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Deep stocks avoid competition migrating horizontal and vertically: The example of two scabbardfishes (*Aphanopus* spp.) targeted by long-liners in grounds next to an oceanic archipelago

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HIGHLIGHTS

- Two *Aphanopus* species are vertically segregated.
- Adults of both species more abundant in deeper bottoms (>2500 m).
- *A. intermedius* is caught at deeper seafloor (>4500 m) than *A. carbo*.
- Food source overlap may explain the vertical segregation of both species.

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ABSTRACT

Fishing is occurring all over the globe, with an increase trend of exploiting deep stocks. Several species are currently targeted from the deep ocean, and some artisanal fisheries developed fishing gears, e.g. long lines, with limited impact to the environment but scarce information is available on biological aspects of these exploited stocks. In the Macaronesian region and specifically in Madeira archipelago, two *Aphanopus* sympatric species have been extensively exploited for decades but no detailed information is available on the spatial and vertical distribution of both species (*Aphanopus carbo* and *Aphanopus intermedius*). Currently, they represent an important percentage of landings from artisanal fishermen of Madeira (27% of the total catches in 2017). We herein observed that they showed a pattern of depth segregation, where adults of both species are more abundant (*ca.* 80%) at deeper seafloor (> 2500 m). *A. intermedius* was more numerous in fishing areas with greater seafloor depth (> 4500 m) compared to *A. carbo*. This pattern may be explained by a food source overlap between both species, and also the vertical segregation within the same species may be considered as a pattern to avoid cannibalism. Also, migration patterns were found in both species being more pronounced for *A. intermedius* where > 86% of individuals were collected offshore (> 12 n.m.). The present results constitute a step forward to start developing integrative management actions to preserve stocks of both species in the medium and long term in the study region.

1. Introduction

Worldwide, fishing has outstandingly changed the distribution of fishes and fisheries far from the consumers and ports (Norse

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et al., 2012), occurring now near the seafloor far off the continental shelf break (including slope areas, seamounts, and seamount ridges) (Troyanovsky and Lisovsky, 1995; Japp and Wilkinson, 2007) in deeper sea waters since the 1950s to maintain extraction rates (Morato et al., 2006). In the succeeding decades, deep-water fisheries expanded worldwide to all oceanic regions as a result of the advances in fishing technologies, being especially important in the Northeast Atlantic (Sissewine and Mace, 2007). This fast development is a consequence of the decrease (or collapse) of many traditional near shore and easily accessible stocks (FAO, 2010; Garcia and Rosenberg, 2010). Consequently, a general decline in fish biomass has been reported (Baum et al., 2003; Christensen et al., 2003; Myers and Worm, 2003) since the late 1980s (Watson and Pauly, 2001; Zeller and Pauly, 2005) and many marine species, in a state of over exploitation, are current conservation concerns (Casey and Myers, 1998; Spotila et al., 2000; Baum et al., 2003). Regardless, an overall increase of fishing effort and catching power has pursued (Gréboval, 2003).

Deep fishing has many environmental concerns specially those ones related to highly vulnerable species (Devine et al., 2006; Bailey et al., 2009). Deep-sea fish species caught in waters deeper than 400–500 m (ICES, 2007) are characterized by several features that make them very sensitive to over exploitation such as, large size, slow growth, late maturation and low mortality rates (Morato et al., 2006; Baker et al., 2009; Clark et al., 2010).

However, the effects of extensive deep fishing are not restricted to targeted species, for example, Bailey et al. (2009) showed that the apparent impacts of fishing extend deeper than the reach of fishing gear but greatly depends on the fishing method, e.g. bottom trawls, longlines, among others. In the Northeast Atlantic, the longline and trawl fisheries prevail, varying from artisanal fisheries to highly mechanized high-seas operations (Large et al., 2003). Longline fishery off Madeira and mainland Portugal, targeting mainly black scabbardfish (*Aphanopus carbo* Lowe, 1839), is one of the longest established fisheries in the Northeast Atlantic (Large et al., 2003). In Madeira, this fishery dates back to the 17th century (Merrett and Haedrich, 1997) and for several decades this was the only fishery targeting this species in the Northeast Atlantic (Bordalo-Machado and Figueiredo, 2009). First evidence showed that this fishing gear has a lower impact on deep sea ecosystems compared to deep bottom trawling (Pham et al., 2014). In several geographic areas, deep fishing grounds constitute an important fraction on fisheries landings such as oceanic islands characterized by coastal fish depletion (Menezes et al., 2013). Thus, integrative management of these artisanal fisheries is of utmost importance for the stock conservation in the medium and long term.

