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Mesopelagic fishes across the tropical and equatorial Atlantic: Biogeographical and vertical patterns

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ABSTRACT

In this investigation we analysed the changes in fish species occurrences and relative abundances across the tropical and equatorial Atlantic, and their vertical distribution patterns in relation to the different environmental scenarios. The study covers a wide region encompassing different water masses, and marked differences in productivity, from an oligotrophic zone close to the Brazilian coast, to a very productive upwelling region close to the Northwest African upwelling. Fishes were collected with a medium-sized midwater trawl (Mesopelagos), complemented by hauls made with a macrozooplankton net (MOCNESS). Species richness in the region was higher than in subtropical, temperate and cold regions. The total number of species and their overall abundance was lower in the stations closer to the Brazilian coast. Abundant species across the entire region were the gonostomatids *Cyclothone alba*, *Cyclothone acclinidens*, *Cyclothone pallida* and *Cyclothone pseudopallida*, the myctophid *Lampanyctus alatus*, the sternoptychid *Sternoptyx diaphana*, and the phosichthyid *Vinciguerria nimbaria*. The occurrences and abundances of *C. parapallida*, *Lampanyctus nobilis* and *Lepidophanes guentheri* were related to zones where AAIW waters occupied the mesopelagic layers, while other species such as *Cyclothone livida* and *Polyipnus polli* increased their abundance when AAIW disappears from their living depths. The presence of Eastern North Atlantic Central Water (ENACW) was associated with the occurrence of several myctophids (*Benthosema glaciale*, *Ceratoscopelus maderensis*, *Diaphus holti*, *Diaphus rafinesquii*, *Hygophum hygomii*, *Lampanyctus crocodilus*, *Myctophum punctatum*, *Symbolophorus veranyi*), and the gonostomatid *Cyclothone braueri*. In spite of the important differences in hydrographic features across the tropical and equatorial Atlantic, all stations showed either the general night migration into the epipelagic layers carried out by myctophids, phosicthyids, and some stomiids, or the presence of the several species of *Cyclothone*, sternoptychids and melamphaeids that remain in the mesopelagic layers, both day and night. The oxygen minimum zone (OMZ) at mesopelagic depths in the north-eastern sector does not seem to disrupt diel vertical migration. Day-night distributions in our study proved that mesopelagic migratory species are capable of crossing these wide hypoxic layers, and that some species such as *Diaphus vanhoeffeni* remain in these layers during the day. Other non-migratory fishes (*Cyclothone* spp. and *S. diaphana*) proved to be widely tolerant to these low oxygen concentrations, as shown by their high numerical abundances in the OMZ.

1. Introduction

Open ocean fishes include a variety of families living in the epipelagic, mesopelagic and bathypelagic zones, with epipelagic families being taxonomically very different from the meso- and bathypelagic families (Haedrich, 1997). Together they constitute the most diverse and abundant fishes of the deep ocean. Mesopelagic fishes comprise generally small luminous species of the families Myctophidae (Hulley, 1992), Gonostomatidae, Sternoptychidae, Phosichthyidae, Stomiidae, Argentinidae, and Bathylagidae (Weitzman, 1997). Although these populations are often described as diverse and with non-dominant species (Wienerroither et al., 2009), the emerging patterns are different when sampling methods allow for the capture of the small *Cyclothone* species of the family Gonostomatidae. These species

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are numerically dominant in the lower mesopelagic layers of all oceans (Badcock, 1970; Badcock and Merrett, 1976; Roe and Badcock, 1984; Miya and Nemoto, 1991; Ross et al., 2010; Olivar et al., 2012). Another important aggregation layer for mesopelagic species is the near surface region (0–200 m), into which many mesopelagic fishes migrate at night on a diel basis (Sutton, 2013; Duhamel et al., 2014).

Estimations of the biomass of mesopelagic fishes are contentious and strongly biased by the methods and assumptions used. Fish abundances obtained through net collections are influenced by haul performance, by net avoidance and by net escape due to mesh size. Acoustic methods depend on the different acoustic responses between organisms and depths, and on the frequency used (Sutton, 2013; Peña et al., 2014), and they rely on hauls for species ground-truthing. As a result, biomass estimates presented up to now have enormous variations, often by several orders of magnitude (Gjøsaeter and Kawaguchi, 1980; Lam and Pauly, 2005; Koslow, 2009; Koslow et al., 2011; Irigoien et al., 2014).

Investigations on mesopelagic fish distributions and on biogeography have used oceanographic parameters, most notably temperature and salinity to set the preferred distribution ranges for the different species (Backus et al. 1977; Duhamel et al., 2014; Hulley, 1981, 1992; Koubbi et al., 2011; Flynn and Marshall, 2013; Olivar et al., 2016a, 2016b). Major changes in species composition have been reported at convergences, oceanic-neritic boundaries and transitional areas (Backus et al., 1970; Krefft, 1974) due to the changing trends in water column depth, water mass properties, nutrient levels and differences in the depths of the mixed layer (Olson, 1986). The influence of oxygen concentrations, particularly in the oxygen minimum zone (OMZ) of the water column is a subject of increasing interest (Childress and Seibel, 1998; Butler et al., 2001; Torres et al., 2012), particularly in the present climate change scenario, where there is expansion and shoaling of the OMZ's (Gilly et al., 2013).

