

Paper II

Distribution and biology of blue hake, *Antimora rostrata* (Pisces: Moridae), along the mid-Atlantic Ridge and off Greenland

Inge Fossen^{a,*}, Odd Aksel Bergstad^b

^a University of Bergen, N-5020 Bergen, Norway

^b Institute of Marine Research, Flødevigen, N-4817 His, Norway

Received 6 April 2006; received in revised form 21 August 2006; accepted 28 August 2006

Abstract

Data on *Antimora rostrata* are presented from 42°N on the mid-Atlantic Ridge to approximately 65°N on the slope off West and East Greenland, a north–south range of approximately 1400 nm (~2600 km). The species occurred in the depth interval 669–3059 m in trawl and longline experiments that sampled the depth range 450–4300 m. Length frequencies indicated both latitudinal and depth-related variation. Around Greenland small specimens occurred at shallower depths (<1000 m) while larger specimens were more frequent deeper than 1000 m. Abundance peaked between 1200 and 2700 m with generally low or no catches shallower and deeper. Sagittal otoliths were examined for 302 specimens, and zonation patterns in transverse sections suggested the existence of annuli. Counts of presumed annuli indicated a maximum age of 25 years, and length-at-age indicated linear growth within the age range sampled. Females grow larger than males and seem to live longer. Estimates of natural mortality varied from 0.11 to 0.25. Estimates of growth and mortality rates correspond to those that might be expected in virgin populations.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Ageing; *Antimora rostrata*; Blue hake; Central North Atlantic; Distribution; Population structure

1. Introduction

Antimora rostrata, often referred to as blue hake, belongs to the gadiform family *Moridae*. The Genus *Antimora*, previously considered to have a number of species, currently comprises only two species; *A. microlepis* restricted to the North Pacific, and *A. rostrata* occurring in all other oceans from 62°S to 62°N (Small, 1981; Turnov, 1992). Presently the two *Antimora* species appear more similar than previously indicated (Iwamoto, 1975; Kulka et al., 2003).

Numerous studies include references to *A. rostrata* (Campbell et al., 1980; Siebenaller and Murray, 1990; Gauldie et al., 1991; Baily et al., 2003) but none offers a comprehensive account of its distribution and biology. General species characteristics (Iwamoto, 1975; Small, 1981), information on distribution and abundance from selected geographical areas (Wenner and Musick, 1977; Gordon and Duncan, 1985a; Kulka

et al., 2003), and biological data (Magnússon, 2001; Kulka et al., 2003) have been presented.

The species is distributed outside the areas sampled by most scientific surveys. Previous records of occurrence of *A. rostrata* are from 200 to 3000 m, but abundance seems generally to peak at depths >1400 m (Wenner and Musick, 1977; Gordon and Duncan, 1985a; Kulka et al., 2003). Although *A. rostrata* was often found to dominate catches from deep slope waters, previous studies have not sampled the entire depth range of the species. Our study complements previous studies by sampling a wider depth range and expanding observations from the continental slopes of the North Atlantic onto the mid-Atlantic Ridge.

In this study, we compile and analyse occurrence and abundance data from scientific surveys and trial fisheries carried out within a large geographic area extending from waters just north of the Azores to the Davis Strait, corresponding to a range in latitude from 42° to 65°N. Spatial variations in occurrence and size structure are discussed in light of findings in this and previous studies. First assessments of longevity, growth pattern, and mortality are presented based on age estimates from otolith sections.

* Corresponding author at: Møre Research, Section of Fisheries, P.O. Box 5075, N-6020 Ålesund, Norway. Tel.: +47 70 11 16 00; fax: +47 70 11 16 01.

E-mail addresses: inge@mfaa.no (I. Fossen), oddaksel@imr.no (O.A. Bergstad).

Table 1
Summary of different sources of data, area covered, which year individual surveys were conducted, and the number of length measurements made of *A. rostrata*

Vessel	Area	Year	Gear	N Length
MS Loran	Mid-Atlantic Ridge	2004	Long line	1109
RV G.O. Sars	Mid-Atlantic Ridge	2004	Trawl	435
RV Paamiut	West Greenland	2003 and 2004	Trawl	825
RV Paamiut	East Greenland	2004	Trawl	314
MS Leinebris	East Greenland	2004	Long line	100
MS Loran	East Greenland	1997	Long line	350
MS Borgarin	Reykjanes ridge	1996	Long line	196
MS Skarheim	West Greenland	1992	Long line	2184

2. Materials and methods

2.1. Sampling at sea

Data was retrieved from more than 300 trawl and longline stations. A summary of the different data available to the study is given in Table 1 and Fig. 1. From the mid-Atlantic Ridge (MAR) the bulk of the data was collected on the MAR-ECO expedition between Iceland and the Azores in July 2004. Details regarding gear and sampling locations were given by Bergstad and Godø (2004) for the bottom trawling carried out by the RV “G.O. Sars” and by Dyb and Bergstad (2004) for the longlining

on the MS “Loran”. From off Greenland, trawl samples were collected by RV “Paamiut” in 2003 and 2004. Details regarding gear and stations were given in Jørgensen (1998, 2004, 2005a,b).

In addition, size distribution data were available from longline samples from East Greenland. These data originate from fishing experiments conducted by MS “Loran” in 1997 (Gundersen et al., 1998) and MS “Leinebris” in 2004 (Møre Research, unpublished data), all from the Kap Bille Bank (62°14'N). From West Greenland (NAFO areas 1D and 1E) corresponding data were available from a longline survey with MS “Skarheim” in 1992 (Møre Research, unpublished data). Also, from the northern part of the MAR length and catch data were

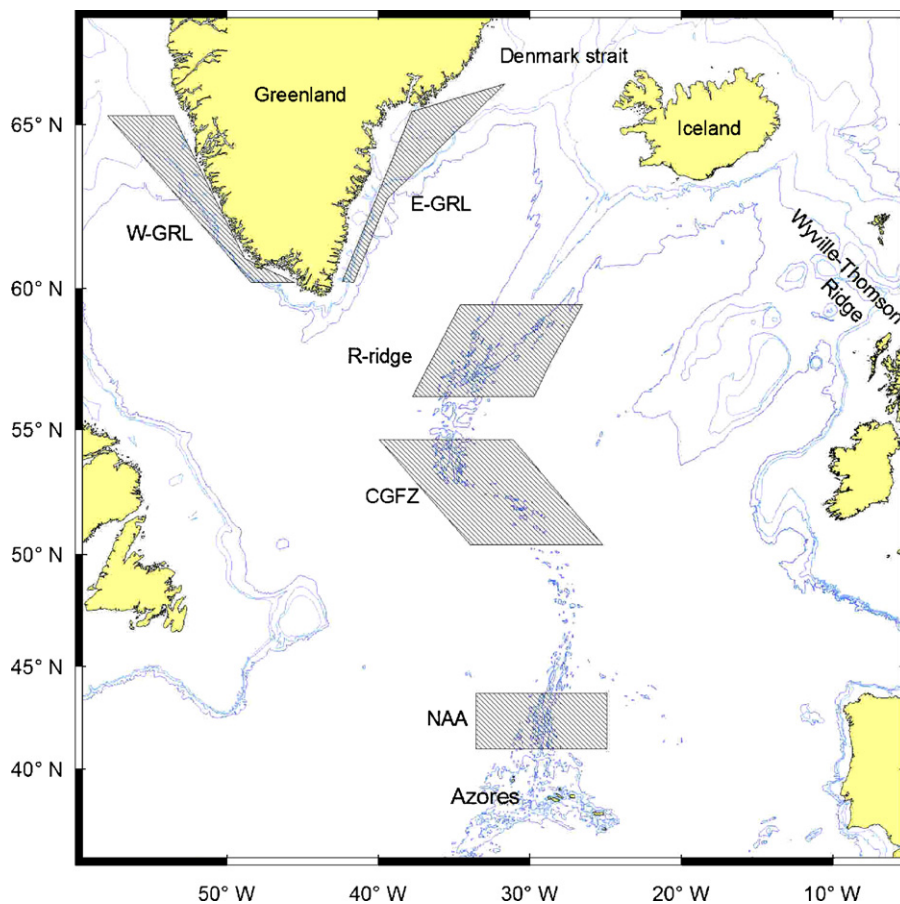


Fig. 1. Map showing the sampling areas used in this study. Both longline and trawl data were available from the sub-area just north of the Azores archipelago (NAA), the Charlie-Gibbs fracture zone (CGFZ), West Greenland (W-GRL) and East Greenland (E-GRL). Longline data were also available from southern part of the Reykjanes Ridge (R-ridge). See text for further details.

retrieved from a longline survey with MS “Borgarin” during 1996 (Hareide et al., 1996).

