Biological features of nine deep-water fishes from the midslope of the Northwest African coast

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ARTICLE INFO

ABSTRACT

The size distribution, sex ratio, spawning activity, and maturity of *Alepocephalus bairdii*, *Alepocephalus productus*, *Alepocephalus rostratus*, *Bathygadus favosus*, *Bathygadus melanobranchus*, *Nezumia aequalis*, *Mora moro*, *Trachyscorpia echinata* and *Hoplostethus mediterraneus* inhabiting the middle slope off Northwest Africa were analysed. Maturation takes place during the winter months, when a high proportion (>62%) of large individuals were observed in the mature, spawning or postspawning stage, with the exception of *H. mediterraneus* (57.3%). Negative allometric growth was recorded as a general pattern in both sexes, but isometric growth was recorded in females of *A. productus*, *A. rostratus*, and *B. melanobranchus*. Positive allometric growth was only observed in females of *T. echinata*. The length frequency distribution showed significant differences between sexes, except in *A. productus* and *A. bairdii*. Females of Macrouridae species were found to be larger and heavier than males. Sex ratios were generally unbalanced, but no bias was observed in *N. aequalis*, *T. echinata,* and *H. mediterraneus*. Relative size at sexual maturity ranged mainly between 0.66 and 0.72, but *B. favosus*, *H. mediterraneus,* and *N. aequalis* showed lower values (0.54–0.61). Sexual maturity is reached mainly at a size between 1 and 5 cm smaller in males than in females, except in *A. bairdii* and *T. echinata*.

1. Introduction

Coastal upwelling systems are located along the northwestern coast of Africa, which constitutes one of the main eastern coastlines of the world (Eberwein and Mackensen, 2006). This upwelling system is characterized by its singular hydrography and productivity and its ability to support high biomasses of marine populations, which makes this area one of the most important and productive fishing areas of the world (Arístegui et al., 2009). Catches on the northwestern coast of Africa reach more than 2 million tons per year, representing more than 70% of the average catches of small pelagic species (FAO, 2018). The FAO State of the Fisheries estimated in 2015 that only 63% of pelagic stocks were considered biologically sustainable (Lakhnigue et al., 2019). Of the 27 demersal stocks, the majority are fully exploited, and 13 stocks are overexploited (FAO, 2020).

Coastal benthic and coastal pelagic species are the main target resources due to their generally elevated market value and have shown a general decreasing trend in catches since 1999 (FAO, 2018, 2020; Lakhnigue et al., 2019). These resources are fished by artisanal and industrial fleets of seiners, trawlers, and longliners in a multipurpose fishery, with a high number of benthic species caught as bycatch of other fisheries (FAO, 2018, 2020). However, as deep benthic species are secondary resources in the area, published information is scarce (Pajuelo et al., 2016). A relatively small number of studies have examined the deep-sea fish community and its relationships with the environmental conditions in the area (Merrett and Marshall, 1981; Merrett and Domanski, 1985a,b; Bianchi, 1992a,b; Pajuelo et al., 2016). Most of these studies have focused on the fish community in the upwelling areas of Cape Blanc, Cape Bojador or Cape Juby (Merrett and Marshall, 1981; Merrett and Domanski, 1985a,b; Bianchi, 1992a,b). In these areas, the main fish fauna is composed of species of Alepocephalidae such as *Alepocephalus bairdii* (Goode & Bean, 1879), *Alepocephalus productus* (Gill, 1883), and *Alepocephalus rostratus* (Risso, 1820); species of Macrouridae such as *Bathygadus favosus* (Goode & Bean, 1886), *Bathygadus melanobranchus* (Vaillant, 1888) and *Nezumia aequalis* (Günther, 1878); species of

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Moridae such as *Mora moro* (Risso, 1810); species of Sebastidae such as *Trachyscorpia echinata* (Köhler, 1896); and species of Trachichthyidae such as *Hoplostethus mediterraneus* (Cuvier, 1829) (Merrett and Marshall, 1981; Merrett and Domanski, 1985a,b; Pajuelo et al., 2016). However, published information on the biological traits of these species in the Atlantic is scarce.

The main goal of this study is to provide information on the size distribution, length–weight relationship, sex ratio, spawning activity, and maturity of *A. bairdii*, *A. productus*, *A. rostratus*, *B. favosus*, *B. melanobranchus*, *N. aequalis*, *M. moro*, *T. echinata* and *H. mediterraneus*, which are deep-sea species inhabiting the middle slope off Northwest Africa (26 °N–33 °N). This valuable and useful information will support the management of these species in a context where the increase in exploitation of deep-sea fish species must ensure the sustainability of these resources.

2. Materials and methods

Specimens were collected from a total of 1027 hauls during commercial surveys conducted from November 2006 to April 2007 on the Northwest African continental slope (González et al., 2014; Pajuelo et al., 2016). Hauls were performed at depths between 800 and 1515 m, and the mean trawled area was 4.02 km^2 (González et al., 2014; Pajuelo et al., 2016).

Individual fish were sorted on board to the species level. Of the total species caught, only the nine species showing large individuals (> 50% maximum size) in active spawning were studied. The species analysed were *A. bairdii*, *A. productus* and *A. rostratus* (Alepocephalidae); *B. favosus*, *B. melanobranchus* and *N. aequalis* (Macrouridae); *M. moro* (Moridae); *T. echinata* (Sebastidae) and *H. mediterraneus* (Trachichthyidae). For the selected species, a random subsample of individuals was obtained, and four traits from each fish were recorded: total length (TL), total weight (TW), stage of maturity and sex. Total length (TL) was measured to the nearest 0.1 cm, and total weight (TW) was measured to the nearest 0.1 g. The total length was considered for all species, including the grenadiers (Macrouridae) because of the extensive use of different measurements for this group such as head length, preanal length, preanal fin length or total length. Additionally, in the grenadiers, the tip of the tail is frequently missing, and thus the preanal length was also measured from the tip of the snout to the front edge of the anus and used to estimate the total length in incomplete individuals. The sex and the maturity stage of each specimen were ascertained macroscopically using the five-stage scale (immature, resting, maturing, spawning, and postspawning) of Holden and Raitt (1974). Indeterminate individuals corresponding to immature fish with undifferentiated gonads or fish not macroscopically distinguishable were excluded from the analyses by sex.

For each species, a Student's *t* test was used to evaluate the null hypothesis of equality in mean TL and mean TW between sexes using a significance level of 5% and a critical value of $t_{0.05,>100} = 1.984$. Differences in TL distribution between males and females of each species were analysed using the Kolmogorov–Smirnov nonparametric *Z*-test. This test evaluated the null hypothesis of equality in TL distribution between the sexes using a critical value of $Z_{0.05} = 1.36$ (Sokal and Rohlf, 2012). The TL–TW relationship was estimated for males and females of each species using a power equation. The equality of the two TL–TW regressions by sex was tested using an *F* test (Sachs, 1982). This test evaluated the null hypothesis of equality of the two regressions estimated by sex using a critical value of $F_{0.05,1,>1000} = 3.851$ (Sokal and Rohlf, 2012). Differences between the expected value for isometric growth and values of the regression coefficient (*b*) were compared with a *t* test. This test evaluated the null hypothesis $H_0: b = 3$ in the TL–TW relationship

between the sexes with a critical value of $t_{0.05,>100} = 1.984$ (Sokal and Rohlf, 2012). The sex ratio was estimated for the total sample and by size class for each species. The Pearson chi-square goodness-of-fit test was used to evaluate the null hypothesis of equality of frequencies between the sexes using a critical value of $\chi^2_{0.05,1} = 3.84$ (Sokal and Rohlf, 2012). The reproductive period was established following the temporal evaluation of the maturity stages. Length at sexual maturity (TL$_{50}$, the length at which 50% of individuals are in maturity stages III–V) was determined from the relationship between the percentage of individuals in maturity stages III–V and the TL classes. The percentage of mature individuals (P) by length class was fitted to a logistic equation $P = 100/(1+\exp(-c*(TL-TL_{50}))$, where c is the model parameter and TL$_{50}$ is the length at sexual maturity. A Student's *t* test was used to evaluate the null hypothesis of equality in mean TL between individuals with maturity stages I–II and III–V for each sex using a critical value of $t_{0.05,>100} = 1.984$. To compare the results between populations or species studied, the relative size at sexual maturity (R_{SAM}), modified from Charnov (1990), was calculated using the following equation: $R_{SAM} = TL_{50}/TL_{max}$, in which TL$_{max}$ is the maximum size attained by the species.

