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Notes on age determination, size and age structure, longevity and growth of co-occurring macrourid fishes

Odd Aksel Bergstad[1] | Rebecca H. Hunter[2] | Nicola J. Cousins[3] | David M. Bailey[2] | Terje Jørgensen[1]

[1]Institute of Marine Research, Bergen, Norway

[2]Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK

[3]Zoology Building, University of Aberdeen, Aberdeen, UK

Correspondence
Odd Aksel Bergstad, Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway.
Email: oabergstad@gmail.com

Abstract

Nineteen species of the deep-water fish family Macrouridae inhabit the Mid-Atlantic Ridge (MAR) of the North Atlantic. Size and age structure, longevity and length at age were explored for seven of the more abundant species: *Coryphaenoides armatus*, *Coryphaenoides brevibarbis*, *Coryphaenoides carapinus*, *Coryphaenoides guentheri*, *Coryphaenoides mediterraneus*, *Coryphaenoides rupestris* and *Macrourus berglax*. The otoliths from these species had growth increments resembling those accepted as annuli in other deep-water species for which validation experiments have been conducted. Based on the counts of these growth increments, age estimates were derived as the basis for studies of age structure, growth and longevity. All the species appeared to have relatively low growth rates, but the interspecific variation in longevity illustrates that there is a considerable variation within the family and among species inhabiting the same deep-sea environment. Most of the species likely complete full life cycles on the MAR, but it is probable that both the youngest and the largest-oldest individuals of some of the species were not sampled adequately.

KEYWORDS
Coryphaenoides, deep water, life history, *Macrourus*, Mid-Atlantic Ridge, North Atlantic

1 | INTRODUCTION

Compared with fishes of the more productive shelf and coastal waters, deep-water demersal fishes inhabiting waters beyond continental shelves are often described as having extended life span, slow growth, high ages at first maturation and therefore low productivity (*e.g.*, Drazen & Haedrich, 2012; Merrett & Haedrich, 1997; Priede, 2017). Cailliet *et al.* (2001) hypothesised that longevity increases with depth of occurrence due to altered physiological processes or diminishing food supply.

Large *et al.* (2003) suggested, however, that long-lived species often perceived as typical deep-water species, *e.g.*, orange roughy

(*Hoplostethus atlanticus*) and roundnose grenadier (*Coryphaenoides rupestris*), were really rather exceptions than representative examples of a wide range of traits displayed by deep-water demersal fish. The deep sea may have comparatively more species with low productivity than the shelf and coastal waters, but diversity is probably higher than commonly perceived.

Nonetheless, life-history traits have been described satisfactorily for surprisingly few of the several hundred demersal deep-water species known. In particular, few attempts have been made to compile and compare data on the diversity of life histories for co-occurring taxonomically closely related species that are members of the same deep-water fish assemblage. In this paper the authors

consider size and age distributions, longevity and growth of seven species of the same family Macrouridae, all inhabiting the same geographical area and general habitat, *i.e.*, a mid-ocean ridge system. Some of the species were studied elsewhere (Allain & Lorance, 2000; Bergstad, 1990; Drazen & Haedrich, 2012; Gordon & Swan, 1996; Kelly *et al.*, 1997; Rodríguez-Marín *et al.*, 2002; Swan & Gordon, 2001), and this study thus supplements earlier studies of macrourid growth and longevity.

The Macrouridae ranks as one of the most prominent deep-water demersal fish families (Marshall, 1965; Merrett & Haedrich, 1997; Priede, 2017) with over 400 known species (Iwamoto, 2008), 19 of which have been reported from the Mid-Atlantic Ridge (MAR) between Iceland and the Azores (64–38° N) (Bergstad *et al.*, 2008a; Porteiro *et al.*, 2017). The MAR is a major deep-water habitat with a suitable depth range for macrourid fishes, and patterns of abundance and depth distributions revealed that although the habitats of different species partially overlap, some segregation by depth occurs (Bergstad *et al.*, 2008a). It is not clear if all the species observed on the MAR complete their life cycle there. The length and age ranges help infer which species complete their life cycle on the MAR and therefore may have self-contained populations in the area.

Good estimates of age are prerequisites for the estimation of life histories. This study therefore attempted to reveal and define annual growth zones in the sagittae (saccular otolith) of the species for which an age determination method had not been described previously.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

Samples of macrourids were collected during the 2004 ecosystems of the mid-atlantic ridge (MAR-ECO) cruises to the MAR in the area between 40° and 55° 30′ N. Bottom trawls were deployed by the
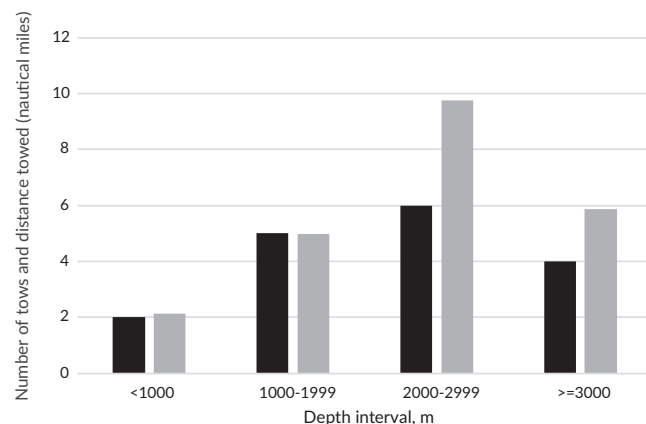

