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Reproduction and growth of *Aphanopus carbo* and *A. intermedius* (Teleostei: Trichiuridae) in the northeastern Atlantic

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Summary

Commercial fishery landings of the black scabbardfish, *Aphanopus carbo,* from the Madeira mid-water drifting longline fleet (northeastern Atlantic) were studied for 2 years within a Portuguese government programme for fishing management. The process noted that 20% of the total catch corresponded to the intermediate scabbardfish, *Aphanopus intermedius*. Length-frequency distribution, and age, growth and reproduction of both species were analysed and compared. The results revealed significant differences in age and growth in influencing the length-frequency distributions. Intermediate scabbardfish attained the largest size (148 cm TL) and age (15 years). However, the two species had similar reproductive strategies. According to data published on *A. carbo* in this region, it is thought to be very likely that previous studies unintentionally mixed both species together in their analyses.

Introduction

The black scabbardfish, *Aphanopus carbo* Lowe, 1839, is a deep-water benthopelagic species that rises in the water column at night. It has been captured between depths of 200 and 1700 m, although is most abundant at 700–1300 m. *A. carbo* is usually caught at shallower depths on the continental shelf and at deeper depths on the island slopes (Nakamura and Parin, 1993; Morales-Nin and Sena-Carvalho, 1996). Due to the growing commercial importance of the fisheries of deep-water species, in recent years there has been an increase in studies on fishery ecology and biological parameters (Howe et al., 1980; Martins et al., 1989; Martins and Ferreira, 1995; Morales-Nin and Sena-Carvalho, 1996; Kelly et al., 1998; Machado et al., 1998, 2001; Lorance and Dupouy, 2001; Morales-Nin et al., 2002; Figueiredo et al., 2003; Gordo, 2009; Machete et al., 2010; Santos et al., 2013). Some indicators suggest that the abundance of this resource is declining in some areas of the northeast Atlantic (Lorance and Dupouy, 2001; ICES, 2008; Machete et al., 2010). Although there are no studies that correlate this decrease with the increase in fishing pressure on *A. carbo* in the North Atlantic, it is possible that the status of the resource is being affected by juveniles and immature fish being caught before they move to reproduction areas off Madeira, the Canary Islands and the northwest coast of Africa (Figueiredo et al., 2003; Pajuelo et al., 2008; Perera, 2008; Vieira et al., 2009). On the basis of otolith microchemistry, Swan et al. (2003) found that there is a single stock in the northeastern Atlantic. The study of the reproductive strategy of *A. carbo* performed by Santos et al. (2013), highlighted a large scale dispersal of this species in the northeast Atlantic with a geographical quasi-complete separation of the immature and mature individuals being the only known spawning grounds of this species located off the Madeira and the Canary islands. These authors suggested that this species needs to be treated as a highly migratory species and managed as a single population. Conversely, Gordo et al. (2009) determined variations in age and growth, otolith shape, parasites and contaminants among Azores, Madeira and mainland Portugal populations.

Using mtDNA analyses, Stefanni and Knutsen (2007) detected the presence of a sympatric species in the Azores, the intermediate scabbardfish, *A. intermedius* Parin, 1983. This led to a joint project among researchers from the Azores, Madeira and Canary Islands aimed at investigating the occurrence of intermediate scabbardfish in central and northeastern Atlantic waters. Specimens from the above-mentioned archipelagos, Morocco, the Western Sahara and mainland Portugal were analysed in terms of genetic and morphological features (Biscoito et al., 2011). The study demonstrated that the distribution range of black scabbardfish extends southwards to at least 27°N, off the Western Sahara coast, while the northern distribution limit of the intermediate scabbardfish is in Azorean waters. The authors concluded that the intermediate scabbardfish is more common in northeastern Atlantic waters than previously believed (Biscoito et al., 2011). So why haven't they been separated in the landings? Basically, there are no conspicuous external characteristics that differentiate the two species (Nakamura and Parin, 1993; Parin, 1995; Biscoito et al., 2011), although both species can be identified using the otolith contour (Tuset et al., 2013). Therefore, it is logical that all biological and fishery data currently recorded are in fact a mixture of information on the two scabbardfishes. For these reasons, the research team of the fisheries laboratory of Direção de Serviços de Investigaçãoe Desenvolvimento das Pescas (DSIDP) at Madeira collected, identified and quantified the occurrence of the two scabbardfishes in the Madeira fleet landings over the past two years. The objective of this paper is to provide biological information regarding the reproduction and growth of both species.

