

Paper III

Frequency distributions of fish length, otolith weight, and interpretation of zone pattern in otoliths as means of estimating age of blue hake, Antimora rostrata

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Abstract

Frequency distributions of fish length and otolith weight were analysed and compared with interpretations of zonation patterns in otoliths. The objective was to compare these techniques and methods with the purpose of achieving the most reliable age estimates of the deep-sea morid fish, Antimora rostrata. Material was collected during several surveys within the central and eastern part of the North Atlantic Ocean.

Frequency distributions of fish length and otolith weight comprised a number of modes, suggesting groups of specimens of similar size and age. A higher number of modes, which were easier to separate, were found in frequency distributions of otolith weight compared to total fish length. In general, however, the two measures reflected a similar mode pattern. When distributions were divided by sex the modes became clearer, suggesting sexual dimorphism. Distances between modes were consistent and corresponded to what might be expected based on interpretations of the zonation pattern observed in the otoliths.

Assuming the patterns of zonation in the otoliths reflect the true age, the growth rate of A. rostrata was relatively constant with age for both otolith weight and fish length within the length range investigated. Growth rates of otolith and fish corresponded to approximately 25 mg/y and 4 cm/y respectively. The results imply that reliable age estimation of the relatively long lived deep-sea A. rostrata might be within reach by the use of objective and cost effective methods. The results suggest that more work should be directed towards using frequency distributions, especially otolith weight, for direct age determination of fish stocks in general.

Keywords: Ageing methods, length distribution, otolith weight, Antimora rostrata, Central and Eastern North Atlantic.

1. Introduction

Blue hake, Antimora rostrata, is a widespread and abundant deep-sea species of the family Moridae often found to dominate both bottom trawl and longline catches from ± 1500 to 2500 m (Fossen & Bergstad, 2006). Little is known of its biology and life history (Kulka et al., 2003; Fossen & Bergstad, 2006). Previous studies have noted the problems of estimating the age of Antimora rostrata from zonation patterns in sagittal otoliths (Magnusson, 2001; Fossen & Bergstad, 2006). Although it was not possible to validate the ageing methodology these studies have indicated a longevity of about 20-25 yr.

Any evidence for a strictly rhythmical pattern of recruitment or growth will lead to greater confidence in the age estimates of A. rostrata, thus increasing our understanding of its poorly understood life history. Adults in advanced stages of maturation and juvenile specimens are seldom encountered with the result that our understanding of maturation and spawning cycle of the species is poor (Wenner and Musick, 1977; Gordon and Duncan, 1985; Fossen and Bergstad, 2006). Evidence of

any annual patterns would confirm previous studies suggesting that annual growth and recruitment patterns are common among deep-sea fishes (Haedrich, 1997; Morales-Nin, 2001; Swan & Gordon, 2001; Gordon, 2003) and as such encourage further studies on A. rostrata. This study also investigates the possibility of a direct ageing of populations of A. rostrata rather than estimating this from the age of individual specimens. A direction previously suggested used for teleosts in general, although comparisons of different methods have only rarely been carried out (Francis and Campana, 2004).

The well documented proportionality between otolith size, fish size, and age has resulted in several studies that aim to achieve a more cost effective and standardized ageing procedure (Boehlert, 1985; Worthington et al., 1995 b; Cardinale et al., 2000). For instance some studies of otolith weight have shown that it might provide a good alternative ageing method to the interpretation of zonation pattern in otoliths (Worthington et al., 1995 a; Cardinale et al., 2000; Campana, 2001; Dougall, 2004; Francis and Campana, 2004; Pino et al., 2004).

In this study, data are compiled for A. rostrata, from different areas and years from the central and eastern North Atlantic. Frequency distributions of fish length and otolith weight have been compared with interpretations of the zonation pattern in transverse sections of otoliths, as a possible method of describing the age structure of populations. A validation of the age estimates was not possible with the material available to this study. An important objective was to evaluate the periodic pattern previously described in otoliths of A. rostrata (Fossen & Bergstad, 2006) through focusing on alternative ageing methods and techniques.

Few comparisons of age interpreted from frequency distributions and zone interpretations have previously been carried out. Indications of a common pattern between the different methods might imply the existence of a strong cyclical factor which might form the bases for age estimation of A. rostrata and other deep-sea species. In a wider perspective this might suggest an alternative for routine age

determination of fish populations in general and also increase our understanding of the structure of deep-sea fish assemblages.