Information on occurrence and abundance was derived from catch per unit effort data. For longlines the measure used was kg/1000 hooks, and for trawl kg/nm². For the RV “G.O. Sars” data from 2004 exact door spread information was not available and the width was therefore assumed to be 60 m, i.e. slightly wider than previous measurements of door spread without the use of strapping in shallower waters (Arill Engås, Institute of Marine Research, Bergen, Norway, personal communication).

Depth in this study is average depth between start and end positions of the trawl tows and the longline sets. While start and end depths were usually similar for the trawl stations (normally within 20 m), some of the longline stations spanned a wider depth interval, in some cases as much as 500 m.

Hydrographic data were collected by CTD casts associated with all trawl stations on the RV “G.O. Sars” (Bergstad and Godø, 2004). Temperature profiles were used to indicate levels and possible gradients by depth and latitude. The results are compared to distribution patterns of *A. rostrata* from both RV “G.O. Sars” and MS “Loran” since both vessels operated at the same time in the same areas.

Total length (TL, snout to tip of caudal fin) was measured to the nearest cm below. On the RV “G.O. Sars”, MS “Loran”, and RV “Paamiut” sex and stage of maturity of the gonads were determined by macroscopic visual examination (Table 2).

2.2. Otoliths

Otoliths were extracted from most specimens and these were stored dry in paper envelopes until further laboratory processing. Sagittal otoliths were mounted in black plastic resin (Laminering 275A and Härdare 275B produced by Nils Malmgren AB) before transverse sections through the nucleus were cut with a high-speed diamond saw. The 0.35 mm thick sections were mounted on glass slides in clear resin (Renlam CY 219 and Ren HY 5162 produced by Vantico Ltd.) and covered with a clear cover glass.

Digital images were taken of the sections using a Nikon digital camera (DXM1200F) connected both to a Leica wild M10 binocular and a computer. Both reflected and transmitted illumination was used for comparison but identical or similar zone counts were achieved. Reflected light was chosen for routine

Table 2
Macroscopic maturity scale used for *Antimora rostrata* (after Mjanger et al., 2003)

Stage	Description
1	Juvenile/immature: gonads are small, eggs or milt not visible to naked eye.
2	Maturing: gonads are developing (maturing). Eggs and milt visible to naked eye but not running.
3	Running: ovaries and testes are in running condition.
4	Spent: shortly after spawning. Gonads are usually loose and reddish. Eggs or milt not visible to naked eye.
5	Uncertain: not possible to distinguish between immature and mature.

use since zones seemed clearer and readability better with this lighting.

In two previous attempts to count annuli in otoliths of *A. rostrata* the edge of the central opaque area was considered the nucleus and the edge of this was counted as 1 (Gauldie et al., 1991; Magnússon, 2001). The same convention was adopted here. The otolith sections revealed growth zones similar to those regarded as annuli in many other fish species, but validation by classical techniques such as seasonal variation in otolith edge character, mark-recapture experiments, or radiometric dating of otolith nuclei (Campana, 2001) was beyond the scope of this study.

Alternate hyaline and opaque zones occurring in otoliths are used to age fish based on the assumption that the zones are formed regularly in time, normally one of each type annually and hence that the zones represent annuli. Age determination by counting annuli in otoliths is used widely but validation is often problematic. In this study, none of the above-mentioned classical methods of age validation was applicable since surveys were only carried out during the summer months and information from mark and recapture studies are non-existent. The only option was to study the completeness of the zone being formed at capture, i.e. the marginal increment at different sampling events (Campana, 2001). If at a given sampling time all otoliths have marginal zones at the same stage of completeness, and if this is the case for several sampling times, then this would indicate a synchronous cyclic deposition. On the contrary, if no such pattern is found, it would indicate asynchronous deposition and hence that the zones cannot be interpreted as regular time markers, i.e. annuli.

The completeness of the marginal increment from sectioned otoliths was expressed as a proportion of the preceding zone (Fig. 2; Fowler and Short, 1998; Campana, 2001). The mid-point in a hyaline band was selected as the starting point of a zone since this might easily be determined by eye (dark band in

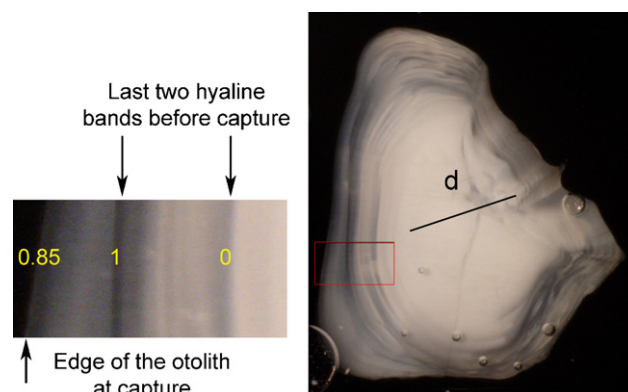


Fig. 2. Right: Transverse section of a sagittal otolith of *A. rostrata* photographed with reflected light. Nucleus diameter was measured along a direction as indicated by the line d. Left: Enlargement of marginal section of, i.e. the red frame shown in the image to the right. In the image 0 represent the start of the second last zone, 1 the end of the second last zone and the start of the marginal zone. The completeness of the marginal zone was scored as 0.85 in this case, indicating that an opaque zone had almost been completed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

Table 3
Index of readability

1	Believed to be reliable, clear definition, no obvious alternative interpretation of the zonation pattern.
2	Confident determination within ± 1 year.
3	Confident determination within ± 2 years.
4	Determination difficult, alternative interpretation of zonation pattern possible. Error margin ± 3 years or more.
5	Interpretation very difficult or impossible. Age estimate not reliable.

Fig. 2). Hyaline material formed bands that were narrower than the opaque bands and do normally represent the period of slow growth (e.g. winter period) in other fish species (Pannella, 1980; Gauldie and Nelson, 1990). To standardise the values where the material deposited changes between hyaline and opaque material the width of the hyaline band was set to be 10% of a completed zone. Start and stop point of one hyaline band will therefore always represent values of 0.95 in one zone to 0.05 in the next zone according to this.

Zonation patterns in the otoliths were complex and in many cases alternative interpretations were possible, each resulting in different zone counts. In an attempt to check consistency of the interpretation between otoliths, both the width of the nucleus and the widths of first zones outside the nucleus were measured. The width of the nucleus will also depend upon the position of the transverse section through the nucleus. The width of the first zones was expected to be relatively similar between specimens. Marked differences in zone width or especially large nuclei might indicate inconsistency regarding the interpretation of the zonation pattern. In images where the *sulculus* was visible, the width of the nucleus was measured as the distance from the *sulculus* across the nucleus (d in Fig. 2), not the longest and not the shortest distance. In other images the distance was measured as a simple average diameter. The average width of the first two zones outside the nucleus was calculated to obtain information on deposition patterns early in the life of the individual. The average width of the two first zones was determined as the average of 2–4 measurements in several directions around the nucleus.