FIGURE 1 Depth distribution of sampling effort on the Mid-Atlantic Ridge. Number of tows and accumulated distance towed, by depth zone. Data for MAR-ECO sampling on the RV *G.O. Sars*, 2004 (■) Number of trawl tows, MAR-ECO; (▨) Total distance towed, nautical miles

research vessel *G.O. Sars* (ship 1) and baited longlines by the chartered fishing vessel *Loran* (ship 2) (Bergstad *et al.*, 2008b; Fossen *et al.*, 2008; Wenneck *et al.*, 2008). The slopes on either side of the ridge were sampled, with pre-planned sampling effort distributed throughout the depth range from the summit of the ridge at 800–900 m to 3500 m. Seventeen successful trawl tows were made, within the depth range 985–3512 m. The depth distribution of sampling effort is plotted against depth in Figure 1. Trawling distance was highest in the 2000–2999 m interval because bottom conditions there allowed longer tows compared with the rougher grounds in shallower areas. A similar strategy was adopted by the fishing vessel (ship 2) which distributed 59 longline sets across the ridge axis at depths ranging from 433 to 4200 m (Fossen *et al.*, 2008), *i.e.*, extending into somewhat shallower and deeper areas than the trawl operations which were inaccessible with the trawl. Due to rough ground, trawling on the minor shallow areas is dangerous, but longlining was feasible. The maximum trawling depth was limited by the wire range of the research vessel to *c*. 3500 m, but longlining was possible somewhat deeper. The single 4200 m set was exceptional, however, and the depth distributions of the longline and trawl effort corresponded well although more longline effort was directed at the minor shallowest areas. The two-gear approach was selected to sample relatively flat soft-substrate areas with the bottom trawl and steep and hard-substrate areas with the longline, within the same depth range.

Size and age distributions were based on MAR-ECO (2004) cruises keeping separate data from bottom trawling and longline. Nonetheless, to complement the observed ages for the growth analysis, the authors used samples from a second project (UK ECOMAR using the RSS *James Cook*, ship 3) that deployed a 14 m semi-balloon otter trawl at three sites at about 2500 m in the northern part of the MAR near the Charlie-Gibbs Fracture Zone (Cousins *et al.*, 2013).

The sampling protocol was the same for the three vessels. The entire catch, or a random sub-sample, was sorted to species, weighed and counted, and for selected species such as the macrourids, ungutted weight (g) and length (mm) of individual specimens were recorded. At sea a heave-compensated scale and an electronic measuring board were used. Some specimens were frozen at sea and weighed and measured in the laboratory after thawing. Data from fresh and frozen–thawed specimens were pooled under the assumption that the changes in length and weight caused by freezing and thawing would be a minor source of imprecision for these species. Macrourid caudal fins are frequently broken or regenerated; therefore pre-anal fin length (PAFL) was measured, defined as the distance from the snout to the base of the first ray of the anal fin. Otoliths (sagittae) were extracted at sea or, in the case of frozen and thawed specimens, in the laboratory. Otoliths were stored either in paper bags or in 70% ethanol, and in the laboratory, one otolith from each pair was cleaned and air-dried (if stored in ethanol).

Also included in this account are a few incidental catches of juvenile *C. rupestris* by midwater trawls aimed at sampling micronekton and plankton (Wenneck *et al.*, 2008).

2.2 | Age estimation

Whole otoliths were embedded in clear epoxy resin (2:1 epoxy:hardener mix) to allow cutting of transverse sections by a low-speed double-blade diamond saw (McCurdy, 1985). Multiple sections were taken to ensure at least one or two of the sections contained the nuclear region and were of readable quality. The selected sections were then mounted on glass slides under cover slips using the same epoxy mix as a mounting medium. A light microscope with $25\times$ and $100\times$ magnification and transmitted light was used for examining the sections.

For *C. rupestris* presumed annuli were counted in accordance with illustrations and descriptions provided by Bergstad (1990). That account showed how the first 10–12 growth zones were wide and resembled those found in other gadoids, including juvenile macrourids (Swan & Gordon, 2001). Some of the early opaque zones appeared as bundles of smaller growth zones, together forming a prominent feature which was regarded as the annulus. Further zones, also proposed as annuli, were often narrow but distinctive. These zones were prominent only on the proximal surface of the otolith as the otolith appeared to grow in thickness rather than along the anteroposterior and dorsoventral axes. For *Macrourus berglax* Rodríguez-Marín et al. (2002) and Orlov et al. (2018) described and illustrated an age determination method based on counting otolith growth zones, and the present approach was compatible with that. For all species in the present study, including *C. rupestris* and *M. berglax*, a consistent counting procedure had to be developed based on a common understanding among readers of what patterns should be accepted as annuli. Initially two readers counted independently the presumed annuli in a limited set of otoliths. The two readings were then compared, and each otolith was viewed and discussed. Specimens with a large difference between readings were particularly studied with the aim to resolve or explain significant inconsistencies. Approaches for regular counting were considered. Decisions were made on what sector of the otolith section or along what direction from the nucleus to the margin counting should proceed to achieve the most repeatable counts. The occurrence of "bundles" (see earlier) was a challenge when defining the more prominent feature to be regarded as one opaque zone. A guiding principle used was that successive initial growth zones should normally become narrower with increasing distance from the nucleus. Another indication of "bundled" annuli was that, as they extend some distance around the section, they normally (but not always) merge into a single zone. Therefore, although counting was done along a specific line or within a specific sector, full viewing of the entire section was necessary. Also, focusing and zooming was required to explore the prospective growth zones, normally on several sections of the same otolith.

The result of these discussion sessions was agreement on a common definition of growth zones to be counted as annuli and a method that generated repeatable annuli counts to be regarded as proposed age estimates. Despite the uncertainties created by variable growth zone patterns within and between species, it was possible to define growth structures for all species that could provide consistent counts. Otolith growth zones are, either in the entire otolith or in parts, often indistinctive. Although precision remained lower than desired, it was considered acceptable for further pursuing the study.

Each otolith was then read twice by Reader 1, and a random subset from each species was read once by Reader 2. Consistency between paired readings was tested using bias plots (Campana et al., 1995) and Wilcoxon signed-rank tests.