3. Results

3.1. Alepocephalidae species

A total of 1680 individuals of *A. bairdii*, *A. productus* and *A. rostratus* were collected (Table 1). *A. bairdii* showed the greatest size and weight range. *A. productus* and *A. rostratus* showed similar size and weight ranges (Fig. 1). These differences in size range were also observed by sex (Table 1). In *A. bairdii*, no significant differences were found in mean TL or TW between males and females (TL *t* = 0.428 < $t_{0.05,>100}$ = 1.984, *p* = 0.669; TW *t* = 0.315 < $t_{0.05,>100}$ = 1.984, *p* = 0.753). *A. productus* did not show significant differences in mean TL (*t* = 1.13 < $t_{0.05,>100}$ = 1.984, *p* = 0.258) and TW (*t* = 1.280 < $t_{0.05,>100}$ = 1.984, *p* = 0.201) between males and females. However, *A. rostratus* showed significant differences in mean TL (*t* > 3.77 > $t_{0.05,>100}$ = 1.984, *p* < 0.0001) and TW (*t* > 6.18 > $t_{0.05,>100}$ = 1.984, *p* < 0.0001) between males and females. The *Z*-test did not show significant differences in the TL distribution between sexes for *A. productus* and *A. bairdii* (Z < 0.785 < $Z_{0.05}$ = 1.36, *p* > 0.293). However, the Z-test showed significant differences in the TL distribution between sexes for *A. rostratus* (Z = 2.40 > $Z_{0.05}$ = 1.36, *p* < 0.0001).

For *A. bairdii*, the *F* test for the TL–TW relationship between the sexes did not show a significant difference (*F* = 2.41 < $F_{0.05,1,>100}$ = 3.97, *p* > 0.05). The null hypothesis of equality in the regression coefficient b=3 was rejected (negative allometric growth in all cases) (*t* > 4.24 > $t_{0.05,>100}$ = 1.984, *p* < 0.05) (Fig. 2 and Table 2). However, *A. productus* and *A. rostratus* showed significant differences between the sexes for the TL–TW relationship (*F* test; *F* > 13.09 > $F_{0.05,1,>100}$ = 3.97, *p* < 0.001). In *A. productus*, negative allometric growth was observed for males and all fish but isometric growth was observed for females (*t* test; all, *t* = 5.57 > $t_{0.05,>100}$ = 1.984, *p* < 0.05; males, *t* = 6.50 > $t_{0.05,>100}$ = 1.984, *p* < 0.05; females, *t* = 1.92 < $t_{0.05,>100}$ = 1.984, *p* > 0.05) (Fig. 2 and Table 2). *A. rostratus* showed negative allometric growth for males, but isometry for females and for all fish (*t* test; all, *t* = 0.70 < $t_{0.05,>100}$ = 1.984, *p* > 0.05; males, *t* = 2.79 > $t_{0.05,>100}$ = 1.984, *p* < 0.05; females, *t* = 0.96 < $t_{0.05,>100}$ = 1.984, *p* > 0.05) (Table 2).

In *A. bairdii*, the sex ratio (1:1.03) was unbiased and similar among size classes (χ^2 = 0.07 < $\chi^2_{0.05,1}$ = 3.84, *p* = 0.805) (Fig. 1). In *A. productus* (1:0.73) and *A. rostratus* (1:0.61), a bias towards males over females was observed (χ^2 > 10.23 > $\chi^2_{0.05,1}$ = 3.84, *p* < 0.0001). The sexes were present at the same frequency

Table 1

Number of individuals (N), minimum (min.), maximum (max.), mean total length (TL, cm) and total weight (TW, g) of *Alepocephalus bairdii*, *Alepocephalus productus* and *Alepocephalus rostratus* specimens.

Species	Group	N	Min. TL	Max. TL	Min. TW	Max. TW	Mean TL	Mean TW
Alepocephalus bairdii	all	361	17.2	80.1	47.8	4752.0	55.7	1710.6
	males	176	33.1	79.6	295.8	4400.7	56.1	1714.2
	females	181	32.0	80.1	250.1	4752.0	55.7	1741.7
Alepocephalus productus	all	510	16.3	57.1	30.5	1853.6	41.5	754.7
	males	246	21.3	56.9	80.2	1853.6	44.7	862.8
	females	180	24.3	57.1	102.3	1815.2	45.5	906.7
Alepocephalus rostratus	all	810	16.9	33.8	251.7	1876.4	40.3	950.8
	males	446	28.7	52.7	251.7	1653.1	42.4	891.5
	females	276	29.5	54.6	308.2	1876.4	43.8	1045.7
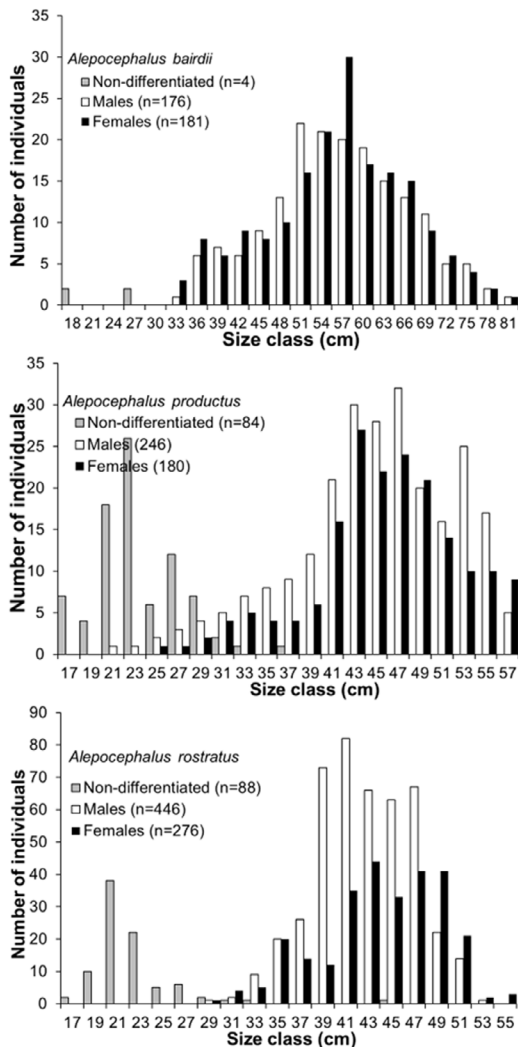
Fig. 1. Size distribution by sex of *Alepocephalus bairdii*, *Alepocephalus productus* and *Alepocephalus rostratus* collected between 800 and 1500 m off Northwest Africa.

in sizes smaller than 33 and 35 cm TL for *A. productus* and *A. rostratus*, respectively ($\chi^2 < 2.78 < \chi^2_{0.05,1} = 3.84$, $p > 0.100$) (Fig. 1). Males were more common than females in sizes from 35–57 cm and 37–55 cm TL for *A. productus* and *A. rostratus*, respectively ($\chi^2 > 8.04 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$).

A high proportion of large individuals of *A. bairdii* (> 69.7%), *A. productus* (> 62.1%) and *A. rostratus* (> 71.3%) in the maturing,

Table 2

Parameters of the TL–TW relationship (TW = a*TL^b) for males, females and all fish. a, intercept; b, regression coefficient (allometric coefficient); s.d., standard deviation; r^2, determination coefficient; t, t test value.

