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Age estimation, growth, maturity and distribution of the roundnose grenadier from the Rockall trough

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This paper summarizes the history of commercial exploitation of roundnose grenadier *Coryphaenoides rupestris* in the North Atlantic. Length frequencies of *C. rupestris* in 1993, from 400 to 1200 m on the slopes of the Rockall trough indicate a reduction since the 1970s in the modal length of fish found at 700–1000 m. Ages ranged from 2 to 50 years for males and 2 to 60 years for females, with most between 10–38 years. Females attained a greater asymptotic pre-anus length (L_∞=19·5 cm) than males (L_∞=15·5 cm) and had a greater weight for a given age (male W_∞=761 g, female W_∞=1132 g). This species may have a protracted spawning period. Using pre-anus lengths, 50% of male fish were mature at 10 cm (ages 8–10) while 50% of female fish were mature at 12 cm (ages 9–11). At the greatest depths sampled the length frequency of fish was bimodal with a hiatus between 9 and 11 cm (ages 8–12). Highest catch rates occurred on the Donegal slope in September at a depth of 800–1000 m.

Key words: deep-water fish; otolith; reproduction; exploitation; NE Atlantic.

INTRODUCTION

Macrouridae (grenadiers) are the most widespread family of fish occurring on the continental slope of the North Atlantic and along the mid-Atlantic ridge (Kotthaus & Kreft, 1967; Marshall, 1979; Gordon *et al.*, 1994). Roundnose grenadier *Coryphaenoides rupestris* (Gunnerus 1765) is the most heavily exploited of these species.

C. rupestris reaches total lengths >100 cm, although up to 50% of this consists of the whip-like tail. It is benthopelagic, feeding on copepods and amphipods, and becomes more piscivorous as it grows (Mauchline & Gordon, 1984; Gordon & Mauchline, 1990). It occurs at 180–2200 m depth (Haedrich & Merrett, 1988; Cohen *et al.*, 1990), but off north-west Ireland it is normally present at 600–1800 m (Gordon unpublished, ICES 1978). It occurs along the continental slope from North Africa, Europe, Iceland, Greenland, Canada to the south-eastern United States, generally 37°–66° N and occasionally as far south as 20° N in the eastern Atlantic and 24° N in the western Atlantic (Cohen *et al.*, 1990). Around south-west Iceland and eastern Canada most specimens are small (<20 cm TL). In the denser popuations to the south-east and west of the Iceland–Faro ridge there are no juveniles (Magnusson & Magnusson, 1994). Juveniles and adults are present in the other areas of its range. There is disagreement over the number of *C. rupestris* stocks in the North Atlantic. Some authors claim that fish in the north-east and north-west Atlantic form part of a

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central spawning concentration along the Reykjanes ridge (Dushchenko, 1988; Dushchenko & Savvatimsky, 1988). This has been disputed (Dupouy & Kergoat, unpublished; Atkinson, 1994). Gene frequencies of fish from all areas of the North Atlantic show a high degree of homogeneity in muscle enzyme loci (Dushchenko, 1988) suggesting a hierarchical system of populations between which there is a large scale exchange of individuals. However the study could not explain the low level of homogeneity in muscle enzyme loci in local populations.

The fishery for roundnose grenadier began on the Donegal and Hebridean slopes in 1989, and in 1992, 49% of the total international catch of roundnose grenadier (9573 tonnes) was taken in ICES Divisions VIa and VIb (Fig. 1, Dupouy & Kergoat, unpublished). The total 1992 landing of roundnose grenadier from all ICES divisions was 17 009 tonnes (Anon., unpublished). In the north-west Atlantic, the commercial fishery for the roundnose grenadier began in 1967 on the continental slope to the east of Newfoundland. During the period 1973–1978, the fishery was yielding up to 82 500 tonnes, but by 1993 this had declined to <10 000 tonnes (Atkinson, 1994; Troyanovsky & Lisovsky, 1994).

This paper presents the first estimates of age and growth for roundnose grenadier in the Rockall trough since the advent of the deep-water fishery. Results are compared with length and growth data from the virgin stock in the same area (Gordon, unpublished; Bridger, 1978). Maturity, length frequency and catch rate data are also presented for samples taken with commercial fishing gear during surveys undertaken in 1992 and 1993.

METHODS

SAMPLING CRUISES

Seven research, exploratory, and commercial cruises to the Rockall trough were made between May 1992 and September 1993 on the same 39-m whitefish stern trawler (1900 bhp) using the same large commercial deep-water rockhopper trawl with 3800-kg Polyice doors. The trawl net was fitted with a fine 10-mm mesh cod-end. Most samples were collected during 1993 (Connolly & Kelly, 1994). Seven areas were fished within the Rockall trough proper (Areas 1–4, 9–11; Fig. 1) at depths from 500 to 1250 m. The western slopes of the Rockall trough (Areas 9–11) were fished only in September. Areas 1–4 on the eastern slopes of the trough were fished in both April and September allowing a seasonal comparison of catch rates.

EXAMINATION OF SPECIMENS

A total of 8166 specimens was measured, of which 1406 (448 fresh, 958 frozen and iced) were examined in more detail in the laboratory. Pre-anus length (Fig. 2) was measured to the nearest cm below. Weight was measured to the nearest g, and sex and maturity were determined by visual examination of the gonads based on an eight-point maturity scale (Elder, 1976).

The conversion of pre-anus to total length was derived by linear regression of total length *v*. pre-anus length from a sub-sample of 89 fish with complete tails, selected over a range of pre-anus lengths 10–22 cm (Table I).

Sagittal otoliths from 1406 fish were cleaned, dried and stored in plastic trays. Some stomachs and gonads were preserved in 4% formaldehyde. Conversion equations were derived to convert iced and frozen weights to fresh weight equivalents (Table II).