Materials and methods

A total of 1525 specimens were sampled between June 2008 and 2010. Samples were taken randomly from the commercial

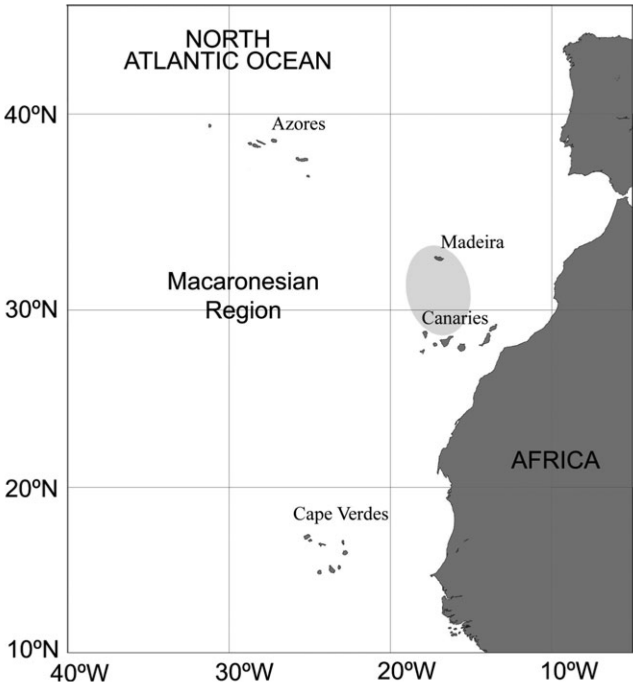

Fig. 1. Geographical origins of studied samples

mid-water drifting longline fishery at Funchal fishing port (Madeira). This fishing fleet includes vessels that operate both near and far from Madeiran waters (Fig. 1). Species were identified based on morphological and meristic criteria following Biscoito et al. (2011). The data analyses were performed for whole samples.

Total length (TL, cm), total weight (TW, g), gutted weight (GW, g) and gonad weight (GNW, g) were recorded for each fish. Relationships between TL-TW and TL-GW were calculated according to the sex using a power function to fit the data (TW or GW = $a\text{TL}^b$). Analysis of covariance (ANCOVA) was used to detect species variations in the relationships.

Sex and maturity stages (MS) were assessed macroscopically using a maturity scale with five stages (Neves et al., 2009): I, immature/resting; II developing; III, pre-spawning; IV, spawning; V, post-spawning. The spawning season was determined according to the monthly changes in the percentage frequency of the maturity stages and the value gonadosomatic index (GSI = 100(GNW/GW)) (West, 1990).

Sagittal otoliths were extracted from 587 black scabbardfish specimens and 134 intermediate scabbardfish specimens. They were cleaned and stored to determine fish age according to Morales-Nin et al. (2002). For ageing, the left otolith of each pair was immersed whole in a 1 : 1 glycerin-alcohol solution. The *sulcus acusticus* was placed downward under a stereomicroscope with a micrometric ocular lens and magnification of 18× using reflected light and a dark background. The posterior region of the whole otolith was selected for reading. Two people with experience in reading otoliths (readers) counted the translucent bands in each otolith independently, and only coincident readings were accepted. The coefficient of variation (CV = SD/mean) was used to measure the precision of the annuli counts, and a paired *t*-test was used to statistically compare differences between readers (Chang, 1982; Campana, 2001). The age of each fish was determined according to the number of annuli, the assumed birth date (1 January, Figueiredo et al., 2003; Vieira et al., 2009) and the sampling date. The von Bertalanffy growth equation was used to describe growth and was fitted to the observed length-at-age to determine the variability in individual growth (Pajuelo et al., 2008). The annual periodicity of the growth increments was determined as explained above (Morales-Nin et al., 2002; Vieira et al., 2009). As there were no juveniles in the samples, the back calculation methodology was applied to estimate fish growth (Francis, 1995). The relationship between otolith radius (OR) and total length (TL) was calculated using a power function, $\text{TL} = a\text{OR}^b$ (Vieira et al., 2009), in a random sample of 100 individuals (50 males and 50 females) for each species. The von Bertalanffy growth model was applied to the back calculated mean length-at-age values (Gayanilo et al., 2005) and the growth parameters were compared using Hotelling's T^2 test (Gordo, 1996).