Species	Group	a	b	s.d. (b)	r^2	t
Alepocephalus bairdii	All	0.0313	2.695	0.0451	0.928	6.76[a]
	Males	0.0315	2.689	0.0575	0.939	5.40[a]
	Females	0.0310	2.706	0.0693	0.915	4.24[a]
Alepocephalus productus	All	0.0213	2.776	0.0402	0.953	5.57[a]
	Males	0.0414	2.604	0.0609	0.916	6.50[a]
	Females	0.0153	2.864	0.0705	0.925	1.92
Alepocephalus rostratus	All	0.0127	2.975	0.0356	0.942	0.70
	Males	0.0193	2.859	0.0505	0.888	2.79[a]
	Females	0.0150	2.940	0.0622	0.915	0.96
Bathygadus favosus	All	0.0435	2.542	0.0385	0.905	11.89[a]
	Males	0.1070	2.240	0.0833	0.900	9.12[a]
	Females	0.0659	2.427	0.0437	0.893	13.11[a]
Bathygadus melanobranchus	All	0.0012	3.312	0.0601	0.917	3.52[a]
	Males	0.0266	2.412	0.0873	0.887	6.73[a]
	Females	0.0046	2.969	0.0728	0.879	0.42
Nezumia aequalis	All	0.0071	2.875	0.0357	0.913	3.51[a]
	Males	0.0320	2.435	0.0351	0.928	16.1[a]
	Females	0.0048	3.003	0.0403	0.959	0.74
Mora moro	All	0.0124	2.946	0.0186	0.910	2.95[a]
	Males	0.0304	2.696	0.0288	0.882	10.5*
	Females	0.0197	2.831	0.0269	0.882	6.28*
Trachyscorpia echinata	All	0.0133	3.115	0.0293	0.931	3.90[a]
	Males	0.0023	2.969	0.0382	0.933	0.81
	Females	0.0071	3.282	0.0447	0.925	6.32[a]
Hoplostethus mediterraneus	All	0.1267	2.465	0.0444	0.848	12.04[a]
	Males	0.0501	2.733	0.0494	0.907	5.40[a]
	Females	0.1052	2.548	0.0501	0.893	9.02[a]

[a]Null hypothesis of isometric growth rejected at significance level $\alpha = 0.05$.

spent or postspawning stages was observed from November to March, mainly during the winter months (Fig. 3). The smallest female of *A. bairdii* with ovaries in stages III–V measured 35.9 cm TL, and the smallest reproductive male measured 37.6 cm TL. In *A. productus*, the smallest reproductive female was 35.8 cm TL, and the smallest reproductive male was 35.2 cm TL. In *A. rostratus*, the smallest female with ovaries in stages III–V measured 35.0 cm TL, and the smallest reproductive male measured 34.9 cm TL. The respective TL$_{50}$ for males and females was estimated at 54.0 and 53.3 cm for *A. bairdii*, 39.6 and 40.4 cm TL for *A. productus*, and 37.8 and 39.2 cm TL for *A. rostratus* (Fig. 4). The R$_{SAM}$ was ranged from 0.65–0.68 for *A. bairdii*, 0.70–0.71 for *A. productus*, and 0.71–0.72 for *A. rostratus*.

3.2. Macrouridae species

A total of 1651 individuals of *B. favosus*, *B. melanobranchus* and *N. aequalis* showed wide ranges of sizes and weights (Table 3 and
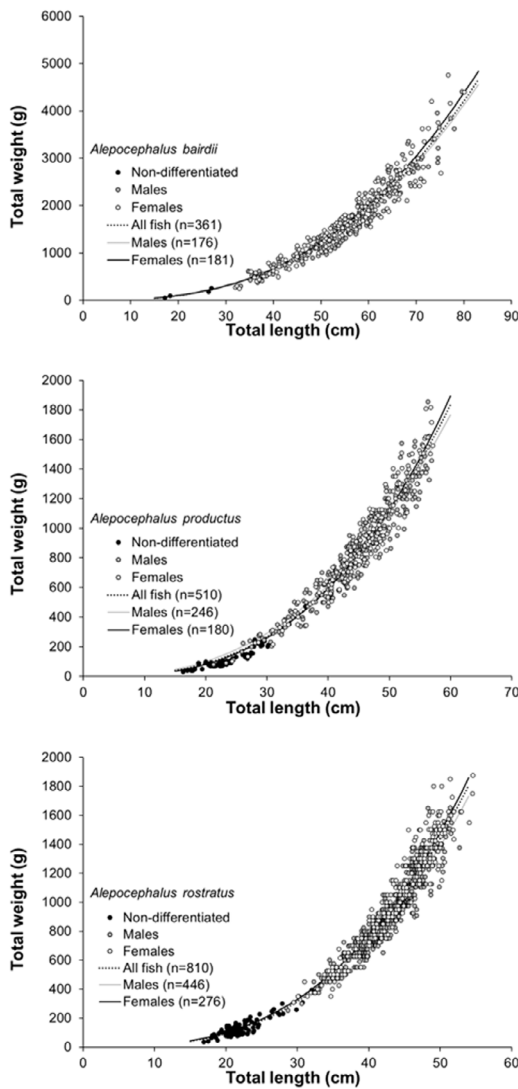
Fig. 2. Length–weight relationship by sex of *Alepocephalus bairdii*, *Alepocephalus productus* and *Alepocephalus rostratus* collected off Northwest Africa. *n*, number of individuals.
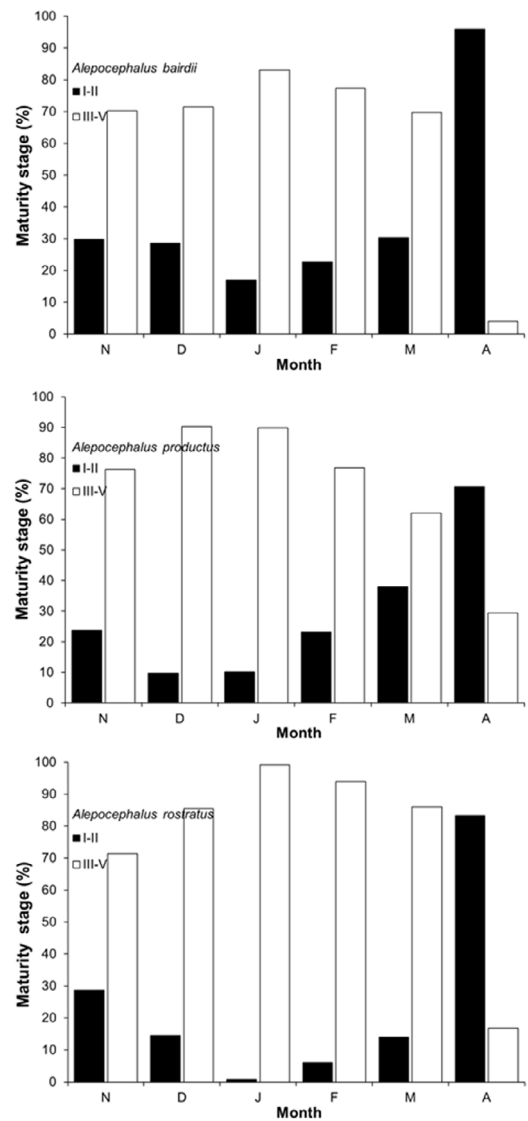

Fig. 3. Maturity stages by month of *Alepocephalus bairdii*, *Alepocephalus productus* and *Alepocephalus rostratus* collected off Northwest Africa.

Fig. 5). Females of *B. favosus*, *B. melanobranchus* and *N. aequalis* were larger and heavier than males. For the three species, significant differences in mean TL and TW between males and females were found (TL, $t > 3.28 > t_{0.05, >100} = 1.984$, $p < 0.001$; TW, $t > 7.34 > t_{0.05, >100} = 1.984$, $p < 0.001$). The Z-test showed significant differences in TL distribution between the sexes for the three macrourids ($Z > 1.878 > Z_{0.05} = 1.36$, $p < 0.002$). The F test for the TL–TW relationship showed significant differences between the sexes for the three macrourids ($F > 14.66 > F_{0.05, 1, >100} = 3.97$, $p < 0.05$). *B. favosus* showed negative allometric growth in all cases ($t > 9.12 > t_{0.05, >100} = 1.984$, $p < 0.05$) (Table 2 and Fig. 6). *B. melanobranchus* showed isometry for females ($t = 0.42 < t_{0.05, >100} = 1.984$, $p > 0.05$) negative allometry for males ($t = 6.73 > t_{0.05, >100} = 1.984$, $p < 0.05$) but positive allometry for all fish ($t = 3.52 > t_{0.05, >100} = 1.984$, $p < 0.05$) *N. aequalis* showed isometry for females ($t = 0.74 < t_{0.05, >200} = 1.96$, $p > 0.05$) bur negative allometry for males and all fish ($t > 3.51 > t_{0.05, >100} = 1.984$, $p < 0.05$) (Table 2 and Fig. 6).

