Diversity and distribution of hyperiid amphipods along a latitudinal transect in the Atlantic Ocean

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A B S T R A C T

As commensals and parasitoids of gelatinous plankton, hyperiid amphipods play unique and important ecological roles in pelagic food webs. Because the diversity and biogeography of this group in oceanic waters is poorly known, we examined diversity and distribution patterns of hyperiids along a basin-scale meridional transect in the Atlantic Ocean (Atlantic Meridional Transect cruise 22). Hyperiids were collected from epipelagic and upper mesopelagic depths at 27 stations between 39°N and 45°S. A total of 70 species in 36 genera and 17 families were identified, the majority of which belonged to the epipelagic Physocephalata infraorder. We observed maximum species and genus richness in the equatorial upwelling region (up to 35 species, 27 genera per station; 7°N–8°S), which appeared largely driven by increased diversity in the superfamily Platysceloidea, as well as a significant and positive relationship between species richness and sea surface temperature. Cluster analyses of hyperiid species assemblages along the transect broadly supported a division into gyral, equatorial, transitional, and subantarctic assemblages, congruent with Longhurst's biogeochemical provinces. Steepest transitions in hyperiid species composition occurred at the southern subtropical convergence zone (34–38°S). The majority of zooplankton groups show maximal diversity in subtropical waters, and our observations of equatorial maxima in species and genus richness for hyperiids suggest that the mechanisms controlling diversity in this group are distinct from other zooplanktonic taxa. These patterns may be driven by the distribution and diversity of gelatinous hosts for hyperiids, which remain poorly characterized at ocean basin scales. The data reported here provide new distributional records for epipelagic and upper mesopelagic hyperiids across six major oceanic provinces in the Atlantic Ocean.

1. Introduction

The amphipod suborder Hyperiidea is an exclusively pelagic marine group, distributed from the sea surface to abyssopelagic depths worldwide. With 292 species currently described and accepted in the World Register of Marine Species (WoRMS: http://www.marinespecies.org), this peracarid crustacean group is a diverse component of the marine zooplankton. The majority of hyperiid species are commensals and parasitoids of gelatinous zooplankton (e.g., Harbison et al., 1977; Madin and Harbison, 1977; Laval, 1980), with tunicates, medusae, ctenophores, and siphonophores serving as primary hosts and additional associations reported for heteropod and pteropod molluscs and radiolarians (e.g., Harbison et al., 1977; Phleger et al., 1999; Gasca and Haddock, 2004). Characterization of host-parasite relationships is an active area of research (e.g., Gasca et al., 2015; Riascos et al., 2015), and some hyperiid genera and families appear to be restricted to particular host groups while others are less selective (e.g., Harbison et al., 1977; Madin and Harbison, 1977; Laval, 1980; Lavaniegos and Ohman, 1999). The association of the hyperiid with its host may encompass the entire life history or may be restricted to particular life stages of the amphipod. A small number of hyperiid amphipods, primarily in polar environments, are free-living, and they are often biomass dominants and important prey for seabirds (Bocher et al., 2001; Waluda et al., 2010), squids (Laptikhovsky, 2002), and fishes (Shreeve et al., 2009) in these ecosystems. Predatory fishes in other ecosystems also prey on commensal hyperiids, and they can make up a large fraction of their diets (Suntsov and Brodeur, 2008; Riascos et al., 2012; Choy et al., 2013). Hyperiids are routinely sampled in net-based oceanographic sampling programs, but their gelatinous hosts are largely destroyed by conventional sampling and preservation methods.

As a result, Remotely Operated Vehicle (ROV) and scuba-based live observations of host-parasite associations derive largely from coastal areas (e.g., Monterey Bay, Gulf of California, Mediterranean Sea), while hyperiid diversity and distributions are known from a broader range of ocean ecosystems (e.g., Vinogradov et al., 1996; Zeidler and De Broyer, 2009).

Hyperiids are classified into two infraorders, the primarily bathypelagic and mesopelagic Physosomata and the epipelagic and mesopelagic Physocephalata (Vinogradov et al., 1996). The majority of hyperiid diversity is contained within the Physocephalata, with approximately 65% of extant species within the 20 families of this infraorder. Particularly diverse hyperiid families include the Scinidae (Physosomata; 45 species) and the Hyperiidae (Physocephalata; 29 species, WoRMS, 2016). Early workers recognized that many morphological features of hyperiids, such as mouthpart deformation (Dittrich, 1988), are correlated with their parasitoid association with gelatinous hosts, and may result from convergent evolution, with the suborder Hyperiidea then viewed as probably polyphyletic in origin (Pirlot, 1932; Vinogradov et al., 1996). Other morphological features, such as hypertrophied olfactory and visual systems, duplications of the eyes and an array of modifications to the appendages also likely derive from their pelagic life style (Harbison et al., 1977; Laval, 1980; Hurt et al., 2013; Baldwin Fergus et al., 2015). Recent molecular phylogenetic studies of the Hyperiidea have supported monophyly of the infraorders as well as reciprocal monophyly of superfamilies Platysceloidea, Vibilioidea, and Phronimoidea within the Physocephalata, but also suggested novel placements for some groups (e.g., Paraphronimidae and Cystisomatidae; Browne et al., 2007; Hurt et al., 2013).

Our knowledge of the biogeography of hyperiids is limited, and most prior studies that report on the diversity of hyperiid assemblages in the Atlantic Ocean focus on particular ocean regions, often reporting species lists (e.g., Gasca, 2003, 2004, 2007). Characterizations of basin-scale patterns in the diversity and distribution of this group are rare (but *see* Tarling et al., 1995, southwest temperate Atlantic). Given the host-parasitoid relationship present for most hyperiid species, the large-scale patterns of hyperiid abundance and distribution are likely driven by gelatinous host abundance and diversity, as has been documented at the mesoscale in other ocean regions (e.g., Lavaniegos and Ohman, 1999; Lavaniegos and Hereu, 2009; Valencia et al., 2013). In other zooplankton groups, latitudinal diversity gradients often include subtropical maxima in diversity (species richness), with slightly lower diversity at equatorial latitudes, and dramatic declines poleward of the subtropical convergence zone (e.g., Reid et al., 1978; McGowan and Walker, 1993; Boltovskoy, 1998; Rutherford et al., 1999; Rombouts et al., 2009). A broad warm water plateau of species richness, across both subtropical and tropical waters, is another common latitudinal pattern observed in pelagic groups (e.g., Macpherson, 2002; Burridge et al., 2017). Characterizing these broad-scale diversity gradients for different pelagic groups is important if we are to better understand the drivers of and controls on pelagic diversity (Macpherson, 2002; Beaugrand et al., 2013).

In this study, we report on the diversity and distribution of hyperiid amphipods across a continuous meridional transect in the Atlantic Ocean (39°N to 45°S) in order to assess large-scale biogeographic patterns and latitudinal diversity gradients for this group. The multidisciplinary Atlantic Meridional Transect programme (www.amt-uk.org, e.g., Rees et al., 2015) provided an ideal platform to sample hyperiid amphipods across a range of open ocean ecosystems (>12,000 km transect), and to examine distribution patterns within a rich oceanographic context. Our goals were to: (1) characterize the hyperiid species occurring in the epipelagic and upper mesopelagic zone across boreal to equatorial ocean provinces in the Atlantic Ocean, (2) test for the co-occurrence of species and identify recurring hyperiid assemblages within Atlantic ocean provinces, and (3) examine whether significant changes in species composition (biogeographical boundaries) are congruent with oceanographic gradients (temperature, salinity, chlorophyll *a*) and/or Longhurst's (1998) biogeochemical ocean provinces.