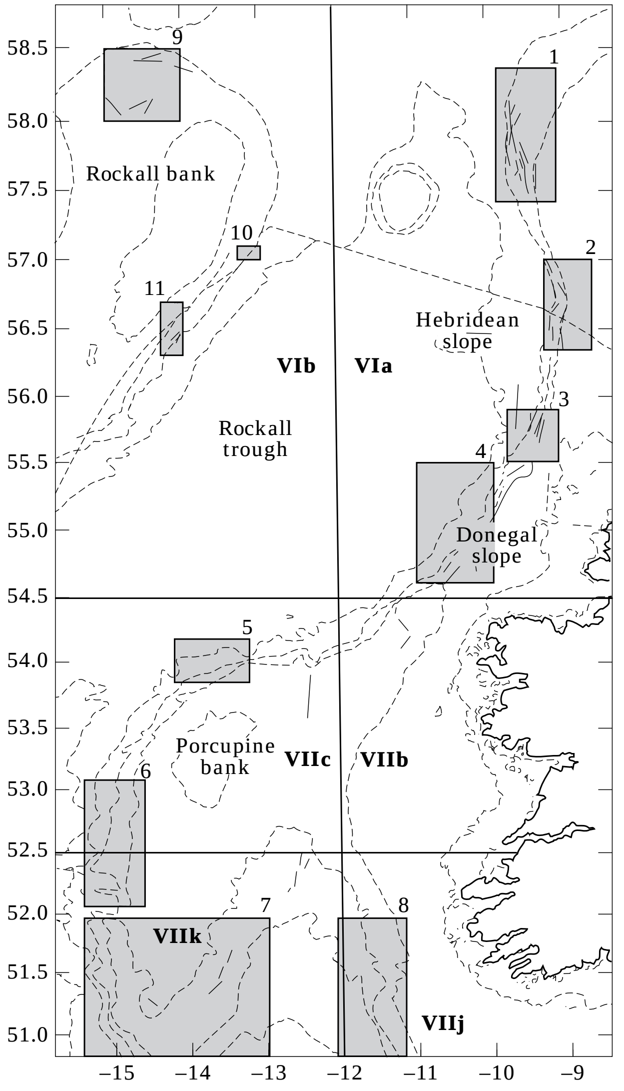

FIG. 1. Map showing ICES divisions and Areas fished (1–11) in April and September 1993 (▨).

AGE ESTIMATION

Otoliths were processed and examined following Williams & Bedford (1975), Chilton & Beamish (1982), and Bedford (1983). Eighty-four whole otoliths from fish <7 cm were viewed immersed in alcohol against a black background in reflected light. In addition, 625 transverse sections were prepared using a low-speed diamond wafering saw (Bedford, 1983; McCurdy, 1985). All sections were etched in a 6% solution of EDTA for *c*. 30 min to improve the clarity of the annual increment structure. Otoliths were viewed by stereo microscope (Wild M8) at between 6–50 × magnification, fitted with a closed circuit, high-definition colour video camera and monitor. Otoliths were illuminated with transmitted and/or reflected light using an optic fibre light source fitted with a ring diffuser. The otolith terminology used was after Jensen (1965) and interpretation of the patterns was based on Chilton & Beamish (1982) and Bergstad (1990). Precision was

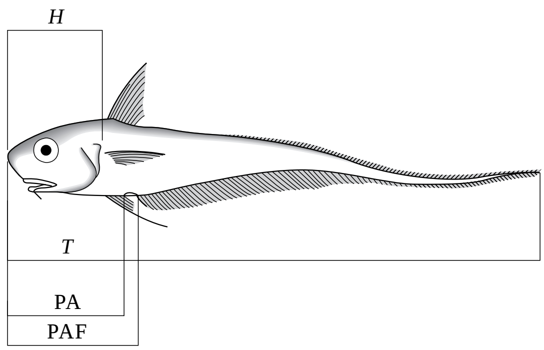

FIG. 2. The various length measurements used for roundnose grenadier. H, head length; T, total length; PA, pre-anus length; PAF, pre-anal–fin length.

TABLE I. Conversion equations for pre-anus length (P) to total length (L) and anal-fin length (A) for roundnose grenadier

$T=4{\cdot}48\ P+0{\cdot}76$	(This paper)
$T=4{\cdot}16\ P+0{\cdot}75$	(Bergstad, 1990)
$A=1{\cdot}063\ P-0{\cdot}38$	(Atkinson, 1981)

TABLE II. Length–weight relationships for fresh (f) iced (ice) and frozen (f_z) roundnose grenadiers, and conversion equations for iced and frozen weights to fresh weight equivalents

Fresh	Iced	Frozen
$W_f=0{\cdot}732(L^{2{\cdot}587})$	$W_{ice}=2{\cdot}287(L^{2{\cdot}176})$ $\mathrm{Ln}(W_f)=1{\cdot}035(\mathrm{Ln}\,W_{ice})-0{\cdot}06$	$W_{fz}=1{\cdot}652(L^{2{\cdot}274})$ $\mathrm{Ln}(W_f)=0{\cdot}991(\mathrm{Ln}\,W_{fz})+0{\cdot}211$

estimated by comparing the age readings obtained from a random sample of 80 otoliths (whole and sections) viewed independently by two readers. The APE (average percentage error) was calculated following the method of Beamish & Fournier (1981).

GROWTH

Von Bertalanffy growth curves $L_t=L_\infty[1-e^{-K(t-t_0)}]$ were fitted using two iterative least squares procedures (SAS NLIN procedure, with DUD option, and Microsoft Excel© solver routine with Newton algorithm option).