The sex ratio of *B. favosus* (1:4.44) and *B. melanobranchus* (1:2.41) significantly favoured females ($\chi^2 > 61.81 > \chi^2_{0.05, 1} = 3.84$, $p < 0.0001$), but there was no bias in *N. aequalis* (1:1.09) ($\chi^2 = 1.43 < \chi^2_{0.05, 1} = 3.84$, $p > 0.120$). The sexes of *B. favosus*

occurred at the same frequency for size classes smaller than 21 cm ($\chi^2 = 0.41 < \chi^2_{0.05, 1} = 3.84$, $p > 0.500$) (Fig. 5). Females were dominant between 22 and 34 cm TL ($\chi^2 = 71.19 > \chi^2_{0.05, 1} = 3.84$, $p < 0.0001$). Above 34 cm TL, only females of *B. favosus* were observed. In *B. melanobranchus*, males were dominant in size classes smaller than 37 cm TL ($\chi^2 = 28.27 > \chi^2_{0.05, 1} = 3.84$, $p < 0.0001$) (Fig. 5), whereas females were dominant in sizes between 39 and 47 cm TL ($\chi^2 = 50.94 > \chi^2_{0.05, 1} = 3.84$, $p < 0.0001$). Above 47 cm TL, only females of *B. melanobranchus* were observed. Males of *N. aequalis* were dominant in size classes between 21 and 35 cm TL ($\chi^2 = 17.01 > \chi^2_{0.05, 1} = 3.84$, $p < 0.0001$), whereas females were dominant in sizes between 37 and 47 cm TL ($\chi^2 = 59.89 > \chi^2_{0.05, 1} = 3.84$, $p < 0.0001$). Above 39 cm TL, only females were observed (Fig. 5).

High proportions of large individuals of *B. melanobranchus* (> 65.3%), *B. favosus* (> 82.0%), and *N. aequalis* (> 62.6%) were observed in the maturing, spent or postspawning stages from November to April, mainly during the winter months (Fig. 7). The smallest female of *B. favosus* with ovaries in stages III–V measured 21.0 cm TL, and the smallest reproductive male measured 19.8 cm TL. For *B. melanobranchus*, the smallest reproductive individuals
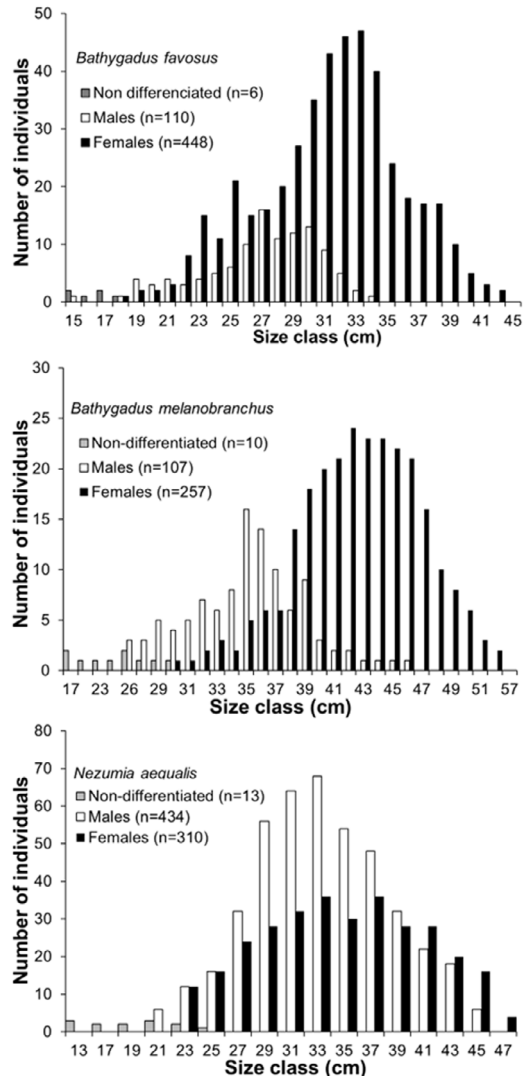
Table 3
Number of individuals (N), minimum (min.), maximum (max.), mean total length (TL, cm) and total weight (TW, g) of *Bathygadus favosus*, *Bathygadus melanobranchus* and *Nezumia aequalis* specimens.

Species	Group	N	Min. TL	Max. TL	Min. TW	Max. TW	Mean TL	Mean TW
Bathygadus favosus	all	564	15.5	43.8	56.0	620.2	30.6	273.3
	males	110	15.5	34.9	56.0	325.0	27.3	181.6
	females	448	18.4	43.8	82.0	620.2	31.6	298.6
Bathygadus melanobranchus	all	374	17.4	54.8	10.2	603.1	40.4	276.5
	males	107	26.4	45.0	61.0	270.2	35.6	147.7
	females	257	30.8	54.8	130.1	600.3	43.3	337.9
Nezumia aequalis	all	757	12.5	47.9	5.7	531.7	33.3	185.5
	males	434	21.5	44.9	41.0	332.0	33.1	166.5
	females	310	22.0	47.9	38.0	531.0	34.4	218.6
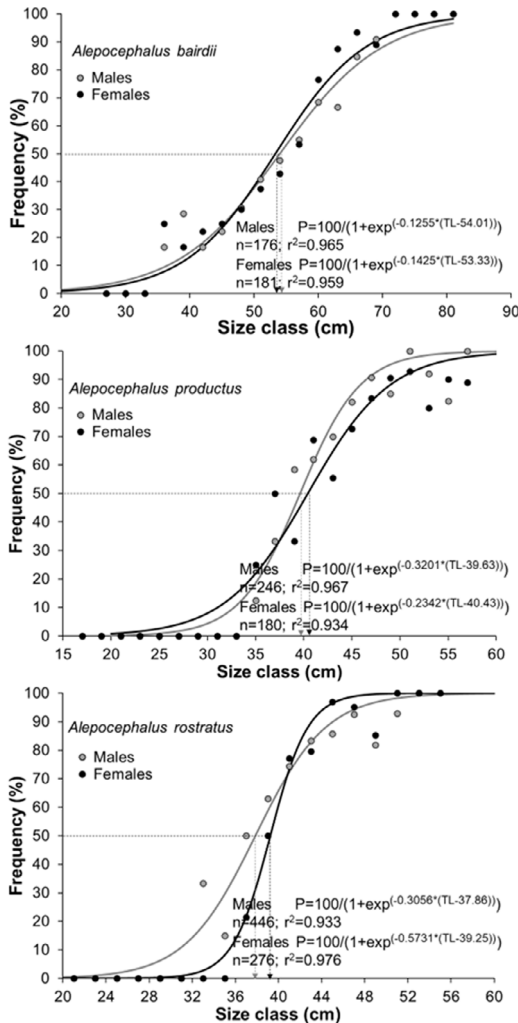
Fig. 4. Ogives of size at first maturity by sex of *Alepocephalus bairdii*, *Alepocephalus productus* and *Alepocephalus rostratus* collected off Northwest Africa. r^2, determination coefficient; n, number of individuals; P, percentage of mature individuals by length class; and TL, total length (cm).
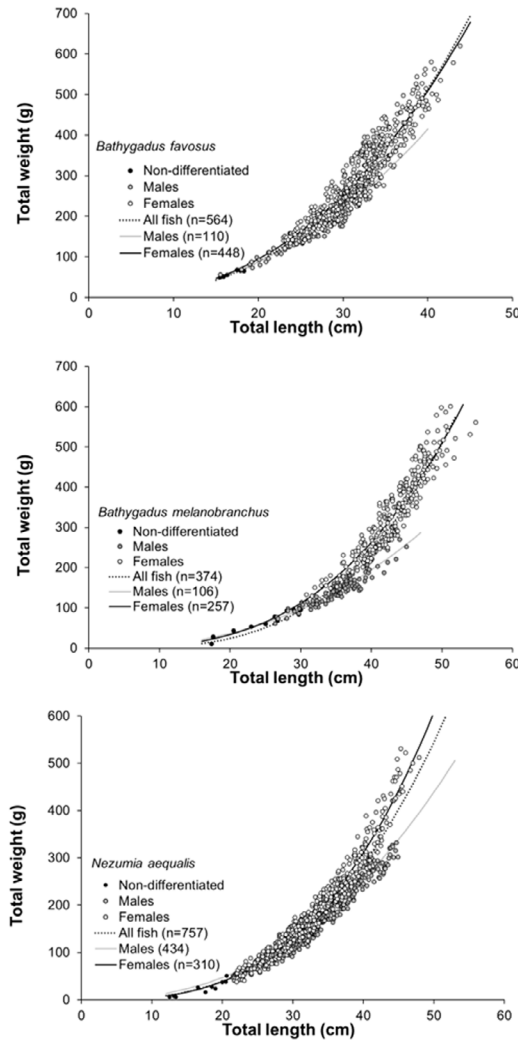

Fig. 5. Size distribution by sex of *Bathygadus favosus*, *Bathygadus melanobranchus* and *Nezumia aequalis* collected between 800 and 1500 m off Northwest Africa.

were 33.0 cm TL (female) and 28.2 cm TL (male), and for *N. aequalis*, the minimum size was 24.3 cm TL (female) and 23.1 cm TL (male). The TL_{50} was estimated as follows: *B. favosus*, 19.7 cm TL (males) and 23.8 cm TL (females); *B. melanobranchus*, 30.5 cm TL (males) and 34.9 cm TL (females); and *N. aequalis*, 27.0 cm TL (males) and 29.4 cm TL (females) (Fig. 8). The R_{SAM} ranged from 0.54–0.56 (*B. favosus*), 0.64–0.68 (*B. melanobranchus*) and 0.60–0.61 (*N. aequalis*).

