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REGULAR ARTICLE

# Reproductive biology of the electric lanternfish *Electrona risso* (Myctophidae) and the bigscale fishes *Melamphaes polylepis* and *Scopelogadus mizolepis* (Melamphaidae)

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## Abstract

This study was the first to investigate the key reproductive traits of the electric lantern fish *Electrona risso* (Myctophidae, $n = 918$) and the bigscale fishes (Melamphaidae) *Melamphaes polylepis* ($n = 260$) and *Scopelogadus mizolepis* ($n = 649$). Specimens of these mesopelagic species were collected in March and April 2015 in the eastern Central Atlantic (0–24° N, 20–26° W). Sex ratio was not significantly different from 1:1 in *E. risso* and *M. polylepis* but significantly skewed toward female dominance in *S. mizolepis*. Reproductive phases were determined macroscopically and by histological analyses on selected individuals. Female length at 50% maturity ($L_{50}$) was 55.1 mm standard length ($L_S$) in *E. risso*, with an observed female maximum length ($L_{max}$) of 81.2 mm $L_S$. *M. polylepis* females had an $L_{50}$ of 40.2 mm $L_S$ and an $L_{max}$ of 86.7 mm $L_S$. *S. mizolepis* had an $L_{50}$ of 46 mm $L_S$ and an $L_{max}$ of 97.9 mm $L_S$. The three species show histological features of iteroparity, but the *E. risso* population appears to occur in two year-classes and experience only one spawning season per lifetime in the study region. All three species are batch-spawners. A batch fecundity of 2668 eggs was estimated from one *E. risso* individual, with a relative batch fecundity of 369 eggs $g^{-1}$ gonad-free body mass. *M. polylepis* had a batch fecundity of 1027 eggs and a relative batch fecundity of 149 eggs $g^{-1}$ ($n = 3$). *S. polylepis* had a batch fecundity of 1545 eggs and a relative batch fecundity of 215 eggs $g^{-1}$ ($n = 21$). The median gonado-somatic index during the actively spawning phase of *E. risso* was 4.5, significantly lower than that of *M. polylepis* (7.5) and *S. mizolepis* (7.1). No regressing or regenerating phases were observed in this study. Batch-spawning in all three species is suggested to be advantageous to cope with intra-annual variability in food supply and other risks for offspring survival. With what appears to be in effect a (facultative) semelparous strategy in combination with a short life span in *E. risso*, inter-annual differences would have a great effect on population dynamics of this species. Knowledge is still lacking on temporal aspects of reproduction such as the duration of the spawning season and the frequency of spawning, as well as age and growth.

KEYWORDS
eastern Central Atlantic, fecundity, gonad histology, length at maturity, mesopelagic fish, ovarian development, reproductive phases

## 1 | INTRODUCTION

The reproductive biology of fishes is central to their population dynamics and recovery from disturbances. Reproductive traits are also included in studies of the functional composition of fish assemblages. However, significant knowledge gaps prevail for most of the fishes in the mesopelagic zone (Caiger et al., 2021; Priede, 2017). The lack of information is partly due to the limited commercial importance of mesopelagic fishes (Gjøsæter & Kawaguchi, 1980) and the habitat, which is difficult to access and requires special equipment to collect samples at 200–1000 m depth (Caiger et al., 2021). Mesopelagic fishes have received renewed attention because of their likely role in the biological carbon pump that facilitates the transfer of atmospheric carbon to depth. Many mesopelagic species perform vertical migrations (Marshall, 1979), feeding in the productive surface layers at night and then exporting carbon to depth (Dam et al., 1995; Longhurst, 1998), where they hide in the dark from visual predators during the day. Mesopelagic fishes also play a central role in the open ocean's food web and are important prey for top predators.

This study focuses on reproduction of the electric lanternfish *Electrona risso* (Cocco, 1829) from the family Myctophidae Gill, 1893, and two species from the family Melamphaidae Gill, 1832, *Melamphaes polylepis* Ebeling, 1962, and *Scopelogadus mizolepis* (Günther, 1878). Myctophids, or lanternfishes, are the most speciose family of mesopelagic fishes (Priede, 2017). *E. risso* is mainly distributed in the temperate to tropical regions of the eastern North Atlantic but also occurs in other oceans (Craddock & Mead, 1970; Kubota & Uyeno, 1972; Nafpaktitis & Nafpaktitis, 1969; Podrazhanskaya, 1993; Tåning, 1918). *E. risso* undertakes vertical migrations of a limited amplitude (Czudaj et al., 2021). It reaches a maximum length of 84 mm (Czudaj et al., 2022), and its diet consists of planktonic copepods as well as small mesopelagic fish (Battaglia et al., 2016). The family Melamphaidae is an abundant but understudied family of meso- to bathypelagic fishes. *M. polylepis* and *S. mizolepis* are circumglobally distributed species that do not perform diel vertical migrations (Bartow, 2010; Priede, 2017). They reach maximum sizes of about 87 and 98 mm, respectively (Czudaj et al., 2022). *M. polylepis* feeds mainly on crustacean zooplankton and Chaetognaths, and *S. mizolepis* feeds mainly on gelatinous and crustacean zooplankton (Bartow, 2010; Randall & Farrell, 1997). Growth and reproductive biology of mesopelagic fishes have been recently reviewed by Caiger et al. (2021). There are several studies on myctophid reproduction, but little is known about *E. risso*.

The main aim of the present study was to analyse the key reproductive traits such as length at maturity, fecundity, reproductive strategy (semelparity *v*. iteroparity), and spawning pattern (batch-spawning vs. total spawning) for the three studied species using macroscopic and histological methods. Further, sex ratios, length–frequency distributions, gonado-somatic index (GSI), and oocyte size were investigated.

## 2 | METHODS

### 2.1 | Sample collection

Samples were collected during the 383rd cruise of the fishery research vessel *FFS Walther Herwig III* in March and April 2015. Mesopelagic ichthyofauna sampling occurred during the second leg of the cruise from Dakar to Bremerhaven, at 18 stations between 0° N and 45° N (Figure 1), usually during night-time except for one daytime haul at each of three 24-h stations. Fish were caught using a pelagic midwater trawl ("Aalnet," Engel Netze, Bremerhaven, Germany) with a mouth opening (16 × 30 m) and equipped with a multiple opening–closing device with three net bags (20-mm mesh-size and 1.8-mm meshes) in the codend container. Based on deep scattering layer depth, night-time sampling was mainly carried out at 50–100 m and about 400 m depth; the maximum sampling depth was 650 m. The study species were caught primarily at 350–400 m depth. Fish were sorted on board into practicable taxa, stored in phosphate-buffered 4% formalin solution, and later identified to the lowest taxonomic level possible in a laboratory setting. About 5% of the total individuals of the three species studied were damaged such that their length could not be measured or the sex not identified; 918 specimens of *E. risso* were in a proper condition for further analysis; 260 specimens of *M. polylepis* and 649 specimens of *S. mizolepis* were usable.