RESULTS

DISTRIBUTION

Overall catch rates (cpue kg h^{-1}) were higher in September (Table III). However many of the greater depth ranges were not sampled in April. The

TABLE III. Catch rates (kg h^{-1}) for roundnose grenadier in April and September 1993

Depth (m)	Area 1		Area 2		Area 3		Area 4	
	April	September	April	September	April	September	April	September
500–649	4·0	6·2	10·4	10·6	1·0	*	36·0	*
650–799	1·9	49·7	0·0	74·7	1·0	37·9	34·2	276·6
800–949	0·7	218·1	0·5	297·3	0·0	425·8	67·5	391·5
950–1099	*	415·4	*	*	*	*	*	367·1
1100–1250	*	166·2	*	*	*	*	*	*

*Depth not fished.

Donegal slope (Area 4) produced consistently higher catch rates in April and September, with a tendency for the greatest concentration of fish to be between 800 and 1000 m (Table III).

LENGTH DISTRIBUTIONS

The length frequencies of 8166 roundnose grenadier caught on the eastern slopes of the Rockall trough, at four different depth ranges, between April and September 1993 showed a mode between 14 and 16 cm (Fig. 3) with a small additional mode at 6 cm below 1000 m. Although present from 600 m, small fish appeared to be more concentrated below 1000 m. Converting these data for fish taken at 700-m and 1000-m depth intervals in September with the equation in Table I, total lengths were compared to those of Bridger (1978) and Gordon (unpublished) (Fig. 4).

AGEING

The opaque and hyaline annual increment pattern was clearly visible on whole otoliths from smaller fish when viewed whole in reflected light (Fig. 5). Ages up to 5 years could be read easily in this fashion. There was some variation in otolith edge types from small otoliths of the same age. However, in larger fish the clarity of the annual increment on whole otoliths was unclear and sectioning was required. There were two major phases of growth. The first was referred to as pre-collar growth (Figs 5(a) and 6: fish $\leq$ age group 20) and post-collar growth [Figs 5(c) and 7] thereafter. In the former, the annual increment pattern was usually readable along the anterio-posterior axis [Fig. 5(b)] but when indistinct the internal axis was used. This post-collar phenomenon has been observed in other studies (Chilton & Beamish, 1982; Bergstad, 1990) and is the result of a shift in the axis of growth from the anterio-posterior to the internal axis.

The first two annual increments could be distinguished despite the presence of checks within the first opaque annual increment of some otoliths. By contrast, Bergstad (1990) had difficulty in distinguishing between the nucleus and first opaque annual increment. Interpretation of annual increments 5–20 (i.e. those observed along the anterio-posterior axis before formation of the collar) presented some problems. The frequent appearance of faint lines between these annual increments, combined with the gradual reduction in the spacing between them, made interpretation difficult. For the purposes of this study the faint lines

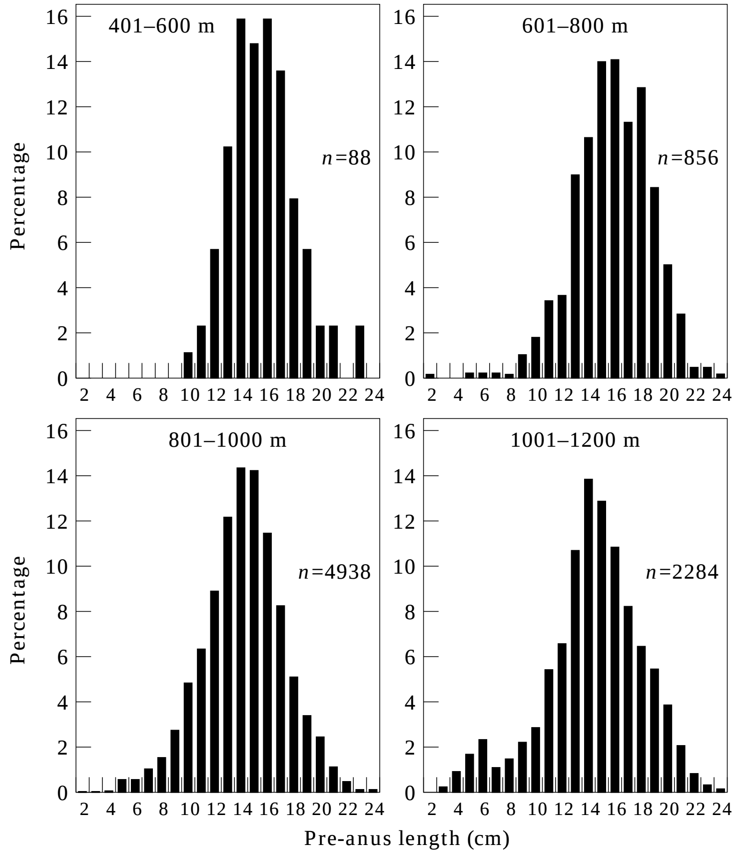

FIG. 3. Percentage length frequency (pre-anus cm) by depth for roundnose grenadier from the Rockall trough (April–September, 1993) using a commercial rock hopper trawl (90-mm mesh) fitted with a 10-mm small mesh cod-end.

in the pre-collar area were treated as check marks, as in Bergstad (1990). A similar protocol has been adopted for redfish (*Sebastes mentella* Travin 1951) otoliths (Kosswig & Rubec, unpublished). The inclusion of these faint lines as annual increments would produce much higher estimates of age.

In fish >age 20 there were no problems with the interpretation of the annual increment patterns on the collar as split rings were not usually evident. Age estimates were made by counting the opaque rings from the nucleus along the internal axis to the edge of the otolith. Otoliths from male and female fish yielded counts of up to 50 and 60 annual increments respectively. Assuming one annulus consists of a successive opaque and hyaline ring, then the samples were dominated by fish of age groups 10–38. The oldest fish was a female aged 60 but there were few fish over age 50. Closeness of the annuli made it increasingly difficult to age fish over 50. There was a low relative abundance of 1–5-year-old fish in both samples and a scarcity of age groups 9–11 particularly in the females (Fig. 8). Precision estimates gave APE of 8·3% for whole otoliths (ages 1–5), and 4·9% for sectioned ones (ages 1–58) (Table IV).