2. Materials and Methods

Material for this study was collected from a number of areas and surveys in the central and eastern North Atlantic Ocean (Figure 1, Table I). Descriptions of gear and data from trawl surveys at Greenland (GRL) and longline surveys from the Mid Atlantic Ridge (MAR) are given in Fossen & Bergstad (2006, and references therein) and Fossen *et al.* (2007). Additional information regarding bottom trawling on the MAR is given by Wenneck *et al.* (2007). The sampling in the Porcupine Seabight (PSB) was carried jointly by the Scottish Association for Marine Science (SAMS) and the UK Institute of Oceanographic Sciences (IOS) between 1979 and 1983. Different bottom trawl types were used to sample the demersal fish populations but because of its depth distribution, 982 to 2970 m, only one trawl the semi-balloon otter trawl (OTSB) sampled *A. rostrata* over its entire depth range (Merrett *et al.*, 1991 a, 1991 b). Fisheries Research Service (FRS), Aberdeen began a series of biannual surveys to the Rockall Trough (RT) in 1998 and since 2004 they have become annual. The trawl is a commercial design fitted with a fine mesh codend. The depth of sampling varied between years and only in 2002, 2004 and 2005 did it reach 1800 m. This would explain the lack of large fish in 1998 and 2000 because this species has a marked bigger deeper trend in the Rockall Trough (Gordon and Duncan 1985).

Not all data sources provided the same kind of information, i.e. frequency distribution of fish length exist from all surveys whereas fewer otoliths were available in general and were lacking from some surveys (Table I).

At sea total length, L_{TL} , of *A. rostrata* was measured to the nearest cm below of specimens caught off Greenland, along the MAR and in the RT. The fish caught in the PSB were measured to the nearest mm standard length (L_{SL}).

In the laboratory samples of otoliths were weighed to a precision of 0.1 mg and otoliths from the same fish were generally of similar weight. In the analyses the first weighed otolith for each specimen was used.

The study is organised in two parts. The first part comprises a descriptive analysis of fish length and otolith weight distributions. Modal progression analysis (MPA) and the FISAT II software (Gayanilo *et al.*, 2002) was used to determine and describe how distributions from different surveys were made up of several modes, suggesting separate year-classes. Each survey was analysed separately, and the results were derived from the Bhattacharya procedure (Bhattacharya, 1967; Gayanilo *et al.*, 2002).

In the MPA, an indication of how well different modes were separated from each other was given by the Separation index (S.I.) (Gayanilo *et al.*, 2002). Values less than 2 indicate that separation of modes is virtually impossible in a frequency distribution (Sparre & Venema, 1998). An S.I. value was not estimated for the first mode found. To be able to display these modes graphically an S.I. value of 0 was used in Figures 2, 3 and 4.

In the second part the pattern of modes found within distributions of fish length and otolith weight are compared to see if there is a similar cyclic pattern. If the patterns are caused by the same periodic event then both measures might be used as proxies for describing this phenomenon. Comparison of the two measures was carried out through several steps to elucidate similarities and differences. Finally these results were compared to age estimates obtained by interpreting the otolith zonation pattern.

3. Results

3.1. Modes within Distributions:

Fish length distributions appeared to be made up of several modes, however, it was difficult to separate the modes in some data sets (Figures 2 & 3, Table II). Although fewer observations were available for otolith weight than for fish length, the otolith weight distributions appeared to be made up of a number of well defined modes (Figure 4, Table III). The first visible mode in fish length was found at around 10 cm in several of the UK surveys especially from the RT (Figure 3). Similarly, for otolith weight, the first modes were found at approximately 35 mg. For both measures a number of modes seemed to follow this first mode.

When the data were separated by sex the mode patterns became clearer (Figures 2, 3 and 4). Similarly the separation index, S.I., for otolith weight suggested that modes were more easily separated when data were analysed by sex rather than both sexes combined (Table III). For fish length, however, no such indication was found (Table II). Within the different data sets and for both measures, the coefficient of variation (CV) of the between mode distances suggested a more stable pattern for males and females compared to data for both sexes combined (Table II, Table III). The results are interpreted as being indicative of sexual dimorphism.

For fish length the total material from the PSB and RT surveys has the highest average between mode distances recorded (Table II). This is probably because the generally low number of observations spread over a wide range of size groups did not allow the detection of all modes within the distribution, causing both larger between modes distance and CV values (Figure 3; Table II). A similar phenomenon is believed to have caused the results for females from the GRL samples with regards to otolith weight (Figure 4, Table III).

3.2. Comparison of measures and methods:

The analysis revealed what seems to be a rather strict cyclical pattern of modes within all frequency distributions of the two measures. Further comparisons between the two measures were carried out taking into consideration sexual dimorphism and the limitations of individual data sets.