2. Methods

2.1. Sampling and identification

Bulk plankton samples were collected at 27 stations along Atlantic Meridional Transect Cruise 22 (AMT22) between October 16 and November 19, 2012 (Table 1; Fig. 1A). Oblique tows were conducted with paired bongo (200 μm, 333 μm mesh) and Rectangular Midwater Trawl (RMT1, 333 μm mesh) plankton nets in the epipelagic and upper mesopelagic zone during night time at all stations except St. 42. Bongo tows were conducted on average between 319 m and the sea surface (range 150–488 m), while RMT tows were conducted over a shallower depth range (average maximum depth 152 m, range 62–216 m; Table 1). A LAT tag 1100 time-depth-recorder (LOTEK Wireless) was attached to the net frame to record the maximum depth of the tow. Tow durations averaged 50 min (range 38–90 min). Bulk samples were well-mixed and preserved in multiple jars. All hyperiid material examined in this study derived from the 333 μm nets (Bongo and RMT1) and was fixed in ethyl alcohol. Depending on the size of the total plankton sample, approximate fractions were examined for hyperiids, ranging from the entire original sample in oligotrophic waters, to 1/10 of the sample in very high biomass and low diversity regions (e.g., stations 64–74; see Table 1). Our approach was non-quantitative, and we therefore have focused our analyses primarily on species presence-absence, as well as on large-scale trends in diversity and species distributions. All hyperiids were counted and removed from the examined sample fraction. Hyperiids were identified based on the taxonomic keys of Bowman (1973), Bowman and Gruner (1973), Shih (1991), Vinogradov et al. (1996), and Zeidler (1999, 2003a,b, 2004a,b, 2006, 2009, 2012a,b, 2015). Representatives of all species were imaged using a Zeiss automated stacking light microscope. Voucher specimens were deposited in the Crustacea collection of Naturalis Biodiversity Center, Leiden, The Netherlands.

Conductivity-temperature-depth (CTD) casts in the upper 500 m of the water column were conducted at similar locations as the plankton tows. All plankton stations were matched to CTD casts based on geographic proximity. Seawater temperature and chlorophyll *a* concentration data were obtained using a Sea-Bird Electronics 3P Temperature Sensor and Chelsea MKIII Aquatracka Fluorometer, with data calibrated and archived by the British Oceanographic Data Centre (BODC: http://www.bodc.ac.uk).

2.2. Diversity and species assemblages

The species richness R and genus richness D for each station were used to summarize the diversity of hyperiid amphipods along the transect. We excluded juveniles of *Scina* sp. from the calculation of species richness because these specimens could not be confidently assigned. Lycaeidae sp. 1 was excluded from the calculation of genus diversity because this undescribed species shared morphological features of *Lycaea* as well as *Simorhynchotus* (Table S1). To gain insight into the underlying causes of the latitudinal trends in species richness, we tested for relationships between species diversity and environmental data by linear regression with species richness R as the dependent variable and sea surface temperature, chlorophyll *a* concentration at the deep chlorophyll maximum (DCM), or the integrated chlorophyll *a* concentration in the upper 300 m of the water column as independent

Table 1

Collection information for all samples included in this study from Atlantic Meridional Transect 22. Samples indicated with an asterisk (∗) by the Sample ID had sample sizes smaller than 30 specimens and were not included in statistical analyses. Oceanic provinces by Longhurst (1998) are given as 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).

AMT22 station	Sampling date	Latitude	Longitude	Net	Start tow	Max. depth [m]	Part of sample analyzed	Longhurst province
9∗	2012-10-16	39°39′N	22°28′W	RMT1	3:23	174	1	NAST E
11∗	2012-10-17	36°40′N	24°27′W	Bongo	3:17	306	1	NAST E
13	2012-10-18	34°21′N	27°38′W	RMT1	3:14	143	1/3	NAST W
17	2012-10-20	29°48′N	33°35′W	RMT1	2:45	195	1/3	NAST W
27	2012-10-25	17°42′N	36°27′W	Bongo	2:41	318	1/3	NATR
29	2012-10-26	15°18′N	34°40′W	RMT1	0:00	152	1	NATR
31	2012-10-27	12°14′N	32°23′W	Bongo	2:40	302	1/5	NATR
35	2012-10-29	6°37′N	28°19′W	Bongo	2:44	404	1	WTRA
37	2012-10-30	4°16′N	26°37′W	RMT1	0:01	216	1/2	WTRA
39	2012-10-31	1°08′N	25°00′W	Bongo	2:40	339	1	WTRA
42	2012-11-01	2°55′S	25°01′W	RMT1	11:54	161	1	WTRA
43	2012-11-01	4°55′S	25°01′W	Bongo	23:54	150	1	WTRA
45	2012-11-03	8°05′S	25°02′W	Bongo	2:42	488	1/2	WTRA
47	2012-11-03	11°18′S	25°03′W	RMT1	23:57	166	1	SATL
51	2012-11-06	18°30′S	25°06′W	Bongo	2:42	373	1	SATL
53	2012-11-08	20°06′S	24°31′W	Bongo	2:24	330	1	SATL
55	2012-11-09	22°57′S	25°00′W	Bongo	2:25	305	1	SATL
57	2012-11-09	25°29′S	25°00′W	RMT1	23:53	153	2/3	SATL
58	2012-11-11	28°22′S	25°28′W	RMT1	1:43	62	3/4	SATL
60	2012-11-12	30°01′S	27°43′W	RMT1	0:00	128	1	SATL
62	2012-11-14	34°07′S	33°30′W	Bongo	2:39	376	1	SATL-SSTC
64	2012-11-14	35°52′S	36°00′W	RMT1	23:53	132	3/16	SATL-SSTC
66	2012-11-16	38°05′S	39°19′W	Bongo	2:43	292	3/8	SSTC
68	2012-11-16	39°53′S	42°03′W	RMT1	23:57	146	3/8	SSTC
70	2012-11-18	42°08′S	45°36′W	Bongo	1:46	309	1/8	SSTC
72	2012-11-19	43°56′S	48°32′W	Bongo	1:45	281	1/10	SSTC
74	2012-11-19	45°30′S	51°21′W	Bongo	1:46	211	1/10	SANT-FKLD

variables using PAST 2.17 (Hammer et al., 2001). The sea surface temperature was represented by values sampled at 10 m depth in order to minimize missing data.

Comparisons of hyperiid assemblages across stations were conducted primarily with presence-absence based measures. We completed a second analysis incorporating species relative abundance, but only including stations for which the entire sample was examined (St. 29, 35, 39, 42, 43, 47, 53, 55, 60, 62). For all analyses, we reduced our dataset to exclude stations with small sample size (<30 specimens, stations 9 and 11). We also excluded the infraorder Physosomata because these species occur primarily at bathypelagic and mesopelagic depths (Vinogradov et al., 1996), and thus were inconsistently sampled in this study. We quantified inter-station similarities by means of hierarchical cluster analysis, similarity profile analysis (SIMPROF), and non-metric multidimensional scaling analysis (nMDS) in PRIMER 6 (Clarke, 1993; Clarke and Warwick, 2001; Clarke and Gorley, 2006). First, we used a Bray-Curtis similarity matrix derived from species presence-absence data including stations 13–74 and also, separately, for warm water stations 13–64. For the second analysis incorporating relative abundance, we used a Bray-Curtis similarity matrix based on standardized and transformed ($\log(x + 1)$) species counts. The hierarchical cluster analyses were performed using the group average setting. We performed SIMPROF analyses to test the significance of the clusters using 1000 permutations and a significance level of $p < 0.05$. The nMDS ordinations were performed with 25 restarts. We inferred rank abundance curves in order to identify patterns of species dominance across ocean provinces and reported the most common species at each site.