Stefanni et al. (2009) first developed a genetic method for discrimination of the two Atlantic cryptic deep-sea species of scabbardfish, *Aphanopus intermedius* Parin, 1983 and *Aphanopus carbo* Lowe, 1839. Subsequently, Biscoito et al. (2011) thoroughly detailed the morphological identification of these two sympatric species from the NE Atlantic (including a large sample from the Azores, Madeira, Canaries, mainland Portugal, Atlantic Morocco and Western Sahara) based on the combined use of both external (basically fins' formulae) and internal (vertebral formula) morphological characters; these authors also provided a re-description of *A. intermedius* incorporating the new meristic and morphometric character ranges found. Consequently, biological studies on *Aphanopus* from the NE Atlantic are generally based on samples with a mixture of both species (*A. carbo* and *A. intermedius*).

In Madeira, an oceanic and volcanic archipelago in the Northeastern Atlantic Ocean, the mid-water drifting longline fishing is a major contributor to fisheries landings along the year with only two target species (*A. carbo* and *A. intermedius*) (Delgado et al., 2013). Both scabbardfish species occur at a wide depth range, from 200 m in the northern part of the NE Atlantic (Nakamura and Parin, 1993) to 2300 m off the Canary Islands (Pajuelo et al., 2008) for *A. carbo*, although more frequent at 800–1300 m in Madeira (Morales-Nin and Sena-Carvalho, 1996) and to 1350 m for *A. intermedius* (Delgado et al., 2013). *Aphanopus carbo* and *A. intermedius* seem to be adapted to a strong activity of migrating upwards at night to feed on crustaceans, cephalopods and fishes (Tuset et al., 2010). Surprisingly, only one previous work (Tuset et al., 2010) made a reference to the coexistence of both species (*A. carbo* and *A. intermedius*) through their depth range, since studies on scabbardfishes have been concerning on reproduction and growth (Delgado et al., 2013). Moreover, most of the information published on this genus in the NE Atlantic Ocean is limited to one species: *A. carbo*, relating to reproductive cycle and strategies (Figueiredo et al., 2003; Neves et al., 2009; Ribeiro Santos et al., 2013a), age, growth and length structure (Morales-Nin et al., 2002; Pajuelo et al., 2008; Vieira et al., 2009), diet (Bordalo-Machado et al., 2009; Ribeiro Santos et al., 2013b), migration (Farias et al., 2013), stock discrimination (Farias et al., 2009; Santos et al., 2009; Gordo et al., 2009), fisheries (Bordalo-Machado et al., 2009; Delgado et al., 2018), heavy metals contents (Costa et al., 2009) and fish quality (Bandarra et al., 2009; Cruz et al., 2009).

We herein aim to explore the existence or lack of differences in seafloor depth ranges of the fishing areas of both scabbardfish species, *A. carbo* and *A. intermedius*, in Madeira (NE Atlantic Ocean). We used a 4-year database (2014–2017) of biological samples using individual total lengths of specimens collected at a depth range of 800–1300 m. We hypothesized that the distribution of total length for both species is similar throughout the seafloor depth range but differs on the proportion of occurrence of each species according to the seafloor depth where they occur. Additionally, we hypothesized that the geographical distribution of both species differs according to distance from the coast (<12 n.m. *vs.* >12 n.m.). The information herein obtained is important for the optimal management of both *Aphanopus* species that constitute the most economically important resource of the Madeiran artisanal fishery.