2.3. Age determination

Based on the assumption that the zones observed were annuli, individual specimens were assigned to age groups by an experienced otolith reader. The conventional adoption of 1 January as the common birth date was applied. For each age reading an index of readability was recorded (Table 3). All otolith sections were read twice and the first reading was regarded as training. In general, readability and hence confidence was improved in the second reading.

3. Results

3.1. Occurrence and abundance:

On the expedition along the MAR in 2004 catches of *A. rostrata* were made in the depth range 949–3059 m. In the sub-

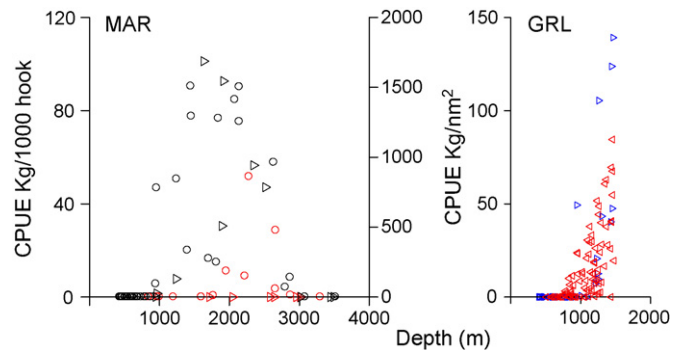


Fig. 3. Left: CPUE values from different stations along MAR, longline (\circ) and trawl (\triangleright). Colour represent areas, red = NAA, black = CGFZ. Right: CPUE values from different trawl stations along Greenland, east-coast (\triangleright) and west-coast (\triangleleft). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

area just north of the Azores archipelago, NAA, (42–43°N) *A. rostrata* was only caught by longline, at depths between 1772 and 2876 m (Fig. 3). In the Charlie–Gibbs fracture zone (51–54°30'N), the species was caught both by trawl and longline from 949 to 2870 m. Deeper and shallower trawls and longline sets failed to catch any *A. rostrata*, however, the deepest recording was made from an experimental gillnet set on plain bottom at 3059 m (Dyb and Bergstad, 2004).

Along the MAR the depth distribution was unimodal with a peak in abundance between 1200 and 2700 m (Fig. 3). The trawl data from West and East Greenland seem only to sample the upper section of the depth distribution of the species and are not fully representative. The shallowest recordings were made at 669 m off West Greenland in NAFO 1C, and at 768 m in NAFO 1D further south, and at 905 m off East Greenland (in ICES Division XIVb).

There were indications of geographical patterns in occurrence and abundance. In the sub-area associated with the Charlie–Gibbs fracture zone all stations between 1000 and 3000 m contained *Antimora* (Fig. 3). Similarly, all stations deeper than 1000 m off East Greenland had *Antimora*, indicating widespread occurrence. The abundance seemed lower in the NAA sub-area and off West Greenland compared to the CGFZ and East Greenland, respectively (Fig. 3).

A comparison between longline catch rates in the CGFZ and NAA sub-areas of the MAR, all stations within the depth range 1000–3000 m, revealed significant differences in CPUE (Student's *t*-test, $t = 3.59$, d.f. = 18.9, $p = 0.002$). Differences were due to higher average CPUE in the CGFZ than in the NAA sub-area, 51.4 kg/1000 hook versus 11.7 kg/1000 hook, respectively.

Within its peak depth range (1200–2700 m) *A. rostrata* was among the dominating species in all datasets. Along the MAR *A. rostrata* contributed between 10 and 80% to the total number of fish caught on longlines set at depths between 1500 and 3000 m. Similar figures were also seen off East Greenland, even in experiments where the chartered vessels had other species as their main target, e.g. Greenland halibut (*Reinhardtius hippoglossoides*).

At the main distribution depth of *A. rostrata* (1000–3000 m) only relatively small differences in temperature were recorded,

Table 4

Temperature range (°C) at depths in two different areas, the Azores archipelago (NAA) and the Charlie–Gibbs fracture zone (CGFZ), along the MAR from GO Sars survey 2004 (Bergstad and Godø, 2004)

Depth (m)	CGFZ	NAA
500	4.25–7.37	5.50–7.30
1000	<u>3.50–3.74</u>	3.89–4.42
2000	<u>3.02–3.17</u>	<u>3.18–3.28</u>

Underlined numbers represent depths where *A. rostrata* were caught.

both in the NAA and CGFZ sub-areas on the MAR (Table 4). A more detailed and spatially comprehensive analysis of distribution and occurrence in relation to depth and temperature was not possible due to sample size limitations and limited availability of temperature recordings (temperature recordings were only made for trawl tows by the research vessel).

3.2. Spatial variation in size structure

Length frequencies varied both between gears, depths and areas (Fig. 4). For longline samples, modal length varied between 40 and 60 cm in all data sets. For trawl samples, modal lengths were between 20 and 40 cm in Greenland waters and between 40 and 60 cm along the MAR. The smallest specimens caught were found in the trawl samples from Greenland. Few specimens smaller than 35 cm were caught along the MAR. In general, larger specimens tended to occur more frequently at depths exceeding 1000 m (Figs. 4 and 5). Length distributions were unimodal from most gears areas and depth strata. The exception was a bimodal distribution from the 1000–2000 m depth strata from Greenland, especially noticeable in the longline data.

When all datasets were considered together, an overall increase of average size with depth was observed. However, except perhaps off Greenland, no ‘bigger deeper’ trend was apparent in individual data sets (Fig. 5).

3.3. Sex distribution

In the trawl data from Greenland the overall proportion of females was 42.7% in stations shallower than 1000 m ($n = 236$, unsexed specimens not included). At greater depths and in all other waters, females dominated. In depths between 1000 and 1500 m at Greenland the proportion of females increased to 55.6% ($n = 692$). In trawl hauls from the MAR similar numbers were 70.5% at depths between 1000 and 2000 m ($n = 342$) and 98.8% at depths exceeding 2000 m ($n = 181$). Along the MAR very few males were taken by longlines. Of the 768 sexed specimens caught on longlines in the CGFZ and NAA region only 12 males were recorded (1.5%).

3.4. Sexual maturation

Only very few specimens were found with visible eggs. This was reflected in the GSI calculations from the trawl material from the CGFZ that revealed that only 3 of the 69 females examined had a GSI higher than 2% (from 8 to 12%). The other

females had GSI between 0.5 and 1.5%. Similar observations were made from the longline samples from CGFZ and NAA for which most specimens were sexed and large gonads kept for further analyses. Here 15 of 756 females had gonads with visible eggs.

3.5. The use of otolith growth zones to determine age

The completeness of the marginal zone being formed at capture was assessed for 132 otoliths caught between 20 June and 13 July 2004 along the east side of Greenland and along the MAR (Fig. 6). Samples from Greenland were caught in the beginning and samples from the MAR at the end of this approximately 3 week long period. No between area differences were found with respect to the completeness of the marginal zone being formed (K–S, $p = 0.396$). In 45 of the 132 otoliths a hyaline zone was being formed. The results showed that a zone was either being nearly completed or had just started to form, indicating a synchronised zone formation in the otoliths.

Measurements of the diameter of the nucleus showed a unimodal distribution with a modal width of about 1.2 mm (Fig. 7). Most measurements of the widths of the inner zones were between 0.16 and 0.20 mm/zone. The results suggest similar zone widths among otoliths, indicating a consistency in the interpretation of the zonation patterns.