3. Results

3.1. Diversity

A total of 3645 hyperiid specimens were counted and identified to 70 species belonging to 17 families (Fig. 1A; Table S1). The most common species found along the AMT22 transect for each family are shown in Fig. 1B. Sixty-six of the species sampled belonged to the Physocephalata infraorder ($N = 3509$ specimens), while four species belonged to the Physosomata ($N = 136$, including *Scina* specimens not identified to species). In our samples, Physocephalata were represented by four of the five described superfamilies, 15 of the 20 described families and 34 of the 56 described genera. Of the four Physocephalata superfamilies sampled, Platysceloidea was the most diverse (6 families, 17 genera, 33 species), followed by Phronimoidea (6 families, 14 genera, 25 species). The least diverse superfamilies were Vibilioidea (2 families, 2 genera, 7 species) and Lycaeopsoidea (1 family, 1 genus, 1 species). The most abundant and diverse Physocephalata family was Lestrigonidae ($N = 903$; 8 species). The Physosomata infraorder was represented by two superfamilies, each represented by a single family (Lanceolidae, Scinidae) and genus (Tables 2 and S1).

Hyperiid diversity was high in warm waters, with species richness R ranging from 15 to 36 species and genus diversity D from 13 to 27 genera at stations between 34°N and 36°S (Fig. 2). Diversity peaked at stations located just north of the equator (4°N–15°N, St. 29, 31, 35, 37) with 29–36 species present in this region. In cooler waters south of 38°S (St. 66–74), hyperiid diversity declined to between 3 and 9 species (Fig. 2A; Table S1). A peak in species diversity associated with the equatorial upwelling region is apparent for Platysceloidea (Physocephalata), the most diverse superfamily in our data, with a maximum of 18 species present at station 35 (Fig. 2B; Table S1). Phronimoidea (Physocephalata), the second most diverse superfamily in our study, showed a different pattern with highest species diversity observed between 29°N and 11°S at stations 17–47 (11–15 species). Species richness for this superfamily was between 7 and 11 species in the central and southern parts of the southern gyre between 18°S and 36°S at stations 51–64 (Fig. 2B; Table S1). We found a significant and positive relationship between hyperiid species richness and sea surface temperature ($R^2 = 0.65$; $N = 27$; $p < 0.001$; Fig. 3). However, there was no significant relationship between species richness and
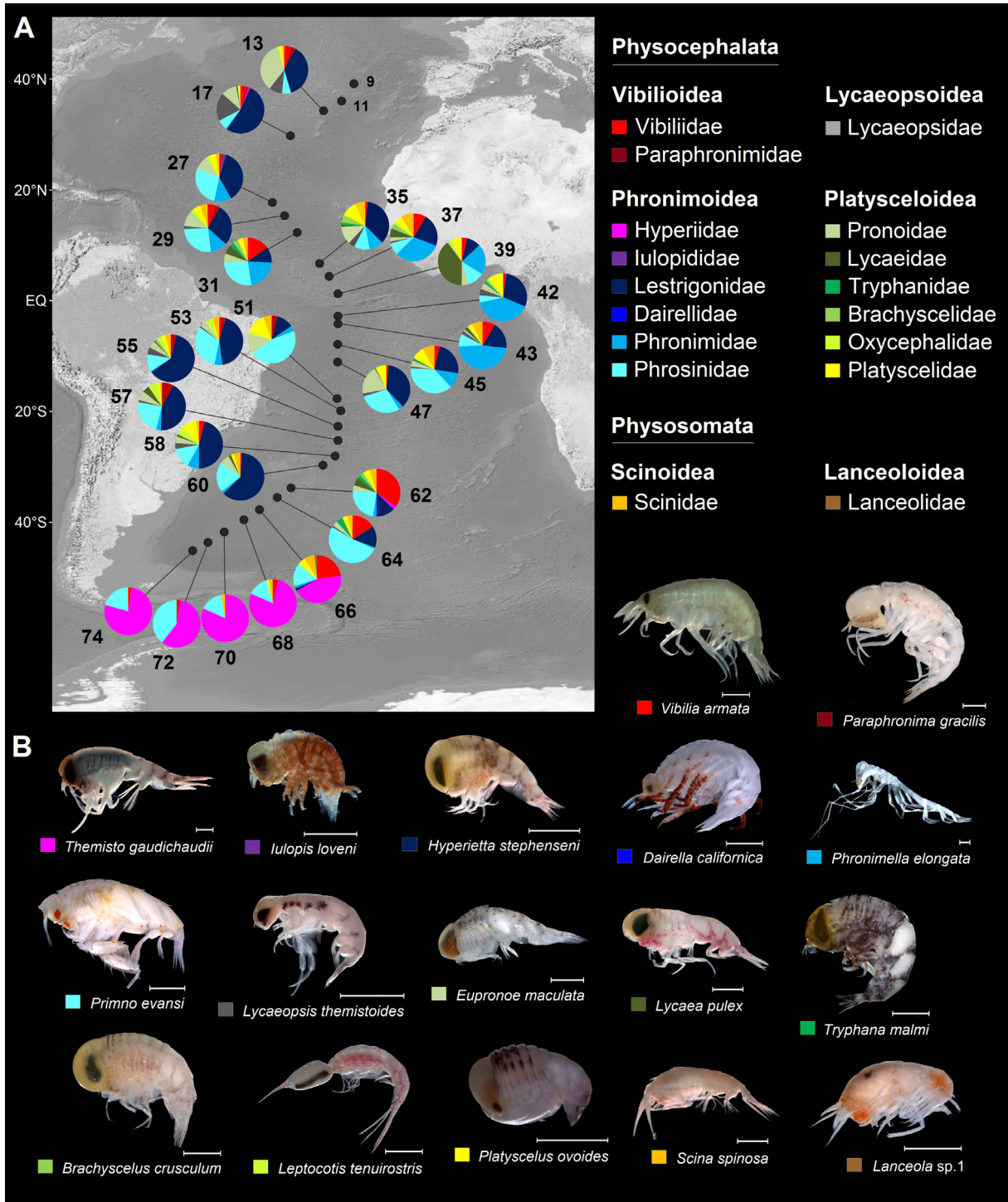
Fig. 1. Overview of hyperiid diversity observed in open waters of the Atlantic Ocean. (A) Distribution of hyperiid families along Atlantic Meridional Transect 22. Piecharts indicate relative abundances of families at each station >30 specimens. (B) Most commonly found representatives of the 18 families that were sampled along Atlantic Meridional Transect cruise 22. Legend colors are arranged by infraorder and superfamily of hyperiids (following the current taxonomy as presented in the World Register of Marine Species: http://www.marinespecies.org). All scale bars represent 1 mm.

maximum chlorophyll *a* concentration ($R^2 = 0.02$; $N = 27$; $p > 0.05$) or between species richness and integrated chlorophyll *a* in the upper 300 m ($R^2 = 0.14$; $N = 27$; $p > 0.05$).

We found two species that have previously been reported to occur only in the Pacific and Indian oceans: *Scina curilensis* and *Tullbergella cuspidata* (Table S1). We also found six morphologically distinct hyperiids that may represent undescribed species, and are treated as species herein. These were listed as *Lanceola* sp. 1, *Lestri-*

gonus sp. 1, *Brachyscelus* sp. 1, *Lycaea* sp. 1 and 2, and Lycaeidae sp. 1.