2. Material and methods

From October 2014 to December 2017, a total of 1662 scabbardfish (1330 *A. carbo* and 332 *A. intermedius*) caught off Madeira and nearby seamounts were sampled every two weeks from the commercial drifting longline fisheries in Port of Funchal, Madeira, NE Atlantic (Fig. 1). From all specimens, individual total length (TL, ±0.01 mm), total weight (TW, ±0.1 g), the total number of dorsal-fin spines and rays, and the total number of pre-caudal and caudal vertebrae were recorded. All sampled specimens from both species, *A. carbo* and *A. intermedius* were identified based on the combination of external (fins' formulae) and internal (vertebral formula) morphological characters following Biscoito et al. (2011).

The Global Positioning System (GPS) positions of each vessel under Vessel Monitoring System control (VMS) were obtained from electronic logbooks of each drifting longline vessel in the study period (2014–2017) (data provided by the Regional Fisheries Department — DRP). Each of the 66 fishing events (5 in 2014, 30 in 2015, 11 in 2016, and 20 in 2017) was spatially plotted using QGIS vs 3.0, and the percentage of each species per fishing event was estimated and assigned to a seafloor depth interval. For further analysis, two fishing areas, namely coastal (fish caught at less than 12 nautical miles, n.m.) and offshore (fish caught greater than 12 n.m.) were established using QGIS v3.0.

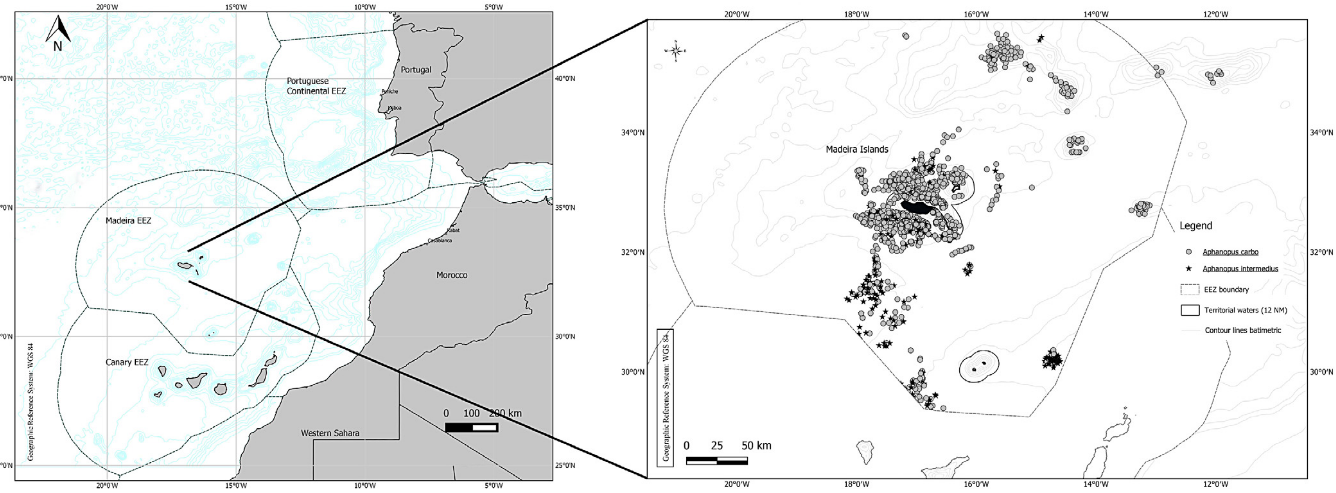

Fig. 1. Map illustrating the geographical distribution of the fishing sets for both *Aphanopus* species, *A. carbo* (grey circles) and *A. intermedius* (black stars), between 2014 and 2017, according to the distance from the coast (<12 and >12 nautical miles).
Source: DRP.

2.1. Data analysis

Data were tested for normality of size distribution and for homogeneity of variance using the Kolmogorov–Smirnov test and the Levene's statistics respectively. All analysis of variance were performed considering the Brown–Forsythe F test, when data were not homogeneous.

All statistical analyses were performed using SPSS v. 24.0 (IBM Corp, 2016).