3.2.1. Separation of modes by measure:

Among males caught off Greenland, S. I. values for modes determined from otolith weight were higher than those determined from distributions of total length, mean S.I. = 5.3 and 3.2 respectively (ANOVA, $p=0.015$, $F_{1,44}=6.43$). Suggesting a better separation of modes within distributions of otolith weight compared to fish length. For females from MAR, a higher number of modes was determined in distributions of otolith weight compared to the total length, 16 vs. 9, however, no differences in S.I. values between the two measures was detected ($p=0.875$, $F_{1,25}=0.025$). Combined with indications from the other data series a rather strong pattern is suggested (Tables II & III). The results indicate that modes in distributions of otolith weight are better separated compared to modes in fish length, and due to this a higher number of modes might be found in distributions of otolith weight especially among bigger and older specimens (see also below).

3.2.2. Between mode distance by measure:

In an attempt to verify that the pattern found in the two measures reflect the same cyclic event, comparisons of the between mode distances were examined. This would indicate if the actual time lag between modes is similar and how it might vary.

When MPA data from the MAR and GRL was used to plot frequency distributions of the distances between subsequent modes, these distributions were dominated by a mode at about 4 cm for fish length and 25 mg for otolith weight (Figure 5). For fish length, median values indicate a somehow shorter distance between modes from males (4.19 cm) than females (4.61), and for combined sexes the distance was 4.63 cm. However, no significant differences were found (KW-test=2.44, $n=2.44$, $p=0.294$).

Similarly for otolith weight, median values indicate a somehow shorter distance between modes for the combined sexes (19.9 mg) than in data from males (26.3 mg) and females (31.3 mg). The between group distances were significant (KW-test=25.48, $n=77$, $p<0.0001$). Differences were due to females having a larger between mode distance than both the combined sexes and only the males. When data for females from GRL were excluded no differences was found between females from the MAR and males from GRL (Mann-Whitney U test=161.00, $n=36$, $p=0.911$), supporting the above comment on data limitations.

Furthermore, the relationship between otolith weight and fish length suggests that an increase in fish length of between 4 and 4.5 cm would result in an increase in otolith weight of 27 to 31 mg ($OW=6.804*L_{TL} -73.09$, $N=428$, $r^2=0.85$ estimated for specimens with a L_{TL} of between 20 and 45 cm). Thus, indicating that the general distance between modes from the two measures are similarly separated in time (Figure 5).

Both histograms of between mode distances, for fish length and otolith weight, showed a tail to the right of the modal peak, which was more pronounced in the data for otolith weight than for fish length (Figure 5). The pattern is interpreted as resulting, at least partly, from modes not being detected due to small sample sizes (see above). This will have the effect of increasing the between mode distance (Figures 2; 3 and 4). Despite this, the analysis suggests an overall consistency between the two measures where the between mode distances follows a similar pattern in all datasets and seem to be generally consistent within the size range investigated.

3.2.3. Fish length and otolith weight:

As modes seems to be consistent across years, data sources, measures, and size groups the next question which needs to be answered is whether as a general rule a mode in fish length actually reflects a mode in otolith weight? To investigate this and to describe how different number of modes can be found in the two measures, data for males collected at GRL during September 2003 have been used as an example.

Although the data set only includes a limited number of observations for both measures (approximately 60) it indicates the general differences between the two.

The placement of most modes in otolith weight overlapped with a mode in fish length (Figure 6). However, some differences were observed. A mode seems to be missing in data from the MPA of otolith weight at about 100 mg reflecting a fish length of 25 cm. Similarly, a mode consisting of larger specimens was found in the otolith weight data, which was not detected in the data of fish length (Figure 6). As reflected by the CV values, modes from otolith weights seemed, in general, to be more evenly spaced compared to fish length data. As expected the results suggest that modes in frequency distributions of otolith weight generally reflect modes in distributions of fish length from the same material. The observed differences are again believed to be connected by the low number of observations combined with a more distinct mode pattern in distributions of otolith weight compared to fish length.

3.2.4. Frequency distributions and otolith zonation pattern:

Modes in the distributions of fish length and otolith weight appear to be consistent over time, between datasets, sexes, size groups, and measures. As this pattern is unlikely to be caused by random variation the results have been compared to existing age estimates based on zonation patterns within the otolith. With the objective of determining whether the modes and zoning patterns might be connected to the same cyclical phenomenon. The age estimates were derived from interpretation of transverse sections of otoliths by Fossen & Bergstad (2006) which utilised some of the same material.