Results

Population structure

A total of 1238 black scabbardfish individuals and 287 intermediate scabbardfish specimens were identified. Intermediate scabbardfish represented 20% of the landings of the fishing fleet. Black scabbardfish specimens ranged from 99.7 to 140.1 cm TL, and reached a mean size of 118.0 ± 6.6 cm TL; they were mainly caught between 112 and 120 cm TL (Fig. 2). Intermediate scabbardfish individuals varied between 105.4 and 148.0 cm TL, and attained a mean size of 128.3 ± 8.4 cm TL; they were most common from 126 to 136 cm TL (Fig. 2). A comparative analysis of the mean size and length-frequency distributions indicated that there were differences between the two species (U test = −17.30, $P < 0.001$; K-S test = 7.83, $P < 0.01$, respectively). The analysis of size structure by sex and species revealed significant differences in mean size (U test = −16.04 and −5.32, $P < 0.001$ for black and intermediate scabbardfish, respectively) and length-frequency distribution (K-S test = 7.02 and 2.95, $P < 0.001$, respectively), reaching greater lengths in females of both species (Figs. 2b, c).

The overall ratio of males to females was 1 : 1.03 for black scabbardfish and 1 : 1.26 for intermediate scabbardfish. The chi-square test did not show significant differences ($P > 0.05$) from the theoretical 1 : 1 sex-ratio in either species. However, the analysis by size class of black scabbardfish showed significant differences between sexes in all cases, except for the size range 120-124 cm TL. Significant variations were only detected in the highest size class (>134 cm TL) for intermediate scabbardfish. In both species, there was a clear tendency for females to predominate with the increase in size (Fig. 3).

Age and growth

There were no significant differences ($P > 0.05$) between the ages estimated by the two readers (CV = 5.05%, $t = -0.217$ for black scabbardfish; CV = 4.52%, $t = 0.001$ for intermediate scabbardfish) and the agreement percentage varied between 92.6 and 94.5%, respectively. The maximum age for black scabbardfish was 14 years and the population showed a clear bimodal distribution (8 and 11 years) (Fig. 4a). The maximum age for intermediate scabbardfish was 15 years and the population structure was asymmetric bimodal (8 and