### 2.2 | Specimen processing and macroscopic analysis

Standard length ($L_S$) was measured for every individual to the nearest 0.1 mm. To access the gonads, the body cavity was opened using scissors. The sex was identified following the morphological descriptions of Bartow (2010) and Brown-Peterson et al. (2011), using a dissecting microscope for the smallest individuals. Further analysis focuses on female individuals, as their reproductive biology typically has the greater effect on the reproductive potential of fish populations (Lowerre-Barbieri, Brown-Peterson, et al., 2011) To determine the reproductive phase of each female fish, the ovaries were observed under a dissecting microscope. The standardized terminology for reproductive development in fish by Brown-Peterson et al. (2011) was applied, and five reproductive phases were distinguished (Table 1). Total weight (TW) and gonadal weight (GW) were determined to the nearest 0.001 g. If the weight was <0.009 g, the tissue was weighed to the nearest 0.00001 g.

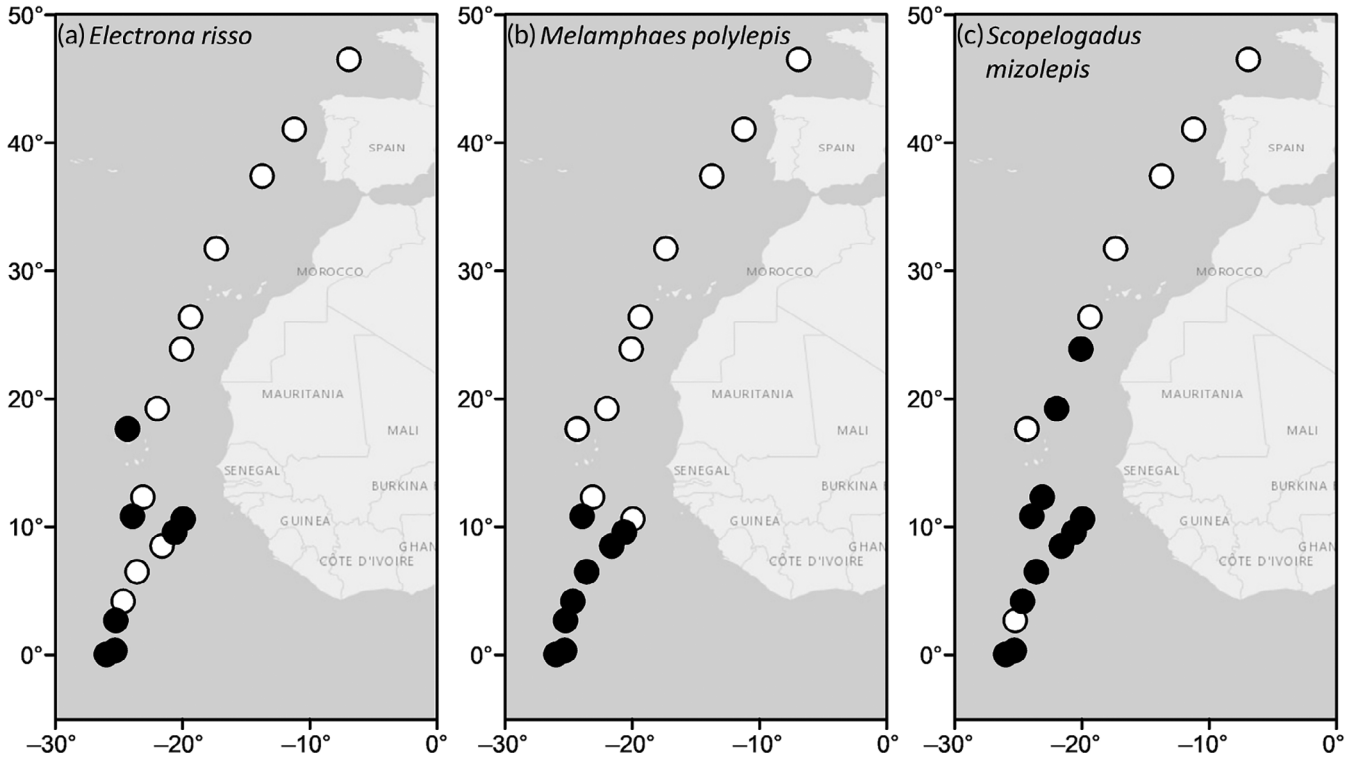


**FIGURE 1** Mesopelagic net sampling stations (circles) and locations where (a) *Electrona risso*, (b) *Melamphaes polylepis*, and (c) *Scopelogadus mizolepis* were caught (black circles) in the eastern Central Atlantic during the 383rd cruise of the *FFS Walther Herwig III* in March and April 2015. Land mass is shown in light gray and ocean in dark gray.

## 2.3 | Microscopic analysis

Batch fecundity was estimated for 1 *E. risso*, 3 *M. polylepis*, and 21 *S. mizolepis* in the actively spawning phase using the gravimetric method (Hunter et al., 1985; Hunter & Goldberg, 1979; Murua et al., 2003). The observations were conducted on one half of each ovary, which was divided into two weighed subsamples. This reduced the counting effort compared to the whole ovary and left the option of using the other half for histological analysis. Oocytes were carefully removed from the tissue with tweezers and placed in a counting chamber, and the most advanced oocytes were counted under a dissecting microscope. In *E. risso*, the ovaries with hydrated eggs were either damaged or had been used for histological analysis, and the most advanced oocytes in an ovary before hydration were counted. Therefore, only a preliminary value is given for this species. For the other two species, only hydrated eggs were counted. The number of eggs divided by the respective subsample weight was multiplied by the ovary weight (gravimetric method; Hunter & Goldberg, 1979; Hunter et al., 1985; Murua et al., 2003). Relative batch fecundity was calculated by dividing batch fecundity by gonad-free fish weight.

For determining oocyte size, at least five hydrated eggs of each of five actively spawning *E. risso*, three actively spawning individuals of *M. polylepis*, and five actively spawning individuals of *S. mizolepis* were measured under a dissecting microscope. For *E. risso*, oocytes from the other reproductive phases were measured (presented in Supporting Information). At least five of the most advanced oocytes from 5 to 69 different specimens of each phase (Table A1, Figure A1) were measured under the dissecting microscope and from microimages using ImageJ software (version 1.49).

## 2.4 | Histological analysis

To validate the macroscopic classification of reproductive phases and to identify reproductive strategies and spawning patterns, the oocyte stages present during the different phases were examined in histological cross-sections. In a standard procedure (Mulisch & Welsch, 2015), gonadal tissue was cut into 2-µm thin sections and stained with Gill hematoxylin and eosin at the Institute of Pathology of the University Medical Centre Schleswig-Holstein, Kiel (one or three ovaries for each observed phase of *E. risso*; see Table 1), and the Pathological Institute Bremerhaven (three ovaries for each observed phase of *M. polylepis and S. mizolepis*). The gonad histology was evaluated following Brown-Peterson et al. (2011, tab. 1), supported by Lowerre-Barbieri, Brown-Peterson, et al. (2011) and Murua and Saborido-Rey (2003).

## 2.5 | Data analysis

Sex ratios were analysed for deviation from 1:1 using $\chi^2$ test, and length distributions were analysed for differences between sexes using Kolmogorov–Smirnov (K–S) test.