2.3 | Data analysis

Sample sizes differed between species. Size and age distributions were derived for all species although the confidence in the results is higher for well-sampled species than for species with small samples, i.e., *Coryphaenoides carapinus* and *Coryphaenoides guentheri*. Size distributions from individual stations were raised to standardised numerical catches to derive distributions reflecting the size composition in the entire catch. Maximum observed age was determined from an examination of age distributions, and the maximum age observed was assumed to represent an estimate of longevity.
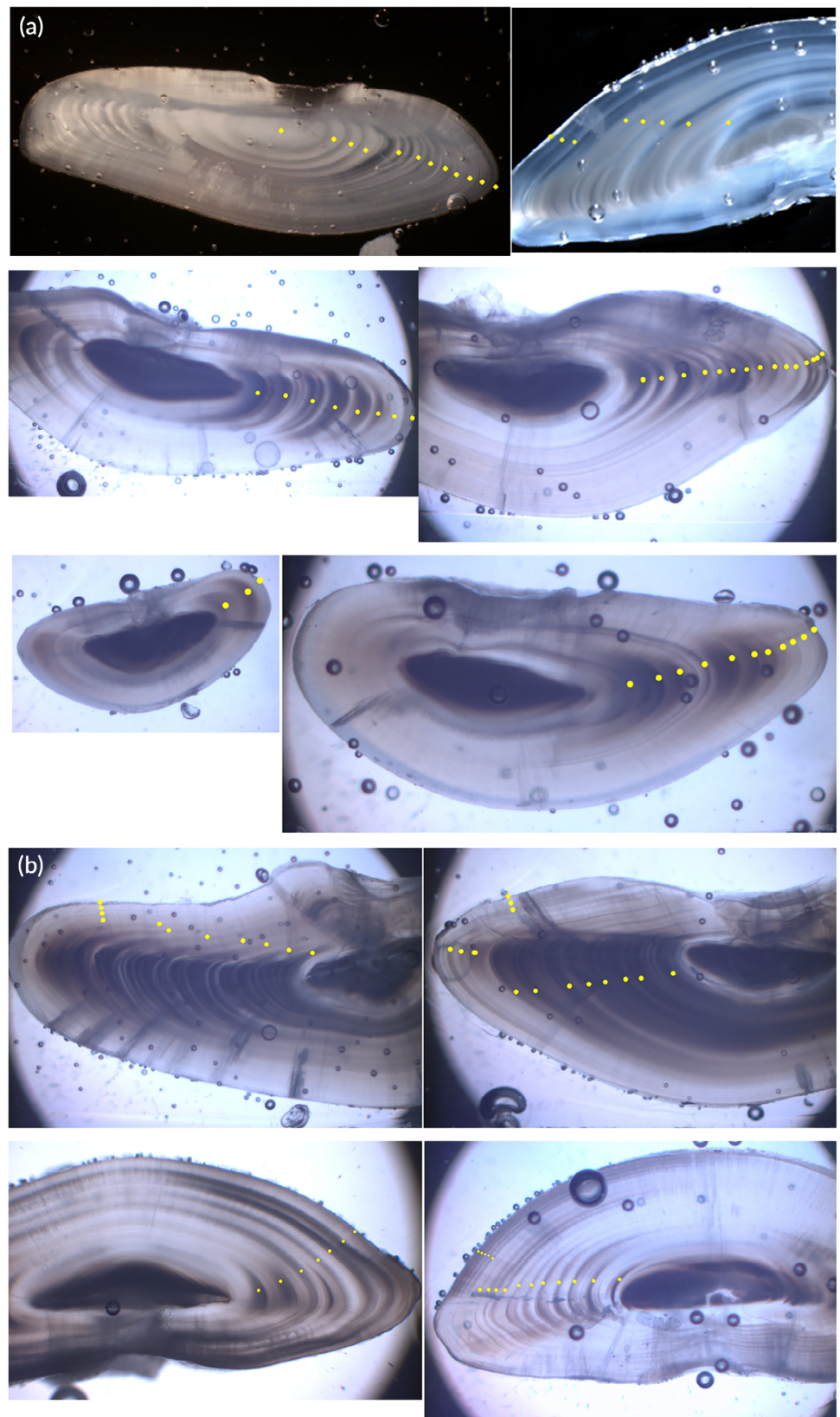
Despite several cases of low sample sizes and suspected limited age ranges, the initial exploratory attempts were made to fit von Bertalanffy growth curves in terms of length to PAFL at age data, i.e., $L_t = L_\infty(1 - \exp(-K(t - t_0)))$, where L_t is the PAFL length at age t, L_∞ is the asymptotic PAFL, K is the growth constant (expressing the rate at which length approaches the asymptote) and t_0 is the age at which $L = 0$. The von Bertalanffy function was chosen as it is a commonly used function in fish and fisheries research, and other options were not explored. Statistical calculations were performed using R version 3.6.3 (R Core Team, 2020). Growth equation parameters were estimated by non-linear regression using the nls function of the R package stats (R Core Team, 2020). Starting values were obtained from a Ford–Walford plot. Ninety-five percent confidence bands of the estimated growth curves were estimated by bootstrapping, using the Boot function of the package car (Fox & Weisberg, 2019) with 1000 bootstrap samples. The bootstrap estimates were bias corrected and accelerated. Statistical evidence of an effect of sex on growth was examined using Kimura's likelihood ratio test (Kimura, 1980), implemented in the *growthlrt* function of the R package *fishmethods*, version 1.11-1 (Nelson, 2019). Parameters a and b of the L–W relationship $W = aL^b$ were derived by fitting power function trendlines to scatter plots using EXCEL, with fish weight (W) and PAFL (L) as input data.

3 | RESULTS

3.1 | Age estimation

Discernible growth zones were observed in the transverse sections of the sagittal otoliths of all examined specimens of the seven species (Figure 2), and the zones resembled those accepted as annuli in other deep-water teleosts (*e.g.*, Bergstad, 1994). The techniques adopted produced technically acceptable sections for most specimens and often several sections of the same otolith. Acceptable sections displayed growth zones for the entire radius of the otolith from the centre to the margin, allowing an uninterrupted count to

be recorded, preferably in several directions. After readers had agreed on a common interpretation and procedure, consistent estimates of zone counts were derived for all species. Paired readings were compared with bias plots as proposed by Campana *et al.* (1995). Because there were no indications of non-linear bias, Wilcoxon signed-rank tests were run and showed that bias was unlikely ($P > 0.5$). Nonetheless, the precision varied between species and was highest for *Coryphaenoides mediterraneus*, which had

very clear otolith growth patterns, and lowest for *C. guentheri* and *C. carapinus*.