Distributions of otolith weight and fish length appear to show similar signals, but because otolith weight shows a better separation of modes, otolith weight data was used for this analysis. Again males from the three GRL trawl surveys were used as an example. The increase in otolith weight between subsequent modes seems to be identical to what is predicted by the between assumed age group differences, suggested by the interpretation of the zoning pattern (Figure 7). This result was

consistent within all three surveys and indicates a similar time lag between the modes in otolith weight and zone deposition in otoliths. All mode values were placed well above the expected otolith weight at age relationship, suggesting that the youngest year-classes were not included in our samples, as also suggested by Figures 2, 3 and 4. The results imply that modes in otolith weight are caused by the same strictly cyclical event that also causes zonation pattern in the otoliths.

4. Discussion

The use of multiple data sources are believed to have strengthened the results in two ways. First, it ensures that data from most size and age groups are included in the analysis thus allowing a general description to be made. Secondly, detecting the same pattern across areas, years and size groups implies that there is a consistent underlying pattern. Furthermore, separating frequency distributions into a number of normal distributions is not necessarily a straight forward process (Sparre & Venema, 1998; Gayanilo *et al.*, 2002). The tools available for separating modes from distributions have limitations especially with respect to their use as an alternative method of age estimation (Sparre & Venema, 1998; Gayanilo *et al.*, 2002). For the general approach used in this study the tools were found sufficient.

Detailed descriptions of frequency distributions of fish length or otolith weight were not possible because sampling was inadequate for most data sets. This is particularly the case for the youngest year-classes in all areas and for the accumulated biomass of larger fish at greater depths at GRL and the RT. Overall, however, a rather clear and consistent pattern can be seen within all data series and size groups. The large between mode distances observed within some distributions was interpreted as being caused by modes not being detected within the material because of limited sample size.

In distributions of fish length the first visible mode was found at approximately 10 cm, which is assumed to reflect the mode in otolith weight found at about 35 mg (Figures 3, 4 and 6). These specimens represent members from the smallest year-class available to the gear. Based on the other findings presented both here and by Fossen and Bergstad (2006), these modes might represent specimens originating from spawning two years earlier.

Despite the limitations found in some data series, distances between modes were found equally spaced both in frequency distributions of fish length and otolith weight. In general, a mode in fish length seemed to reflect a mode in otolith weight. The modes in distributions of otolith weight were more consistent and allowed more modes to be separated, especially among the larger specimens. This might be explained by a closer connection between otolith growth and age compared to fish length and age (Boehlert, 1985). The fact that 7 modes could be identified in both measures in a small sample of approximately 60 male specimens from GRL suggests a well defined and strict pattern (Figure 6).

The increase in otolith weight between subsequent modes was identical to what is predicted from the estimated relationship between otolith weight and age estimates from the zonation patterns within the otolith (Figure 7). The indicated time lag between modes was consistent over time and between areas and suggests a strictly cyclical pattern. Furthermore, Fossen & Bergstad (2006) suggest that the zonation pattern itself is formed synchronously between specimens and thereby also implying the influence of a strong and strictly cyclical event.

Based on previous experiences from other species the most likely explanation of a strict cyclical pattern is annual fluctuations in biotic and or abiotic parameters (Pannella, 1980; Campana & Neilson, 1985; Wilson, 1988; Gauldie & Nelson, 1990; Gauldie *et al.*, 1991; Haedrich, 1997). The actual cause of the zonation pattern in otoliths is generally poorly understood and is thought to be a combined effect of several variables (Gauldie & Nelson, 1990). Within the deep-sea the seasonal variation

in light and temperature is negligible and fluctuations are expected to be found elsewhere (Merrett & Haedrich, 1997). In the deep-sea it is probable that these cyclical patterns are linked to the annual fluctuation in production in the euphotic zone followed by a seasonal supply of food to the deep sea floor (Haedrich, 1997; Merrett & Haedrich, 1997).

As Francis and Campana (2004) point out, the purpose of estimating the age of fishes is to describe the age related stock structure as inputs for stock assessments. This is usually done by ageing of individual specimens although the goal is to describe the age structure of the population. In this study we show that alternative methods, using frequency distributions, might be an alternative to conventional age determination of Antimora rostrata. Similar studies have previously been carried out on other species (Boehlert, 1985; Pawson, 1990; Worthington et al., 1995 b; Araya et al., 2000; Cardinale et al., 2000; Francis and Campana, 2004; Pino et al., 2004). This method is particularly relevant for situations where zone interpretation is difficult, time consuming, and or can result in biased age distributions, e.g Campana and Neilson, (1985); Beamish and McFarlane, (2000); Cardinale et al., (2000); Campana, (2001); Francis and Campana, (2004). This method represents an important step towards more automated age determination (Boehlert, 1985; Pawson, 1990; Worthington et al., 1995 a, 1995 b; Cardinale et al., 2000; Pino et al., 2004).