**TABLE 1** Classification of female reproductive phases of *Electrona risso*, *Melamphaes polylepis*, and *Scopelogadus mizolepis*.

| Reproductive phase | Macroscopic features (Brown-Peterson et al., 2011, Gartner, 1993) | Histological features (Brown-Peterson et al., 2011) | Specific observations for *E. risso* | Specific observations for *M. polylepis* and *S. mizolepis* |
|---|---|---|---|---|
| Immature | Ovaries small, thin, and translucent, blood vessels indistinct; located anteriorly above stomach; small clear oocytes visible only under higher magnification, few in number.<br>*E. risso*: $N = 197$<br>*M. polylepis*: $N = 15$<br>*S. mizolepis*: $N = 258$ | Only O and PG oocytes present; rarely atresia, no muscle bundles; thin ovarian wall and little space between oocytes.<br>*E. risso*: $n = 1$<br>*M. polylepis*: $n = 3$<br>*S. mizolepis*: $n = 3$ | In addition to O and PG, a few individual CA oocytes were present. | As described. |
| Early developing (subphase of "developing") | Pale and still ribbonlike ovaries but extending posteriorly, blood vessels becoming more distinct; more oocytes, larger and clearly visible under low magnification.<br>*E. risso*: $N = 49$<br>*M. polylepis*: $N = 95$<br>*S. mizolepis*: $N = 147$ | Only PG and CA oocytes present.<br>*E. risso*: $n = 1$<br>*M. polylepis*: $n = 3$<br>*S. mizolepis*: $n = 3$ | In addition to PG and CA, Vtg1 oocytes and atresia were present. | As described. |
| Developing | Enlarging ovaries, reaching end of peritoneal cavity, oocytes becoming visible to naked eye.<br>*E. risso*: $N = 32$<br>*M. polylepis*: $N = 17$<br>*S. mizolepis*: $N = 84$ | PG, CA, Vtg1, and Vtg2 oocytes present; no evidence of POFs or Vtg3 oocytes; some atresia can be present.<br>*E. risso*: $n = 1$<br>*M. polylepis*: $n = 3$<br>*S. mizolepis*: $n = 3$ | Atresia observed. | No atresia observed. |
| Spawning capable | Large ovaries fill most of the peritoneal cavity; blood vessels prominent; individual oocytes visible macroscopically.<br>*E. risso*: $N = 87$<br>*M. polylepis*: $N = 8$<br>*S. mizolepis*: $N = 96$ | Vtg3 oocytes or POFs present. PG, CA, Vtg1, Vtg2, and atresia may also be present; early stages of OM can be present.<br>*E. risso*: $n = 1$<br>*M. polylepis*: $n = 3$<br>*S. mizolepis*: $n = 3$ | PG, CA, Vtg1, and Vtg2 oocytes were also present. No POF and no early stages of OM or hydrated oocytes observed. | PG, CA, Vtg1 and Vtg2 oocytes, and early stages of OM (GVM) were also present; several POFs in one histological sample of each species. |
| Actively spawning (subphase of "spawning capable") | Ovaries filling entire posterior area of the peritoneal cavity; body walls usually expanded; oocytes fragile and easily torn.<br>*E. risso*: $N = 73$<br>*M. polylepis*: $N = 3$<br>*S. mizolepis*: $N = 54$ | Oocytes undergoing late GVM, GVBD, hydration, or ovulation are present. PG, CA, Vtg1–3, and POFs may also be present.<br>*E. risso*: $n = 3$<br>*M. polylepis*: $n = 3$<br>*S. mizolepis*: $n = 3$ | GVM, GVBD, or HYD present; PG, CA, Vtg1 and Vtg2 but no Vtg3 observed. | GVM, GVBD, or HYD present. Vtg1–3 oocytes and a few PG and CA were also observed. |

*Note*: Macroscopic criteria from Brown-Peterson et al. (2011) and Gartner (1993); histological criteria from Brown-Peterson et al. (2011). Species-specific details are given for characteristics that are optional for a phase. No regressing or regenerating ovaries were observed.
Abbreviations: CA, cortical alveoli oocyte; GVBD, germinal vesicle breakdown oocyte; GVM, germinal vesicle migration oocyte; HYD, hydrated oocyte; *N*, number of individuals assigned to phase; *n*, number of individuals with histological samples; O, Oogonia; OM, oocyte maturation; PG, primary growth oocyte; POF, postovulatory follicle; Vtg1–3, primary to tertiary vitellogenic oocytes.

Maturity was categorized per individual as either 0 for immature or 1 for mature. All specimens past the immature phase were considered mature. Maturity ogives were then calculated using logistic regression by fitting a generalized linear model with a binomial error distribution and a logit link function to the data. $L_S$ was the explanatory variable and maturity the response variable. The logistic regression can be expressed in linear form as

$$\ln\left(\frac{p}{1-p}\right) = a + b \times L_S, \quad (1)$$

where $p$ is the probability of being mature and $a$ and $b$ are parameters to be estimated. For the length at which 50% of the individuals are mature, $p$ is 0.5 and length at 50% maturity ($L_{50}$) can then be calculated from the obtained parameters as

$$L_{50} = -\frac{a}{b} \quad (2)$$

(Ogle, 2016). Further, the ratio of $L_{50}$ to the maximum observed length ($L_{max}$) was calculated ($L_{50}/L_{max}$), because it has been empirically associated with reproductive strategies (Froese & Pauly, 2013), albeit using asymptotic length.

A GSI as a measure of reproductive investment was calculated for each individual as

$$\text{GSI} = \frac{\text{GW}}{\text{TW} - \text{GW}} \times 100, \quad (3)$$

where GW is the gonad weight and TW is the total body weight. For comparisons of GSI between reproductive phases and between species, pair-wise Wilcoxon rank-sum test with Holm correction for multiple testing were used.

All calculations were performed using the open-source software R, version 4.2.0 (R Core Team, 2022), and $p$ values ≤0.05 were considered statistically significant. The data are publicly available (Knorrn et al., 2023).

## 3 | RESULTS

### 3.1 | Length distributions and sex ratios

For *E. risso*, 434 female and 484 male individuals were found (sex ratio: 1:1.12, females to males; $\chi^2$ test, $\chi^2 = 2.723$, $p = 0.10$). The lengths ranged from 30.5 to 81.2 mm $L_S$ (Figure 2a). Two major size groups appeared with modal sizes of about 51 and 64 mm. Length distributions were similar between sexes (K–S test, $D = 0.076$, $p$-value = 0.146). For *M. polylepis*, 139 male and 121 female individuals were found (sex ratio: 1.14:1, females to males; $\chi^2$ test, $\chi^2 = 1.246$, $p = 0.264$). The lengths ranged from 28.7 to 86.7 mm (Figure 2b), with the majority of individuals between 45 and 55 mm $L_S$. Length distributions were similar between sexes (K–S test, $D = 0.133$, $p = 0.206$). In *S. mizolepis*, the majority were females (641 individuals); only 8 individuals were sexed as male (sex ratio: 80:1, females to males; $\chi^2$ test, $\chi^2 = 617.4$, $p < 0.001$). This species had a length range between 26.6 and 97.9 mm $L_S$ (Figure 2c). The length–frequency distribution shows two major groups, one with a maximum frequency of about 45 mm $L_S$ and another with individuals between 60 and 80 mm $L_S$. The number of males was too low for a meaningful comparison of length distributions between sexes.