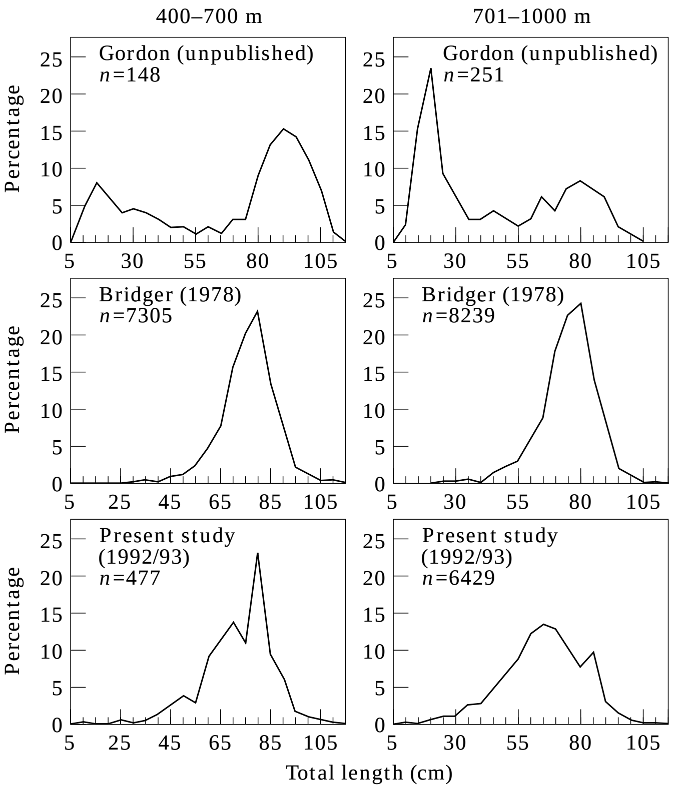

FIG. 4. Comparison of length–frequency distributions (total length in 5-cm intervals) between Gordon (unpublished), Bridger (1978) and the present study. Lengths recorded from the eastern slopes of the Rockall trough in September at depth intervals 700 and 1000 m.

GROWTH

All the observations of length at age were used when fitting the von Bertalanffy curves. Females attained a greater asymptotic length than males (Fig. 9, Table V) and were heavier than males at a given age (Fig. 10). The asymptotic weight of females ($W_\infty \equiv 1573$ g) was substantially greater than that of males ($W_\infty \equiv 922$ g). The presence of individual exceptionally large fish seemed to be characteristic of the female population. The Brody growth coefficient K suggests that the fish were slow growing.

MATURITY

The majority of fish were spent or recovering in April and ripe in September (Fig. 11). This may indicate at least two spawning events over the year. The pre-anus length at which 50% of the fish became mature (LM50) as determined by probit analysis was 10 cm (95% C.I. 4–11 cm) for males and 12 cm (95% C.I. 10·5–13 cm) for females. Probit analysis of maturity at age was less clear possibly because of the poorly represented age groups at the onset of maturity (Fig. 8). This may imply that maturation in the roundnose grenadier is a function of body size rather than age.

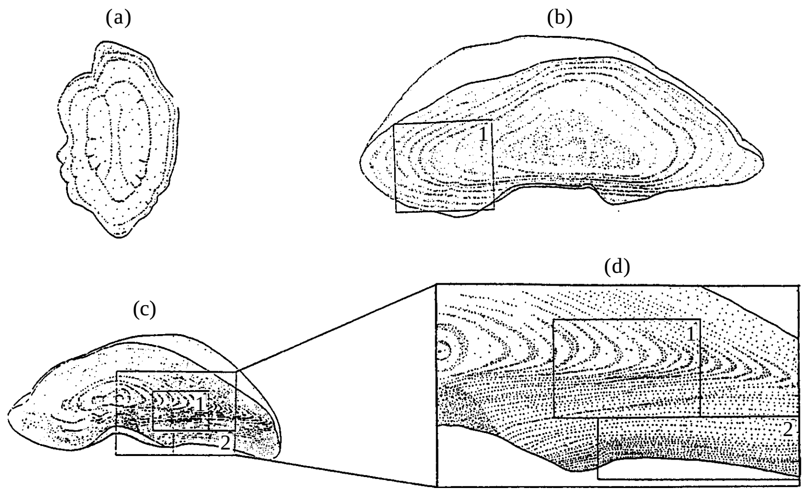

FIG. 5. Drawings of: (a) whole otolith of 3-year-old roundnose grenadier; (b) section of a pre-collar otolith showing region where checks occur (box 1); (c) section of a post-collar otolith showing region of finely spaced bands on the collar (box 2); and (d) detail of (c) showing fine bands toward the edge of the collar (box 2) and area with check marks (box 1).

DISCUSSION

C. rupestris was most abundant on the Donegal slope at 800–1000 m depth. Higher catch rates on the eastern slopes of the Rockall trough may have been an artefact of less efficient trawling on the rough coral ground frequently encountered on the western slopes, or of the different depths fished during the two surveys. The magnitude of difference between catch rates in April and September may also reflect the increased trawling experience during the latter survey.