Weighing otoliths for analysis of frequency distributions is less time consuming than conventional age reading and therefore it is possible to dramatically increase sample size and thereby reduce costs (Worthington et al., 1995 b; Cardinale et al., 2000; Dougall, 2004). Whether or not it will lead to a marked increase in precision and accuracy will vary from species to species. However, such methods might be applicable to a number of fish stocks (Worthington et al., 1995 a; Araya et al., 2000; Francis and Campana, 2004; Pino et al., 2004)

Assuming that the observed cyclic pattern described here reflects an annual cycle and therefore different year-classes the study supports the results of previous studies on

growth and longevity of A. rostrata (Magnusson, 2001; Fossen & Bergstad, 2006). The results suggest a relatively linear growth within the data range. Also the estimated otolith growth of about 25 mg/y appears to be reasonable compared to estimates for the Patagonian grenadier, Macruronus megallanicus, off Chile (~31 mg/y) (Pino et al., 2004) and the macrourid, Coelorhynchus coelorhynchus, off Greece (34 mg/y) (Labropoulou and Papaconstantinou, 2000).

The differences in the mode patterns between males and females suggest different growth rates. Females appeared to have a faster growth rate than males, although the differences were not significant. The lack of significance could be either because the differences might be small (Fossen & Bergstad, 2006) or that the sample size is less than optimal or both. Previous studies have shown that the larger specimens of A. rostrata are dominated by females (Kulka et al., 2003; Fossen & Bergstad 2006). The indications of faster growth rates for females in this study suggests that given appropriate sample sizes this method has the potential to estimate separate growth rates for males and females.

Utilization of deep-sea resources is expected to increase in the coming decades as fisheries continuously explore new and deeper waters for resources (Gordon et al., 2003; ICES, 2006).

A major problem for the assessment and management of these deep-water resources is a lack of knowledge of the age composition of the stocks (Large et al., 2003).

Validation of traditional age reading methods is particularly difficult and has seldom been achieved and then only for juveniles (Swan & Gordon 2001 and references cited therein). This study indicates the possible usefulness of this alternative method for estimating the age of deep-water species.

5. Acknowledgement

We would like to thank the scientific staff and crew on all the involved vessels for excellent seamanship and thorough processing of catches. We also want to thank Odd Aksel Bergstad for making data available from the MAR-ECO project, Ole A. Jørgensen and Micael Rosing for making data from the Greenland surveys available. The UK Natural Environment Research Council supported the collection of the Porcupine Seabight material by Nigel Merrett and one of us (JDMG). Thanks to Fisheries Research Services, Aberdeen for supplying the Rockall Trough length data and allowing one of us (JDMG) to collect otoliths.

The study was an element of MAR-ECO (www.mar-eco.no), a field project of the Census of Marine Life (www.coml.org).

6. References

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Tables:

Table I Summary of sources of data: Area, year, sampling method, number of length measurements and number of otoliths available.

Area	Year	Gear	No. Lengths measured	No Otolith Weighed
Mid Atlantic Ridge	2004	Long line	1109	387
Mid Atlantic Ridge	2004	Trawl	435	0
West Greenland	2003 & 2004	Trawl	825	660
East Greenland	2004	Trawl	314	297
UK – Porcupine S. B.	1979 – 1983 [^]	Trawl	894	0
UK – Rockall Trough	1998 – 2005	Trawl	882	51*

[^] Includes data from 9 surveys

* Data from 2005 only

Table II Summary output from the Modal Progression Analysis of frequency distributions of fish length. For each data set (where possible the total distributions were also separated by sex), number of modes found, median value of the modes' Separation Index, Median and Mean distance between subsequent modes, and CV of mean is shown. GRL= Greenland, MAR = Mid Atlantic Ridge.

Data	No. modes	Median S.I.	Median distance	Mean dist. (CV%)
GRL-15/9-03 - total	10	4.28	3.84	4.58 (32.2)
GRL-15/6-04 - total	10	4.19	4.9	5.44 (44.1)
GRL-15/11-04 - total	10	3.83	4.8	4.81 (22.7)
GRL-15/9-03 - males	7	3.61	3.83	3.57 (44.9)
GRL-15/6-04 - males	7	4.56	4.53	4.53 (17.5)
GRL-15/11-04 - males	6	2.87	3.95	4.05 (8.2)
GRL-15/9-03 - females	9	5.27	4.87	5.23 (36.4)
GRL-15/6-04 - females	10	4.5	4.5	4.76 (28.8)
GRL-15/11-04 - females	9	4.31	4.31	4.59 (20.9)
MAR – females	8	2.84	4.68	4.60 (24.2)
Porcupine Seabight - all data *	52	4.33	5.07	6.20 (71.8)
Porcupine Seabight -females*	47	4.08	3.58	4.16 (54.8)
Rockall Trough – all data*	26	4.86	4.91	5.06 (22.2)

*The nine surveys from Porcupine Seabight presented in Figure 3 was treated as separate surveys but presented as one set here. This was also done for the 5 surveys from the Rockall Trough.