3.2 | Size and age distributions and longevity

Seven species that were comparatively abundant were given special attention: *Coryphaenoides armatus*, *Coryphaenoides brevibarbis*, *C. carapinus*, *C. guentheri*, *C. mediterraneus*, *C. rupestris*, and *M. berglax*. The size ranges for these and some less-abundant species are provided in Table 1. Extensive size ranges of all the seven species except *M. berglax* occurred in the trawl catches (Table 1; Figure 3), including juveniles of 20 mm PAFL, probably the smallest to be expected in demersal trawls. For *C. rupestris*, the most abundant species, such small juveniles were captured only in midwater trawls.

C. armatus occurred in bottom-trawl catches from ship 1 as well as in the longline catches from ship 2. The longline samples comprised very large fish, including specimens of PAFL > 250 mm not captured by the trawls (Figure 3). *M. berglax* was infrequent in the bottom-trawl catches, therefore the small sample size, but common on longline.

Maximum observed age estimates varied substantially between species from 12 years in *C. carapinus* to the oldest-observed *C. rupestris* and *M. berglax* of near 40 years (Figure 4; Table 2). For *C. armatus*, a number of otolith sections suggested ages of 30 years or more. Nonetheless, the precision between repeat counts was low, and these were excluded from the analysis.

As sample sizes were low for *C. carapinus* and *C. guentheri*, the results for these species are less certain than for the others. Young *M. berglax* (<10 years) were not observed and were probably not sampled by the longlines. *C. mediterraneus* aged <5 years and *C. guentheri*

<6 years were missing in the otolith samples, but the size distributions comprised very small fish that may have been undersampled, primarily because priority was given to secure samples for museum curation. Once conserved in formaldehyde, the specimens were unavailable for otolith sampling. Another challenge was that small juvenile macrourids are difficult to identify to species level.

3.3 | Length–weight relationships and growth

The length–weight relationship parameters for all species are provided in Table 1.

Size-at-age plots are shown in Figure 5. For the four species (*C. brevibarbis*, *C. rupestris*, *C. armatus* and *C. mediterraneus*) with sample sizes exceeding 50 individuals, von Bertalanffy growth functions were fitted (Figure 5a; Table 3). In three of the species, *C. armatus*, *C. brevibarbis* and *C. mediterraneus*, the scatter plots suggested an almost-linear increase in length with age. Asymptotic lengths were thus poorly estimated. The data allowed for separate calculations of growth by sex only for *C. rupestris*. There was evidence of a marginal statistical difference ($P = 0.048$).

4 | DISCUSSION

4.1 | Age determination

Otolith growth zones resembling annuli observed in shallow-living fishes were recognised in a range of deep-water fishes (*e.g.*, Beckman & Wilson, 1995; Bergstad, 1994; Cailliet *et al.*, 2001; Morales-Nin & Panfili, 2005; Swan & Gordon, 2001). Zones found previously in some

TABLE 1 Sample sizes, length and weight ranges and parameters of the length–weight relationships of macrourids from the Mid-Atlantic Ridge

| Species | Sample size | | Pre-anal fin length (cm) | | Weight (g) | | L–W parameters | | | |
	Length	Age	Minimum	Maximum	Minimum	Maximum	a	b	n	r²
Coryphaenoides armatus	874	232	2.5	35.0	1	5280	0.08	3.09	590	0.977
Coryphaenoides brevibarbis	1808	77	2.0	12.5	1	195	0.09	3.17	415	0.943
Coryphaenoides carapinus	166	23	2.4	12.0	5	210	0.15	2.88	34	0.949
Coryphaenoides guentheri	58	15	2.8	15.0	17	480	0.03	3.59	25	0.957
Coryphaenoides mediterraneus	168	68	1.8	21.0	2	1340	0.23	2.79	90	0.960
Coryphaenoides rupestris	636	180	1.9	22.5	2	1980	0.12	3.17	602	0.985
Coryphaenoides leptolepis	56		2.3	22.0						
Coryphaenoides profundicolus	1		35.5							
Macrourus berglax	288	44	14.5	49.0	290	11,270	0.10	2.97	259	0.983
Paracetonurus flagellicauda	41		4.0	9.0						
Sphagemacrurus hirundo	8		2.5	4.6						
Squalogadus modificatus	1		6.1							
Bathygadus favosus	1		91 cm total length							