3.3. Mora moro

A total of 2822 individuals were collected (Table 4, Fig. 9). Significant differences in mean TL and TW were found between males and females (TL, $t = 31.02 > t_{0.05, >100} = 1.984$, $p < 0.0001$; TW, $t = 36.48 > t_{0.05, >100} = 1.984$, $p < 0.0001$). The Z-test showed significant differences in TL distribution between

Table 4
Number of individuals (N), minimum (min.), maximum (max.), mean total length (TL, cm) and total weight (TW, g) of *Mora moro*, *Trachyscorpia echinata* and *Hoplostethus mediterraneus* specimens.
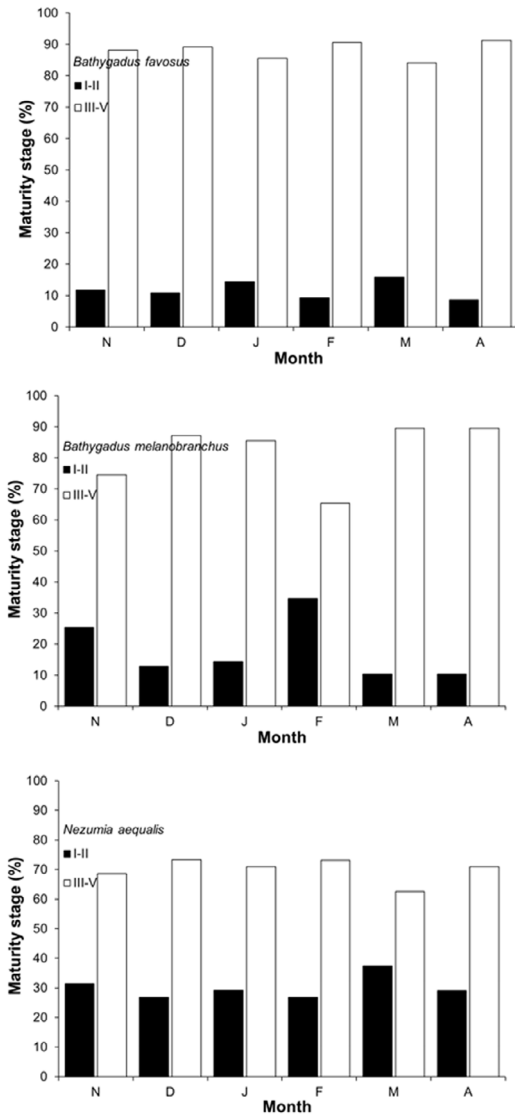
Species	Group	N	Min. TL	Max. TL	Min. TW	Max. TW	Mean TL	Mean TW
Mora moro	all	2822	25.0	61.6	125.3	2753.8	44.5	965.1
	males	1143	25.2	52.8	125.3	2051.2	41.63	728.6
	females	1661	25.6	61.6	201.0	2753.8	47.49	1134.9
Trachyscorpia echinata	all	1193	20.1	60.7	159.2	4501.4	44.9	1971.9
	males	582	20.4	60.7	200.5	4375,0	45.6	2035.9
	females	594	25.3	55.8	375.1	4501.4	44.8	1952.7
Hoplostethus mediterraneus	all	892	10.4	28.3	20.7	509.0	22.9	293.9
	males	429	10.6	28.3	40.6	458.2	22.8	293.8
	females	442	12.3	27.9	50.5	509.0	23.2	305.1

Fig. 6. Length–weight relationship by sex of *Bathygadus favosus*, *Bathygadus melanobranchus* and *Nezumia aequalis* collected off Northwest Africa. *n*, number of individuals.

Fig. 7. Maturity stages by month of *Bathygadus favosus*, *Bathygadus melanobranchus* and *Nezumia aequalis* collected off Northwest Africa.

the sexes ($Z = 12.39 > Z_{0.05} = 1.36$, $p < 0.0001$). The F test for the TL–TW relationship showed significant differences between the sexes in both regressions ($F = 6.70 > F_{0.05,1,>100} = 3.97$, $p < 0.001$). The t test showed negative allometric growth for all cases ($t > 2.95 > t_{0.05,>100} = 1.984$, $p < 0.05$) (Table 2 and Fig. 10).

A high proportion (> 77.1%) of large individuals in the maturing, spent or postspawning stage was observed from November to February (Fig. 11). The sex ratio (1:1.453) showed significant deviation from 1:1 in favour of females ($\chi^2 = 95.69 > \chi^2_{0.05,1} =$