### 3.2 | Ovarian and oocyte development

Five reproductive phases were distinguished in each of the studied species (Table 1; Figures 3 and 4; Figure A2). The sizes of the gonads ranged from small, immature gonads to large, ripe gonads that filled most of the cavity. No specimens in the regressing or regenerating

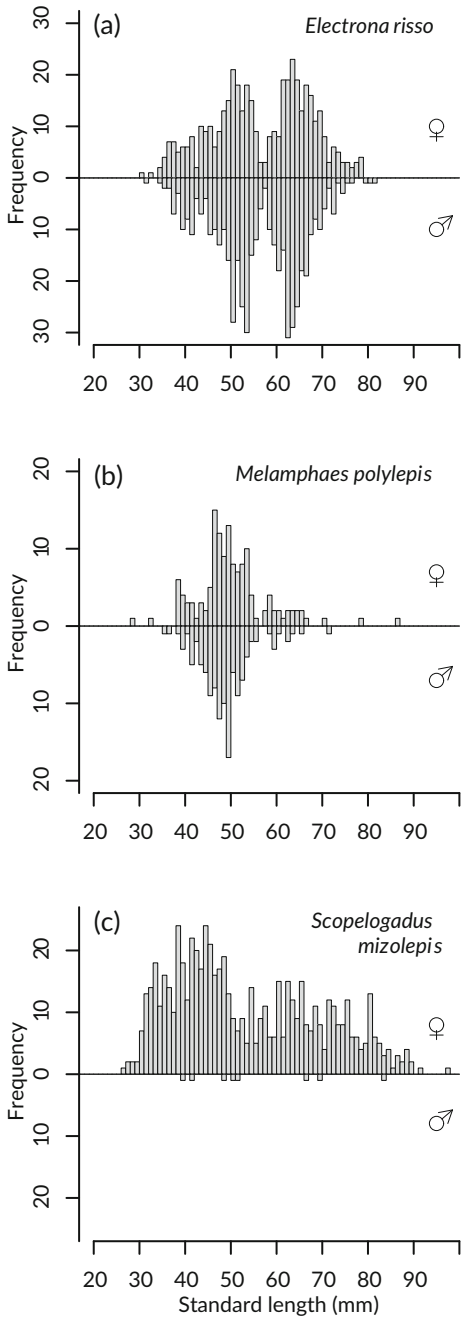


**FIGURE 2** Length–frequency distributions of (a) *Electrona risso*, (b) *Melamphaes polylepis*, and (c) *Scopelogadus mizolepis* by sex (upper panels, females; lower panels, males).

phase were observed. The macroscopic descriptions are summarized in Table 1.

To validate the macroscopic findings and to reveal the spawning strategy, oocyte development was examined in histological cross-sections from the different reproductive phases (one or three samples per phase per species; Table 1; Figures 3 and 4; Figure A2). In the ovaries from the immature phase, almost all oocytes were primary growth (PG) oocytes; a few individual cortical alveoli (CA) oocytes (0.1%–0.2% of cells) were present in the sample from *E. risso* (Figure 3). The developing phase is characterized by the presence of PG and CA in its

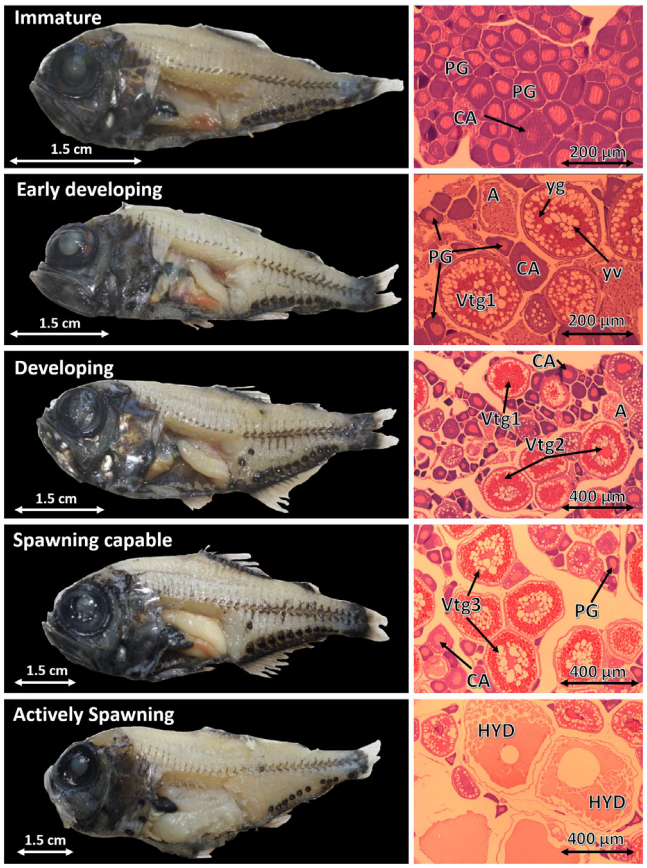


**FIGURE 3** *Electrona risso* ovarian development. Reproductive phases based on Table 1. Macroscopic development in female gonads (left panels) and histological cross-sections of ovaries (right panels). A, atresia; CA, cortical alveoli oocyte; GVBD, germinal vesicle (nucleus) breakdown oocyte; GVM, germinal vesicle migration oocyte; HYD, hydrated oocyte; PG, primary growth oocyte; Vtg1–3, primary to tertiary vitellogenic oocyte; yg, yolk granules; yv, yolk vesicle. Photography by K. Wieben.

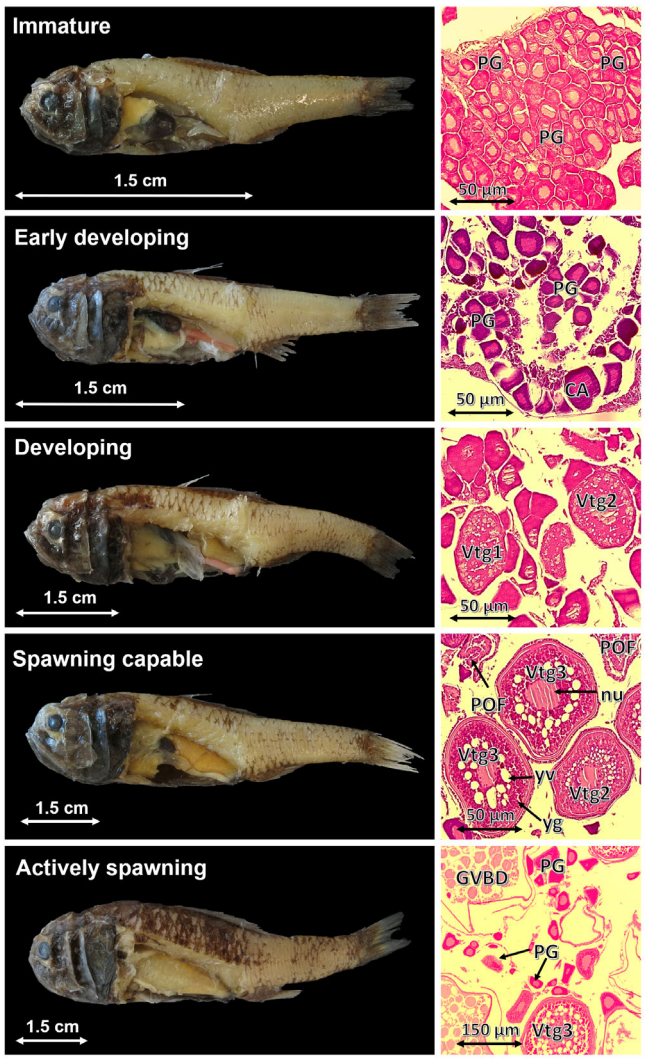


**FIGURE 4** *Melamphaes polylepis* ovarian development. Reproductive phases based on Table 1. Macroscopic development in female gonads (left panels) and histological cross-sections of ovaries (right panels). CA, cortical alveoli oocyte; GVBD, germinal vesicle (nucleus) breakdown oocyte; nu, nucleus; PG, primary growth oocyte; POF, postovulatory follicle; Vtg1–3, primary to tertiary vitellogenic oocyte; yg, yolk granules; yv, yolk vesicle. Photography by A. Knorrn.

