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

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ABSTRACT

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 basinscale 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.

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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 freeliving, 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.

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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., 2016). 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 wellmixed and preserved in multiple jars. All hyperiid material examined in this study derived from the 333 um 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

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