3.2. Distribution patterns

Some of the well-sampled hyperiid families were present in both warm and cold waters along the AMT22 transect (Phrosini-dae, Platyscelidae, Scinidae, Vibiliidae), while other families were

Table 2

Overview of relative abundances of hyperiid species across six Longhurst ocean provinces sampled on Atlantic Meridional Transect cruise 22 (AMT22). Species are listed by superfamily and family. Relative abundances report the percentage (%) of total specimens averaged within each oceanographic region. The first column per oceanographic region lists how common species are within that region: rare (R: <5.0% of total specimens averaged within that region); common (C: 5.0–<15.0%); or abundant (A: = or >15.0%). The number of stations in which the species was found in each province is noted within brackets.

(Super)family	Species	NAST W	%	NATR	%	WTRA	%	SATL	%	SATL-SSTC	%	SSTC, SANT-FKLD	%
		St. 13, 17		St. 27, 29, 31		St. 35, 37, 39, 42, 53, 45		St. 47, 51, 53, 55, 57, 58, 60		St. 62, 64		St. 66, 68, 70, 72, 74	
Lycaeopsoidea													
Lycaeopsidae	*Lycaeopsis themistoides*	Common (2)	13.7	Rare (1)	1.2	Rare (3)	2.6	Rare (5)	2.3	Rare (1)	0.5		
Phronimoidea													
Dairellidae	*Dairella californica*					Rare (1)	0.2			Rare (1)	0.5		
Hyperiidae	*Hyperoche medusarum*					Rare (1)	0.1						
	Hyperoche martinezii									Rare (1)	0.5		
	Laxohyperia vespuliformis	Rare (1)	0.4										
	Themisto gaudichaudii									Rare (1)	0.5	Abundant (5)	76.9
	Themisto libellula									Rare (1)	0.5		
Iulopididae	*Iulopis loveni*			Rare (1)	0.2								
Lestrigonidae	*Hyperietta luzoni*	Rare (2)	3.4	Rare (1)	0.2	Rare (2)	0.8	Rare (3)	0.7	Rare (1)	1.0		
	Hyperietta stebbingi	Common (2)	6.0	Rare (3)	1.7	Common (5)	3.6	Rare (5)	1.6				
	Hyperietta stephenseni	Common (2)	5.6	Common (3)	7.3	Common (6)	12.1	Common (7)	12.3	Common (2)	7.4		
	Hyperietta vosseleri	Rare (2)	2.6	Rare (1)	0.2	Rare (4)	1.2	Rare (1)	0.4				
	Hyperioides longipes	Common (2)	6.8	Common (2)	6.8	Rare (5)	1.7	Abundant (7)	21.7	Rare (2)	4.5	Rare (1)	0.1
	Lestrigonus bengalensis			Rare (1)	0.2								
	Lestrigonus sp. 1	Abundant (2)	16.2	Common (3)	5.8	Rare (5)	4.0	Common (7)	5.1	Rare (1)	0.5		
	Phronimopsis spinifera	Rare (2)	4.3	Rare (3)	2.2	Rare (6)	3.0	Rare (6)	3.1				
Phronimidae	*Phronima atlantica*			Rare (2)	4.8	Common (5)	7.1	Rare (2)	0.7	Rare (2)	1.5		
	Phronima sedentaria			Rare (3)	3.4	Common (6)	6.7	Rare (4)	0.5	Rare (1)	0.5		
	Phronima solitaria					Rare (3)	0.3	Rare (1)	0.1			Rare (1)	0.1
	Phronima stebbingi	Rare (1)	0.4	Rare (2)	2.4								
	Phronimella elongata			Rare (3)	4.8	Common (6)	13.3	Rare (7)	2.6				
Phrosinidae	*Anchylomera blossevillei*			Common (2)	6.3	Common (6)	6.0	Common (5)	5.1				
	Phrosina semilunata	Rare (1)	1.3	Rare (3)	4.6	Rare (6)	3.0	Common (5)	8.0	Rare (1)	3.5		
	Primno johnsoni			Rare (2)	0.7								
	Primno evansi	Rare (2)	3.0	Common (2)	5.6	Rare (1)	2.2	Common (7)	6.8	Abundant (1)	18.3	Abundant (5)	17.9
	Primno latreillei	Rare (2)	2.1	Common (3)	10.7	Rare (6)	2.4	Rare (7)	4.8	Common (1)	14.9		
Platysceloidea													
Brachyscelidae	*Brachyscelus crusculum*			Rare (2)	1.7	Rare (4)	2.0	Rare (1)	0.1	Rare (1)	1.0		
	Brachyscelus globiceps					Rare (1)	0.1	Rare (1)	0.1	Rare (1)	0.5		
	Brachyscelus macrocephalus					Rare (2)	0.2						
	Brachyscelus sp. 1					Rare (1)	0.1	Rare (1)	0.1				
	Thamneus rostratus					Rare (1)	0.2						
Lycaeidae	*Lycaea pulex*	Rare (1)	0.4	Rare (2)	2.2	Rare (3)	2.0	Rare (5)	1.2	Rare (1)	3.5		
	Lycaea serrata					Rare (1)	0.1						
	Lycaea sp. 1					Rare (3)	3.8						
	Lycaea sp. 2					Rare (1)	0.4						
	Lycaeidae sp. 1					Rare (2)	0.2						
Oxycephalidae	*Calamorhynchus pellucidus*			Rare (2)	0.5			Rare (1)	0.1				
	Cranocephalus scleroticus			Rare (1)	0.2	Rare (1)	0.1						
	Leptocotis tenuirostris					Rare (1)	0.1	Rare (4)	1.2				
	Oxycephalus piscator	Rare (1)	0.4			Rare (2)	0.2	Rare (4)	0.7				
	Rhabdosoma minor			Rare (1)	0.2	Rare (1)	0.2	Rare (2)	0.2				
	Streetsia challengeri	Rare (1)	0.4	Rare (1)	0.2	Rare (2)	0.4	Rare (2)	0.4	Rare (1)	0.5		
	Streetsia mindanaònis					Rare (1)	0.1						
	Streetsia porcella			Rare (2)	1.0	Rare (1)	0.1						
	Tullbergella cuspidata							Rare (1)	0.1				
Platyscelidae	*Amphithyrus bispinosus*			Rare (1)	0.5	Rare (2)	0.2						
	Amphithyrus sculpturatus	Rare (1)	0.9			Rare (4)	0.6	Rare (1)	0.8				

Table 2 (continued)