The most appropriate method for measuring grenadier length has been addressed by several authors (Atkinson, 1981; Savvatimsky, unpublished; Shibanov & Savvatimsky, unpublished; Atkinson, 1989, 1991). Although NAFO (North Atlantic Fisheries Organization) and ICES (International Council for the Exploration of the Sea) have adopted pre-anal-fin length as the standard length measurement for roundnose grenadier (Sahrhage, 1986), pre-anus length was used here for its convenience when measuring large numbers of fish, as in recent studies (Bergstad, 1990; Connolly & Kelly, 1994; Charuau *et al.*, 1994).

This study found *C. rupestris* to be sexually dimorphic with females growing almost 4 cm longer than males at maximum lengths, similar to results from the Skagerrak (Bergstad, 1990). As in many fish species, the females were heavier than males of the same length. The population also contained a few anomalously large and heavy females, as in the Skagerrak (Bergstad, 1990).

Juvenile fish (pre-anus length <4 cm) were poorly represented, possibly owing to the selectivity of the large commercial gear used in the sampling surveys. Even though this commercial gear was fitted with a sprat bag (10-mm mesh), small fish may have been forced out of the trawl before reaching the cod-end or may have escaped under the bobbins on the trawl foot-rope. Age groups 8 and 9 (10–12 cm) around the onset of first maturity, were poorly represented also. This feature was apparent from the data of Gordon (unpublished) who sampled

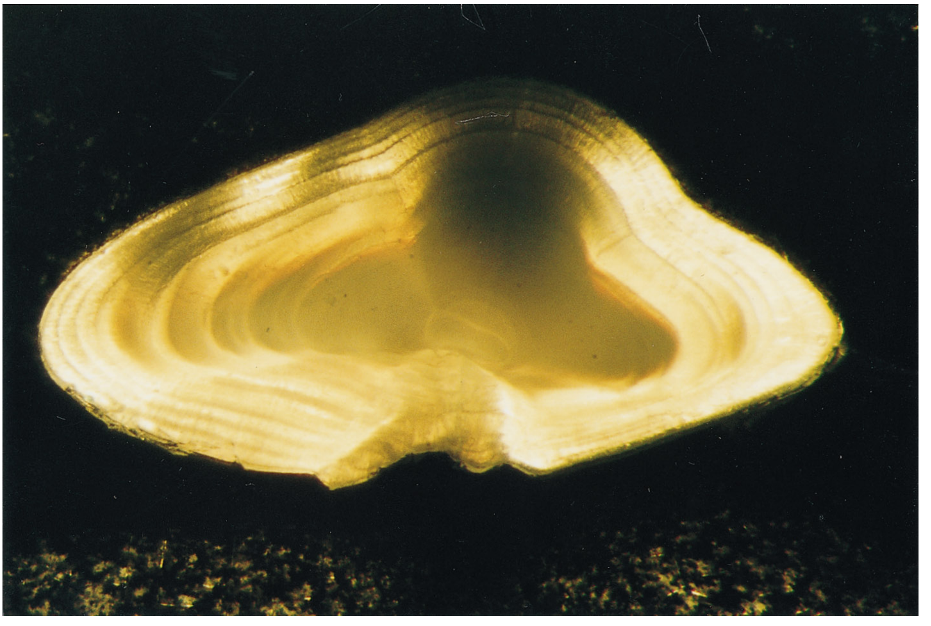

FIG. 6. Photomicrograph of *Coryphaenoides rupestris* otolith in reflected light. The otolith is from an immature fish of pre-anus length 5 cm, estimated at age group 8, captured in September 1993. This otolith is an example of pre-collar growth phase.

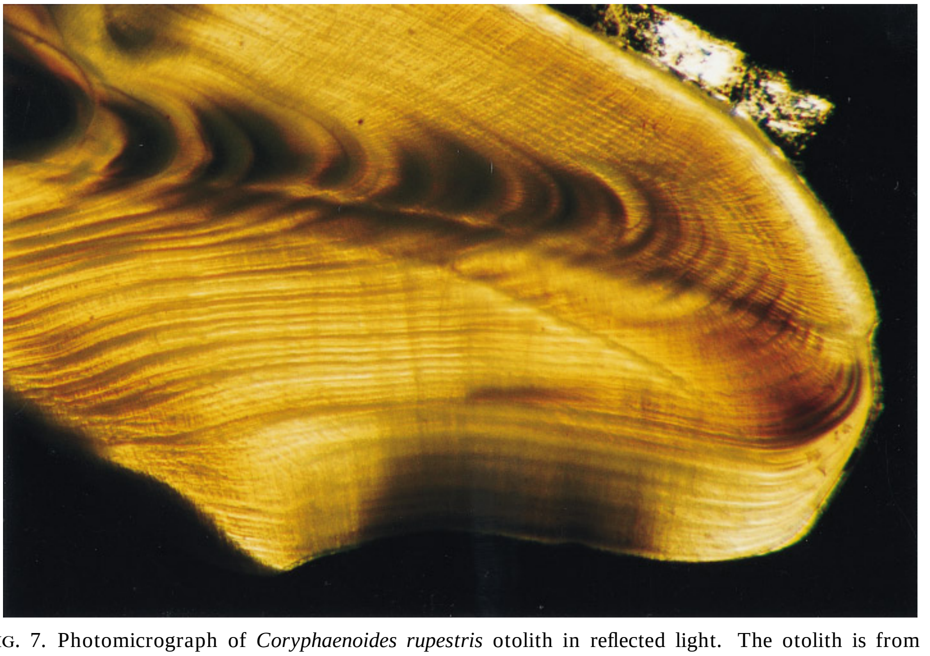

FIG. 7. Photomicrograph of *Coryphaenoides rupestris* otolith in reflected light. The otolith is from a mature male fish of pre-anus length 18 cm, estimated at age group 35, captured in September 1993. This otolith is an example of post-collar growth phase.