3.84, $p < 0.0001$). Males were dominant in size classes below 43 cm ($\chi^2 = 154.58 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$) (Fig. 9), whereas females were dominant at sizes greater than 45 cm TL ($\chi^2 = 546.71 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$). Only females were observed above 53 cm TL. The smallest female with ovaries in stages III–V measured 33.5 cm TL, and the smallest reproductive male measured 29.9 cm TL. The TL$_{50}$ was estimated at 39.6 cm TL
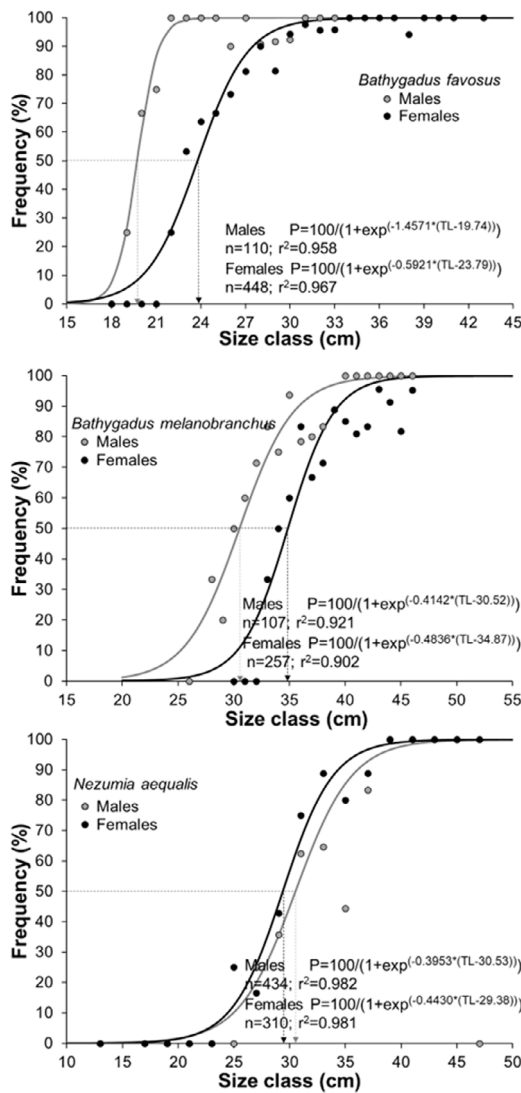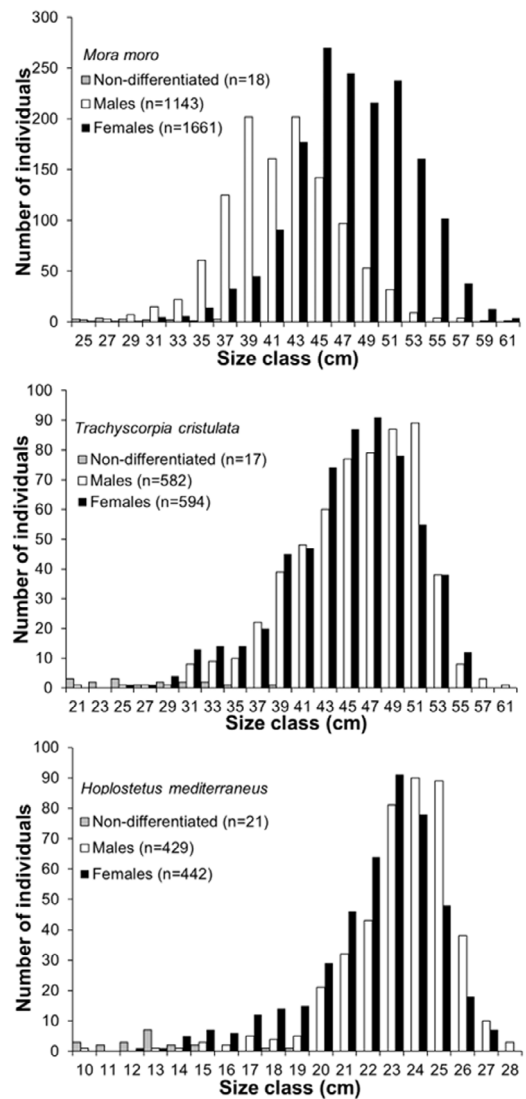
Fig. 8. Ogives of size at first maturity by sex of *Bathygadus favosus*, *Bathygadus melanobranchus* and *Nezumia aequalis* collected off Northwest Africa. r^2, determination coefficient; n, number of individuals; P, percentage of mature individuals by length class; and TL, total length (cm).
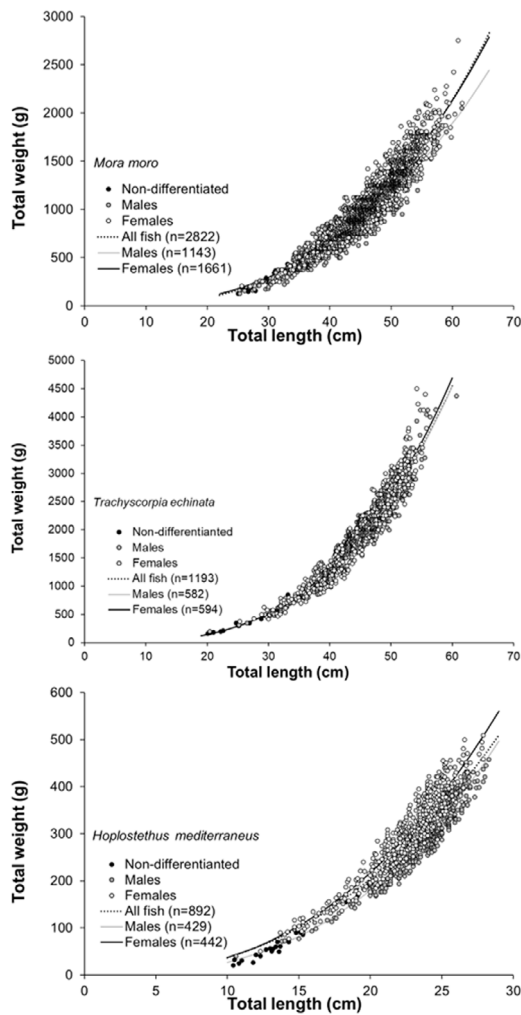

Fig. 9. Size distribution by sex of *Mora moro*, *Trachyscorpia echinata* and *Hoplostethus mediterraneus* collected between 800 and 1500 m off Northwest Africa.

for males ($R_{SAM} = 0.75$) and 44.6 cm TL ($R_{SAM} = 0.72$) for females (Fig. 12).

3.4. Trachyscorpia echinata

A total of 1193 individuals were collected (Table 4, Fig. 9). Significant differences in the mean TL and TW were found between males and females (TL, $t = 2.45 > t_{0.05,>100} = 1.984$, $p = 0.014$; TW, $t = 1.981 > t_{0.05,>200} = 1.96$, $p = 0.048$). The Z-test shows significant differences in TL distribution between the sexes ($Z = 1.61 > Z_{0.05} = 1.36$, $p = 0.011$). The F test for the TL–TW relationship did not show significant differences between the sexes in either regression ($F = 1.91 < F_{0.05,1,>100} = 3.97$, $p > 0.05$). The null hypothesis of equality in the regression coefficient (H_0: b=3) was rejected (positive allometric growth was observed in all cases and females) (all, $t = 3.90 > t_{0.05,>100} = 1.984$, $p < 0.05$; females, $t = 6.32 > t_{0.05,>100} = 1.984$, $p < 0.05$) and isometric for males (males, $t = 0.811 < t_{0.05,>100} = 1.984$, $p > 0.05$) (Table 4 and Fig. 10).

The sex ratio (1:1.02) was not significantly different from 1:1, and the null hypothesis of equal frequencies between the sexes

was accepted ($\chi^2 = 0.12 < \chi^2_{0.05,1} = 3.84$, $p = 0.738$). The sexes showed equal frequencies among the size classes (Fig. 9). A high proportion (> 76.04%) of large individuals in the maturing, spent or postspawning stage was observed from November to February (Fig. 11). The smallest female with ovaries in stages III–V measured 36.2 cm TL, and the smallest reproductive male measured 31.3 cm TL. The TL_{50} was estimated at 40.4 cm TL ($R_{SAM} = 0.67$) for males and 38.8 cm TL ($R_{SAM} = 0.70$) for females (Fig. 12).

3.5. Hoplostethus mediterraneus

A total of 892 individuals were collected (Table 4 and Fig. 9). Significant differences in mean TL or TW between males and females were found (TL, $t = 6.57 > t_{0.05,>100} = 1.984$, $p < 0.001$; TW, $t = 2.016 > t_{0.05,>100} = 1.984$, $p = 0.04$). The Z-test shows significant differences in TL distribution between the sexes ($Z = 2.87 > Z_{0.05} = 1.36$, $p < 0.001$). The F test for the TL–TW relationship shows significant differences between the sexes $F = 8.81 > F_{0.05,1,>100} = 3.97$, $p < 0.001$. The t test showed

Fig. 10. Length–weight relationship by sex of *Mora moro*, *Trachyscorpia echinata* and *Hoplostethus mediterraneus* collected off Northwest Africa. *n*, number of individuals.
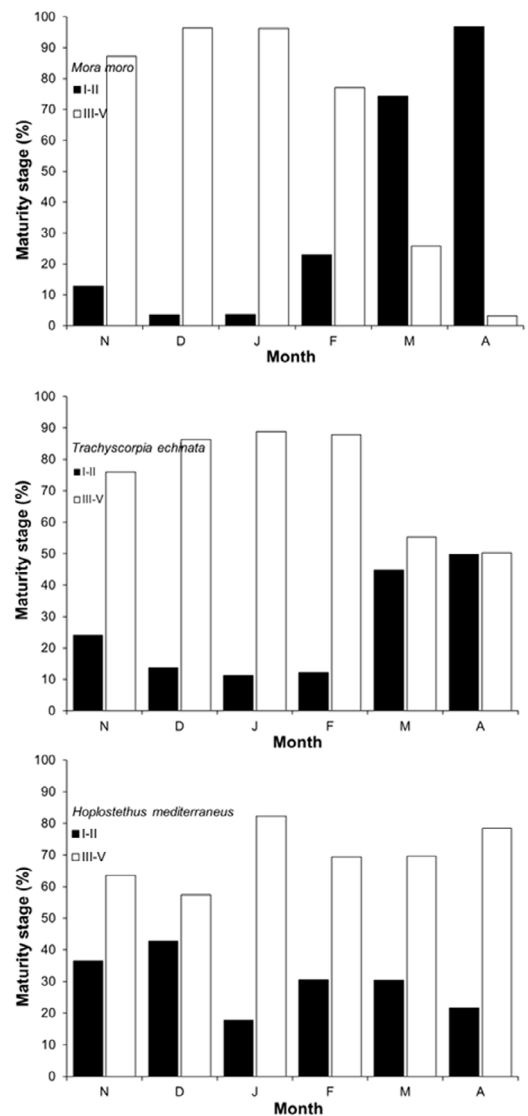

Fig. 11. Maturity stages by month of *Mora moro*, *Trachyscorpia echinata* and *Hoplostethus mediterraneus* collected off Northwest Africa.

negative allometric growth for females, males, and all fish ($t > 5.40 > t_{0.05,>100} = 1.984$, $p < 0.05$) (Table 2 and Fig. 10).