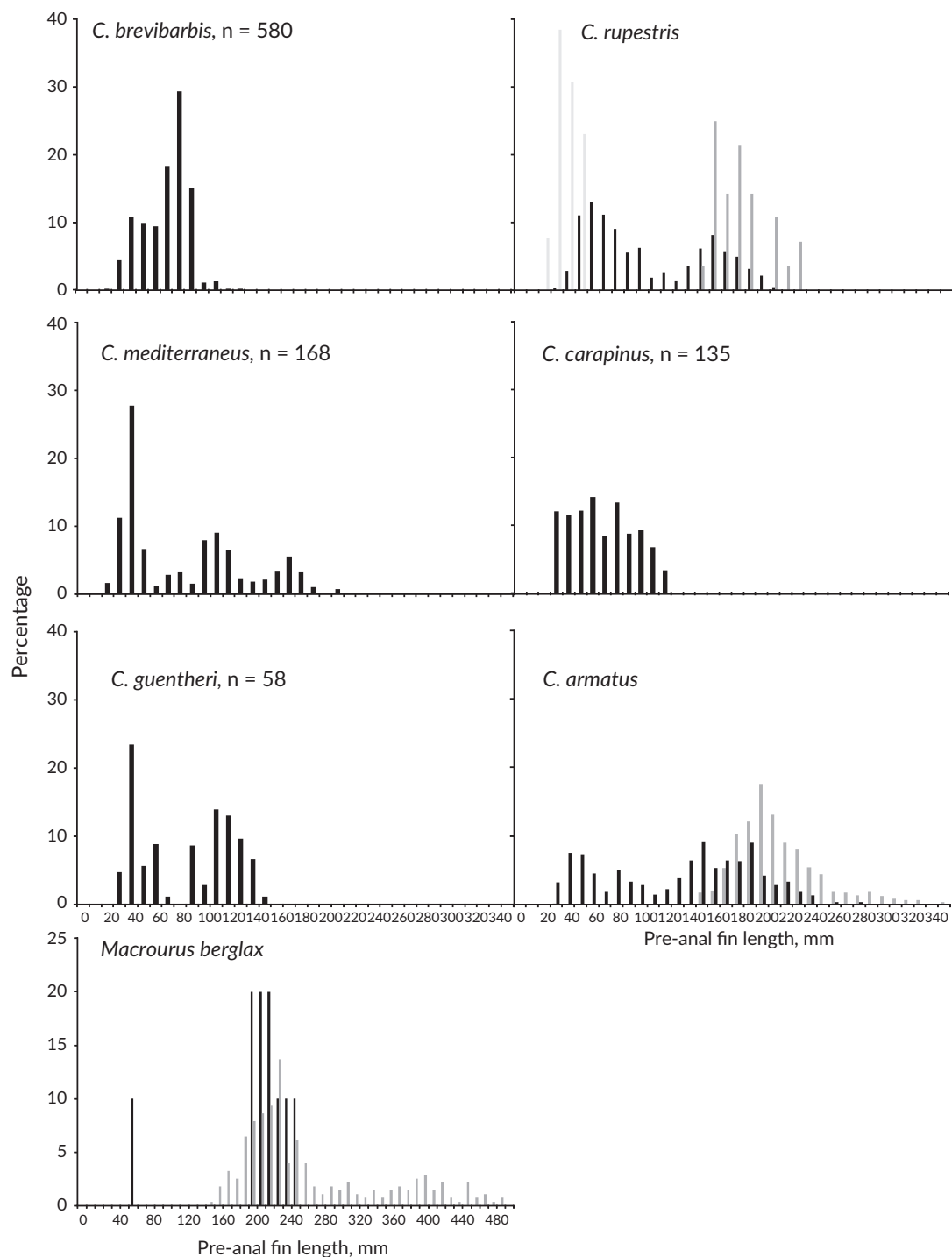*Note.* Data are from the MAR-ECO expedition, 2004.

FIGURE 3 Size distributions of seven macrourid species on the Mid-Atlantic Ridge. Data collected by trawls and longlines on the MAR-ECO expedition in 2004 (■) Bottom-trawl samples, *n* = 595; (▢) Longline samples, *n* = 28; (■) Midwater trawl samples, *n* = 13; (▢) Longline samples, *n* = 586; (▢) Bottom-trawl samples, *n* = 202; (▣) Bottom-trawl samples, *n* = 10; (■) Longline samples, *n* = 278

macrourids were assumed to reflect the alternate growth periods of the year, and a complete annulus is therefore counted as 1 year in the life of the fish (*e.g.*, Bergstad, 1990, 1994; Gordon & Swan, 1996; Swan & Gordon, 2001).

A range of methods using scales and otoliths have been used to determine the age of macrourid fishes, and Swan and Gordon

(2001) summarised approaches and results of early studies. They also considered several of the species used in the present study except *M. berglax* and examined whole otoliths from juveniles on which they observed clear growth zones proposed to represent annuli. Subsequently, *M. berglax* otoliths were used by Rodríguez-Marín *et al.* (2002) and Orlov *et al.* (2018) to determine age, and
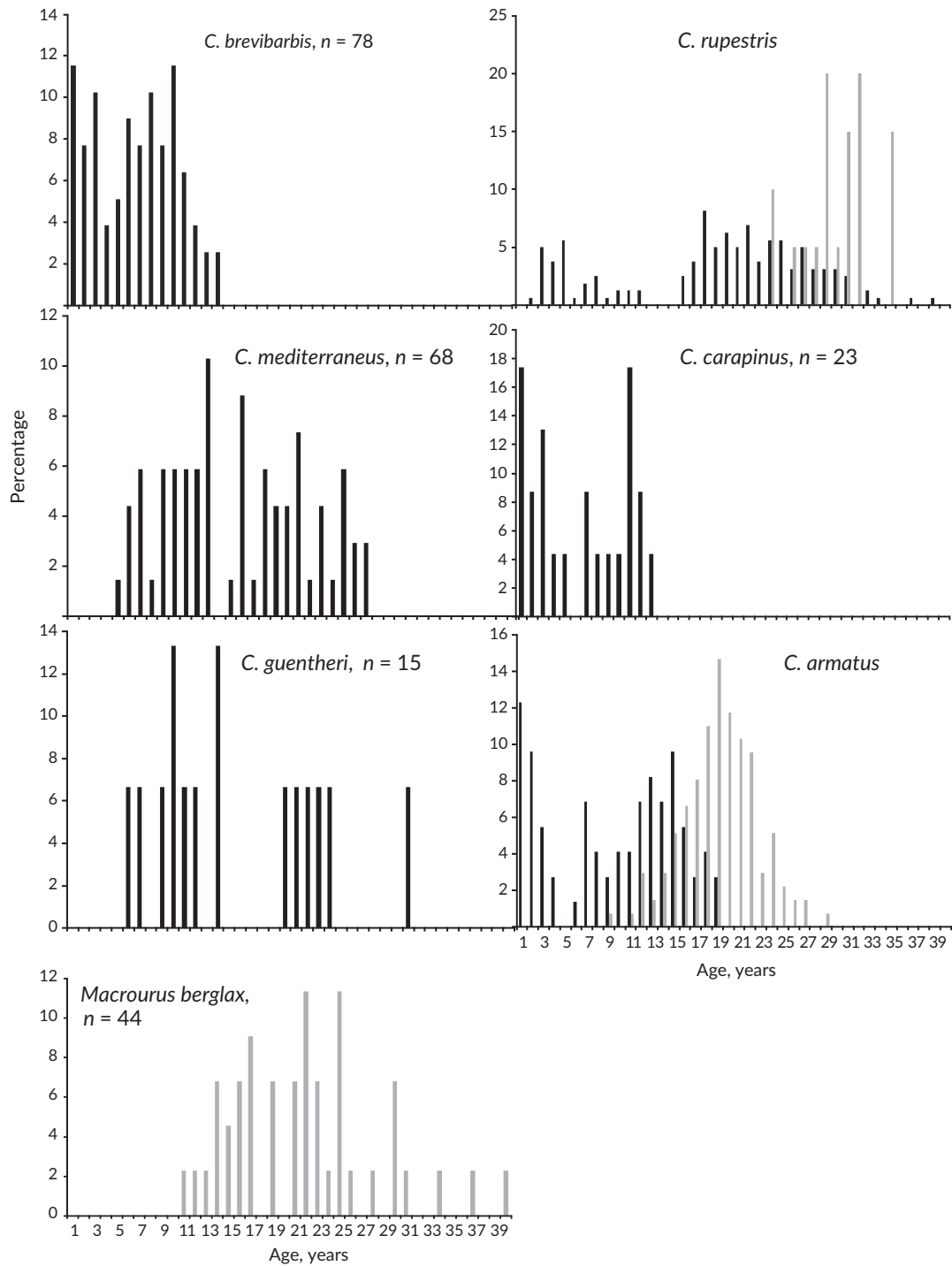
FIGURE 4 Age distributions of seven macrourid species on the Mid-Atlantic Ridge. Data collected by trawls and longlines on the MAR-ECO expedition in 2004. Age estimates used are "proposed ages" as determined from counts of growth zones on otoliths assumed to represent annuli (■) Trawl samples, $n = 160$; (□) Longline samples, $n = 20$; (■) Trawl samples, $n = 73$; (□) Longline samples, $n = 136$