early subphase and the subsequent addition of primary and secondary vitellogenic oocytes (Vtg1 and Vtg2). Early vitellogenic oocytes (Vtg1) also appeared in the sample of the early developing subphase of *E. risso*. The spawning-capable phase is indicated by the presence of tertiary vitellogenic oocytes (Vtg3) or postovulatory follicles (POF). In all three species, oocytes in all earlier stages from PG to Vtg2 were also present. Several POFs were observed in one histological sample each from *M. polylepis* (Figure 4) and *S. mizolepis* (not shown). In the actively spawning subphase, oocytes mature and the germinal vesicle migration, germinal vesicle breakdown, or hydration stage is observed. Notably, whereas in the two melamphaid species, less advanced cells from PG to Vtg3 occurred alongside the maturing oocytes, in *E. risso*, PG to Vtg2 but no Vtg3 were observed.

## 3.3 | Length at maturity

The logistic regressions showed that $L_S$ had a highly significant effect on the probability of maturity ($p < 0.001$; Figure 5). Probability of maturity as a function of length differed between the three species ($p < 0.001$). The length at which 50% of the female *E. risso* population are mature ($L_{50}$) was 55.1 mm $L_S$ (54.2–56.1 mm, bootstrapped 95% C.I.). The female maximum length ($L_{max}$) observed was 81.2 mm $L_S$, and $L_{50}/L_{max}$ was 0.68; that is, they mature at 68% of their maximum length. Among all assessable *E. risso* females ($n = 438$), 55% were mature, of which 30% were in the actively spawning phase. *M. polylepis* females had an $L_{50}$ of 40.2 mm $L_S$ (95% C.I.: 37.4–42.2 mm). $L_{max}$ was 86.7 mm $L_S$, and $L_{50}/L_{max}$ was 0.46; individuals mature at 46% of the maximum observed $L_S$ for females described in this study. For *M. polylepis*, 89% were mature, 2.4% of which were actively spawning ($n = 138$). *S. mizolepis* had a length at maturity of 46 mm $L_S$ (95% C.I.: 45.3–46.7 mm) with an $L_{max}$ of 97.9 mm $L_S$ and an $L_{50}/L_{max}$ of 0.47. Sixty percent of *S. mizolepis* females were mature, 14% of which were in the actively spawning phase.

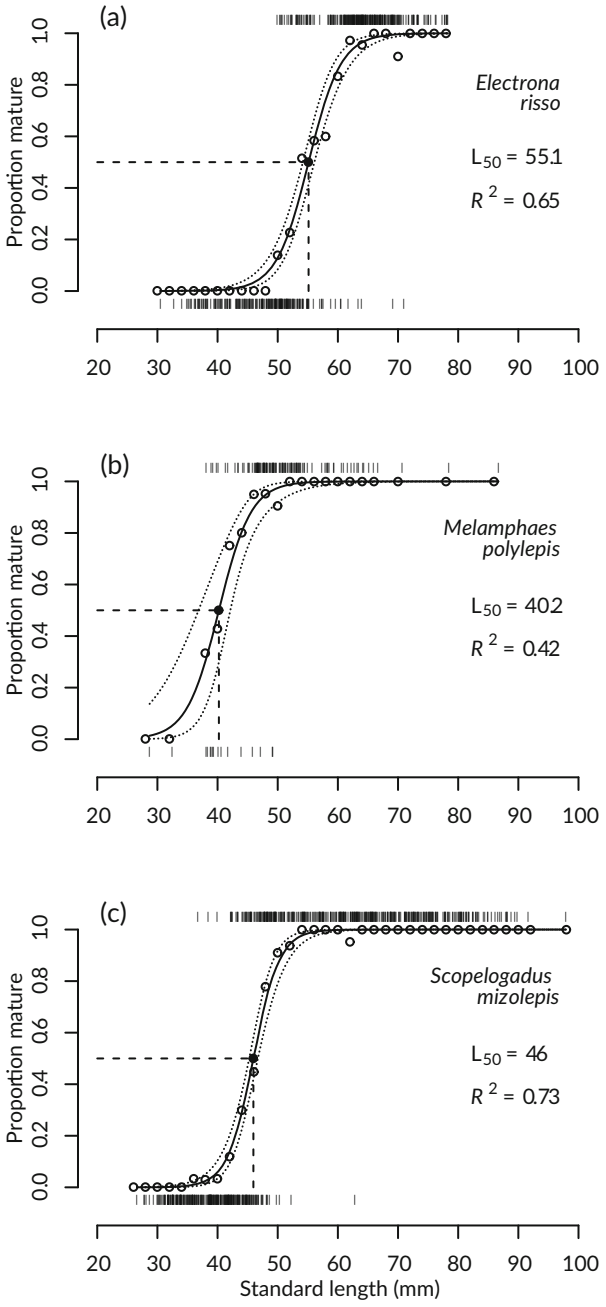


**FIGURE 5** Maturity ogives (solid lines) for females of (a) *Electrona risso*, (b) *Melamphaes polylepis*, and (c) *Scopelogadus mizolepis*. Vertical slashes are single observations, and open circles illustrate the proportions of mature individuals per 2-mm size class. Dotted lines are 95% C.I., and dashed lines and filled black dots indicate the length at which 50% of the individuals are mature ($L_{50}$). $R^2$ values are McFadden's $R^2$.

### 3.4 | GSI, fecundity, and oocyte size

The GSI increased with advancing ovarian development in females of the three species (Figure 6). The differences between the reproductive phases in each species were significant (pair-wise Wilcoxon rank-sum test, $p < 0.05$); however, the ranges of GSI values overlapped (Figure 6). During each of the first three phases, GSI values also differed significantly between all species (pair-wise Wilcoxon rank-sum test, $p < 0.005$). *E. risso* initially had the highest values, but by the actively spawning phase, its GSI (median 4.5) was exceeded (pair-wise Wilcoxon rank-sum test, $p < 0.02$) by *M. polylepis* (median 7.5) and *S. mizolepis* (median 7.1), with no significant difference between the latter.

Batch fecundity for the single *E. risso* was 2668 eggs, with a relative batch fecundity of 369 eggs $g^{-1}$ gonad-free body mass. *M. polylepis* had a batch fecundity of 1027 ± 1120 eggs (mean ± S.D.) and a mean relative batch fecundity of 149 eggs $g^{-1}$ ($n = 3$). *S. polylepis* had a batch fecundity of 1545 ± 644 eggs and a mean relative batch fecundity of 215 eggs $g^{-1}$ ($n = 21$). The sizes of hydrated eggs before spawning were 0.73 ± 0.05 mm for *E. risso*, 0.86 ± 0.1 mm for *M. polylepis*, and 0.91 ± 0.05 mm for *S. mizolepis*.

## 4 | DISCUSSION

This study was the first to describe the ovarian development in *E. risso*, *M. polylepis*, and *S. mizolepis* females, along with other key reproductive traits. An overview of the main results is provided in Table 2.