2.1.1. Occurrence of A. carbo and A. intermedius as a function of seafloor depth

The analysis of occurrence of both *Aphanopus* species by seafloor deep was performed by assigning each data entry to a specific fishing area corresponding to a seafloor depth interval. Five seafloor depths were established considering depth intervals of 1000 m, i.e. (i) <1500 m; (ii) 1500–2500 m; (iii) 2500–3500 m; (iv) 3500–4500 m; (v) >4500 m. The length distribution of the catch is herein analysed with respect to the seafloor depth where longlines were deployed by fishermen at the catching location. Hence, it does not correspond to the depth range of occurrence of each *Aphanopus* species, since longlines are conventionally deployed between 700–1300 m depth. The existence of differences in the occurrence of *A. carbo* and *A. intermedius* according to seafloor depth was tested using Pearson's Chi-square statistics ($p < 0.001$). Additionally, the distribution of *A. carbo* and *A. intermedius* as a function of seafloor depth was plotted dividing the territorial waters in compartments of 10 per 10 km and a density map showing the mean density values in each compartment, covering a search radius of 10 km of the study area was generated using Kernel Density Estimation (KDE) approach (Wolters, 2012).

2.1.2. Size distribution of A. carbo and A. intermedius by seafloor depth

The size distribution of both *Aphanopus* species was evaluated considering the previously described five seafloor depths and four size classes established considering size intervals of 150 mm. The first corresponding to sizes between 900 and 1049 mm, the second from 1050 to 1199 mm, the third from 1200 to 1349 mm and the fourth from 1350 to 1500 mm (Table 1).

The relationship between size and depth gradient of the seafloor for both species was determined using a Pearson χ^2 statistic test ($p < 0.001$). A univariate comparison of the mean size per seafloor depth was performed for each *Aphanopus* species using an analysis of variance (ANOVA). Pairwise comparison was carried out using Tamhane's T2 when variance was not homogeneous and LSD when variance was homogeneous.

Table 1
Number (N) of individuals of both *Aphanopus* species, *A. carbo* and *A. intermedius*, from each of the four size classes (TL) established (900–1049 mm; 1050–1199 mm; 1200–1349 m; 1350–1500 mm), sampled between 2014 and 2017.
Source: DRP.

Species	Size class (mm)	N Fish sampled
Aphanopus carbo	900–1049	17
	1050–1199	27
	1200–1349	663
	1350–1500	623
Aphanopus intermedius	900–1049	2
	1050–1199	77
	1200–1349	179
	1350–1500	74

2.1.3. Distribution of A. carbo and A. intermedius as a function of distance from the coast

The geographic distribution of *A. carbo* and *A. intermedius* in relation to distance from the coast (<12 n.m. *vs.* >12 n.m.) was investigated using a Pearson χ^2 statistic test ($p < 0.001$), for the studied period.

3. Results

A total of 1330 specimens of *A. carbo* (947–1478 mm TL; mean size of 1203 ± 68 mm TL) and 332 of *A. intermedius* (1026–1483 mm TL; mean size of 1272 ± 96 mm TL) were sampled. The sampled data showed a normal distribution ($Z = 1.429$, $p < 0.05$) and a non-homogeneous variance ($W = 88.739$, $p < 0.01$). The mean length of *A. carbo* was significantly smaller than that of *A. intermedius* ($F = 148.873$, $p < 0.05$).

3.1. Occurrence of A. carbo and A. intermedius as a function of seafloor depth

The percentage of occurrence of *A. carbo* and *A. intermedius* varied along the seafloor depth. *A. carbo* was dominant in fishing areas with seafloor depths <4500 m while *A. intermedius* dominated in fishing areas with seafloor depths >4500 m (χ^2 =