The equatorial and tropical Atlantic is an interesting region to investigate these groups of fishes due to its varying geographic and oceanographic properties, and important productivity gradients, with the western sector typified as one of the most oligotrophic subtropical zones of the global ocean (Morel et al., 2010) and the area near the North African coast as one of the most productive in the world due to the upwelling (Mittelstaedt, 1983). This region is characterized by the convergence of water masses originating in both southern and northern hemispheres, which results in a complicated current system with zonal westward currents and eastward undercurrents (Equatorial Current, Equatorial Counter Current), as well as the equator-ward currents along the Brazilian and African coasts (North Brazilian Current and Canary Current) and the Guinea Dome cyclonic gyre, close to the African coast (Stramma and Schott, 1999). Additionally, the eastern tropical North Atlantic zone is distinguished by a permanent mesopelagic oxygen minimum zone (OMZ) at approximately 300–600 m depth (Karstensen et al., 2008, 2016).

Background information on the distribution of mesopelagic fishes in the Atlantic is broad and goes back to the mid-1900s, with some studies on zoogeographical patterns (Backus et al., 1965, 1970, 1977; Krefft, 1974, 1976; Hulley, 1981, 1986; Hulley and Krefft, 1985; Boltachev, 1987; Hulley and Paxton, 2016a,b), and others analysing diel vertical migrations (Badcock, 1970; Badcock and Merrett, 1976; Roe and Badcock, 1984, for the eastern North Atlantic). Particular attention has been devoted to more northern latitudes (van der Spoel and Bleeker, 1991; Fock et al., 2004; Sutton et al., 2008, 2010; Sutton, 2013), and to the area near Canary upwelling from investigations dating back to the 1960s and 1980s (Backus et al., 1965, 1970, 1977; Krefft, 1974, 1976; Hulley, 1981; Boltachev, 1987), to the more recent studies by Wienerroither et al. (2009) and Hulley and Paxton (2016a,b). Finally, there have also been numerous investigations in the western central Atlantic (e.g., Gibbs and Krueger, 1987; Gartner et al., 1987; Craddock and Hartel, 2003; Ross et al., 2010).

Diel vertical migration (DVM) is a recurrent event in open-ocean waters, and is carried out by both zooplankton and micronektonic organisms (Pearcy et al., 1977; Roe and Badcock, 1984; Angel and Pugh, 2000; Ross et al., 2010; Bianchi et al., 2013; Sutton et al., 2008; Sutton, 2013). It has been extensively documented that most Myctophiformes and some Stomiiformes are the most common fishes performing such migrations, with nocturnal aggregations in the epipelagic layers, where they feed, and with deeper day distributions (Willis and Pearcy, 1982; Gartner et al., 1987; Koslow et al., 1997; Kenaley, 2008; Olivar et al., 2012; Duhamel et al., 2014). The diel migration behaviour of many mesopelagic fishes would be expected to have an even more important integrating effect on potential species interactions than the horizontal component (Haury, 1986) because it involves the nightly coincidence in a relatively narrow layer of a large number of species and individuals that may have more segregated day distributions.

Information on the species involved (or not) in these nocturnal excursions have appeared in a number of studies around the world ocean, and have become more frequent following the use of fishing gears able to sample discrete water layers (Roe and Badcock, 1984; Williams and Koslow, 1997; Andersen et al., 1998; Watanabe et al., 1999; Ross et al., 2010). Nevertheless, due to the difficulties of net deployments and time consuming operations, there is still a large proportion of the oceanic regions where such studies have not been conducted. The closest geographical zone to our study region where the vertical migration of mesopelagic fishes has been investigated, at the species level, was at more northern latitudes, in the Northeast Atlantic; the results have been reported in the seminal works of Badcock (1970), Goodyear et al. (1972), Badcock and Merrett (1976), Backus et al. (1977) and Roe and Badcock (1984). Similarly, Kinzer and Schulz (1985) have presented results for the equatorial region. More recent investigations in this regard were also related to subtropical and temperate zones like the Canary region and the Mediterranean Sea (Wienerroither et al., 2009; Olivar et al., 2012).

Vertical migration has a fundamental role in the active transport of carbon from the upper surface layers, where fish feed at night, to the darker deeper layers, where through respiration and excretion they release the carbon assimilated at the surface. Therefore, knowledge of the species involved, and their particular migratory patterns, are basic issues for any further investigations of carbon fluxing. The aim of the present study is to determine the influence of productivity, vertical structure of the water column and water masses on the species diversity and patterns of distribution of mesopelagic fish populations across the tropical and equatorial Atlantic.

2. Material and methods

2.1. Oceanography

The study was conducted in the tropical and equatorial Atlantic, from near the Brazilian coast to south of the Canary Islands, and covered some 5000 km (Fig. 1). Twelve hydrographic stations separated by 420 km, from 500 km off the Brazilian coast (13°S 38.3°W) to 200 km south of the Canary Islands (28°N 15.6°E), were occupied and included both day and night measurements (Fig. 1). Two CTD casts were performed at each of the 12 stations using a Seabird 911Plus conductivity-temperature-depth (CTD) instrument with a Seabird-43 Dissolved Oxygen Sensor and a Seapoint Chlorophyll Fluorometer Sensor. The first cast was performed at