3.6. Readability

The interpretation of the zonation patterns in otolith sections from *A. rostrata* was difficult. This is reflected in the frequency distribution of readability scores given to the 275 individual readings (otolith sections) (Table 5). None was given readability 1, and 45% were given a readability indicating an uncertainty of 3 years or higher.

3.7. Age and growth

Assuming that the growth zones counted represented annuli, fish were assigned to age-groups from 1 to 25 years (Fig. 8). In general most of the specimens caught were between 7 and 14 years old, covering lengths from 30 to 65 cm. In the samples from the MAR fish were assigned ages from 6 to 25 years, but only 16 out of 114 (14%) were less than 10 years of age. Similarly, the age range of the fish from Greenland was from 1 to 20 years but only few, 15 of 162 (9.3%), were above 10 years.

Individual total length is plotted against age in Fig. 8. Von Bertalanffy growth curves were fitted to the data for males and females independently, and for all data pooled (Fig. 8; Table 6). While males seldom exceeded 50 cm, many females were larger than this. At the same age, however, no marked differences

Table 5
Frequency distribution of readability scores in the otolith readings

	Readability				
	1	2	3	4	5
N observations	0	30	122	105	18

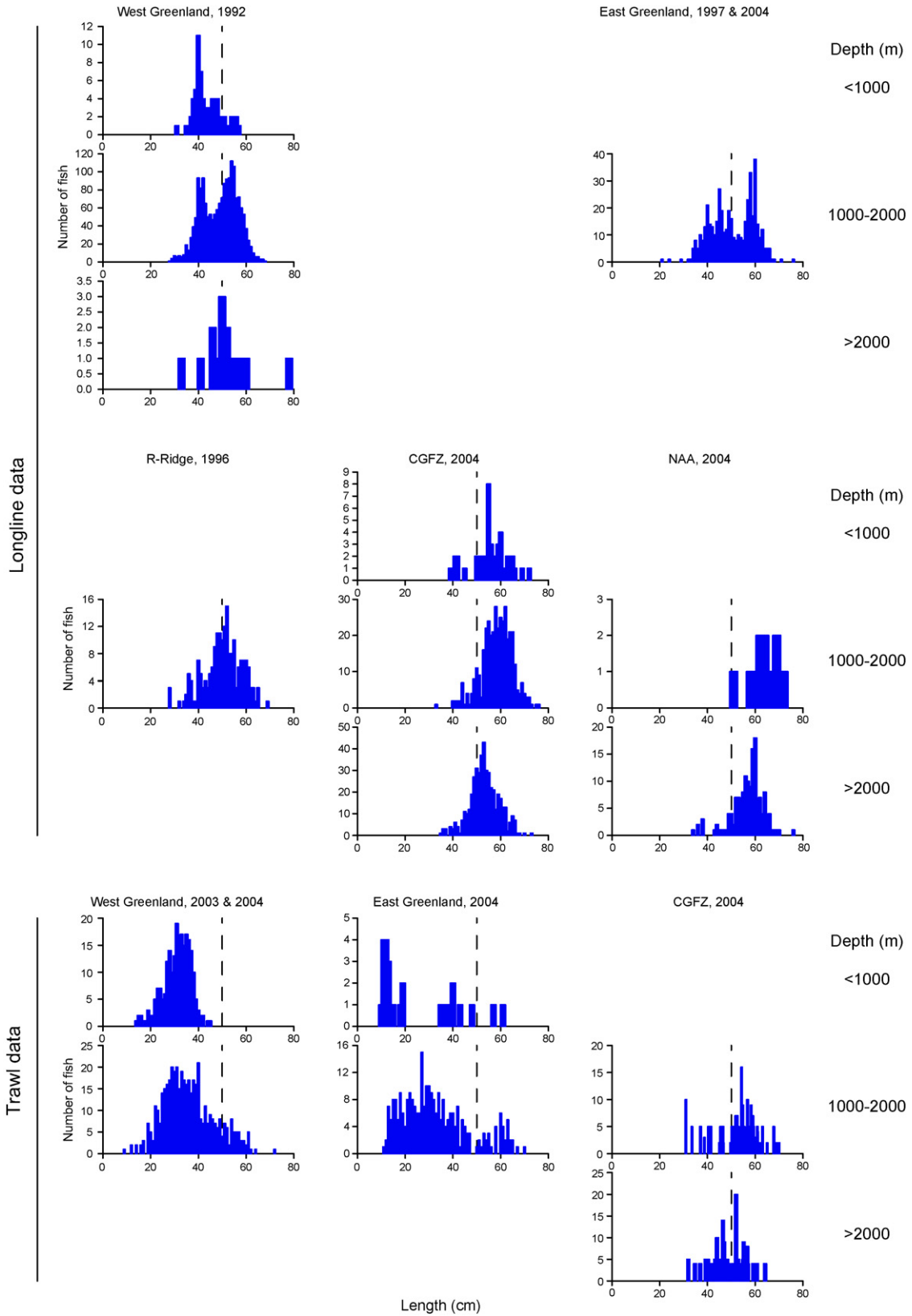


Fig. 4. Length frequencies by area and depth for longline (LL) surveys on top. Left to right data from West- and East-Greenland. Middle: Reykjanes Ridge, CGFZ and NAA (see Fig. 1 for details). Bottom: Trawl data from West Greenland, East Greenland and CGFZ. For all areas data is divided into three depth strata. Dotted line placed at 50 cm length, in all graphs, for easier comparisons.

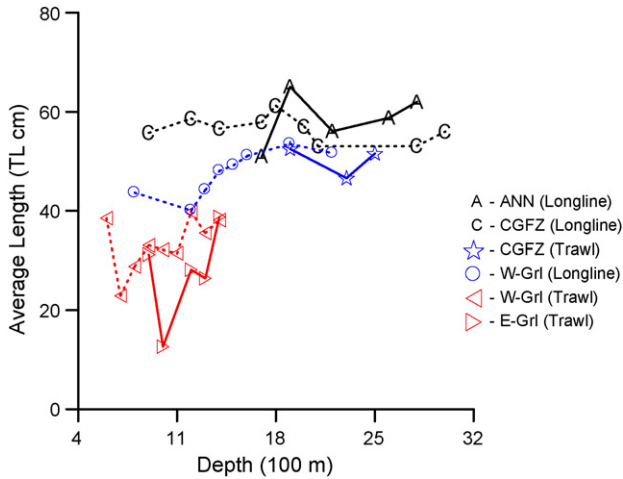


Fig. 5. Average lengths at depths for separate gears and areas.

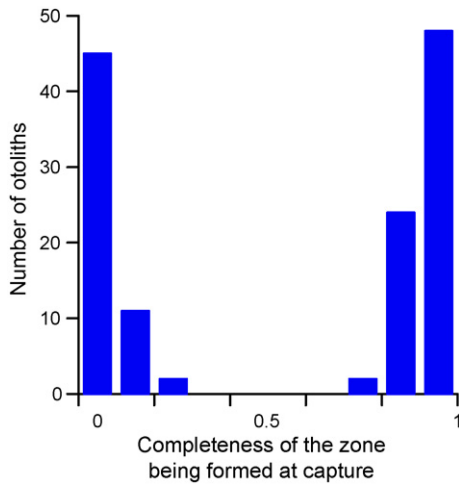


Fig. 6. The completeness of the zone being formed at capture, frequency of occurrence. Specimens caught between 20 June and 13 July 2004.

between sexes in length at age were found. Females seem to grow bigger and may live longer than males. The corresponding growth estimates from Magnússon (2001) were also included (Fig. 8; Table 6). Although Magnússon (2001) did not split the data by sex, the growth curve might indicate a somewhat slower growth and smaller L_{∞} . These estimates were, however, calculated from 57 individuals with a narrower size range than those in the present study (Table 6; Fig. 8).