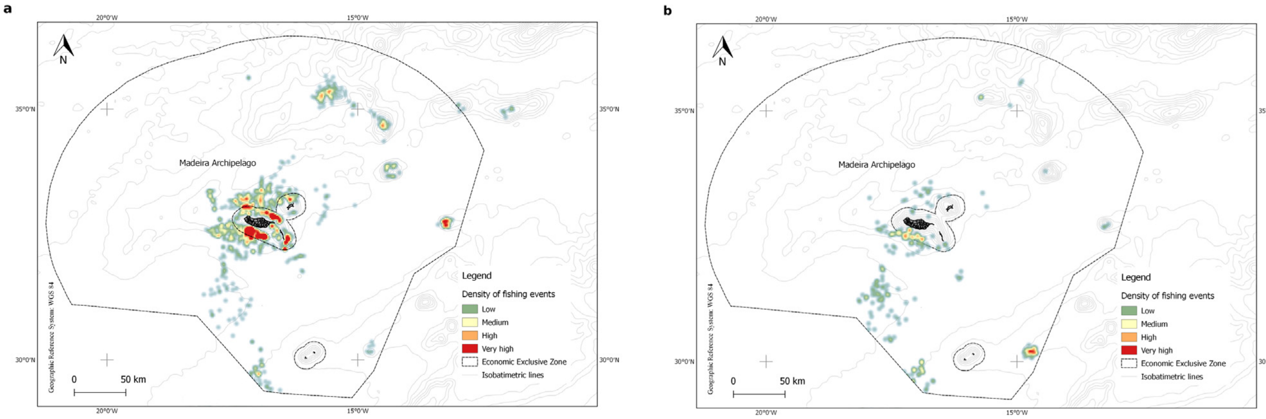

Fig. 2. Kernel Density Estimation (KDE) plot showing the mean density values of both *Aphanopus* species, *A. carbo* (a) and *A. intermedius* (b), per compartment of 10 per 10 km generated for the study area and for the period 2014–2017.
Source: DRP.

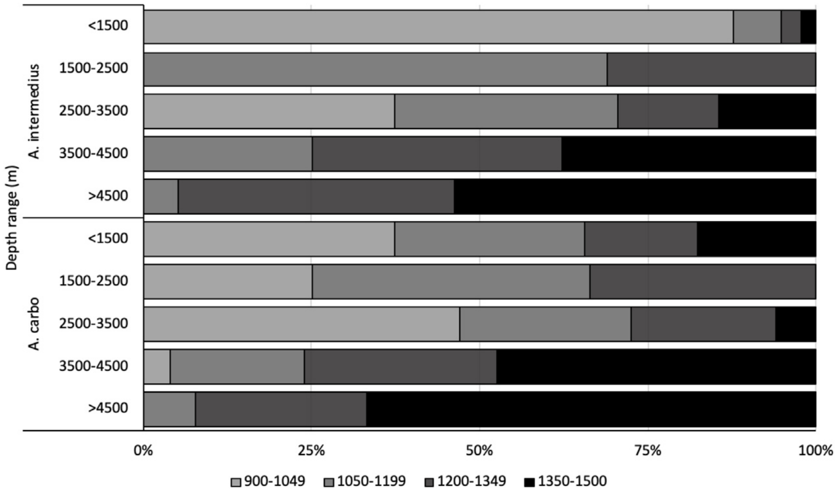

Fig. 3. Proportion of individuals of both *Aphanopus* species, *A. carbo* and *A. intermedius*, from each of the four size classes (TL) established (900–1049 mm; 1050–1199 mm; 1200–1349 mm; 1350–1500 mm) by the five seafloor depths established: <1500 m; 1500–2500 m; 2500–3500 m; 3500–4500 m; >4500 m), between 2014 and 2017.

168.610, $p < 0.001$). In fact, it was evident a decrease in the proportion of *A. carbo* with increasing seafloor depth and the opposite trend for *A. intermedius* with proportion increasing with seafloor depth. According to the KDE map (Fig. 2), the distribution of both *Aphanopus* species showed different cluster spatial patterns.