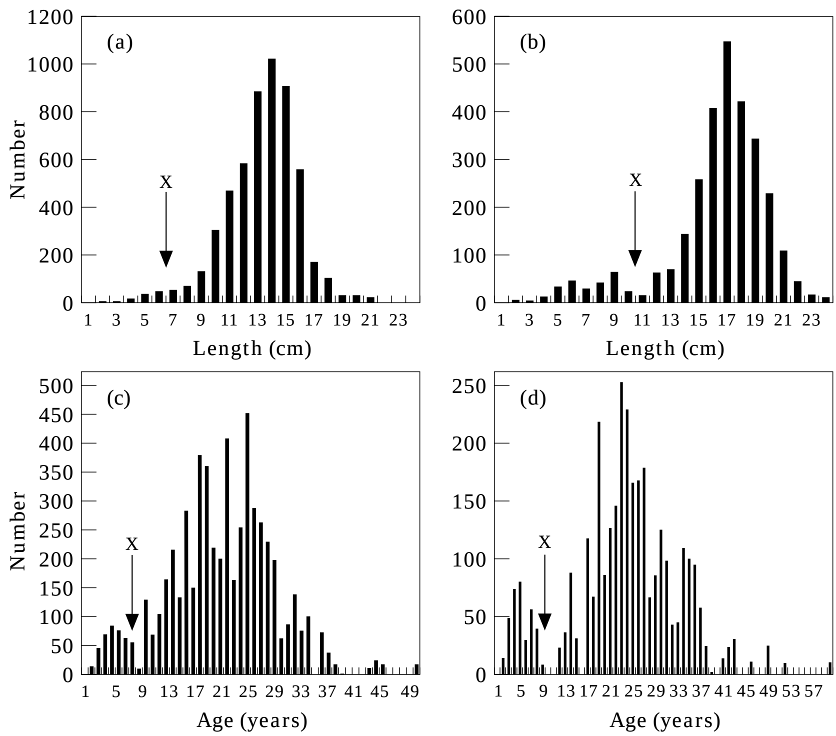

FIG. 8. Pre-anus length frequencies of male [(a); $n=5723$] and female [(b); $n=3245$] roundnose grenadier from the Rockall trough and age distributions for male [(c); $n=5723$] and female [(d); $n=3245$] fish. X indicates corresponding length and age of poorly represented part of population in sample.

TABLE IV. Precision estimates from roundnose grenadier otolith readings

Type of reading	No. of otoliths	No. of readers	No. of readings	A.P.E.	0 years (%)	1 year (%)	2 years (%)
Flat	32	2	3	8·3	63	22	15
					0–5 years (%)	6–10 years (%)	11+ years (%)
Section	48	2	2	4·9	75	17	8

Flat otoliths were read from 2–7 years and percentage agreement calculated over 0-, 1-, and 2-years difference. Sectioned otoliths were read from 2–58 years and the percentage agreement calculated over 0–5, 6–10, and greater than 10-years difference.

depths in excess of 1800 m in the Rockall trough and Bergstad (1990) who sampled the greatest depths available in the Skagerrak. Mauchline & Gordon (1984) observed an ontogenetic shift in the diet of grenadier during the onset of maturity, which may increase competition with the adult population for the limited available food resources. The low relative numbers of first maturing fish may reflect increased mortality or migration to feed higher in the water column and out of range of a demersal trawl net.

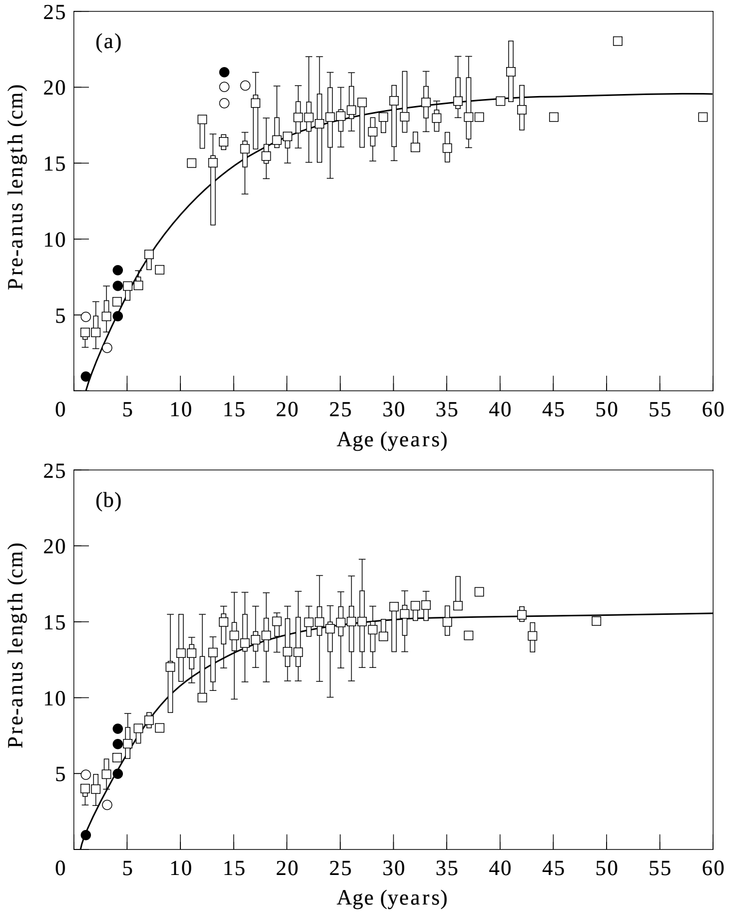

FIG. 9. Box plots of lengths *v.* age for (a) female and (b) male roundnose grenadier overlain with von Bertalanffy curves. □ = median, ▭ = interquartile range, vertical bars indicate 95 percentile. ○, value outside ± 2 S.E. ●, outlying values.