Shaded: data assumed to be heavily biased due to inadequate sampling.

Table III Summary output from the Modal Progression Analysis of frequency distributions of otolith weight. For each data set (where possible the total distributions were also separated by sex), number of modes found, median value of the modes' Separation Index, Median and Mean distance between subsequent modes, and CV of mean is shown. GRL= Greenland, MAR = Mid Atlantic Ridge.

Data set	N modes	Median S.I.	Median distance	Mean and CV%
GRL-15/9-03 - total	7	4.17	21.29	20.4 (11.3)
GRL-15/6-04 - total	9	3.84	18.57	19.4 (22.2)
GRL-15/11-04 - total	7	3.26	22.53	21.1 (23.1)
GRL-15/9-03 - males	7	6.04	29.88	30.3 (22.6)
GRL-15/6-04 - males	8	6.01	26.27	24.5 (28.3)
GRL-15/11-04 - males	9	4.44	23.54	25.8 (24.4)
GRL-15/9-03 - females	5	4.00	42.78	64.2 (72.9)
GRL-15/6-04 - females	9	9.49	33.46	45.2 (51.5)
GRL-15/11-04 - females	6	4.20	53.33	48.7 (35.8)
MAR – females	16	3.58	26.32	26.7 (23.7)
Rockall Trough - 2005	3	6.77*	42.82*	42.82 (7.9)

* Mean of two values

Shaded: data assumed to be heavily biased due to inadequate sampling.

Figures:

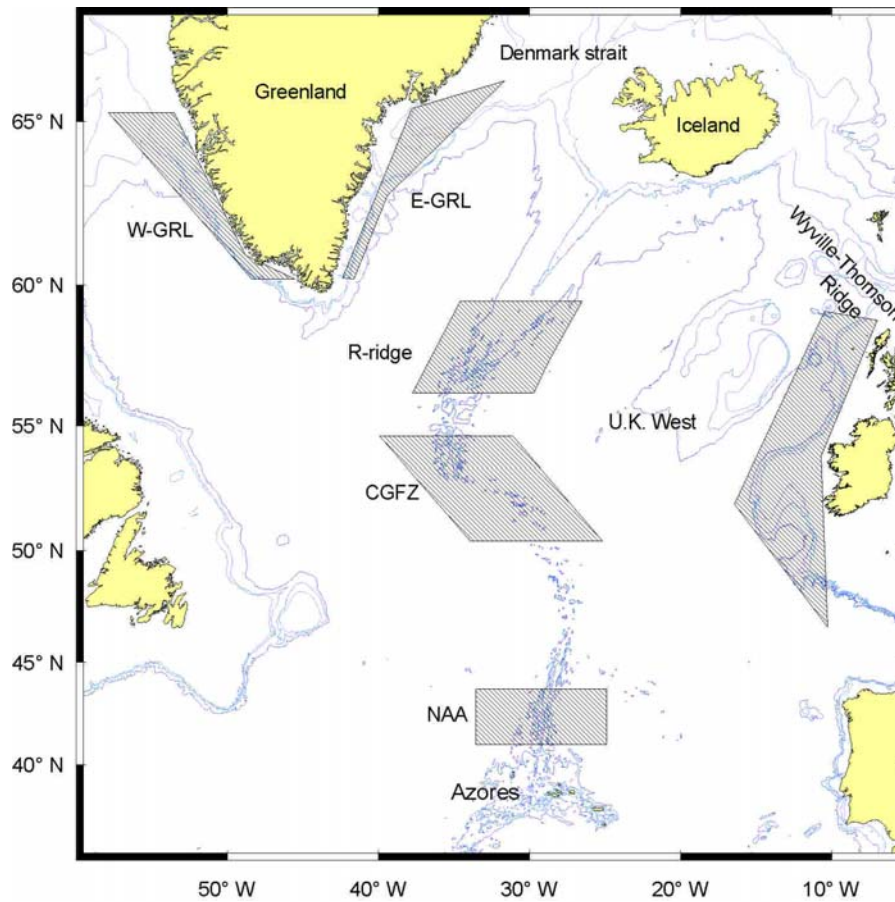


Figure 1 Map showing the sampling areas used in this study, shaded. Both longline and trawl data were available from the sub-area just north of the Azores archipelago (NAA), the Charlie Gibbs fracture zone (CGFZ), West Greenland (W-GRL) and East Greenland (E-GRL). Trawl data were available from the areas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