3.2. Size distribution of A. carbo and A. intermedius by seafloor depth

Size distribution of *A. carbo* along the depth gradient of the seafloor showed that 58.8% of the smaller specimens (900–1049 mm TL) were found at fishing areas with seafloor depths ranging from 2500 to 3500 m (Fig. 3). 61.4% of individuals with 1050 to 1199 mm TL and 69.3% of the individuals with a total length comprised between 1200 and 1349 mm TL were caught at fishing areas with seafloor depths from 2500 to 4500 m (Fig. 3). 81.5% of the largest specimens (1350–1500 mm TL) appeared at fishing areas with seafloor depths greater than 3500 m (Fig. 3). The differences in size distribution per seafloor depth were statistically significant ($\chi^2 = 76.012$, $p < 0.001$).

The size analysis of *A. carbo* per seafloor depth showed that the mean length varied from 1187 ± 66.84 mm in fishing areas with seafloor depths <1500 m to 1269 ± 73.87 mm in fishing areas with greater depths (>4500 m). In seafloor with depths between 1500 m and 3500 m, mean size of *A. carbo* was similar, contrarily to the mean size from fishing areas at greater seafloor depths (>3500 m) where the largest sampled specimens were caught ($F = 24.273$, $p < 0.001$).

Concerning *A. intermedius*, a similar pattern was observed, with smaller individuals being more commonly caught at fishing areas with lower seafloor depths. Most individuals with sizes ranging from 1050 to 1199 mm TL (78.4%) were found at fishing areas with seafloor depths between 2500 and 4500 m, while 71.5% of specimens with size ranging from 1200 to 1349 mm TL were caught at fishing areas with depths greater than 3500 m. 79.2% of the largest specimens (1350–1500 mm TL) were found in the deepest seafloors (>3500 m). For this species, differences in size distribution were also statistically significant ($\chi^2 = 66.165$, $p < 0.001$).

The mean length of *A. intermedius* showed a similar trend to *A. carbo* varying between 1202 ± 105.24 mm in seafloors with depths <1500 m and 1316 ± 71.23 mm in seafloors depths >4500 m. Significant differences were found in mean size among the seafloor depth ranges ($F = 12.113$, $p < 0.001$). The mean size of *A. intermedius* was less variable in seafloors with depths <3500 m contrarily to the size of the specimens caught in fishing areas at greater seafloor depths.

Comparing the size distribution of both species, it becomes evident that both for *A. carbo* and for *A. intermedius* the larger specimens are more common in fishing areas with greater seafloor depths. However, *A. intermedius* specimens between 1200 and 1350 mm appear at deeper seafloors than individuals of *A. carbo* with the same size range ($\chi^2 = 188.45$, $p < 0.001$).

3.3. Distribution of *A. carbo* and *A. intermedius* as a function of distance from the coast

A. carbo (64.4%) and *A. intermedius* (86.7%) were both more commonly caught at distances >12 n.m. However, a greater proportion of *A. carbo* (35.6%) was caught closer to the coast (<12 n.m.) comparatively to *A. intermedius* (13.3%). The differences in proportions according to distance from the coast were statistically significant ($\chi^2 = 62.061$, $p < 0.001$).

4. Discussion

Both species seems to be segregated by depth range, with larger individuals of both species being more abundant in deeper seafloors (>3500 m). The two *Aphanopus* species (*A. carbo* and *A. intermedius*) display a typical behaviour of species avoiding niche competition, i.e. depth range, and this trend is also discernible in specimens of different size range within the same species, probably to avoid cannibalism from large adults on juveniles and preadults. Also, spatial segregation patterns were found in both species being more pronounced for *A. intermedius* where >86% of individuals were collected offshore (>12 n.m.) in fishing areas with greater seafloor depth (>3500 m). Such horizontal segregation of the available niches by these two sympatric species can be seen in the context of both foraging and predation-risk avoidance in a coastal and offshore competition.