(Super)family	Species	NAST W St. 13, 17	%	NATR St. 27, 29, 31	%	WTRA St. 35, 37, 39, 42, 43, 45	%	SATL St. 47, 51, 53, 55, 57, 58, 60	%	SATL-SSTC St. 62, 64	%	SSTC, SANT-FKLD St. 66, 68, 70, 72, 74	%
	Platyscelus armatus	Rare (1)	0.4			Rare (3)	0.8						
	Platyscelus crustulatus			Rare (1)	0.2	Rare (1)	0.1						
	Platyscelus ovoides	Rare (1)	0.4	Rare (3)	2.2	Rare (6)	3.8	Rare (6)	4.3	Rare (2)	4.0	Rare (2)	1.0
	Tetrathyrus forcipatus			Rare (2)	1.5	Rare (5)	2.6	Rare (2)	0.6	Rare (1)	0.5		
Pronoidae	*Eupronoe armata*	Rare (2)	3.8	Rare (3)	1.0	Rare (4)	1.2	Rare (3)	2.5	Rare (1)	0.5		
	Eupronoe maculata	Rare (1)	2.1	Common (3)	5.8	Rare (6)	3.3	Common (6)	6.9	Rare (2)	2.0		
	Eupronoe minuta	Abundant (2)	17.9	Rare (2)	1.7	Rare (2)	0.2	Rare (6)	1.4				
	Parapronoe campbelli	Rare (1)	0.4			Rare (1)	0.2						
	Parapronoe crustulum			Rare (1)	0.2	Rare (3)	0.4			Rare (2)	1.0		
	Parapronoe parva			Rare (1)	0.2	Rare (2)	0.2						
	Pronoe capito					Rare (2)	0.2						
Tryphanidae	*Tryphana malmi*			Rare (1)	1.0	Rare (4)	0.9			Rare (2)	3.5		
Vibilioidea													
Paraphronimidae	*Paraphronima gracilis*	Rare (2)	2.6	Rare (2)	2.2	Rare (2)	0.3	Rare (6)	2.0	Rare (2)	1.0		
Vibiliidae	*Vibilia armata*	Rare (2)	2.1	Common (2)	5.1	Rare (6)	3.8	Rare (2)	0.2	Common (2)	8.9	Rare (4)	1.9
	Vibilia australis	Rare (2)	1.3	Rare (3)	1.0	Rare (2)	0.3	Rare (2)	0.6	Rare (1)	1.5	Rare (1)	0.1
	Vibilia borealis					Rare (4)	0.5						
	Vibilia propinqua			Rare (2)	2.2			Rare (2)	0.4	Rare (1)	2.0	Rare (1)	0.1
	Vibilia pyripes	Rare (1)	0.9			Rare (1)	0.1			Rare (1)	2.0		
	Vibilia stebbingi									Common (1)	13.4	Rare (2)	1.8

restricted to warmer waters, occurring only as far south as 34°S (St. 62; Brachyscelidae, Lycaeidae, Oxycephalidae), 36°S (St. 64; Lycaeopsidae, Paraphronimidae, Pronoidae) or 38°S (St. 66; Lestrogonidae, Phronimidae). The Hyperiidae showed a different pattern: they were found sporadically in warm waters, but dominated in the subantarctic (St. 66–74) (Fig. 1A; Tables 2 and S1). Species distribution patterns were highly diverse (Table S1). Many hyperiid species were present across a broad warm water range, including *Eupronoe maculata*, *Hyperietta stephenseni*, *Lycaeopsis themistoides*, *Phronimella elongata*, *Phronimopsis spinifera* and *Primno latreillei*. Some species were restricted to locations in or near the equatorial region (e.g., *Vibilia borealis*) or the subtropical gyres (*Eupronoe minuta*). Other species were found only in the northern gyre and sometimes also in the (near-) equatorial region, but were absent from or very rare in the southern gyre (e.g., *Amphithyrus bispinosus*, *Hyperietta vosseleri*, *Parapronoe campbelli*, *Phronima stebbingi*, and *Primno johnsoni*). *Themisto gaudichaudii* and *Vibilia stebbingi* were found at southern transitional and subantarctic locations. Several species occurred across a wide range of warm and cold water regions along AMT22, sometimes with intermittent or disjunct distribution patterns. For example, *Vibilia armata* was absent in the central part of the southern gyre and *Primno evansi* was absent in the equatorial region. Such wide distribution patterns are questionable, and it is possible that some of these species represent a complex of morphologically similar, or cryptic, species.

3.3. Species assemblages

Hyperiid species composition differed significantly between stations along AMT22. The cluster and SIMPROF analyses based on species presence-absence identified three clusters ($p < 0.05$; Fig. 4A), which are also apparent in the nMDS ordinations (Fig. 4B, C). The species composition of subantarctic stations in the first cluster (St. 66, 68, 70, 72 and 74; 38–46°S) was most distinct from all other regions (15% similarity). A second cluster represented all stations from 13 to 64 except St. 62 (34°S), which was significantly distinct from all other stations in this analysis. The ordination of St. 64 may be artifactual, caused by the relatively small sample fraction that was examined at this station (Table 1). Stations 62 and 64 are located in southern temperate waters and represent transitional species assemblages between the southern subtropical gyre and subantarctic provinces. The equatorial stations 35, 37, 39, 42, 43 and 45 (7°N–8°S) grouped together, although this cluster was not statistically significant (Fig. 4). In analyses that included relative species abundance data and only included stations that were examined in their entirety (11 stations, excluding the subantarctic region), we obtained three significant clusters ($p < 0.05$; Fig. 5A). One cluster represented the equatorial upwelling region (St. 35, 39, 42, 43), another consisted of the northern and southern gyre stations combined (St. 29, 47, 51, 53, 55, 60), and the southern temperate St. 62 was distinct. These results were congruent with analyses based on presence-absence data only, but these analyses were better able to resolve the equatorial upwelling region as a distinct cluster (Fig. 5).