At 700 m depth, the 80-cm total length modal value is the same as that of Bridger (1978) but slightly less than the 90 cm of Gordon (unpublished). At the 1000-m depth interval, Gordon's and Bridger's modal value of 80 cm is greater than the present 65 cm, which also has proportionately more fish in the 40–60-cm length range. This may indicate that commercial exploitation over the past 5 years has removed many of the larger fish from the eastern slopes of the Rockall trough.

C. rupestris is believed to be a serial spawner and to have a complex reproductive cycle (Grigorev, 1972; Geistdoerfer, 1979; Gordon, unpublished; Alekseyev *et al.*, 1992). The present study found ripe fish in April and in September, but no egg or larval information is available from this area. Gordon (unpublished) found a high proportion of spawning fish during the late summer from the Rockall trough. In the Skagerrak, spawning fish were found in most months of the year with major activity in late autumn, and much reduced activity in early spring. Fertilized eggs were in mesopelagic water from October to

TABLE V. *Coryphaenoides rupestris* from the Rockall trough

Parameter	Estimated length parameter		Estimated weight parameter	
	Females	Males	Females	Males
K	0·101 (0·088–0·115)	0·128 (0·110–0·146)	0·118	0·133
L_∞/W_∞	19·5 cm (18·9–20·1)	15·5 cm (15·1–15·9)	1573 g	922 g
t_0	0·803 (0·393–1·214)	0·654 (0·197–1·112)	1·38	0·99

Estimated parameters of von Bertalanffy growth equation in terms of length and weight. K, coefficient of growth; L_∞, asymptotic length; W_∞, asymptotic weight; t_0, theoretical age when length is zero. Values in parentheses are 95% confidence intervals.

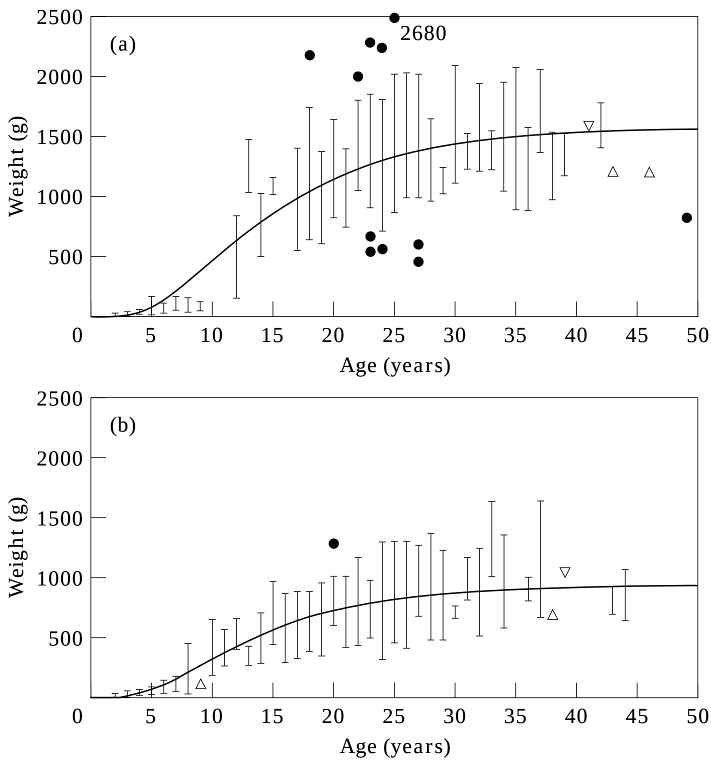

FIG. 10. Plot of weight *v*. age for (a) female (n=317) and (b) male (n=383) roundnose grenadier. Vertical bars indicate the range of values within ±2S.E. △, single value; ●, outliers.

December and juveniles were at the same depths from December to February (Bergstad & Gordon, 1994). In the present study, males matured at a smaller length than females, but age differences were not demonstrable from the relatively small samples available.

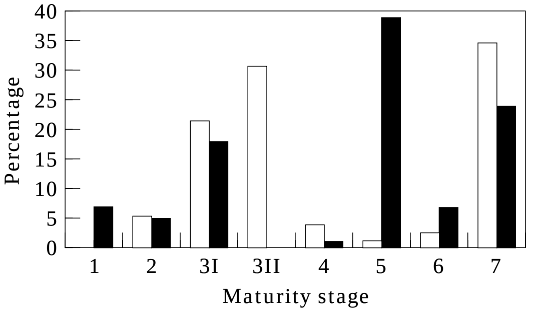

FIG. 11. Percentage occurrence of female roundnose grenadier maturity stages in April $n=75$ (□) and September $n=206$ (■). 1, virgin; 2, developing virgin; 3I, developing; 3II, recovering; 4, maturing; 5, ripe; 6, running; 7, spent.