the approaches were well described and illustrated. In the present study, relatively clear, gradually narrowing growth increments from the centre to the otolith margin were found on otolith sections from the entire size range of all the seven species aged. Therefore, growth zones resembling those accepted as annuli for many shallow-living species appear to be also deposited in these deep-water macrourids throughout their life span. Seasonality in the deep

sea may be dampened compared with that observed in shallow habitats but strong enough to cause seasonal food supply and migrations (Milligan et al., 2020).

Similarity in otolith growth zones between species with or without validated annuli does not per se constitute a validation of the existence of annuli. Even if some previous studies show or strongly suggest that annuli occur in the macrourid otoliths, it is recognised that stringent

TABLE 2 Age range of seven macrourid fishes from the Mid-Atlantic Ridge (MAR) derived from counts of otolith growth zones assumed to be annuli

Species	Observed age range on MAR
Coryphaenoides armatus	1–29+
Coryphaenoides brevibarbis	1–13
Coryphaenoides carapinus	1–12
Coryphaenoides guentheri	6–31
Coryphaenoides mediterraneus	5–27
Coryphaenoides rupestris	2–39
Macrourus berglax	11–40

validation of the age estimation method is still needed for several of the species. Among the species studied here, it is only for *C. rupestris* and *M. berglax* that validation exercises have previously resulted in clear and convincing results, albeit for limited age ranges. Gordon and Swan (1996) studied seasonal frequencies of opaque and hyaline edges in *C. rupestris* juvenile otoliths and concluded that annuli occurred. Similar indications were obtained for *C. guentheri*, *C. armatus* and *C. mediterraneus*, but the seasonal sampling was not sufficient to reach firm conclusions. Rodríguez-Marín *et al.* (2002) validated otolith age readings for *M. berglax* using several approaches such as backcalculation of length at age, length frequency analyses and analyses of the progression of the length mode of an exceptionally large year class. The structures assumed to represent annuli in all the macrourids mentioned earlier, as well as *C. carapinus* and *C. brevibarbis*, were similar in appearance to those observed in the Pacific grenadier, *Coryphaenoides acrolepis*, for which radiometric ageing has closely agreed with age estimates from counting annuli (Andrews *et al.*, 1999).

There was inter- and intraspecific variation in the level of precision of the annuli counts. Despite the fact that the technical quality of the sections was good, the growth zones in some otolith sections were indistinctive and therefore difficult to distinguish and count. This was consistently the case for *C. guentheri* and *C. carapinus* and for large specimens of *C. armatus*. Repeatable counts could be derived based on the agreed definition of assumed annuli and counting procedures, but validating the method and age estimates was beyond the scope of this work and remains a task for the future.

4.2 | Longevity and growth of individual species

The depth distributions of the different species on the MAR were reported by Bergstad *et al.* (2008a), and based on the sampling by ship 1 (*G.O. Sars*) and ship 2 (FV *Loran*) spanning the depth range from the summit to *c.* 3500 m. The results suggest that the sampling included the ranges and maximum depth of occurrence of all the macrourid species in the study area. Weighing of the length frequencies by catch was assumed to result in single species-specific distributions representing the areas and depth ranges on the MAR where the individual species were most abundant.

4.2.1 | *Coryphaenoides armatus*

The size range observed suggested that all life stages of *C. armatus* occurred in the area. The differences between sampling gears illustrate how choice of gear, *i.e.*, trawl or longline, may strongly influence results and the perception of size and age structure in an area. Hook and bait sizes probably prevent small fish from being hooked, and although *C. armatus* species is a known scavenger, attraction to carrion/bait may increase with size. Nonetheless, it was more surprising that the smallest juveniles were missing also in trawl catches, despite that the trawl had an 8 mm liner in the codend. Likely explanations are that the smallest juveniles stay very close to the seabed and pass beneath the groundgear or that they escape through the somewhat larger mesh of the trawl belly. Diving with manned submersibles, Felley *et al.* (2007) frequently observed small grenadiers very close to the seabed on the slopes of the Charlie-Gibbs Fracture Zone (CGFZ) and assumed that many were *C. armatus* (but other species may also have occurred there).

There are no previously published longevity data for this species, but an estimate of *c.* 40 years may be reasonable. It is probable that the species completes a significant part of its life cycle on the MAR because the smallest juveniles were observed in the area (Felley *et al.*, 2007) and large fish occurred on longlines and in trawls.

The near-linear growth curve suggests, however, that the oldest fish may not have been captured. Lorance *et al.* (2003) highlight the inaccuracies created in growth rate analyses conducted on an incomplete size-age range of specimens, namely overestimation of L_∞ and subsequent underestimation of K when large fish are absent or underrepresented. Therefore, the estimates of von Bertalanffy growth parameters presented in Table 3 for this and other species must be treated with some caution.