The geographic distribution of hyperiid species assemblages corresponded to Longhurst's biogeochemical provinces (Longhurst, 1998), with seasonal positions as estimated by Reygondeau et al. (2013). Our analyses separated between the equatorial (western tropical Atlantic, WTRA), gyral (northwest Atlantic subtropical gyral, NAST W; north Atlantic tropical gyral, NATR; south Atlantic gyral, SATL), subantarctic (south subtropical convergence, SSTC; subantarctic water ring – southwest Atlantic shelves, SANT-FKLD), and temperate, transitional (SATL-SSTC) stations (Table 1; Figs. 4 and 5). Stations from the NAST W province had similar species assemblages, although not significantly different from other gyre stations (Table 1; Fig. 4).
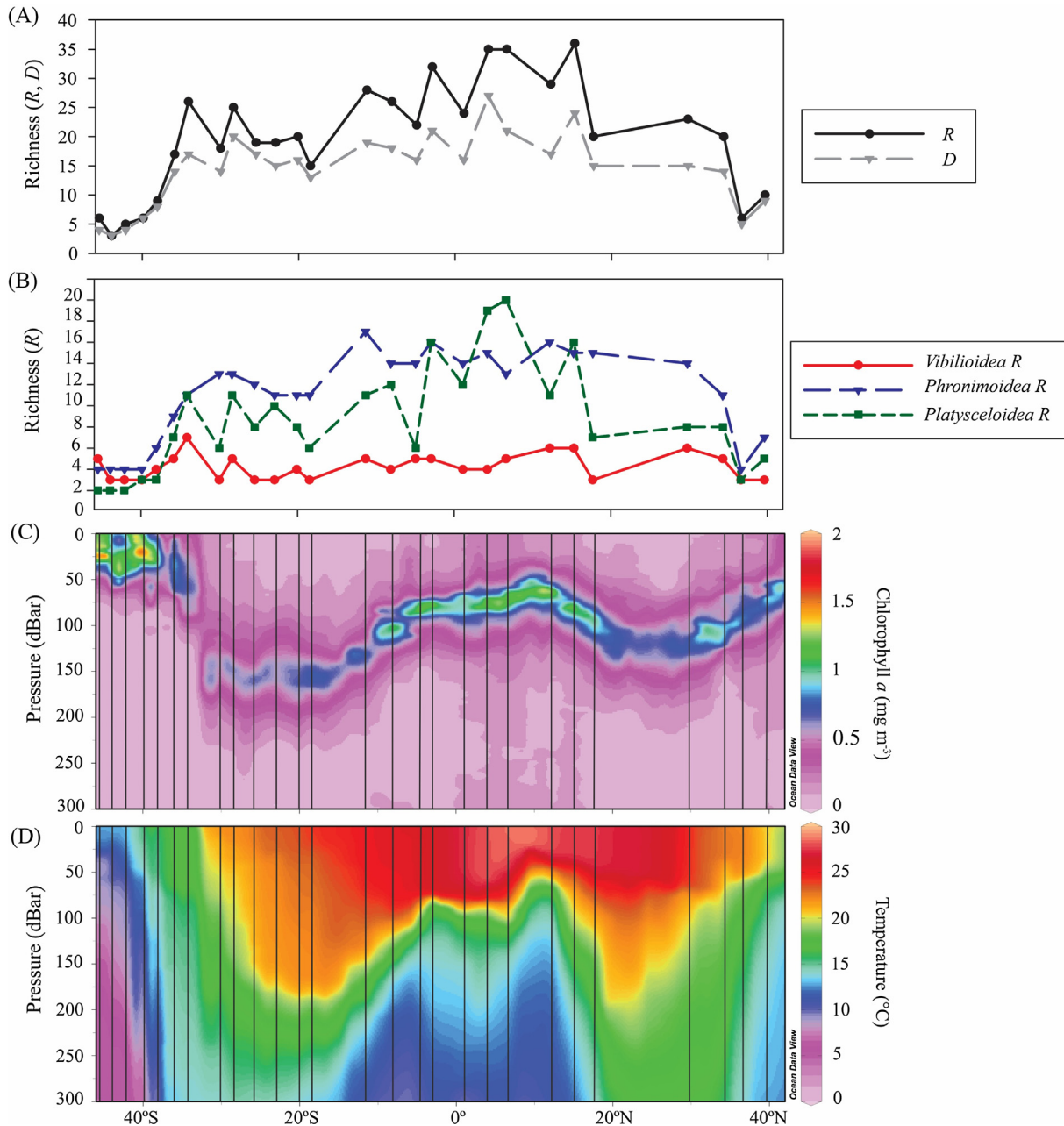
Fig. 2. Basin-scale patterns of (A) total hyperiid species richness *R* and genus richness *D*, (B) species richness *R* of superfamilies Vibilioidea, Phronimoidea and Platysceloidea (Physocephalata), and (C, D) seawater temperature and chlorophyll *a* concentrations in the upper 300 m of the water column along AMT22. Vertical lines in (C) and (D) mark the sampling locations for this study. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
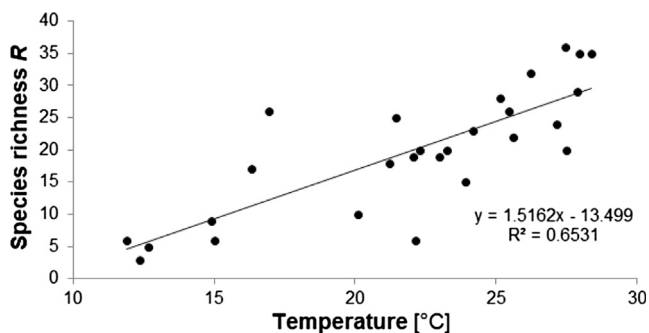
Fig. 3. Relationship between hyperiid species richness *R* and sea surface temperature. Linear regression and R^2 value as reported in the legend.

An overview of species composition and relative abundance of hyperiids in six regions along the meridional transect is presented in Table 2. In the NAST W province (St. 13, 17), *Eupronoe minuta* (17.9%) and *Lestrigonus* sp. 1 (16.2%) were the most abundant species. *Primno latreillei* (10.7%), *Hyperietta stephenseni* (7.3%) and *Hyperioides longipes* (6.8%) were common in the NATR province (St. 27–31). In the equatorial WTRA province (St. 35–43), the most common species were *Phronimella elongata* (13.3%) and *Hyperietta stephenseni* (12.1%). In the southern gyre (SATL, St. 47–60), *Hyperioides longipes* (21.7%) and *Hyperietta stephenseni* (12.3%) were the most common species. The two samples from the southern transition zone (St. 62 and 64, SATL-SSTC) demonstrated a steep transition from species common in the southern gyre toward the subantarctic hyperiid assemblage. Across these stations combined,
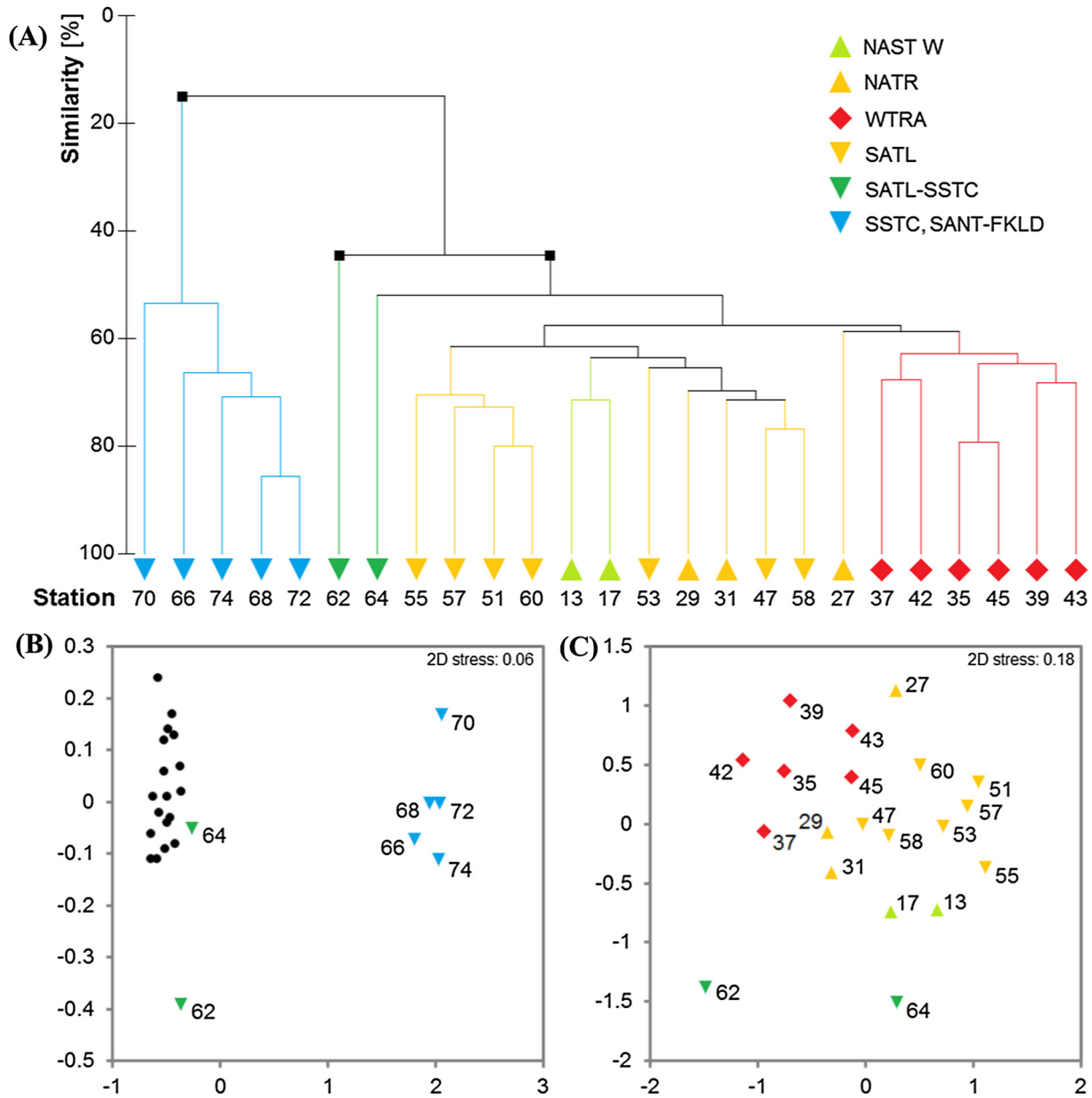
Fig. 4. Species assemblages of Atlantic Physocephalata hyperiids based on presence-absence data for stations with >30 specimens. (A) Hierarchical cluster analysis of stations, according to their species composition. Three significant clusters are shown (SIMPROF *p* < 0.05). (B, C) Non-metric Multi-Dimensional Scaling (nMDS) ordination based on the species assemblage of hyperiids (B) using all stations, and (C) excluding the subantarctic stations 66, 68, 70, 72 and 74. Symbols are colored according to Longhurst provinces, with upward triangles for the northern hemisphere, downward triangles for the southern hemisphere and diamonds for equatorial locations.