### 4.1 | Methodological constraints

All samples were taken during the 383rd cruise of the *FFS Walther Herwig III* from a limited geographic area, but the three species have distribution ranges beyond the subtropical and tropical eastern North Atlantic. Reproductive traits may differ in regions with other environmental conditions. Similarly, reproductive investment may vary between years. With regard to the timing of sampling, this cruise covered the months March and April, and reproductive processes during other seasons have not been investigated. Still, although there appear to be some sampling gaps particularly for larger *M. polylepis*, the individuals from this cruise range from small and immature to actively spawning and reach or exceed the maximum lengths so far reported (Czudaj et al., 2022; Hulley, 1990) in each species. The three species were selected for analysis because a sufficiently large number of individuals had been caught, and damaged specimens with gonads visible indicated that a range of ovarian developmental phases were present. That said, the estimations of batch fecundity are based on only one individual of *E. risso* and three individuals of *M. polylepis*; these values should be updated as more data become available. In *S. mizolepis*, of more than 600 sexed individuals, only 8 were identified as male. It is unlikely that this is the actual sex ratio. Male to female ratios of 2:1 (Clarke, 1983) and 3:1 (Bartow, 2010) have been reported for this species. Males could have been missed with the chosen fishing depths in the present study if they reside apart from the females. A strong dominance of females over males (23:1) had also been reported in spawning aggregations of *Diaphus danae* (Flynn & Paxton, 2012), where a sampling bias through a sex-dependent vertical distribution was suggested (Go, 1981; Hulley & Prosch, 1987).

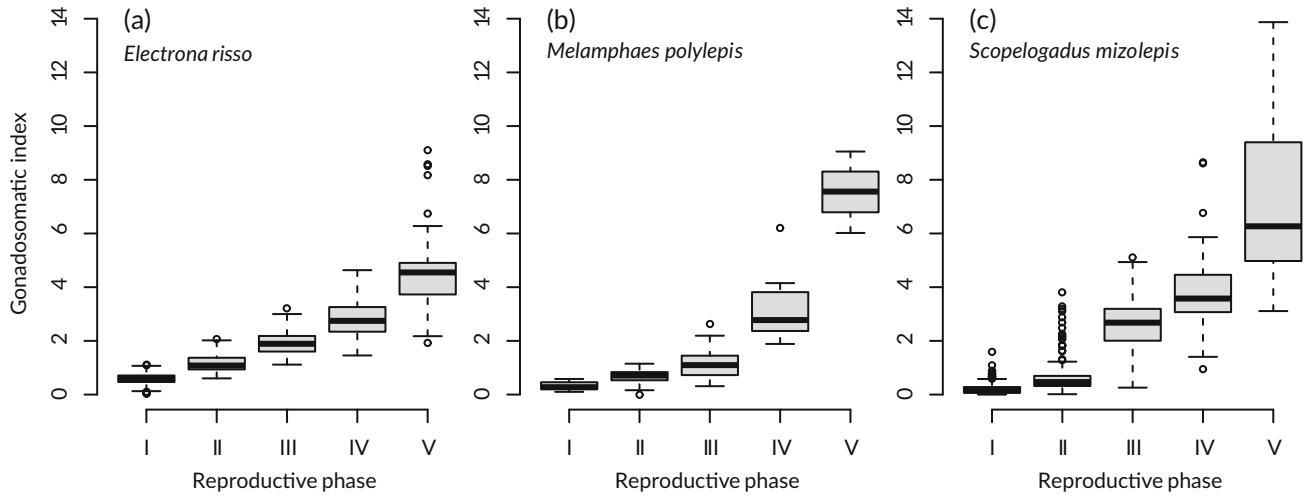


**FIGURE 6** Gonado-somatic index of females of (a) *Electrona risso*, (b) *Melamphaes polylepis*, and (c) *Scopelogadus mizolepis*, per reproductive phase. I, immature; II, early developing; III, developing; IV, spawning capable; V, actively spawning (see also Table 1). All neighboring values differ significantly ($p < 0.05$).

**TABLE 2** Overview of the main reproductive traits of *Electrona risso*, *Melamphaes polylepis*, and *Scopelogadus mizolepis* from the present study.

| | ***E. risso*** | ***M. polylepis*** | ***S. mizolepis*** |
|---|---|---|---|
| Maximum size $L_{max}$ | 81.2 mm (female)<br>84.1 mm (overall) | 86.7 mm (female = overall maximum) | 97.9 mm (female = overall maximum) |
| Size at maturity $L_{50}$ (95% C.I.) | 55.1 mm (54.2–56.1) | 40.2 mm (37.4–42.2) | 46 mm (45.3–46.7) |
| $L_{50}/L_{max}$ | 0.68 (with female $L_{max}$) | 0.46 | 0.47 |
| Breeding opportunities | Histological features of iteroparity, but likely with only one realized reproductive season, at least in the study region | Iteroparous | Iteroparous |
| Spawning pattern | Batch-spawner | Batch-spawner | Batch-spawner |
| Oocyte size (mean ± S.D.) | 0.73 ± 0.05 mm | 0.86 ± 0.1 mm | 0.91 ± 0.05 mm |
| Gonado-somatic index (GSI) in actively spawning phase (median) | 4.5 | 7.5 | 7.1 |
| Batch fecundity (mean ± S.D.) | 2668 | 1027 ± 1120 | 1545 ± 644 |
| Relative batch fecundity (eggs $g^{-1}$ gonad-free fish weight, mean ± S.D.) | 369 | 149 ± 114 | 215 ± 56 |

## 4.2 | Life history

Sex ratios were balanced in *E. risso* and *M. polylepis*, and lengths were similar between sexes in the three studied species. A higher allocation of resources to females is a strategy to achieve a higher egg-producing biomass and occurs in some mesopelagic species (Clarke, 1983), but is not common in most myctophid species (Gartner, 1993; Hussain, 1992; Lisovenko & Prut'ko, 1987).

The $L_{50}$ of *E. risso* showed that females matured at about 55.5 mm, which is slightly lower than an $L_{50}$ of 59 mm estimated from macroscopic appearance by Hulley (1981). The $L_{50}$ in the present study lay between two size groups in the length–frequency distribution. Linkowski (1987) reported an age of 600 days in specimens from the eastern North Atlantic with 60 mm $L_S$, based on analysis of daily growth increments in otoliths. As the individuals in our study grew up to 20 mm larger, we estimate that *E. risso* becomes approximately 2 years old and interpret the two size groups as one largely immature year-class and one reproducing year-class. Using empirical data, Froese and Pauly (2013) found that one-time spawners, as well as bearers and guarders, typically mature about 67% of their asymptotic size, whereas species with an $L_{50}/L_{inf}$ significantly lower than 0.67 spawn more than once. The observed $L_{50}/L_{max}$ (0.68) therefore confirms that the nonguarding *E. risso* reproduces during a single spawning season. However, a robust age and growth analysis are needed.

The length–frequency distributions of the two melamphaid species appear more ragged with no clearly distinguishable cohorts and

may represent overlapping year-classes. A conclusive age determination based on growth increments in otoliths was not possible, as we do not know the periodicity of the ring deposition with certainty, and a large proportion of the otoliths were corroded from fixation in formalin solution. In another study on a species from the melamphaid family, *Poromitra crassiceps* reached an age of 9 years and matured in the last 2 years of life, assuming that growth rings were annual (Childress et al., 1980). *M. polylepis* matured at a slightly smaller size than *S. mizolepis* (40.2 *v.* 46 mm, respectively), yet, with the correspondingly different maximum lengths, the $L_{50}/L_{max}$ values are remarkably similar at 0.46 and 0.47. These values are well below 0.67 and indicate that both species increase their chance of successful reproduction by maturing relatively small, which allows for multiple breeding seasons (Froese & Pauly, 2013).