There remains a lack of knowledge on life-history strategies of this species known also to inhabit abyssal plains. Gravid females are rarely sampled, and ontogenetic migrations into abyssal areas may happen.

4.2.2 | *Coryphaenoides brevibarbis*

The largest fishes observed were at or near previously reported maximum sizes. This is a small, apparently short-lived species, and it is tentatively concluded that this species complete its life cycle in the area. The age samples were too small to split growth curves by sex. Bergstad *et al.* (2008b) found a very high abundance of this species on the MAR, mostly restricted to northern areas near the CGFZ.

4.2.3 | *Coryphaenoides carapinus*

Unlike the other species of this study which are probably benthopelagic feeders or scavengers, this fish is adapted morphologically for benthic feeding (Mauchline & Gordon, 1984). The smallest juveniles <30 mm PAFL were not observed, and it is also uncertain
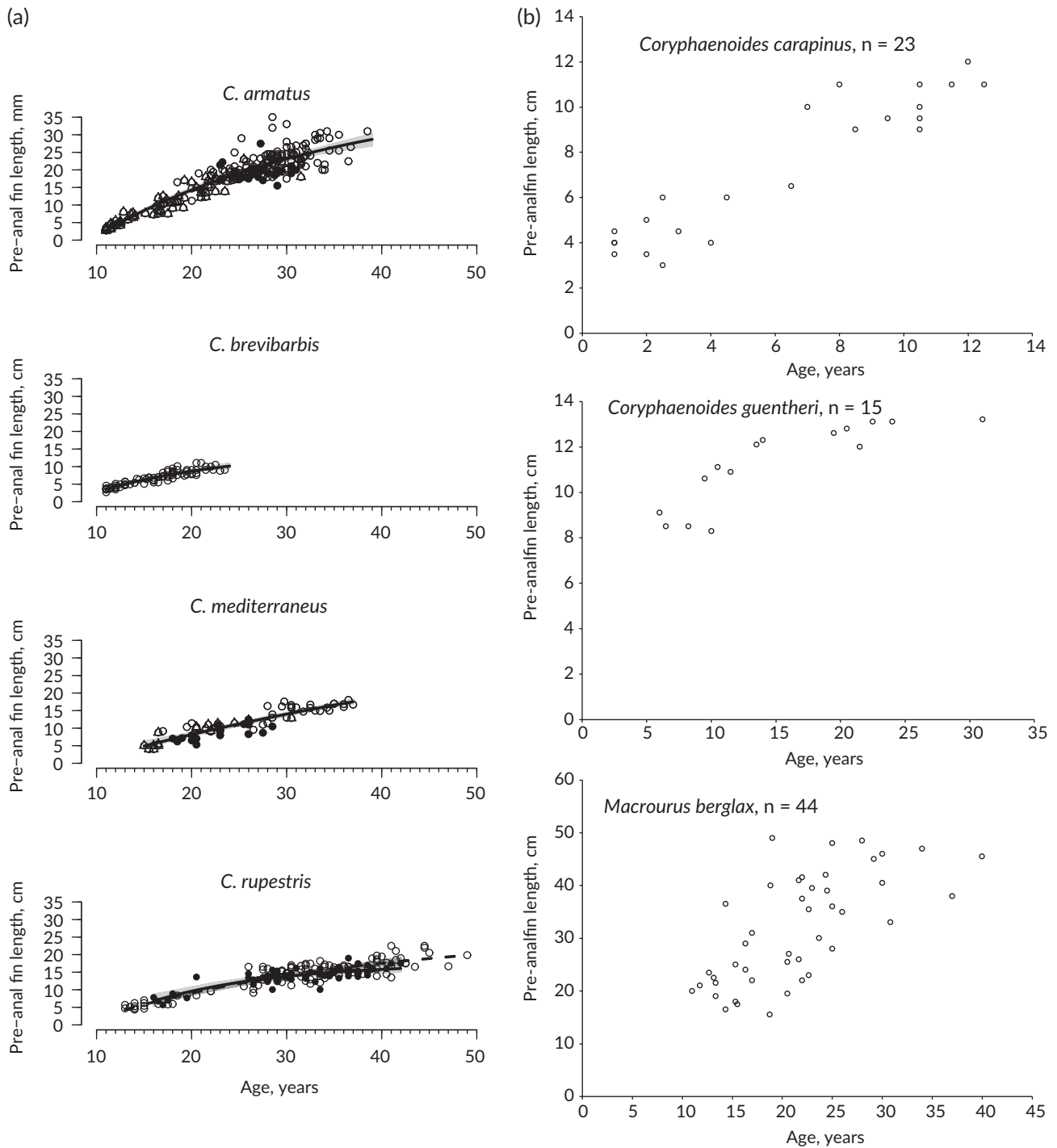
FIGURE 5 (a) Length-at-age data for four macrourid species from the Mid-Atlantic Ridge, with fitted von Bertalanffy growth functions. Growth function parameters and sample sizes are provided in Table 3. Shaded areas are 95% confidence bands. Data are from MAR-ECO and UK ECOMAR samples (○) females; (●) males; (△) unsexed; (○) females; (●) males; (△) unsexed; (○ – – –) females; (● ——) males. (b) Length at age of three macrourids: *Coryphaenoides carapinus*, *Coryphaenoides guentheri* and *Macrourus berglax*. *n* = sample size, *i.e.*, number of specimens with data on age and length. Data are from MAR-ECO and UK ECOMAR samples

whether the largest fish occurred in the catches and whether the species has a full life cycle in the area. The longevity estimate of 12 years may thus be too low, especially in view of the length-at-age data suggesting a linear relationship. On the European slope (Rockall Trough a.o.), J. D. M. Gordon (pers. comm.) found *C. carapinus* of 8–37 cm total length (TL). Assuming that PAFL is roughly 30% of TL, that corresponds to a PAFL range of *c.* 2–11 cm which is similar to that observed on the MAR.