The presence a high proportion of large individuals (> 57.3%) in the maturing, spent or postspawning stages was observed only from November to April (Fig. 11). The sex ratio (1:1.03) was not significantly different from 1:1 ($\chi^2 = 0.190 < \chi^2_{0.05,1} = 3.84$, $p = 0.683$). The sexes showed very similar frequencies in sizes less than 13 cm TL ($\chi^2 = 0.2 < \chi^2_{0.05,1} = 3.84$, $p > 0.600$) (Fig. 9). Females were dominant in size classes from 14–23 cm TL ($\chi^2 = 17.42 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$), whereas males were dominant in sizes greater than 24.0 cm TL ($\chi^2 = 16.38 > \chi^2_{0.05,1} = 3.84$, $p < 0.0001$). The smallest female with ovaries in stages III–V measured 15.3 cm TL, and the smallest reproductive male measured 15.9 cm TL. The TL$_{50}$ was estimated at 16.8 cm TL ($R_{SAM} = 0.59$) for males and 17.4 cm TL ($R_{SAM} = 0.62$) for females (Fig. 12).

## 4. Discussion

4.1. Alepocephalidae species

The presence of high proportions of large individuals of *A. bairdii*, *A. productus* and *A. rostratus* during the winter months in the maturing, spent or postspawning stages coincides with the observations of Golovan and Pakhorukov (1975), who suggested that the spawning time of *A. bairdii* and *A. productus* takes place in the winter season in the eastern-central Atlantic, although a long spawning period cannot be ruled out according to the observations for *A. bairdii* by Nazarov (1983) and Allain (1999, 2001), who indicated that the spawning period appears to occur throughout the year with females maturing asynchronously in the northeastern Atlantic, and for *A. rostratus* by Porcu et al. (2020), who indicated a continuous reproductive cycle in the Mediterranean. In the present work, females of *A. bairdii* larger than 69 cm with gonads in the resting stage were not observed. This coincides with the observations by Nazarov (1983) and Allain (1999, 2001), who indicated that *A. bairdii* is characterized by the absence of large resting females; females only undergo a resting stage during their first spawning season, whereas in the subsequent spawning periods, females could spawn several times per year without a resting phase. In *A. rostratus*, Morales-Nin et al. (1996) observed mature specimens year round, although there was a higher proportion in autumn when the continuous mature condition was more evident in females, with more than 30% of the entire population being always mature (Morales-Nin et al., 1996). This observation coincides with the results
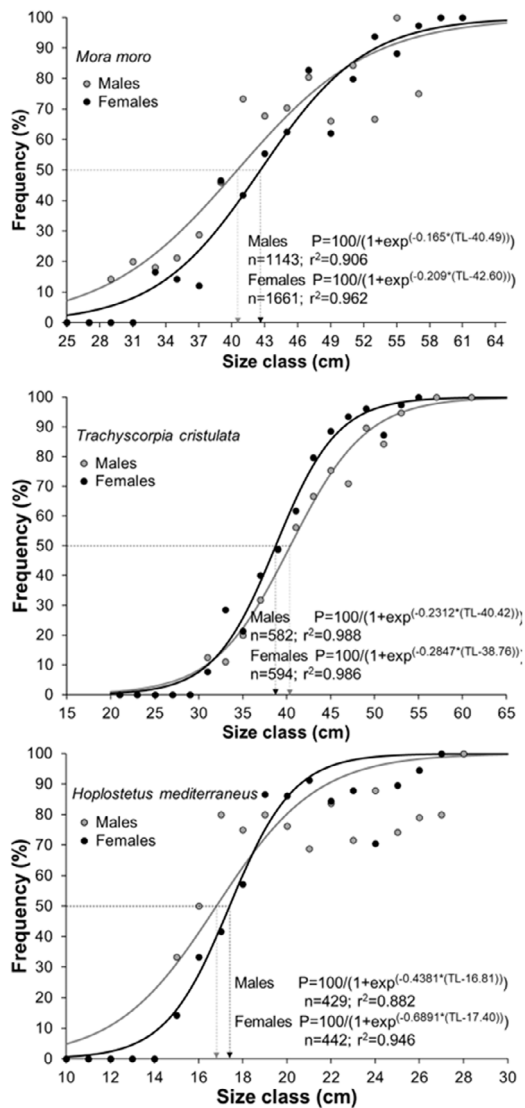
Fig. 12. Ogives of size at first maturity by sex of *Mora moro*, *Trachyscorpia echinata* and *Hoplostethus mediterraneus* collected off Northwest Africa. r^2, determination coefficient; n, number of individuals; P, percentage of mature individuals by length class; and TL, total length (cm).

of Follesa et al. (2007), who observed an unusual multilobed structure of the testis, suggesting that alepocephalids may have a strategy that guarantees continuous spermatogenesis. The high proportion (67.4%) of large reproductive individuals found in this study may be related to the spawning strategy of these species. In this regard, Morales-Nin et al. (1996) suggested that alepocephalids form an aggregation near the sea bottom during spawning, which would increase their vulnerability and the presence of reproductively active individuals in catches from bottom trawlers.

The size at sexual maturity recorded for *A. bairdii* in the eastern-central Atlantic is smaller than that in the North Atlantic (55 cm SL, 15 years) described by Allain (1999, 2001). This smaller size also coincides with the smaller size of the smallest mature female in the eastern Atlantic compared with that in the North Atlantic (Allain, 1999). *A. rostratus* reaches sexual maturity at shorter lengths in the Mediterranean (Morales-Nin et al., 1996; Follesa et al., 2007; Porcu et al., 2020) with a shorter maximum length than that in the Atlantic (Golovan and Pakhorukov, 1980; Morales-Nin et al., 1996), and the results of this work are very

similar to those obtained by Golovan and Pakhorukov (1980). When comparing the relative size at sexual maturity, *A. bairdii* showed a value of 0.59 in the North Atlantic and *A. rostratus* exhibited a range of 0.52–0.61 in the Mediterranean and 0.64–0.67 along the African coast, whereas in this study, alepocephalids showed very similar values among species (0.65–0.72) and with other observations from the northwest coast of Africa (Golovan and Pakhorukov, 1980). The absence of interspecific variation in the relative size at sexual maturity in the same area suggests a genetic basis for these species linked to plasticity in size under different environmental conditions. In the present study, negative allometric growth was observed for *A. bairdii*; however, Meiners-Mandujano et al. (2018) observed positive allometric growth, but with a reduced number of specimens.

4.2. Macrouridae species

B. favosus, *B. melanobranchus* and *N. aequalis* showed a bimodal size distribution, with females reaching larger sizes than males and with a low number of juveniles in the catches. The latter observation suggests a shallower distribution of juveniles located out of the depth soundings of this study. In this regard, Massutí, et al. (1995) pointed out that smaller individuals are located at depths less than 1000 m in the Mediterranean, and Moranta et al. (2007) confirmed a general pattern of increasing size with depth. *B. melanobranchus* was recorded from 450 to 2600 m in the North Atlantic (Merrett and Marshall, 1981). This observation explains the absence of younger individuals of these macrourids at the depth soundings in this study, as has been described for other deep-sea fish species (Massutí, et al., 1995; D'Onghia et al., 2008; Fernandez-Arcaya et al., 2013a,b); this is a consequence of an ontogenetic change in the feeding habits of the species (Macpherson and Duarte, 1991; Morales-Nin et al., 1996). Additionally, Coggan et al. (1999) indicated that *N. aequalis* did not show marked differences in overall population structure across the larger geographical regions of its distribution allowed by its greater temperature tolerance, and Massutí, et al. (1995) suggested that in the Mediterranean, juveniles are concentrated in permanent areas of spawning and recruitment at depths of 500–900 m. However, *B. melanobranchus* was described along the Northwest African coast as a species with restricted vertical range found between 500 and 1200 m (Merrett and Marshall, 1981), and the absence of younger individuals was explained by the selectivity of the fishing gear or the reproductive behaviour of the species (Massutí, et al., 1995). The bimodal distributions observed in the three species are due to sexual size dimorphism (Merrett and Marshall, 1981; Massutí, et al., 1995; Coggan et al., 1999), and changes in mean size with depth cannot be attributable to different sex ratios, as the pattern has been observed for both sexes. Additionally, the larger size of females as well as the bimodal distributions are reflected in the sex ratios for each size interval (Massutí, et al., 1995).