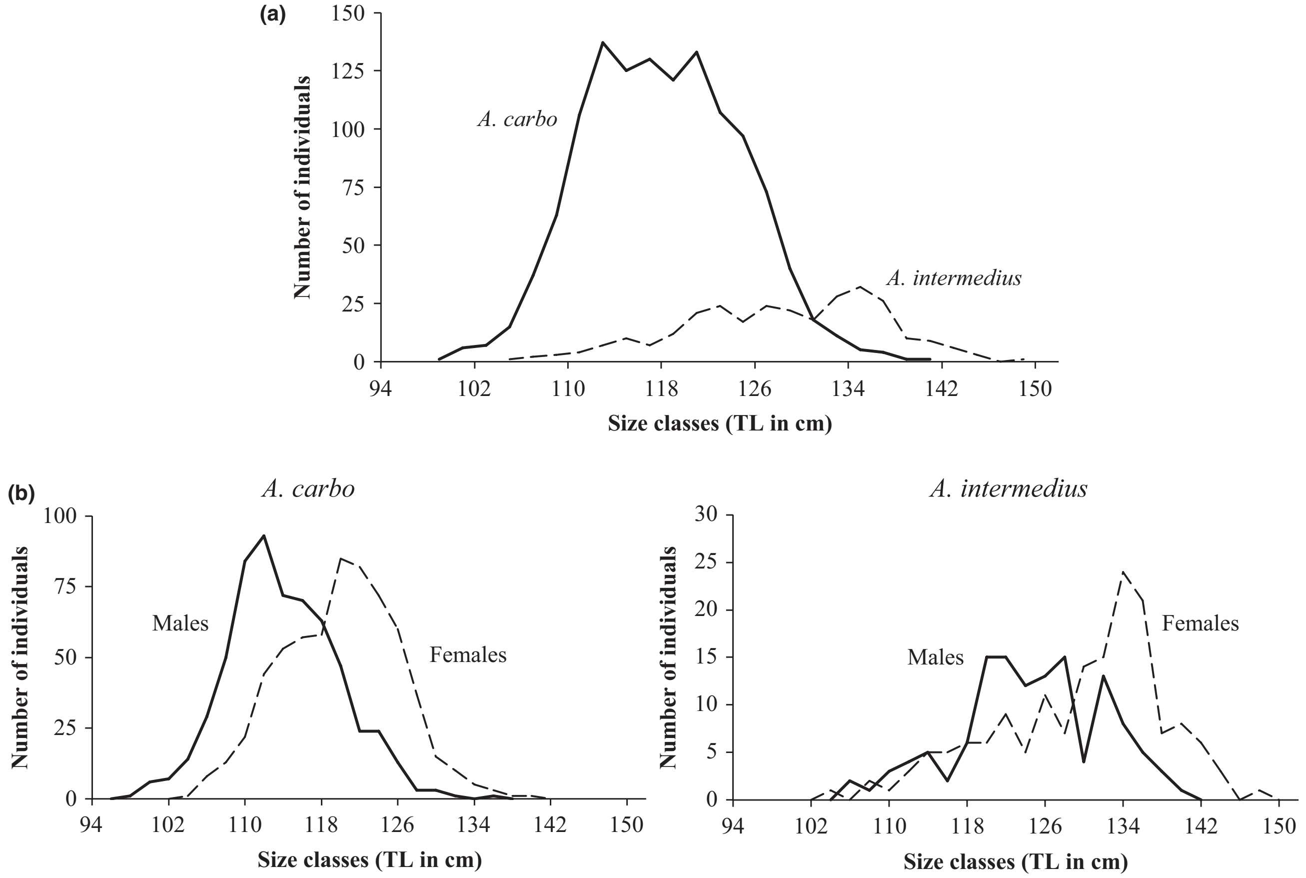

Fig. 2. Length-frequency distribution (a) of black and intermediate scabbardfish, NE Atlantic waters, 2008–2010; (b) by sex for each species

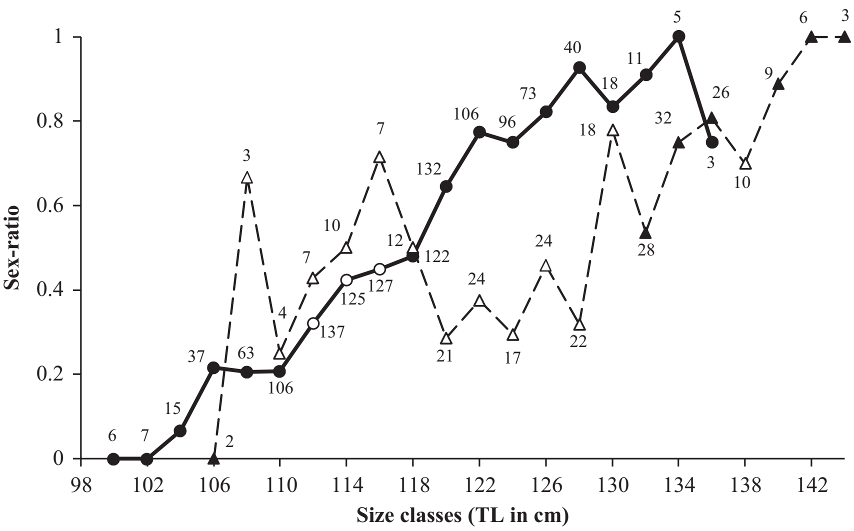

Fig. 3. Variation in sex ratio in relation to size class, black scabbardfish (circle) and intermediate scabbardfish (triangle), NE Atlantic waters, 2008–2010. Black marks, statistically significant differences from a 1 : 1 ratio; white marks, non-significant differences; numbers, no. individuals sampled

12 years), favouring older fish. The mean size by age was higher for intermediate scabbardfish and there were significant differences (*t*-Student, $P < 0.05$) from age 10 years (Fig. 4b).