TABLE 3 Estimates of parameters of the von Bertalanffy growth function for four macrourid fishes from the Mid-Atlantic Ridge

Species	n	Point estimates of parameters			95% C.I.		
		L_{inf}	K	t_0	L_{inf}	K	t_0
Coryphaenoides rupestris, both sexes	180	23.3	0.04	−1.7	20.0–32.1	0.03–0.06	−3.4–0.7
Female	105	25.8	0.04	−2.1	20.4–42.6	0.02–0.06	−4.6–0.5
Male	62	17.6	0.08	−0.5	15.1–23.9	0.03–0.15	−8.0–2.9
Coryphaenoides armatus	230	42.1	0.04	−0.8	34.1–57.3	0.03–0.05	−1.4–0.4
Coryphaenoides brevibarbis	77	14.5	0.07	−2.9	11.1–31.5	0.02–0.12	−4.6–1.9
Coryphaenoides mediterraneus	67	45.8	0.02	−1.7	27.3–197.3	0.003–0.04	−6.1–0.6

Note. Data are from MAR-ECO and UK ECOMAR.

4.2.4 | *Coryphaenoides guentheri*

Beyond the smallest juveniles, it is likely that the entire size range was sampled, and the longevity estimate of *c*. 30 years may be reasonable. Although the age sample was small, and the length-at-age data were limited, the scatter plots suggested that asymptotic level may have been approached. It is tentatively concluded that *C. guentheri* completes its life cycle on the MAR.

4.2.5 | *Coryphaenoides mediterraneus*

The growth zones in the *C. mediterraneus* otoliths were the clearest observed among the species considered, and annuli counts yielded a longevity estimate of 27 years. *C. mediterraneus* thus appear to have an intermediate longevity. Nonetheless, judging from the length-at-age data where there was no levelling off with age (Figure 4), it is suspected that larger individuals were not captured in this study.

4.2.6 | *Coryphaenoides rupestris*

As for *C. armatus* there are clear gear-related differences in length ranges sampled, with the longlines catching only big fish and trawls more or less the entire size range. Very small juveniles occurred in midwater trawls, suggesting a benthopelagic and truly pelagic lifestyle, as observed earlier by Vinnicheno and Khlivnoi (2008). As ages up to 72 years have been previously recorded elsewhere (Bergstad, 1990), it is likely that the maximum age found on the MAR of only 39 years is low. This may reflect the relatively low sampling effort reducing the chance of encountering the few very old individuals. An alternative explanation is that the species does not complete its life cycle in the sampling area. The latter is considered less probable for a species not likely to perform extensive migrations.

The growth curves suggest a sexual dimorphism as observed in other studies, with females growing bigger than males. The roundnose grenadier on the MAR may seem to grow to sizes similar to those observed in the Rockall Trough (Allain & Lorance, 2000; Kelly *et al*., 1997).

4.2.7 | *Macrourus berglax*

Few roughhead grenadiers were caught by trawls, and juveniles were not found in the sampling area. The youngest individual was 11 years. On the longlines, a wider size range, including very large individuals, occurred. This species is sub-Arctic, and the catches were taken near the previously assumed southern range on the MAR (Bergstad *et al*., 2008a, 2008b; Hareide & Garnes, 2001). The absence of young fish and abundance of large fish may reflect an ontogenetical migration southwards along the MAR. No previous studies have exceeded the age estimates obtained in this study, and a longevity of around 40 years may be reasonable and corresponds with earlier comprehensive observations in the Northwest Atlantic by Rodríguez-Marín *et al*. (2002) but were high compared with data from West Greenland waters provided by Orlov *et al*. (2018). Judging from illustrations in these published accounts, the methods used for age determination by different workers appeared to correspond to those used here, but as yet no intercalibration exercises have been published for the species. The restricted size range made fitting growth curves impossible for this species.

4.2.8 | Other species

The checklist of MAR-ECO fishes by Porteiro *et al*. (2017) included some size data for macrourid species. Some additional data not included in the checklist are provided in Table 1.

4.3 | Variation in life-history traits

Albeit that uncertainties remain for some species, the study revealed that there are considerable differences among the seven macrourid species in terms of longevity and probably also in growth patterns. Several of the species are apparently not particularly long lived, whereas some have extensive age ranges, *i.e.*, *C. rupestris*, *C. armatus* and *M. berglax*. It may be generally correct that deep-water fishes often have extended life span, slow growth and so on (*e.g.*, Drazen & Haedrich, 2012; Merrett & Haedrich, 1997; Priede, 2017); nonetheless,

this study also seems to confirm that there is greater variation than that general statement suggests, as also proposed by Large *et al.* (2003). Members of the same family inhabiting the same general habitat displayed a range of strategies. Multispecies studies of this nature are few, and further studies of other deep-water fish families would be needed to determine if the observed variation is special for macrourids or whether interspecific variation is rather extensive also in other families.

Furthermore, longevity was not related to depth. Some of the short-lived species (*C. carapinus* and *C. guentheri*) were among the deepest-living macrourids (Bergstad *et al.*, 2008a), and species with long life span occurred at either end of the depth range on the MAR (*i.e.*, *C. rupestris* and *M. berglax* vs. *C. armatus*).

On the MAR, two of the species, *C. rupestris* and *M. berglax*, have been targeted by fisheries. Others may occur as by-catch. The two target species have extended life span, and because that has been known from other areas within their extensive ranges, it is taken into account in fisheries management advice in, *e.g.*, international council for the exploration of the sea and northwest atlantic fisheries organization (Large *et al.*, 2003; Rodríguez-Marín *et al.*, 2002).

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AUTHOR CONTRIBUTION

O.A.B. helped with ideas, data generation, data analysis, manuscript preparation and funding. R.H.H. assisted with data generation, data analysis and manuscript preparation. N.J.C. was involved in data generation, data analysis and manuscript preparation. D.M.B. assisted with manuscript preparation and funding. T.J. helped with data analysis and manuscript preparation.

ETHICS STATEMENT

The work did not include experiments that required permits pertinent to animal welfare regulations. Only wild-caught deep-sea fish specimens were examined, and all the species of Macrourids studied were dead when they arrived on deck.

ORCID

Odd Aksel Bergstad https://orcid.org/0000-0002-4096-0896

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