer abundances of 845–1730 ind./1000 m³ at 37°N, whereas in our study higher abundances were found south of 31°N in early fall, which may again reflect seasonal variation.

In the Caribbean Sea, not sampled in our study, the average species abundances in the 239 μm mesh size net (aperture 1.0 m) used by Wells (1973) near Barbados resemble our findings in equatorial St. 14. For *Creseis virgula*, Wells (1973) found 16.9 ind./1000 m³, which is highly comparable to the 18.4 ind./1000 m³ in our study. For *Heliconoides inflatus*, Wells (1973) found 257.3 ind./1000 m³ resembling the 239.8 ind./1000 m³ in our study. The major difference was the high abundance of *Creseis conica* in the Caribbean (188.2 ind./1000 m³) reported by Wells (1973; listed as *Creseis virgula conica*), whereas we found only 16.8 ind./1000 m³ at our St. 14.

4.3. Plankton biomass in the global ocean

Qualitatively, the pteropod biomass distribution along AMT24 showed a similar large-scale pattern as the biomass distributions of many other mesozooplankton groups, with high zooplankton biomass in arctic and subantarctic waters, elevated biomass in the equatorial regions, and lowest biomass within the gyres (Moriarty and O'Brien, 2013). Quantitatively, however, biomass data from sampling locations between 10 and 500 m deep in various parts of the Atlantic Ocean as synthesized by Bednaršek et al. (2012a) point at a higher pteropod biomass (dry weight) in the Atlantic Ocean than in the Indian and Pacific oceans. This was true for the equatorial Atlantic north of Brazil, the Mediterranean Sea, and the subantarctic near South Georgia. Our data appear to confirm this. Compared to the global median pteropod biomass of 0.058 mg m⁻³ (only non-zero global data) reported by Bednaršek et al. (2012a), we found a much higher pteropod biomass per m³ in the Atlantic Ocean (Fig. 2B; median of 0.28 mg m⁻³).

4.4. Latitudinal trends in species richness

The dominant paradigm for latitudinal diversity patterns in pelagic systems is a bimodal pattern of species richness, with maxima in the gyres, slightly lower richness in the equatorial province, and a sharp decrease of diversity towards the temperate and polar zones (e.g. Hillebrand, 2004a). Our pteropod data broadly support this pattern, and with the exception of one equatorial station, diversity at most stations in the equatorial province was slightly lower than in the gyres (Fig. 2C). Many hypotheses have been formulated for advancing the ecological, biogeographic, and evolutionary understanding of the latitudinal diversity gradient, and for explaining why the gradient in the pelagic ocean differs from a steady increase of diversity towards the equator, the most widely recognized pattern in benthic and terrestrial environments (e.g. Angel, 1997; Gaston, 2000; Willig et al., 2003; Hillebrand, 2004a, b; Brayard et al., 2005). Examples of such conceptual models are

the evolutionary speed hypothesis and geometric constraints hypothesis (Willig et al., 2003).

Several pelagic groups show latitudinal trends in species richness similar to pteropods, with the highest richness in the subtropical gyres. Such a pattern was reported for hydromedusans (Macpherson, 2002), euphausiids (Angel, 1997; Tittensor et al., 2010), pelagic decapods (Angel, 1997), ostracods (Angel, 1997; Angel et al., 2007), fish (Angel, 1997), foraminifera (Rutherford et al., 1999; Tittensor et al., 2010), and tintinnid ciliates (Dolan and Pierce, 2013). Several other pelagic taxa do not show a bimodal pattern with maximum species richness in the subtropical gyres, but display a diversity peak in the equatorial region or a diversity plateau across subtropical and tropical latitudes. Examples of equatorial maxima are found for salps (Macpherson, 2002) and hyperiid amphipods (Burridge et al., 2016), and our data indicate that heteropods also show maximum species richness in equatorial waters. A wider diversity plateau across the tropics and subtropics was found for copepods (Woodd-Walker et al., 2002; Rombouts et al., 2009), siphonophore hydrozoans and cephalopods (Macpherson, 2002). Larvacean species diversity only had a clear peak in the northern gyre (Macpherson, 2002), and chaetognaths only demonstrated a peak in the southern gyre (Macpherson, 2002) with a distinct decrease in species diversity towards cold North Atlantic waters (42–59°N; Pierrot-Bults, 2008). However, the reported species diversities in the latter two groups were lower (maxima of up to ~50 and ~40 species, respectively) than for hydromedusans or crustaceans. Species diversities registered for pteropods were also comparatively low. Accurate estimates of pteropod species diversities may require more rigorous sampling efforts and more accurate assessments of species boundaries. Our anomaly of high diversity at equatorial station 14 was largely caused by the occurrence of pteropod taxa that are generally known to appear in low abundances and that were only sporadically collected along AMT24, e.g. *Diacavolinia* sp. and *Hyalocylis striata*. Repeated transect studies may compensate for such anomalies. Overall, the latitudinal diversity gradient varies among zooplankton groups, and appears to result from a complex interplay among ecological factors, highly diverse life history strategies and roles in the marine food web, as well as different evolutionary histories.

5. Conclusions

To our knowledge, this is the most comprehensive study of the diversity and abundance of planktonic gastropods across the Atlantic Ocean to date. We found close correspondence between our pteropod assemblages and Longhurst's (1998) biogeochemical provinces. On average, our results point to a substantially higher pteropod biomass in the Atlantic Ocean than in the Indian and Pacific oceans. The dominant paradigm of a bimodal pattern of species richness in pelagic systems, with maxima in the subtropical gyres, was broadly supported by our pteropod data. Our study provides only a snapshot in time, however. Thorough repeated sampling will be essential for examining large-scale, long-term trends in the diversity and abundance of planktonic gastropods, quantifying future changes, and predicting species-specific sensitivities to ocean changes.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.pocean.2016.10.001>.

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