Deep sea ecosystems are, by nature, oligotrophic, with scarcity of food and food availability in extensive areas of these oceanic systems (Tyler, 2003). Most of the food comes from the rain of detritus, mostly decaying remains of microbes, algae, plants and animals from the upper zones of the ocean (Morel et al., 2010; Westberry et al., 2012). The oligotrophy of deep sea greatly determines the whole life cycle of species, i.e. reproduction strategy and ontogenic development, among others (Sánchez-Hernández et al., 2017). One of the most extensive strategies adopted by deep sea species is niche segregation, where different size-ranged specimens of the same species avoid occupying the same physical space, especially concerning juvenile and preadult stages (Suding, 2001). This behaviour may be explained by the occurrence of cannibalism or even predation from similar species in size and food habits (Reif et al., 2018), however, to our knowledge no previous studies have addressed this issue in deep ocean though extensive literature published in marine iconic species such as seabirds (e.g. Paiva et al., 2018) and mammals (e.g. Kiszka et al., 2011).

The two studied species showed this avoiding strategy between them, i.e. predation from *A. carbo* to *A. intermedius* and vice versa, and also within each species where different niches are occupied by small size-ranged species compared to large-sized adults. Although the present study is based on seafloor depths, and not depth ranges where these species were caught by longlines, a consistent trend was observed concerning the size of both targeted species. The larger size individuals of both species tend to occupy consistently the deeper sections of the water column, this may be explained metabolically. Large-sized adults have a lower relationship area-volume that implies lower metabolism in a limiting environment, i.e. food scarcity, low temperatures and high hydrostatic pressure, as the deep sea. These individuals manage to inhabit there in a better fitness than juveniles and small-ranged adults, e.g. preadults. Life-history theory suggests that small short-lived species allocate more energy to reproduction than large long-lived species since they are likely to spawn several times during their lifespan (Stearns, 2000). However, a high variety of reproductive patterns have been observed among fishes, and the reproductive effort – proportion of the available resources invested in reproduction – varies depending on the species size, longevity and environmental variations that affect the feeding, metabolism and mortality rates (McBride et al., 2015; Olsson and Gislason, 2016). Moreover, in order to avoid energy constraints, some species show migratory patterns during the reproductive season, as occurs with both studied species (*A. carbo* and *A. intermedius*) (Delgado et al., 2013; Vasconcelos et al., 2019).

In the present study, a vertical niche segregation has been shown between both species, being *A. carbo* more abundant in seafloors with shallower depths (<2500 m) that showed shorter body size compared to *A. intermedius*. However, both species display the same behaviour regarding body sizes with shorter individuals (<1.200 mm) in shallower seafloors and larger specimens overwhelmingly dominated assemblages from deeper seafloors (>2500 m), even more accentuated in *A. intermedius* with 79% of large-sized individuals in fishing areas with >3500 m depth. The segregation of both species is also spatial, though both species are more abundant in areas far from the coast. It has been observed a clear dominance of *A. intermedius* in offshore areas (>12 n.m. from the coast) compared to *A. carbo*, more abundant in coastal areas (<12 n.m.).

Fishery exploitation also plays an important role in the spatial distribution of *A. carbo* and *A. intermedius* assemblages (Vasconcelos et al., 2019). The intensive fishing of these target species caused an overall decrease in their yields, making the fishing vessels go further away from the regular fishing grounds, leading to a progressive geographical expansion of the fishery (Delgado et al., 2018; Vasconcelos et al., 2019). Nowadays, and since at least the last five years, this fishery is fishing as far as the Southern Azores Seamount Chain and the Canaries Economic Exclusive Zone (Delgado et al., 2018). By determining the common depth and specially segregation of these species, populations in the NE Atlantic can be better monitored and managed. We herein outline biological data on both *Aphanopus* species, specifically concerning their vertical distribution per seafloor depth in fishing areas off Madeira and other Macaronesian archipelagos, e.g. the Canary Islands. This information is of paramount importance to develop integrative management actions that may enable a sustainable fishing of these stocks in the study region. As deep stocks, these species are vulnerable to fishing pressure with an uncertain potential recovery. Hence, management measures are urgently needed to be implemented in Madeira for stock conservation in the medium and long term, e.g. the establishment of a spatial and temporal season during the spawning period. Further conservational studies focusing on these two commercial species (*A. carbo* and *A. intermedius*), based on the spatial distribution of individuals with different maturity stages during spawning (coastal aggregations) and non-spawning periods, are ongoing (e.g. Vasconcelos et al., 2019).

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