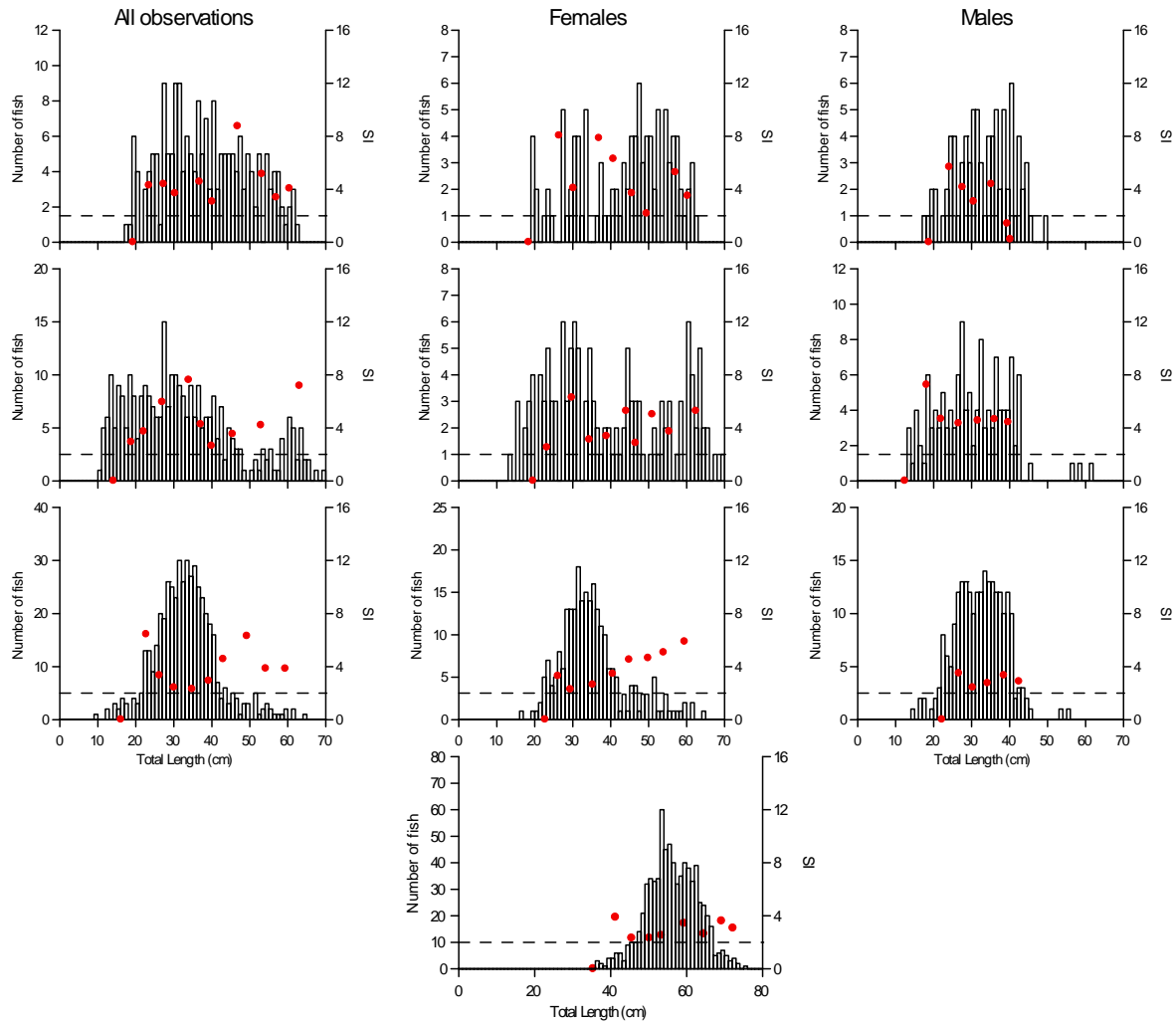


Figure 2 Left: Total length frequencies from Greenland, middle females, and right males. Top West-GRL 2003 September, East-GRL 2004 June, W-GRL 2004 October/November. Bottom MAR, 2004 (females). Also included are estimated mean values for different modes defined in FISAT II, plotted against separation index, S.I. The horizontal lines included in the figures indicate S.I. values of 2.