Female specimens attained greater lengths and had a lower growth rate than males in both species (Table 1). Statistical differences in growth parameters were found by sex for *Aphanopus intermedius* (Hotelling's T^2-test; $T^2 = 21.830$, $P < 0.05$) and for *A. carbo* ($T^2 = 476.449$, $P < 0.05$). Data analysis indicated that intermediate scabbardfish reach a greater length but grow more slowly than black scabbardfish. Comparative analysis of the growth parameters of the two species revealed significant differences ($T^2 = 10.624$, $P < 0.05$).

Length–weight relationships

ANCOVA analyses for TL-TW and TL-GW regressions did not show differences between sexes in either species, thus relationships were calculated for all individuals. The comparative analyses showed differences between species: black scabbardfish had a greater total weight ($F = 21.624$, $P < 0.001$) and

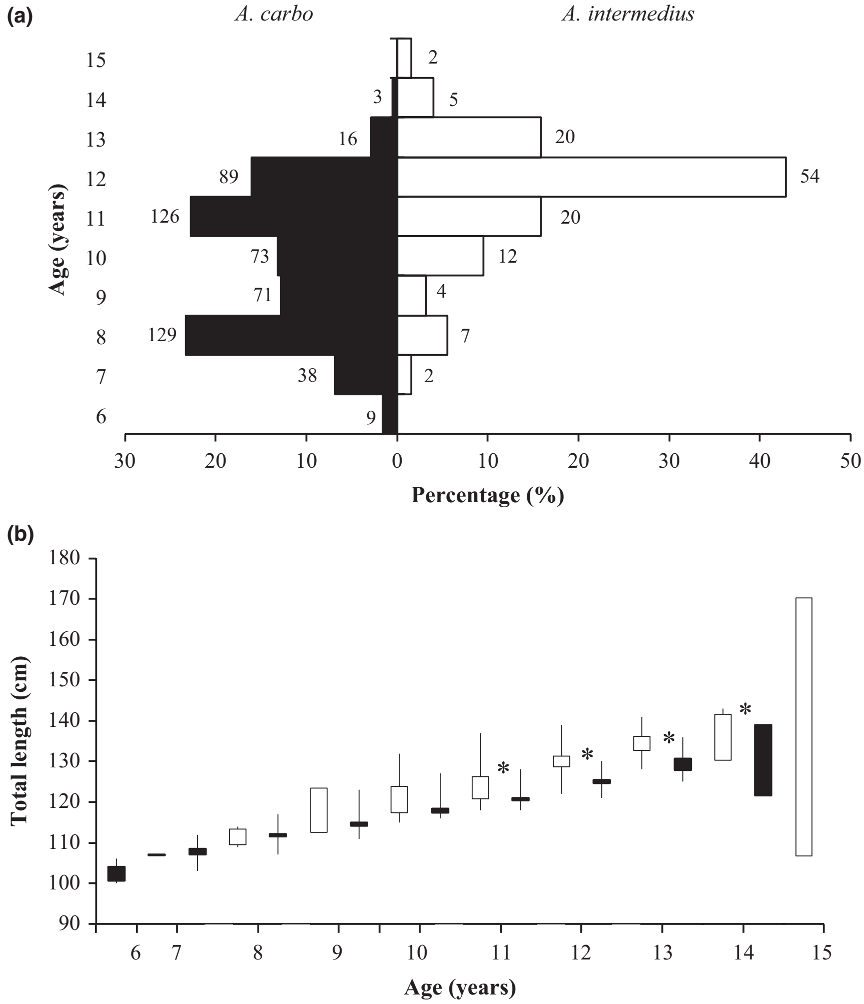

Fig. 4. Age-frequency distribution, (a) black and intermediate scabbardfish and (b) box-plot of total length by age for black scabbardfish (dark) and intermediate scabbardfish (white), NE Atlantic waters, 2008–2010. *indicates statistically significant differences of mean size by species; numbers, no. individuals sampled