the most common species were *Primno evansi* (18.3%), *Primno latreillei* (14.9%) and *Vibilia stebbingi* (13.4%). In the subantarctic (SSTC, SANT-FKLD, St. 66–74), *Themisto gaudichaudii* was overwhelmingly dominant (76.9%), followed by *Primno evansi* (17.9%). The rank abundance curves confirmed a pattern of strong species dominance in the subantarctic, while there was never a dominant species (> 50% per station) in the warm water regions, including southern transitional stations 62 and 64 (Fig. S1).

4. Discussion

Hyperiid amphipods are an enigmatic macrozooplankton group and an important component of pelagic food webs. Despite their abundance in open ocean ecosystems from polar to tropical waters, hyperiid diversity and distribution patterns have not been charac-

terized at basin-wide spatial scales. In this study, we examined the diversity and distribution of epipelagic and upper mesopelagic hyperiids along a meridional transect in the Atlantic Ocean spanning > 80 degrees of latitude (39°N to 45°S). The majority of species sampled belonged to the Physocephalata infraorder, characterized by their large heads and eyes relative to their body length (Fig. 1B). Across this transect, we identified 70 species from 17 families, of which six species represent putative undescribed species. We report new distributional records in the Atlantic Ocean for *Scina curilensis* and *Tullbergella cuspidata,* which were previously only reported from the Indo-Pacific.

4.1. Latitudinal diversity gradients

Overall, the dominant pattern in the latitudinal diversity gradient for hyperiids is a species diversity peak in the equatorial
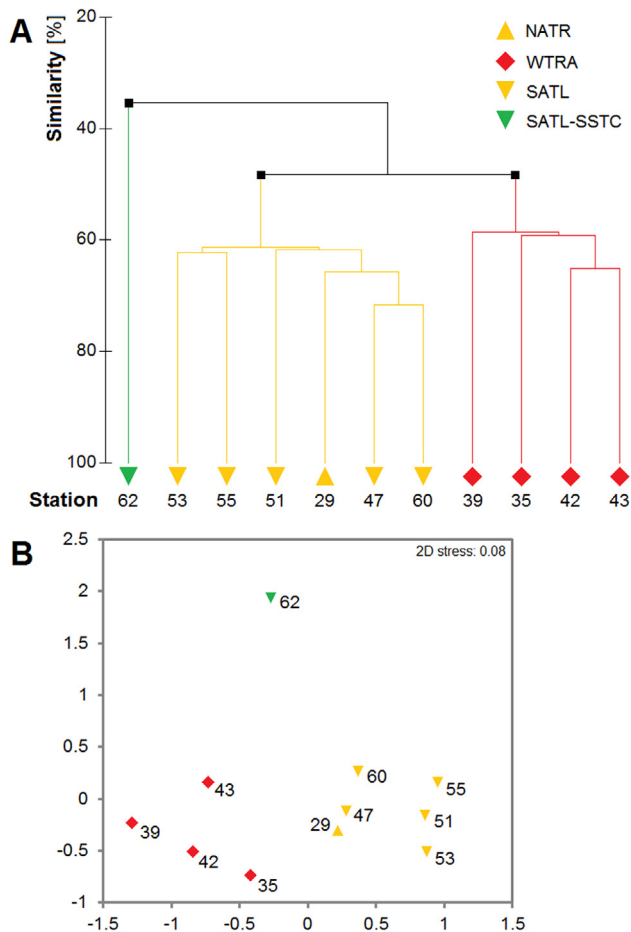
Fig. 5. Species assemblages of Atlantic Physocephalata hyperiids based on relative abundance data for stations that were examined in their entirety (>30 specimens). (A) Hierarchical cluster analysis of stations, according to Physocephalata species composition and relative abundance (see Table 1). Three significant clusters are shown (SIMPROF $p < 0.05$). (B) nMDS ordination based on the species assemblage of hyperiids. Symbols are colored as in Fig. 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

upwelling region, which is mainly caused by high equatorial diversity in the Platysceloidea hyperiids. Although this latitudinal pattern was also observed for salps (Macpherson, 2002), it is not the dominant pattern for latitudinal diversity gradients in the pelagic. A bimodal pattern of species richness is most commonly observed, with highest diversity in the subtropical gyres, (slightly) lower diversity in the equatorial upwelling zone, and a sharp decrease in species diversity poleward of the subtropical convergence (e.g., Rutherford et al., 1999; Brayard et al., 2005; Boyce et al., 2008; Dolan and Pierce, 2013). Such a pattern was reported for anthomedusan hydrozoans (Macpherson, 2002), cephalopods (Rosa et al., 2008) as well as for planktonic crustaceans, including euphausiids (Angel, 1997; Tittensor et al., 2010), decapods (Angel, 1997), and ostracods (Angel, 1997; Angel et al., 2007). Some fishes and microplanktonic groups also demonstrate this bimodal pattern, such as tuna and billfish (Boyce et al., 2008), tintinnid ciliates (Dolan and Pierce, 2013) and planktonic foraminifera (Rutherford et al., 1999; Tittensor et al., 2010). Finally, this pattern was observed for shelled pteropods along AMT24, a similar basin-scale transect in the Atlantic Ocean (Burridge et al., 2017). A second latitudinal diversity pattern reported for some pelagic groups is of a broad plateau of species richness across subtropical and tropical waters (e.g., siphonophores and cephalopods; Macpherson, 2002). The Phronimoidea hyperiids in our study demonstrated this diver-

sity plateau, with species richness relatively constant across warm waters of both subtropical gyres and the equatorial region (Fig. 2B). Collectively, these studies demonstrate that basin-scale latitudinal diversity patterns differ among pelagic groups, and even among different superfamilies within hyperiid amphipods, suggesting that they may result from different drivers.