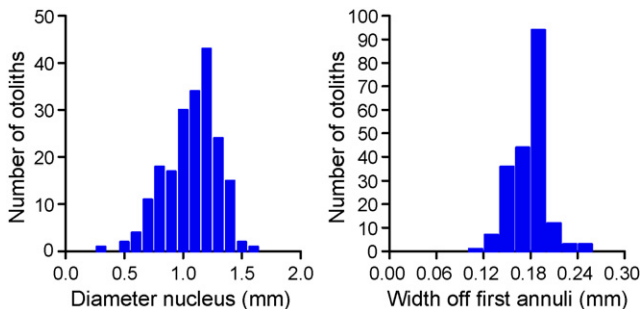


Fig. 7. Histograms of nucleus diameter (left) and width of first annuli (right).

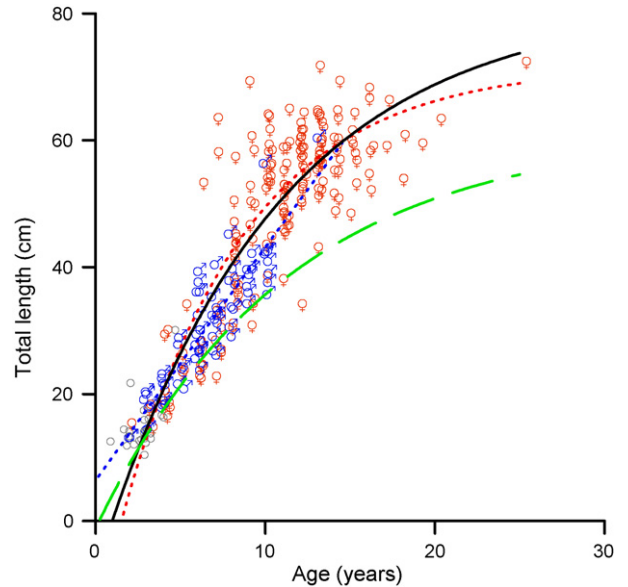


Fig. 8. Length at age by sex including VBGF growth curves for both sexes (dotted line) and the sexes combined (continuous line). Unsexed specimens shown as circles. VBGF from Magnússon (2001) in dashed line.

Otolith weight was closely correlated with fish length (Pearson correlation = 0.955, pairwise $n = 248$) and both body length and otolith weight was similarly correlated with age (Pearson correlation of fish length versus age = 0.887 ($n = 257$), and otolith weight versus age = 0.887 ($n = 248$), only age determinations with readability <5 were included). The results suggest a relationship between the otolith growth, fish length and age similar to what has been described for other species.

3.8. Mortality estimates

Estimates of the coefficient of natural mortality, M , was obtained by empirical calculations (Rikhter and Elfanov, 1976; Pauly, 1980; Alagaraja, 1984; Jensen, 1997). These methods are based on relationships between population parameters, environmental temperature (used by one technique) and mortality for a number of fish stocks worldwide (Table 7). Estimates of M varied from 0.112 to 0.184 and the average of the different methods was 0.152. The VBGF estimates of K and L_{∞} from Table 4 were also used together with the length frequencies from the 2004 longline survey at MAR to derive an estimate of the coefficient of total mortality, Z . Here we assume that Z is equal to

Table 6
VBGF parameters (Von Bertalanffy, 1938) estimated for *A. rostrata* for all data combined and by sex

	L_{∞}	K	t	r^2	N
All	81.70	0.10	0.98	0.84	257
Females	71.86	0.14	1.52	0.74	170
Males	2332.00	0.0016	-1.74	0.81	68
Magnússon all data	64.37	0.089	0.21	-	57

Correlation coefficient, r^2 , and number of observations, N , also included. Only data from 2004 with readability <5 were used. Similar estimates from Magnússon (2001) included.

Table 7
Theoretical calculation of the coefficient of natural mortality, M , based on published relationships between basic biological and environmental data

Formula	Data input	M
Pauly's (Pauly, 1980)	K , L_{∞} , E-temp	0.112
B&H invariant (Jensen, 1997)	K and $M/K = 1.6$	0.155
The 1% rule (Alagaraja, 1984)	Max. age	0.184
Rikhter and Elfanov (1976)	M_{50}	0.158

Input: VBGF parameters K and L_{∞} from Table 3 (sexes combined), max. age: maximum observed/estimated age = 25 year, M_{50} assumed to be 9 years. Average environmental temperature (E-temp) was assumed to be 3.5 °C.

M due to the limited amount of fishing in these areas. The Jones and van Zalinge method (Sparre and Venema, 1998) indicated a Z of 0.25.

4. Discussion

4.1. Species range, and occurrence and abundance in the study area

The data presented yield new information on the range and distribution of *A. rostrata* in the central North Atlantic, i.e. from north of the Azores archipelago at approximately 42°N, to either side of Greenland, at approximately 65°N.

This and previous studies indicate a continuous distribution of *A. rostrata* along the east coast of North America, from Florida in the south to the Davis Strait in the north, and south along and around the coast of Greenland to the Denmark Strait (see Kulka et al., 2003 and references therein) and further to Iceland and southwards along the MAR to the Azores. On the European slope the species is common southwards to the Bay of Biscay and there are single records from the slope off northern Morocco (Cohen, 1986; Haedrich and Merrett, 1988).

The northerly distribution limits of *A. rostrata* in the North-east Atlantic north of the Denmark Strait, Iceland, Faroe Islands and the British Isles remains somewhat uncertain. Kulka et al. (2003), referring to personal communication with P.I. Savvatimskyi, suggests that *A. rostrata* is a minor by-catch in waters north-west of Norway, however, no record of this species is found in Norwegian survey databases at the Institute of Marine Research, which also includes numerous surveys at relevant depths, including those targeting Greenland halibut, *R. hippoglossoides*, normally caught together with *A. rostrata* elsewhere. Bergstad et al. (1998) did not observe the species along the eastern Norwegian Sea slope. It seems unlikely that it occurs regularly north of the Wyville-Thompson Ridge and the Faroe-Shetland Channel.

In the Norwegian Sea slope waters, the temperature falls below 0 °C at the most relevant depth of occurrence for the species, and this appears to be lower than the species' preferred temperature range. Similarly *A. rostrata* is well known to the south and west of Iceland but the few records from the northern and eastern side of Iceland are considered to represent expatriate individuals (J. Palsson, personal communication). The species is therefore probably only sporadic in the Norwegian and Greenland Seas north of the Scotland-Faroe-Iceland-Greenland ridges.

The depth distribution of *A. rostrata* is wide (Haedrich and Krefft, 1978; Snelgrove and Haedrich, 1985; Kulka et al., 2003). In this study, the species was found shallower when moving northwards along West Greenland (768 m in NAFO 1D to 669 m in NAFO 1C). Similarly on the mid-Atlantic Ridge, the upper depth limit appeared to become deeper when moving southwards, i.e. it was 949 m at Charlie-Gibbs fracture zone and 1772 m in the sub-area just north of the Azores. Hareide and Garnes (2001) reported catches at between 600 and 700 m on a seamount just north of the Charlie-Gibbs fracture zone in 1997. These data corroborate from previous studies that there is a cline from north to south in the upper depth limit for the species (Wenner and Musick, 1977; Kulka et al., 2003). This may represent a classical submergence as the surface layers become gradually warmer from north to south along the species' latitudinal range.