Table 1
Von Bertalanffy growth parameters (and errors) by sex, black scabbardfish and intermediate scabbardfish, NE Atlantic waters

Species	Sex	L_∞ (cm)	k (years^{-1})	t_0 (years)	R^2
Black scabbardfish	Males	131.9 (4.7)	0.166 (0.025)	−3.078 (0.510)	0.979
	Females	136.2 (4.8)	0.153 (0.025)	−4.183 (0.667)	0.979
Intermediate scabbardfish	Males	136.5 (3.5)	0.143 (0.017)	−4.950 (0.551)	0.990
	Females	147.6 (3.7)	0.121 (0.012)	−4.703 (0.410)	0.994

Table 2
Length–weight relationships, black scabbardfish and intermediate scabbardfish, NE Atlantic waters

Species	Sex	Equation	r^2	ANCOVA test
Black scabbardfish	Males	$TW = 0.002TL^{2.869}$	0.728	*TL-TW*
		$GW = 0.003TL^{2.825}$	0.734	$F = 0.415$, $P = 0.519$
	Females	$TW = 0.002TL^{2.937}$	0.692	*TL-GW*
		$GW = 0.005TL^{2.722}$	0.705	$F = 1.087$, P = 0.297
	Total	$TW = 0.001TL^{3.004}$	0.763	
		$GW = 0.003TL^{2.837}$	0.770	
Intermediate scabbardfish	Males	$TW = 0.019TL^{2.439}$	0.723	*TL-TW*
		$GW = 0.022TL^{2.393}$	0.733	$F = 0.315$, P = 0.575
	Females	$TW = 0.012TL^{2.538}$	0.774	*TL-GW*
		$GW = 0.019TL^{2.435}$	0.797	$F = 0.068$, P = 0.794
	Total	$TW = 0.011TL^{2.559}$	0.775	
		$GW = 0.015TL^{2.472}$	0.791	

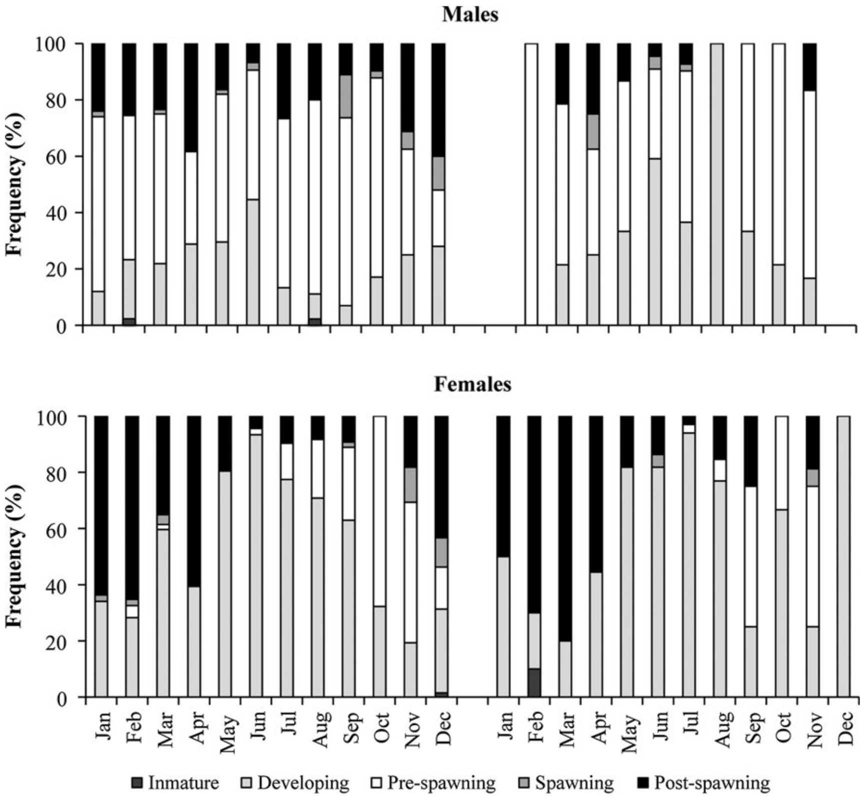

Fig. 5. Monthly variation of maturity stages, (left) black scabbardfish; (right) intermediate scabbardfish, NE Atlantic waters, 2008–2010