Based on GSI, Bartow (2010) estimated that *Melamphaes* spp. at the northern Mid-Atlantic Ridge mature at 70–117 mm, and Clarke (1983) estimated the $L_{50}$ for female *S. mizolepis* caught around Hawaii at 59 mm and the $L_{50}/L_{max}$ at 0.79. Apart from methodological differences between studies, it could be that species adopt different reproductive strategies depending on environmental conditions. In other widely distributed mesopelagic species, geographical variation has been observed in life-history traits such as size at maturity (García-Seoane et al., 2014) or maximum length and the growth speed with which it is reached (Salvanes & Kristoffersen, 2001).

## 4.3 | Spawning strategy

Whether different oocyte stages occur simultaneously or successively in histological cross-sections can elucidate the temporal reproductive strategy. Semelparous fishes, which experience only one spawning season, do not maintain a reserve of PG oocytes: all PG oocytes develop into secondary growth oocytes (Lowerre-Barbieri, Brown-Peterson, et al., 2011). In the three studied species, PG oocytes were present in the actively spawning phase; thus, they all have the histological characteristics of the iteroparous strategy, which allows for multiple breeding opportunities in a lifetime. Still, we concluded that *E. risso* is functionally semelparous, in that only one spawning cycle is realized in the study region. Habitat-dependent facultative semelparity was found in subarctic capelin (Christiansen et al., 2008), which illustrates that the dichotomy between semelparity and iteroparity is not strict. In contrast to the melamphaids in this study, *Poromitra cracciceps* appeared to be semelparous, because it showed no development in ovaries until its seventh year and showed development in mature oocytes only in the ninth year (Childress et al., 1980).

Within a spawning season, eggs can be released during one spawning event (total spawners) or in several batches over a longer period (batch-spawners) (Burton & Burton, 2018). In batch-spawners, only a portion of yolked oocytes is selected to be hydrated and spawned in each batch. The presence of multiple oocyte stages in the spawning-capable phase indicated batch-spawning in our three species. Batch-spawning was further evident in the two melamphaid species by the presence of POFs in gonads with not yet hydrated oocytes, indicating at least one batch had already been released. Both total and batch-spawning occur in different myctophid species around the world, but batch-spawning seems to be the more common strategy, especially in tropical and subtropical waters. *Benthosema suborbitale*, *Lampanyctus alatus*, *Lepidophanes guentheri*, and *Notolychnus valdiviae* have protracted spawning seasons of 4–6 months, with spawning occurring every 1–4 days, whereas *Ceratoscopelus* sp. has a restricted spawning period, with spawning once or twice a year (Gartner, 1993). Batch-spawning increases the chance of successful reproduction in unpredictable environments (Hočevar et al., 2021) and can avoid competition among offspring (Nakayama et al., 2011). Moreover, it is a way to reach a higher annual fecundity despite a small body size (Lowerre-Barbieri, Ganias, et al., 2011).

In the actively spawning phase, all earlier oocyte developmental stages were present alongside the maturing oocytes in both melamphid species, but late vitellogenic oocytes (Vtg3) were not observed in *E. risso*. With a simulation study, Ganias and Lowerre-Barbieri (2018) showed that such different patterns result from different combinations of oocyte growth and spawning intervals, where shorter spawning intervals increase the number of coexisting oocyte batches. The absent group of Vtg3 oocytes points to a longer spawning interval in *E. risso*.

No individuals in the regressing or regenerating phase were observed in this study. Observing numerous females in the regressing phase would indicate the end of the spawning season (Brown-Peterson et al., 2011). Iteroparous species would then remain in the regenerating phase until the next reproductive cycle, but semelparous species would die. The phase "spent" (corresponding to regressing in Brown-Peterson et al., 2011) was rarely encountered in studies on the myctophid *Benthosema pterotum* in the Indian Ocean (Dalpadado, 1988). Dalpadado (1988) hypothesized that females spawn only once and die shortly afterward or that they spawn, recover quickly, and leave no trace of previous spawning. Sampling over a longer time would be needed to solve this in future investigations. The samples for this study were obtained in late March and early April during the spawning season, but with the present temporal coverage, it is not possible to determine the entire spawning period. Of the three species, *E. risso* had the highest percentage of individuals able to spawn, whereas *M. polylepis* may have been the furthest from its peak spawning activity.

## 4.4 | Reproductive investment

There was a significant correlation between increasing GSI and progressing ovarian development, as well as significant differences between successive phases. However, in each species, the GSI ranges overlapped between reproductive phases. This means that the GSI should not be used alone to discriminate between reproductive phases. Comparing our results with other studies on mesopelagic fishes, the GSI values of *E. risso* are within the range of other myctophids. The median GSI of actively spawning females in this study (4.5) was slightly higher than the reported maximum for *Benthosema fibulatum* (3.9; Hussain, 1992) but lower than that of *B. pterotum* females

with hydrated oocytes (10–16; Sassa et al., 2014). The highest GSI value reported for a myctophid was 34.01 in *D. danae* (Flynn & Paxton, 2012). The maximum GSI of 12 female *S. mizolepis* caught in June and early July in the northern Atlantic was 2.38 (Bartow, 2010), much lower than the maximum value of 13.87 in the present study. This confirms that the main spawning season of *S. mizolepis* is more likely during March/April than during June/July.

The fecundity estimates are the first reported for *E. risso* and the first for the family Melamphaidae. The results may be imprecise due to the low number of replicates in combination with a high natural variability. Clarke (1984) reported a strong variation in the fecundity between similar-sized individuals of a myctophid species. *E. risso* showed a higher batch fecundity and a relative batch fecundity than the two melamphaid species. It appears that *E. risso* experiences only one spawning season with longer spawning intervals, which may be partly compensated by its higher fecundity, whereas the melamphaids spread their lifetime reproductive output over several spawning seasons.

Average batch fecundities of myctophids can range from about 100 eggs in *Notolychnus valvidae* to 12,000 eggs per batch in *Ceratoscopelus* sp. (Gartner, 1993). Fecundities can vary geographically within species and between closely related species. *Benthosema glaciale* females in the Mediterranean Sea and the North Atlantic had a comparatively low batch fecundity with 491 ± 228 (mean ± S.D.); the relative batch fecundity was 1031 eggs $g^{-1}$ gonad-free fish weight (García-Seoane et al., 2014), whereas *B. pterotum* females from the Indian Ocean had a batch fecundity up to 3000 (Dalpadado, 1988). The batch fecundity of *B. pterotum* estimated in the East China Sea was between 253 and 1942 (Sassa et al., 2014). The highest fecundity in myctophids was found in *D. danae* in the Australian Coral Sea (Flynn & Paxton, 2012): one female with 106 mm $L_S$ had a batch fecundity of 25,803 eggs, where the relative batch fecundity was 1817 eggs $g^{-1}$ gonad-free fish weight. Overall, the results of this study fit well into the overall range of fecundity in myctophids.