Most previous accounts describe an increasing abundance of *A. rostrata* with increasing depth and a maximum at depths greater than 1300 m (Wenner and Musick, 1977; Gordon and Duncan, 1985a; Magnússon, 2001; Kulka et al., 2003). The depth distribution pattern seen for the data from the CGFZ and the NAA sub-areas suggests that this study, as the first ever, sampled the full depth range of the species. In both sub-areas abundance of *A. rostrata* was higher in the middle of the depth range and gradually lower closer to the depth limits of its occurrence. The species does not seem to have been recorded below 3000 m previously (Wenner and Musick, 1977 (2930 m); Gordon and Duncan, 1985a (2880 m); and Iwamoto, 1975 (2904 m)). The deepest record made at the MAR at 3059 m seems therefore to be the deepest published record of this species.

In the data from the MAR-ECO expedition during 2004 abundance peaked between 1200 and 2700 m and the highest catch rates were recorded around 2000 m in the CGFZ sub-area. The trawl data from Greenland showed an increasing abundance with depth to 1500 m, and this was the lower depth limit of the Greenland trawl surveys. The full depth range in this area is therefore not known. The indication of peaking abundance at depths around 2000 m agrees well with previous indications from other areas (Wenner and Musick, 1977 (1500–2500 m); Gordon and Duncan, 1985b (1750–2200 m)).

Geographical comparisons of abundance were difficult since different vessels used different fishing gears. However, the data from the Charlie-Gibbs fracture zone and the sub-area just north of the Azores archipelago indicated higher abundance of *A. rostrata* in the former. For the different longline surveys, between gear differences in selection and catchability can be expected to be relatively small. In general catch per unit of effort (CPUE) for longline showed little variation between areas and surveys. From West Greenland at depths less than 1500 m, longline CPUE values varied between 0 and 60 kg/1000 hooks, and *A. rostrata* was caught at most stations below 1200 m (Møre Research, unpublished data). A similar pattern was observed at the Reykjanes Ridge (the MAR between Charlie-Gibbs FZ and Iceland) where *A. rostrata* were caught from 700 to 1950 m with most catch rates between 0 and 60 kg/1000 hooks (Hareide et al., 1996).

A. rostrata frequently contributed a substantial proportion of the total catch on both longlines and in trawls. This is especially

true for deeper stations (Bergstad and Godø, 2004; Dyb and Bergstad, 2004). These findings agree with several other studies and confirm that *A. rostrata* ranks among the dominating large species within its main depth range, 1000–3000 m (Fitch and Lavenberg, 1968; Iwamoto, 1975; Wenner and Musick, 1977; Haedrich and Krefft, 1978; Haedrich et al., 1980; Gordon and Duncan, 1985a; Merrett et al., 1991a,b; Kulka et al., 2003). As in previous studies (Kulka et al., 2003), *A. rostrata* occurred within a narrow temperature range, mainly from 3 to 4 °C.

4.2. Spatial variation in size structure

In general, considerable variation in size distribution was found both between gears, areas and depths. Longline catches tended to catch larger specimens than trawl. Small specimens (<20 cm) were only recorded from catches off Greenland. Larger specimens occurred more frequently in depths exceeding 1000 m. This may also account for the increasing predominance of females with increasing depth. Similar patterns were found in previous studies elsewhere (Wenner and Musick, 1977; Gordon and Duncan, 1985a,b; Kulka et al., 2003).

Females dominated the catches in general, indicating a skewed sex distribution. Only in the trawl catches from West Greenland did males occur as frequent as females. Overall the results showed similar patterns to those described by both Wenner and Musick (1977) and Kulka et al. (2003) where males occurred more frequently in shallower stations and larger females deeper. The females were markedly larger than males especially in areas where females dominated. Such a pattern could indicate that the dominance is due to increased longevity among females resulting in an overall dominance among the older and larger individuals.

4.3. Zonation patterns in otoliths

Assessing the state of formation of the marginal otolith increment suggested a synchronous and possibly annual deposition frequency (Gauldie and Nelson, 1990; Campana, 2001). Formation of a hyaline band during mid summer indicates a marked delay in what is often characterised as the winter band, but this has also been shown in other studies of deep-water fishes and has been attributed to a delay in the seasonal energy pulse from the euphotic zone (Wilson, 1988; Randall and Farrell, 1997).

Scoring completeness of the marginal zone seems to be an approach that adds more information about the cycle of zone formation than the classical technique studying the frequency over time in the opaque and hyaline character of the edge zone. This is especially true if so-called false zones occur, and this is quite common (Pannella, 1980; Jerald, 1983; Campana and Neilson, 1985; Beamish and McFarlane, 2000). However, even if synchronous deposition occurs, the deposition frequency may not be annual. More work is needed to determine if the zones counted in this study are annuli.

One of the prerequisites for counting otolith growth zones consistently is that the nucleus and the first few growth zones can be distinguished. It would be expected that the nuclear diameter measurements are unimodal and not very variable, and the

same should be the case for the widths of the first growth zones. The results in this study are in line with these expected patterns, and suggest that the interpretations were quite consistent. However, some very large nuclei were observed and the left tail of the distribution indicated that some of the otolith sections failed to hit the centre of the nucleus. The right tail may represent the few otoliths sectioned exactly through the nucleus centre, but specimens born especially early or that grew especially fast would also fall into this latter group. Alternatively, the first hyaline zones were not detected in these otoliths (e.g. Beamish and McFarlane, 1987).

Most otoliths had an inner zone width of about 0.18 mm. Assuming that the width of the inner zones are similar between otoliths the results indicate that the zonation patterns in the otoliths were interpreted in a similar way.

4.4. Readability

The studies by Fitch and Lavenberg (1968), Gauldie et al. (1991) and Magnússon (1998, 2001) seem to be the only published attempts at determining age of this species using otoliths. Fitch and Lavenberg (1968) wrote a guide to teleost fishes, Gauldie et al. (1991) described the structure and chemical ultrastructure of the *A. rostrata* otolith, and Magnússon (2001) focused primarily on distribution and some biological parameters.

The readability assessments in this study show that there are rather serious interpretation challenges, but that the precision of these exploratory age estimates can still be acceptable, i.e. repeated counts of the same otolith section do not vary much once a certain interpretation of the zonation pattern has been chosen.

Otoliths of *A. rostrata* are roughly conical and elongated along the anteroposterior axis (for details see Gauldie et al., 1991). Previous studies have shown that otolith shape and size contain valuable information about age (Templeman and Squires, 1956; Fletcher and Blight, 1996; Cardinale et al., 2000; Fossen et al., 2003). For *A. rostrata* we observed a strong positive correlation between otolith weight and fish length, and a steady growth of the otolith throughout the lifetime of the fish would therefore be expected. This also supports the indication of a steady body growth with increasing age without any abrupt changes in growth pattern.

4.5. Age and growth

More work is still needed before a precise and accurate ageing method based on otolith zonation patterns is developed for *A. rostrata*. The information presented here on age and growth rests on the assumption that the otolith zones were indeed annuli and that the counts were acceptably precise. Most of the specimens were between 7 and 14 years old, but ages from 1 to 25 years were observed. This indicates that *A. rostrata* has an intermediate longevity compared with other co-occurring deep-water fishes that have been sufficiently studied. It is neither short-lived, nor especially long-lived.