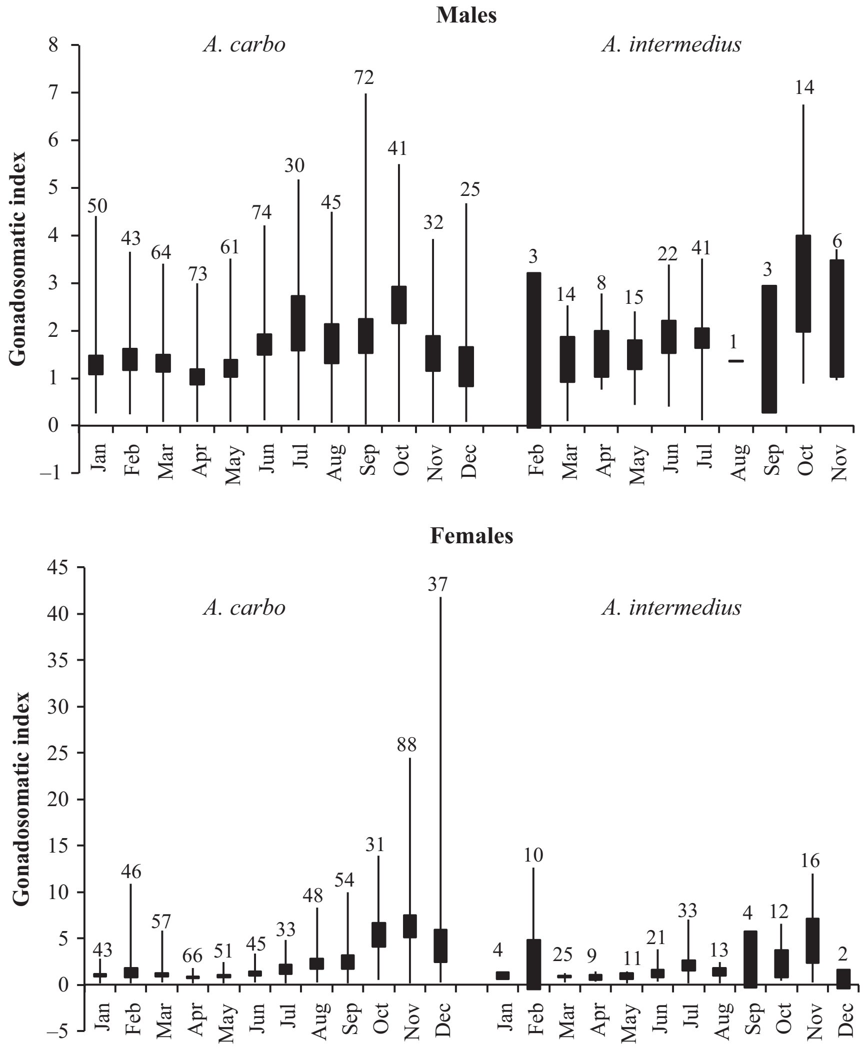

Fig. 6. Box-plots of monthly variation of gonadosomatic index by sex, black and intermediate scabbardfish, NE Atlantic waters, 2008–2010. Numbers, no. individuals sampled

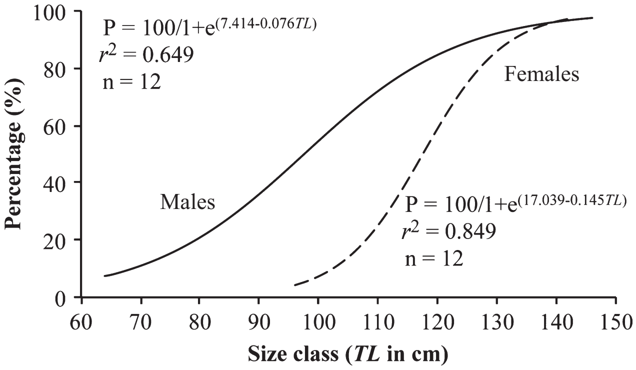

Fig. 7. Theoretical curve of sexual maturity, male and female black scabbardfish, NE Atlantic waters, 2008–2010

gutted weight ($F = 17.052$, $P < 0.001$) than intermediate scabbardfish for the same length (Table 2).