The presence of large individuals of macrourids in the high maturing, spent or postspawning stages coincides with the observations of Merrett and Marshall (1981), who suggested that the spawning time of *N. aequalis* takes place during the winter season in the eastern-central Atlantic, although a long spawning period in the area cannot be ruled out according to observations from the North Atlantic (Coggan et al., 1999) and Mediterranean (Massutí, et al., 1995; Fernandez-Arcaya et al., 2013b; Porcu et al., 2020) that indicated that the spawning period appears to occur throughout the year. This continuous reproduction in macrourids is characteristic of the group (D'Onghia et al., 2008; Fernandez-Arcaya et al., 2013b). However, this possible spawning throughout the year could be erroneous because the reproductive strategies of these species are strongly linked to food availability; *N. aequalis* showed lower fecundity in the Mediterranean

than that in the Atlantic (Carrassón and Matallanas, 1989; Coggan et al., 1999), which was related to limited food availability (Coggan et al., 1999). Food availability can vary latitudinally in the area and seasonally as a consequence of different pulses of intensity in the upwelling and in the formation of filaments (García-Muñoz et al., 2005).

Although the different sizes of macrourids make it difficult to compare results, the size at first maturity obtained for *N. aequalis* is consistent with those reported from the Mediterranean (Massutí, et al., 1995; Porcu et al., 2020) and northwestern Atlantic (Coggan et al., 1998). When values (0.57–0.75) are compared as relative size at sexual maturity, they are similar to those obtained in this study (0.64–0.69). The relative size at sexual maturity (R_{SAM}) attained the lowest values for *B. favosus* (the species with the lowest maximum size) and the highest values for *B. melanobranchus* and *N. aequalis* (species with the highest maximum size), suggesting the presence of interspecific variation in the R_{SAM} in the same region and reflecting differences in plasticity in size among these species under the same environmental conditions.

4.3. Mora moro

The absence of juveniles in the catches suggests the presence of these individuals at shallower depths as described by Fernandez-Arcaya et al. (2013a), who indicated that the recruits are located in the upper slopes at depths between 400 and 800 m. These authors also observed a depth limit of 1500 m, which is similar to the sounding in this study. Similar bathymetric distributions in the two habitats are environmentally different; the Northwest African upwelling and the Mediterranean suggest that pressure could be the main factor limiting the depth distribution of this species as a consequence of increasing pressure affecting the physiology of the fish (Siebenaller et al., 1982; Coggan et al., 1999). The bimodal distribution observed in *M. moro* is due to sexual size dimorphism. This pattern was also observed by Rotllant et al. (2002), who described a dimorphic pattern in size with females larger than males and sex ratios weighted in favour of females in the Mediterranean. These differences have been attributed to slope-dwelling fishes such as *M. moro* as a consequence of a drastic reduction in somatic growth (Gordon et al., 1995; Rotllant et al., 2002). The length at sexual maturity reported in this study is greater than that observed by Rotllant et al. (2002) and Porcu et al. (2020) from the Mediterranean. These differences could be linked to different growth rates associated with higher food availability in the area of Northwest Africa upwelling.

The presence of a high proportion of large individuals in stages of reproductive activity suggests that *M. moro* spawns in winter in the study area. However, different spawning periods have been described for this species. Gordon and Duncan (1985) described the spawning of *M. moro* in the Northeast Atlantic in June or July, and Menezes et al. (2001) described spawning in November off the Azores, whereas Cohen (1986) described the species as a winter or early spring spawner in the Mediterranean. Rotllant et al. (2002) found mature individuals year-round, except in summer, with a quasi-continuous reproductive pattern in the Mediterranean, indicating that in deep-water gadiforms, spawning varies within the distribution. Fernandez-Arcaya et al. (2013a) and Porcu et al. (2020) recorded marked seasonal reproduction in the Mediterranean winter with few spawning females, suggesting a very narrow spawning period. Fernandez-Arcaya et al. (2013a) suggested that this species spawns when plankton blooms occur in the surface water layers and are available to larvae, increasing their survival rate, and Porcu et al. (2020) pointed out that reproduction responds to a natural fluctuation in food pulses reaching bathyal depths.

The growth coefficient of the length–weight recorded for *M. moro* in the eastern-central Atlantic was negatively allometric and differs from that observed by Delgado et al. (2017). This is probably due to the limited size range observed (42–44 cm TL) in the seamounts off the archipelago of Madeira.

4.4. Trachyscorpia echinata

No biological information exists on this species to date, except for the length–weight relationship (Meiners-Mandujano et al., 2018). Massutí et al. (1993) and Ragonese and Giusto (1999) suggest a recent incursion during the last decades into the Mediterranean Sea from the Atlantic populations. In the present study, positive allometric growth was observed; however, Meiners-Mandujano et al. (2018) observed isometric growth, but with an absence of the larger and heavier specimens. From breeding biology of conspecifics is known that these species lay eggs in buoyant gelatinous masses on the seafloor (Nelson, 1994).

4.5. Hoplostethus mediterraneus

The variability in size of both sexes in the sampled population could reflect that this species is a selective or opportunistic feeder that feeds in the water column of the benthopelagic zone, in which case a bottom trawl would not be a good fishing gear for sampling this population (Merrett and Marshall, 1981; Gordon and Duncan, 1987; D'Onghia et al., 1998).

Although Maurin (1970) indicated that many parts of the Mediterranean are not suitable environments for *H. mediterraneus*, a reproductive peak was recorded in summer for this species (D'Onghia et al., 1998; Pais, 2001). However, Gordon and Duncan (1987) indicated that spawning of this species occurs in spring–summer in the northeastern Atlantic, and environmental conditions during autumn are unsuitable for larval or juvenile survival. Given that the upwelling along the northwestern coast of Africa is one of the most suitable environments for fish, the presence of large individuals from November to April with a high proportion in the maturing, spent or postspawning stage suggests an extended spawning season in the area that could run from autumn (as in the northern region) until late spring. The higher maximum size, size of the smallest mature individuals observed, and size at sexual maturity estimated in the Northwest Africa upwelling area compared with data from the Mediterranean (D'Onghia et al., 1998; Pais, 2001; Vitale et al., 2008), suggest higher growth in the Atlantic region linked to higher food availability. The growth coefficient of the length–weight relationship recorded for *H. mediterraneus* in the eastern-central Atlantic was negatively allometric and differs from that observed in the central Aegean Sea (positive allometry) by Soykan and Kınacıgil (2021). This is probably due to the restricted size range observed (4.3–16.6 cm TL) in the Aegean Sea, which is smaller than the size at maturity described in the Mediterranean Sea by D'Onghia et al. (1998).

5. Conclusion

The information presented in this contribution will help to support the sustainability of these species and will be useful to their management. For the species studied, spawning season takes place in winter. The distribution of length frequencies showed significant differences between sexes, except in *A. productus* and *A. bairdii*. Macrouridae species in the region showed a bimodal size distribution, with females reaching larger sizes and higher weights than males. Negative allometric growth was recorded as a general pattern in both sexes, and alternative isometric growth was recorded only in females of *A. productus*, *A.*

rostratus, and *B. melanobranchus*, and positive allometric growth in females of *T. echinata*. Sex ratios were generally unbalanced except in *N. aequalis*, *T. echinata* and *H. mediterraneus*. Relative size at sexual maturity showed a narrow range of similarly high values, except in *B. favosus*, *H. mediterraneus*, and *N. aequalis*. Sexual maturity is reached at smaller sizes in males than in females, except in *A. bairdii* and *T. echinata*. Although data analysed were collected in 2005–2006, the biological information obtained are still valid.

CRediT authorship contribution statement

R. Triay-Portella: Conceptualization, Investigation, Writing – original draft. **J.A. González:** Project administration, Funding acquisition, Formal analysis, Investigation, Writing – original draft. **J.M. Lorenzo:** Data curation, Formal analysis, Investigation, Methodology. **M. Biscoito:** Data curation, Formal analysis, Investigation, Methodology. **J.G. Pajuelo:** Conceptualization, Formal analysis, Investigation, Supervision, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

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