The question around where reproduction occurs has already been discussed by several previous studies (Wenner and Musick,

1977; Kulka et al., 2003). An interesting result in this study was the pronounced difference in age range between specimens caught off West Greenland and those caught along the MAR. It is tempting to suggest that West Greenland is a nursery for the species and that there is a gradual migration onto the MAR. However, the waters deeper than 1500 m were not sampled in the Greenland surveys and the large specimens living deeper may have been missed. It remains however puzzling that so few small juveniles were observed on the MAR. Similarly the survey along the MAR might have failed to catch the smaller specimens. Distances and circulation patterns do not support any close connection between Greenland and the MAR. It is notable that small *A. rostrata* were observed in areas nearer the MAR along the slopes west of the British Isles (Gordon and Duncan, 1985a). However, the observations seem to indicate that *A. rostrata* may have rather pronounced spatial size segregation.

Females grow both bigger and probably older than males, however, no marked between-sex difference in growth rate was indicated. Similar patterns are found in many fish species and are often thought to be connected to reproduction strategies where larger females have a higher relative fecundity than small ones while size might be of less importance to males (Stearns, 1976; Stearns and Crandall, 1984; Randall and Farrell, 1997). This could explain a suggested increased mortality among males (see also Wenner and Musick, 1977). Magnússon (2001) indicated that males were smaller than females at a given age, which is not supported by our study. The difference may be due to spatial population differences, limitations in the material, or differences in interpretation of the otoliths zonation pattern. If females grow bigger than males and both sexes experience similar growth rates, then marked differences in catchability or a higher mortality rate for males is the only explanation for the large difference in occurrence and size distribution between the sexes. Neither of these possibilities can be ruled out.

Except for Fitch and Lavenberg's (1968) note about that zonation pattern in otoliths suggesting a maximum age of 10 years, only one previous study of growth of *A. rostrata* exists in the literature. Magnússon (2001) fitted a Von Bertalanffy growth function to 57 age-length observations from Iceland (Table 6; Fig. 8). The result indicated a somehow slower growth than in our study. However, differences in the size distribution of the specimens used in the two studies together with the lack of sex information in the former makes direct comparisons difficult.

4.6. Estimates of mortality

In most situations, precise estimation of natural mortality is difficult to obtain (Wootton, 1990). Due to the importance of this parameter in fish stock assessment, estimates are often made even with inadequate information. The tentative estimates presented here merely indicate what mortality level one might expect. This is of particular interest since *A. rostrata* is among the dominating species at these depths where generally little is known about the biology and life history of the different species occurring there.

Methods used to estimate natural mortality are then very sensitive to the accuracy of abundance estimates or other biological

parameters used in the calculation (Wootton, 1990; Sparre and Venema, 1998). The Jones and van Zalinge method (Sparre and Venema, 1998) gave slightly higher estimate for total mortality than the other theoretical estimates of natural mortality, 0.25 versus 0.112–0.184, respectively. The indications suggest that natural mortality for *A. rostrata* are expected to be at the same or somewhat lower level than what is normally expected for many of the commercially exploited ground fish species (Roff, 1984; Sinclair, 2001).

4.7. Maturation

Macroscopic staging of gonads is difficult, especially during the resting stages between spawning periods. In *A. rostrata* the difficulties are even greater than normal because few immature or running specimens have been observed and never described (Gordon and Duncan, 1985a; Kulka et al., 2003). No histological studies of this species have been carried out. In this and other studies, most ovaries examined were relatively large and reddish but had no visible oocytes (see also Gordon and Duncan, 1985a). These specimens may have been characterised as immature or maturing, and both conclusions may be correct. There may have been consistent differences between surveys in this classification. It would seem likely that the females that normally dominate the catches should be placed in the same group (see also Wenner and Musick, 1977; Gordon and Duncan, 1985a).

Acknowledgements

We would like to thank the scientific staff and crew on MS "Loran", RV "G.O. Sars" and RV "Paamiut" for excellent seamanship and thorough processing of catches. A special thanks to Ole A. Jørgensen and Micael Rosing for making data from the Greenland surveys available. We are also thankful to our colleagues at Møre Research who have collected data during numerous longline expeditions and made the data available. The work was a contribution to the MAR-ECO project (www.mar-eco.no), a field project of the Census of Marine Life (www.coml.org).

References

- Alagaraja, K., 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. *Indian J. Fish.* 31, 177–208.
- Baily, D.M., Bagley, P.M., Jamieson, A.L., Collins, M.A., Priede, I.G., 2003. In situ investigation of burst swimming and muscle performance in the deep-sea fish *Antimora rostrata* (Günther, 1878). *J. Exp. Biol. Ecol.* 285–286, 295–311.
- Beamish, R.J., McFarlane, G.A., 1987. Current trends in age determination methodology. In: Summerfelt, R.C., Hall, G.E. (Eds.), *Current trends in age determination methodology. Age and Growth of Fish*. The Iowa State University Press, Ames, Iowa, pp. 15–42.
- Beamish, R.J., McFarlane, G.A., 2000. Reevaluation of the interpretation of annuli from otoliths of a long-lived fish, *Anoplopoma fimbria*. *Fisheries Res.* 46, 105–111.
- Bergstad, O.A., Bjelland, O., Gordon, J.D.M., 1998. Fish Communities on the Slope of the Eastern Norwegian Sea. ICES, Copenhagen (Denmark), ICES-CM-1998/O:30, 29 pp.
- Bergstad, O.A., Godø, O.R. (Eds.), 2004. Report from the 2004 MAR-ECO Expedition to the Mid-Atlantic Ridge on RV. G.O. Sars. Available on www.mar-eco.no/sci.

- Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.* 59, 197–242.
- Campana, S.E., Neilson, J.D., 1985. Microstructure of fish otoliths. *Can. J. Fisheries Aquat. Sci.* 42, 1014–1032.
- Campbell, R.A., Haedrich, R.L., Munroe, T.A., 1980. Parasitism and ecological relationships among deep-sea benthic fishes. *Mar. Biol.* 57, 301–313.
- Cardinale, M., Arrhenius, F., Johnson, B., 2000. Potential use of otolith weight for the determination of age-structure of Baltic cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*). *Fisheries Res.* 45, 239–252.
- Cohen, D.M., 1986. Moridae, pp. 713–723. *Moridae*, pp. 713–723. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E. (Eds.), *Fishes of the North-eastern Atlantic and the Mediterranean*, vol. I–III. Unesco, Paris, p. 1473.
- Dyb, J.E., Bergstad, O.A., 2004. The Cruise with M/S Loran Summer 2004. Møreforsking, Å0418 (ISSN: 0804-5380), 98 pp.
- Fitch, J.E., Lavenberg, R.J., 1968. *Deep-water Teleostean Fishes of California*. Cambridge University press, London, England.
- Fletcher, W.J., Blight, S.J., 1996. Validity of using translucent zones of otoliths to age pilchard *Sardinops sagax neopilchardus* from Albany, western Australia. *Marine Freshwater Res.* 47, 617–624.
- Fossen, I., Albert, O.T., Nilssen, E.M., 2003. Improving the precision of ageing assessments for long rough dab by using digitised pictures and otolith measurements. *Fisheries Res.* 60, 53–64.
- Fowler, A.J., Short, D.A., 1998. Validation of age determination from otoliths of the King George whiting *Sillaginoides punctata* (Perciformes). *Mar. Biol.* 130, 577–587.
- Gauldie, R.W., Coote, G., Mulligan, K.P., West, I.F., Merrett, N.R., 1991. Otoliths of deep water fishes: structure, chemistry and chemically-coded life histories. *Comp. Biochem. Physiol.* 100A, 1–31.
- Gauldie, R.W., Nelson, D.G.A., 1990. Otolith growth in fisher. *Comp. Biochem. Physiol.* 97A, 119–135.
- Gordon, J.D.M., Duncan, J.A.R., 1985a. The biology of the family Moridae in the deep-water of the Rockall Trough. *J. Mar. Biol. Assoc. U.K.* 65, 475–485.
- Gordon, J.D.M., Duncan, J.A.R., 1985b. The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, northeastern Atlantic. *Prog. Oceanogr.*, Nr 15, 37–69.
- Gundersen, A.C., Woll, A.K., Boje, J., 1998. Linesurvey etter blåkveite ved Kap Bille Banke, Øst-Grønland, i juli–august 1997. Report from Møre Research, Ålesund, Å9810 (ISSN: 0804-5380), 58 pp. (in Norwegian).
- Haedrich, R.L., Krefft, G., 1978. Distribution of bottom fishes in the Denmark Strait and Irminger Sea. *Deep-Sea Res.* 25, 705–720.
- Haedrich, R.L., Merrett, N.R., 1988. Summary atlas of deep-living demersal fishes in the north Atlantic basin. *J. Nat. History* 22, 1325–1362.
- Haedrich, R.L., Rowe, G.T., Polloni, P.T., 1980. The megabenthic fauna in the deep sea south of New England, USA. *Mar. Biol.* 57, 165–179.
- Hareide, N.-R., Ganes, G., 2001. The distribution and catch rates of deep water fish along the Mid-Atlantic Ridge from 43 to 61°N. *Fisheries Res.* 51, 297–310.
- Hareide, N.-R., Resmussen, H., Thomsen, B., 1996. Rapport frå forsøksfiske på Reykjanesryggen med M/S Borgarin, April–Mai 1996. Report from Møre Research, Ålesund, Å9614 (ISSN: 0804-5380), 19 pp. (in Norwegian).
- Iwamoto, T., 1975. The abyssal fish *Antimora rostrata* (Günther). *Comp. Biochem. Physiol.* 52B, 7–11.
- Jensen, A.L., 1997. Origin of the relation between K and L inf and synthesis of relations among life history parameters. *Can. J. Fisheries Aquat. Sci.* 54 (5), 987–989.
- Jerald Jr., A., 1983. Age determination. In: Nielson, L.A., Johnson, D.L. (Eds.), *Age determination*. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland, pp. 301–324.
- Jørgensen, O.A., 1998. Survey for Greenland Halibut in NAFO Divisions 1C–1D. NAFO SCR Doc. 98/25, 26 pp.
- Jørgensen, O.A., 2004. Survey for Greenland Halibut in NAFO Divisions 1C–1D, 2003. NAFO SCR Doc. 04/19, 26 pp.
- Jørgensen, O.A., 2005a. Survey for Greenland Halibut in NAFO Divisions 1C–1D, 2004. NAFO SCR Doc. 05/13, 28 pp.
- Jørgensen, O.A., 2005b. Survey for Greenland Halibut in ICES Division 14B, June 2004. WP for ICES NWWG, 33 pp.
- Kulka, D.W., Simpson, M.R., Inkpen, T.D., 2003. Distribution and Biology of Blue Hake (*Antimora rostrata* Günther 1878) in the Northwest Atlantic with Comparison to Adjacent Areas. *J. Northwest Atlantic Fisheries Sci.* 31, 299–318.
- Magnússon, J.V., 1998. Age maturity and other biological parameters of two morid species *Lepidon eques* (Günther, 1887) and *Antimora rostrata* Günther, 1878, in Icelandic waters. *ICES CM* 1998, O:32, 22 pp.
- Magnússon, J.V., 2001. Distribution and some other biological parameters of two morid species *Lepidon eques* (Günther, 1887) and *Antimora rostrata* (Günther 1878) in Icelandic waters. *Fisheries Res.* 51, 267–281.
- Merrett, N.R., Gordon, J.D.M., Stehmann, M., Haedrich, R.L., 1991a. Deep demersal fish assemblage structure in the Porcupine Sea Bight (eastern North Atlantic): slope sampling by three different trawls compared. *J. Mar. Biol. Assoc. U.K.* 71, 329–358.
- Merrett, N.R., Haedrich, R.L., Gordon, J.D.M., Stehmann, M., 1991b. Deep demersal fish assemblage structure in the Porcupine Sea Bight (eastern North Atlantic): results of single warp trawling at lower slope to abyssal soundings. *J. Mar. Biol. Assoc. U.K.* 71, 359–373.
- Mjanger, H., Alvsvåg, J., Hestenes, K., Svendsen, B.V., de Lange Wenneck, T., 2003. Håndbok for prøvetaking av fisk og krepsdyr. Versjon 3.15. Institute of Marine Research, Bergen, Norway, 168 pp.
- Pannella, G., 1980. Growth patterns in fish Sagittae. In: Rhoads, D.C., Lutz, R.A. (Eds.), *Growth patterns in fish Sagittae*. Skeletal Growth of Aquatic Organisms. Plenum Press, New York and London, pp. 519–560.
- Pauly, D., 1980. On the interrelationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. CIEM* 39 (2), 175–192.
- Randall, D.J., Farrell, A.P., 1997. *Deep-Sea Fishes*. Academic Press, San Diego, California, USA, 385 pp.
- Rikhter, V.A., Elfanov, V.N., 1976. On one of the approaches to estimation of natural mortality of fish populations. *ICNAF Res. Doc.*, 76/VI/8, 12 pp.
- Roff, D.A., 1984. The evolution of life history parameters in Teleosts. *Can. J. Fisheries Aquat. Sci.* 41, 989–1000.
- Siebenaller, J.F., Murray, T.F., 1990. A₁ Adenosin receptor modulation of adenylyl cyclase of deep-living Teleost fish, *Antimora rostrata*. *Biol. Bull.* 178, 65–73.
- Sinclair, A.F., 2001. Natural mortality of cod (*Gadus morhua*) in the Southern Gulf of St Lawrence. *ICES J. Mar. Sci.* 58 (1), 1–10.
- Small, G.J., 1981. A review of the bathyal fish genus *Antimora* (Moridae: gadiiformes). *Proc. California Acad. Sci.* 42, 341–348.
- Snelgrove, P.V.R., Haedrich, R.L., 1985. Structure of the deep demersal fish fauna off Newfoundland. *Mar. Ecol. Prog. Ser.* 27, 99–107.
- Sparre, P., Venema S.C., 1998. *Introduction to tropical fish stock assessment*. Part I-Manual. FAO Fish. Tech. Pap. (306.1) Rev. 2: 212 p.
- Stearns, S.C., 1976. Life history tactics: a review of the ideas. *Q. Rev. Biol.* 51, 3–47.
- Stearns, S.C., Crandall, R.E., 1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. In: Potts, G.W., Wootton, R.J. (Eds.), *Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress*. Fish Reproduction: Strategies and Tactics. Academic Press Ltd., London, pp. 13–29.
- Templeman, W., Squires, H.J., 1956. Relationship of otolith length and weights in the haddock *Melanogrammus aeglefinus* (L.) To the rate of the growth of the fish. *J. Fisheries Res. Board Can.* 13 (4), 467–487.
- Turnov, I.A., 1992. Fish of the family Moridae from the southeastern Atlantic (Genera *Gadella*, *Halargyreus*, and *Antimora*). *J. Ichthyol.* 32, 38–45.
- Von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquires on growth laws II). *Hum. Biol.* 10 (2), 181–213.
- Wenner, C.A., Musick, J.A., 1977. Biology of the morid fish *Antimora rostrata* in the western north Atlantic. *J. Fisheries Res. Board Can.* 34, 2362–2368.
- Wilson Jr., R.R., 1988. Analysis of growth zones and microstructure in otoliths of two macrourids from the North Pacific abyss. *Environ. Biol. Fishes* 21, 251–261.
- Wootton, R.J., 1990. *Ecology of Teleost Fishes*. Chapman & Hall, London, 404 pp.