Reproduction

Developing and mature males were found throughout the year in both species. Their gonad weight, and therefore the spermatozoa reserve, increased before the females were mature. However, females in the developing stage were mainly observed between July and September and in the mature stage from October to December (Fig. 5). The GSI showed highest values between September and February (Fig. 6). The sizes at first sexual maturity for black scabbardfish were 97.6 cm TL in males and 117.5 cm TL in females, and the determination coefficient (r^2) was very low for males and high for females (Fig. 7). The maturity ogives were not estimated for intermediate scabbardfish due to the low number of individuals.

Discussion

Our results showed clear differences between both species in the length-frequency distribution and growth. In this context, it is highlighted that the length-frequency distribution of black scabbardfish differs from those previously found in Madeiran waters by Morales-Nin and Sena-Carvalho (1996) and Figueiredo et al. (2003).

Scabbardfishes grow relatively quickly during the first two years of life, attaining approximately 54-70% of their maximum length, whereupon growth slows (Morales-Nin and Sena-Carvalho, 1996; Morales-Nin et al., 2002; Pajuelo et al., 2008; Vieira et al., 2009; present study). The results indicate that the growth rate is higher in black scabbardfish, the deeper-swimming species. Theoretically, deep-sea benthic and benthopelagic fishes have lower metabolic rates due to less oxygen, lower temperature and availability of food (Martini, 1998; Drazen and Seibel, 2007). However, black scabbardfish seems to be adapted to a strong activity of migrating upward at night to feed on crustaceans, cephalopods and benthopelagic, mesopelagic and pelagic fish (Howe et al., 1980; Ehrich, 1983; Mauchline and Gordon, 1984; Pshenichny et al., 1986; Figueiredo et al., 2003; Tuset et al., 2010). Some studies on deep species have noted similar variations linking nocturnal activity to forage, which implies higher energy consumption and faster growth (Duarte et al., 1997; Colmenero et al., 2010).

Studies have shown that the black scabbardfish carries out its sexual cycle throughout the NE Atlantic. Immature and non-productive specimens predominate in the British Isles and French and Portuguese continental waters, while mature and larger specimens are found in Macaronesian waters (Figueiredo et al., 2003; Pajuelo et al., 2008). Vieira et al. (2009) showed in an in-depth analysis that only 16.5% of males and 6% of females inhabiting mainland Portuguese waters were over the size of maturity. Neves et al. (2009) suggested that individuals in better condition may migrate, and that fish in poorer condition might remain in continental waters. In this case, fish might interrupt their reproductive development in successive years, increasing in length and not spawning, as also occurs, for example, in sea bass (Pawson et al., 2000). This implies that there are two clusters of adult specimens in Atlantic waters that can be clearly differentiated: one group would show somatic growth influenced by reproduction, and another group would show continuous growth. However, in any case, there would be a genetic flow between them and the survival of the species would depend on the reproductive stock.

On the basis of the current biological information, there is no support for the idea that there are different stocks in NE Atlantic waters (Gordo et al., 2009). We think that results from previous studies may be biased due to an unintended mixing of the two species. We support this hypothesis for several reasons: first, samples were collected from the entire fishing fleet that operates both near and far from Madeiran waters. Secondly, fish sizes were smaller than in other geographical areas such as the Azores (Vinnichenko, 1998; Machete et al., 2010), the Canary Islands (Pajuelo et al., 2008), and other areas of the North Atlantic (ICES, 2006). However, according to the literature the maximum size of the black scabbardfish has not changed in recent years (Morales-Nin and Sena-Carvalho, 1996; Figueiredo et al., 2003; Vieira et al., 2009). And finally, a genetic study with Madeira samples showed greater differentiation-sharing with specimens of the Portugal coast and Hatton Bank (Quinta et al., 2004). Nevertheless, new studies will be necessary to assert or reject this hypothesis.

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