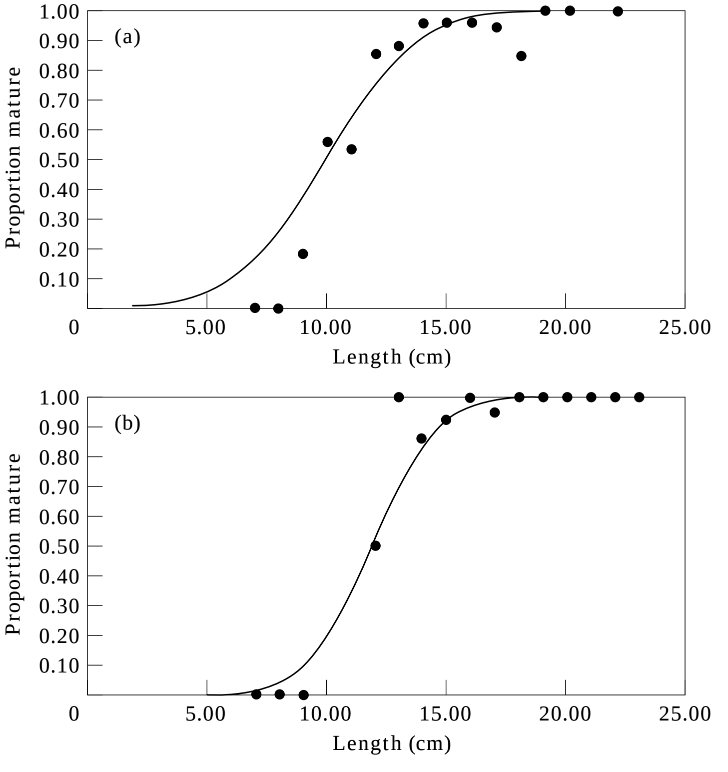

FIG. 12. Plots of proportion mature *v*. length based on maturity at stage 3 for (a) male and (b) female roundnose grenadier. The curve was fitted using Probit analysis and used to calculate LM50. ——, calculated; ●, observed.

The use of whole otoliths and scales for ageing this species is not satisfactory (Savvatimsky *et al*., 1977). Gordon (unpublished) aged roundnose grenadier (2–32 years) by viewing broken sagittal otoliths in transmitted light and burning the surface in more difficult specimens, but 20·4% of the otoliths were unreadable. The present study used standard otolith ageing methods (McCurdy, 1985),

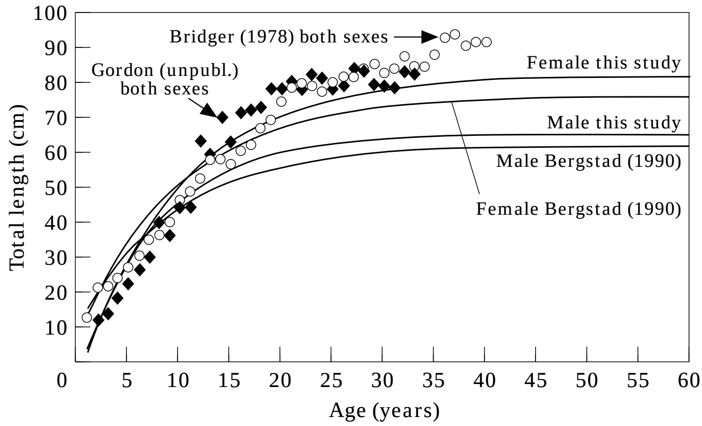

FIG. 13. Comparison of Gordon's (unpublished) and Bridger's (1978) mean length at age data, overlain with von Bertalanffy curves from Bergstad (1990) and this study; note measurement is total length.

modified to account for the observations and methods adopted by Bergstad (1990, 1994). The appearance of the otolith sections in Bergstad (1990) was similar to this study except that in Bergstad (1990) the first and second annuli were obscured by a merging of both opaque zones. Bergstad (1990) aged roundnose grenadiers at 1–72 years recording a predominance of 18–30 year olds. Dupouy & Kergoat (unpublished) reported fish of 13–26 years from commercial landings, but the ageing methods used were not discussed. The present study found ages from 2 to 60 with most between 10–38 years. However no age validation of roundnose grenadiers has been carried out to date (Bergstad, 1994).

Interpretation of the otolith sections was complicated by the presence of fine bands between annual increments 5–20, a problem common in many deep-water species. This study adopted the criteria of Chilton & Beamish (1982) who interpreted any fine lines between annuli 1–20 as checks, and considered the fine increments on the collar of old fish as annular. Kosswig & Rubec (unpublished) noted the inconsistency of this approach but agreed that counting fine increments on the collar of old fish produced the most reliable results. Age counts using these criteria have been corroborated by radiometric ageing for *Sebastes diplopora* (L.) (Bennett *et al.*, 1982) and *S. mentella* (Travin, 1951) (Campana *et al.*, 1990).

Of all ageing studies on roundnose grenadier from the west of the British Isles, only Gordon (unpublished) and Bridger (1978) produced length at age data from age estimations based on otoliths, and are comparable with the present work. Bergstad (1990) stated ' it is likely that the outer thin growth zones were not visible in the broken otoliths by the methods they (Bridger, 1978; Gordon, unpublished) used and therefore the age of fish >20 year is probably underestimated '. Bridger (1978) reported similar age distributions with a peak between 18–35-year-old fish. The predicted L_∞ for both male and female grenadiers from the Skagerrak (Bergstad, 1990) is smaller than that estimated for the Rockall trough by the present study (Fig. 13), while growth rates from Bridger (1978) and Gordon (unpublished) were similar. However, the mean lengths at age of mature fish (i.e. ages >15) from Gordon (unpublished) and Bridger (1978) were larger than those of the present study. This may be due to the conversion factor used from pre-anus length to total length (Table I) or to ageing anomalies. The values of length at first maturity from Gordon (unpublished) were within the range of the present study.

Precision estimates from this study indicate good reproducibility for both whole (ages 1–5) and sectioned otoliths (Table IV). APEs of 8·3% for whole otoliths (age groups 1–5 only) and 4·9% for sectioned otoliths compare favourably to those of 4·4% to 7·6% for whole otoliths of sprat *Spratus spratus* (L.) (Torstensen, unpublished). However it is recognized that the age estimates produced in this study require validation (Beamish & McFarlene, 1983).

It seems likely that commercial exploitation of roundnose grenadier will continue in the Rockall trough. This study has shown roundnose grenadier to be long lived, slow to mature and potentially vulnerable to overfishing. Given our poor understanding of the biology of grenadiers, it would seem prudent to introduce management regulations and an international stock monitoring programme to prevent the overexploitation of this species.

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