Because most hyperiid amphipods are commensal or parasitic on gelatinous hosts, their large-scale patterns in distribution, abundance, and diversity are likely driven substantially by host abundance and diversity (e.g., Madin and Harbison, 1977; Laval, 1980; Lavaniegos and Ohman, 1999; Gasca et al., 2007, 2015). In this study, we find some evidence that distribution patterns of hyperiids may be associated with distribution patterns of their respective hosts. However, we know that these fragile gelatinous plankton groups are not sampled adequately with plankton nets. Within Platysceloidea, the superfamily with a high equatorial peak in species diversity, the host-associations appear to be more specific than in the Phronimoidea superfamily, which had a broad warm water plateau in species richness (Fig. 2B; Harbison et al., 1977, 1978; Madin and Harbison, 1977; Laval, 1980; Gasca et al., 2007, 2015). For example, the Lycaeidae family (Platysceloidea) is strongly associated with salp and pyrosome tunicates (e.g., Harbison, 1976; Madin and Harbison, 1977; Laval, 1980). The Lycaeidae family was most diverse in the equatorial region and contributed to the equatorial species diversity peak for Platysceloidea that was observed in this study (Fig. 2B; Table S1). Likewise, salps show a peak in species diversity in equatorial waters (Macpherson, 2002) and salp blooms have been reported to be associated with increases in primary production (Stone and Steinberg, 2014) and upwelling of nutrients (Li et al., 2011) as occurs in the equatorial upwelling zone. We did not find prior reports in the literature suggesting a higher abundance of siphonophores or ctenophores in the equatorial region that may further explain the high equatorial diversity of Platysceloidea (but *see* Stemmann et al., 2008 for differences in abundance of gelatinous zooplankton between other oceanic regions worldwide). However, we noticed high abundances of pyrosomes, salps and other gelatinous plankton in the equatorial upwelling region along AMT22 (Peijnenburg and Goetze, unpub. observations). In contrast, an example of less specific host associations at the family-level can be found in Hyperiidae (Phronimoidea), with species known to associate with salp tunicates, ctenophores, scyphozoans, and antho- and leptomedusan hydrozoans (e.g., Harbison et al., 1977; Madin and Harbison, 1977; Laval, 1980; Lavaniegos and Ohman, 1999; Kruse et al., 2015). The tropical and subtropical plateau in species diversity of the Phronimoidea superfamily may be linked to this low host specificity.

4.2. Species assemblages and oceanography

Hyperiid species assemblages were distinct for gyral, equatorial, transitional, and subantarctic stations along AMT22 (Figs. 4 and 5). The sharpest transition in hyperiid species composition occurred in the South Atlantic Ocean between the southern subtropical convergence and the subantarctic province, located at ~34 to 38°S. This transition consisted of a sudden drop in species diversity, with *Themisto gaudichaudii* and *Primno evansi* dominating in subantarctic waters (76.9% and 17.9% of the total assemblage; Table 2). The location of this transition is similar to that found for pteropods, which also showed dramatic declines in species richness poleward of the convergence zone along a similar AMT transect (AMT24; Burridge et al., 2017). This region is characterized by a shift from oligotrophic waters with a deep DCM (150–200 m) and very low chlorophyll *a* concentrations (<0.6 mg/m^3 at the DCM) to well-mixed waters with shallow (<75 m) and high (>0.75 mg/m^3) maximum chlorophyll *a* concentrations. We found similar hyperiid

species assemblages in the northern and southern subtropical gyres, a pattern also observed for assemblages of pteropods (Burridge et al., 2017), copepod genera (Woodd-Walker et al., 2002), and cephalopod families (Rosa et al., 2008) within the Atlantic, as well as for several groups in the Pacific basin (e.g., Williamson and McGowan, 2010; Brinton, 1962). However, the northern and southern gyre ecosystems are not exact replicates of one another, as was reflected by the slightly lower hyperiid diversity and higher relative species dominance in the southern gyre (Figs. 2 and S1).

The hyperiid species assemblage in the equatorial region occurred between ∼7°N and 8°S, across a narrower latitudinal band than observed in some other zooplankton groups (e.g., Woodd-Walker et al., 2002; Angel et al., 2007; Hirai et al., 2015; Goetze et al., 2017; Burridge et al., 2017). Specifically, the location of the northern boundary of the equatorial hyperiid assemblage did not extend as far north as is commonly found for other zooplankton. Burridge et al. (2017) found a distinct equatorial assemblage between 14°N and 4°S with transitions at 18°N and 8°S for pteropod species along a similar Atlantic transect (AMT24, 2014). Angel et al. (2007) studied the inter-station similarities of ostracod assemblages in the North Atlantic and found that stations at 18°N, 10°N and 0° grouped closely together, suggesting that the equatorial species assemblage extended much farther north than was observed in hyperiids. For copepod genera, the equatorial assemblage occurred between 17.5°N and 7.5°S (Woodd-Walker et al., 2002). This narrower equatorial distribution for hyperiids may be a consequence of their dependence on gelatinous hosts, which serve as a micro-environment over large parts of the hyperiid life cycle (e.g., Laval, 1980). However, little is known about species diversity and distribution patterns of gelatinous hosts across these Atlantic Ocean provinces (as shown by the distribution of the Jellyfish Database Initiative (JEDI) metadata sets in Condon et al., 2012), impeding our ability to assess whether the boundaries of distinct hyperiid species assemblages reflect those of their gelatinous hosts.

There are several limitations of the sampling in this study, and further work on hyperiids at ocean basin scales is justified. Our material was collected with the primary goal of providing specimens for molecular studies on marine zooplankton, and so while the 200 μm mesh net was handled quantitatively (e.g., calibrated flowmeter mounted in the net), the paired 333 μm mesh bongo net was intended for live collections of larger-bodied animals. Subsequent work should be conducted on a more quantitative collection of material, drawing from the initial taxonomic observations of this study. In addition, more information on the diversity and distribution of gelatinous hosts would enable greater inference from our observations on hyperiids. Although it may not be appropriate to attempt to quantify the gelatinous plankton in our net-collected samples, one fruitful way forward could be to examine the gut contents of hyperiids using a molecular approach in order to establish the taxonomic identities of hyperiid-host relationships (e.g., metabarcoding; Pompanon et al., 2012). Hyperiids often feed on host tissues (Laval, 1980), and DNA sequences from hyperiid stomach contents could reveal host identity in the majority of cases where net-collected animals have been disturbed from their hosts. Similar molecular diet studies have been very informative for detecting novel trophic links in other marine species (e.g., Deagle et al., 2009; Olsen et al., 2014; Albaina et al., 2016).

5. Conclusion

This study is among the first to examine large-scale diversity and distribution patterns of hyperiid amphipods across open waters of the Atlantic, and our data provide important new distributional records across six oceanic provinces. The latitudinal maximum in hyperiid species richness occurred in the equatorial upwelling region, and was largely driven by increases in the diversity of Platysceloidea hyperiids. We also observed a significant positive relationship between species richness and sea surface temperature at the basin scale. The dominant paradigm of a bimodal pattern of species richness in pelagic systems, with maxima in the subtropical gyres, was not supported by our data on hyperiids. Instead we propose that the large-scale patterns of hyperiid diversity are at least partly driven by gelatinous host abundance and diversity. However, limited knowledge of the diversity and distribution of gelatinous zooplankton hosts impedes our inferences regarding drivers of these basin-scale patterns in hyperiids. Species assemblages along AMT22 broadly supported a division into gyral, equatorial, transitional, and subantarctic hyperiid communities, congruent with Longhurst's (1998) biogeochemical provinces. Biogeographic distributions of hyperiids ranged from species that were endemic to specific regions (e.g., *Vibilia borealis*, *Eupronoe minuta*, *Hyperietta vosseleri*, *Vibilia stebbingi*), to species that occurred across broad warm water ranges (e.g., *Hyperietta stephenseni*). Some species occurred in warm-, intermediate, as well as cold water regions (e.g., *Vibilia armata*, *Primno evansi*) often with disjunct distribution patterns. Such broadly distributed species may represent assemblages of cryptic or morphologically similar species, and would be interesting target species for future phylogeographic and taxonomic studies.

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.2016.08.003.

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