## 5 | CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

The three investigated species *E. risso*, *M. polylepis*, and *S. mizolepis* from the subtropical to the tropical North Atlantic are broadcast spawners that release their eggs in batches. *E. risso* is short lived, and females mature at about two-thirds of the maximum size and reproduce in a single spawning season. *M. polylepis* and *S. mizolepis* mature at less than half of the maximum size and reproduce in multiple spawning seasons. Low batch fecundity in broadcast spawners is a feature of an opportunistic life-history strategy (Winemiller, 2005; Winemiller & Rose, 1992), which is an adaptation to unpredictable environments. However, *E. risso* will be especially vulnerable to pressures such as commercial fishing, as it is likely that they would be caught before they were able to release all their eggs. Moreover, as only a few year-classes exist at the same time, a missed reproduction of one cohort can hardly be mitigated at the population level. A withdrawal of an economically profitable quantity would put the *E. risso* population in danger sooner than the two melamphaid species, all with unknown consequences for the ecosystem. Future research is needed to fill in knowledge gaps related to the temporal aspects of reproduction. In particular, age determination and validation, which require knowledge of the periodicity of growth ring formation in otoliths, are needed to analyse growth rates and growth patterns, longevity, and age at maturity. Because actively spawning females were found in the current study, late March and early April must lie in the spawning season. However, the duration of the spawning season and the frequency of spawning, which are needed in combination to estimate annual egg production and lifetime fecundity, are not yet known.

### AUTHOR CONTRIBUTIONS

Heino O. Fock conceived the idea for the study. Alexander H. Knorrn and Kim L. Wieben carried out the practical work with help from Heino O. Fock and Henrike Andresen. Alexander H. Knorrn, Kim L. Wieben, and Henrike Andresen analysed the data and discussed the results with Heino O. Fock, Alexander H. Knorrn, Kim L. Wieben, and Henrike Andresen wrote the text, and Heino O. Fock revised it critically.

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### DATA AVAILABILITY STATEMENT

Data for this study were published open access: Knorrn et al. (2023) Reproductive data of Electrona risso, Melamphaes polylepis and Scopelogadus mizolepis from the Eastern Central Atlantic in March and April 2015. PANGAEA, https://doi.org/10.1594/PANGAEA.962192.

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## APPENDIX

**TABLE A1** Oocyte sizes of *Electrona risso* per reproductive phase (see Table 1).

| Reproductive phase | Diameter ± s.d. (mm) of most advanced oocyte |
|---|---|
| Immature | <0.2<br>$n = 5$ |
| Early developing<br>(subphase of "developing") | 0.20 ± 0.04<br>$n = 11$ |
| Developing | 0.27 ± 0.05<br>$n = 24$ |
| Spawning capable | 0.39 ± 0.04<br>$n = 69$ |
| Actively spawning<br>(subphase of "spawning capable") | 0.73 ± 0.05<br>$n = 5$ (only hydrated oocytes measured) |

*Note*: At least five oocytes have been measured in each of *n* individuals.

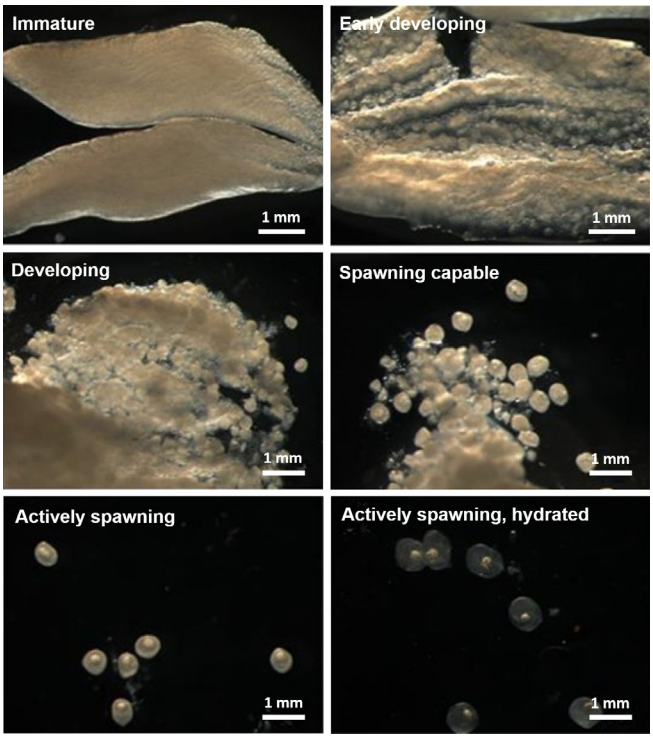


**FIGURE A1** Oocytes. Figure A1: Oocytes of female *Electrona risso* per reproductive phase (see Table 1), photographed with reflected light. Photography by K. Wieben.

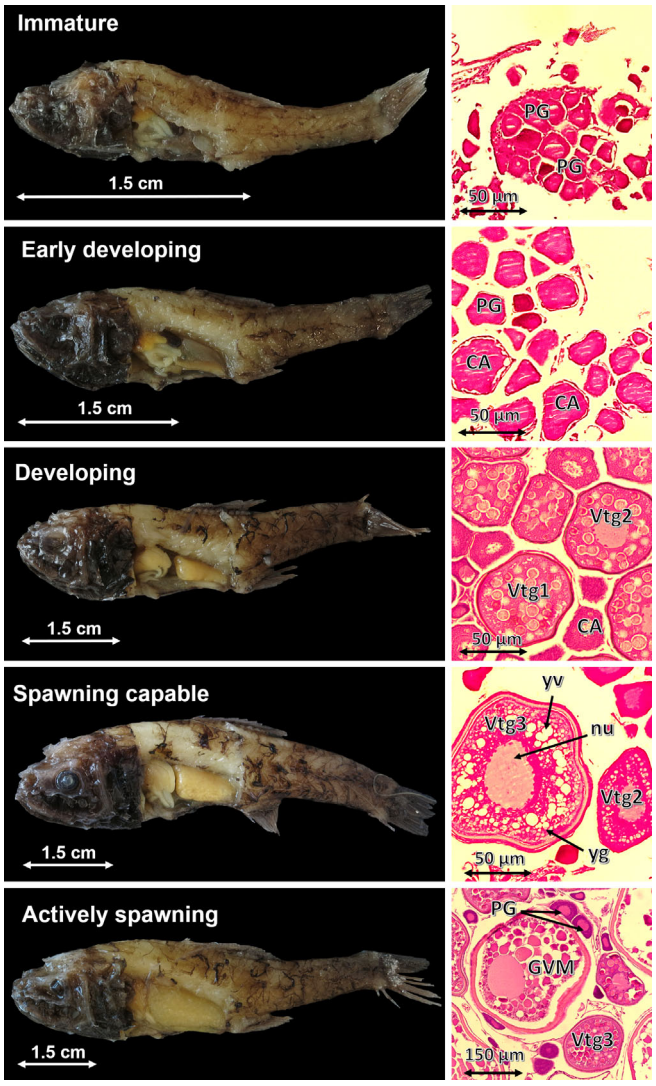


**FIGURE A2** *Scopelogadus mizolepis* ovarian development. Reproductive phases based on Table 1. Macroscopic development of female gonads (left panels) and histological cross-sections of ovaries (right panels). CA, cortical alveoli oocyte; GVM, germinal vesicle migration oocyte; nu, nucleus; PG, primary growth oocyte; Vtg1–3, primary to tertiary vitellogenic oocyte; yg, yolk granules; yv, yolk vesicle. Photography by A. Knorrn.