Porcupine Seabight (SL)

Rockall Trough (TL)

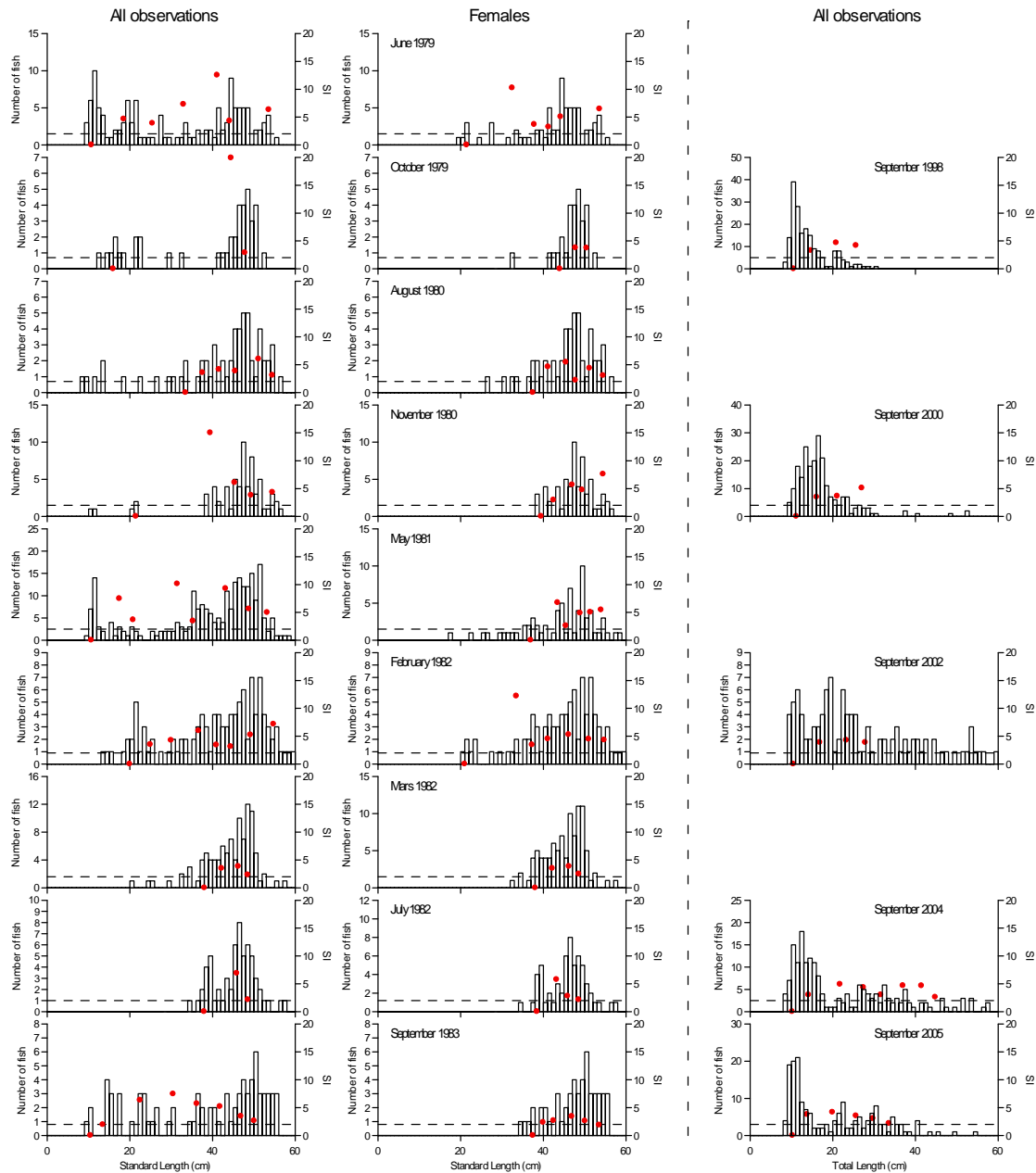


Figure 3 Frequency distribution of Standard Length (SL) from 9 selected surveys between 1979 and 1983 from the Porcupine Seabight (covering a period of 5 years where the number of observations per survey was highest). Left: All measurements. Middle: only specimens determined as females. To the Right: Frequency distribution of Total Length from Rockall Trough (Scotia) surveys from the period 1998 to 2005. In all graphs were estimated mean values of modes detected by the MPA procedure in Fisat II is plotted against the separation index S.I. as red circles. The horizontal lines included in the figures indicate S.I. values of 2.

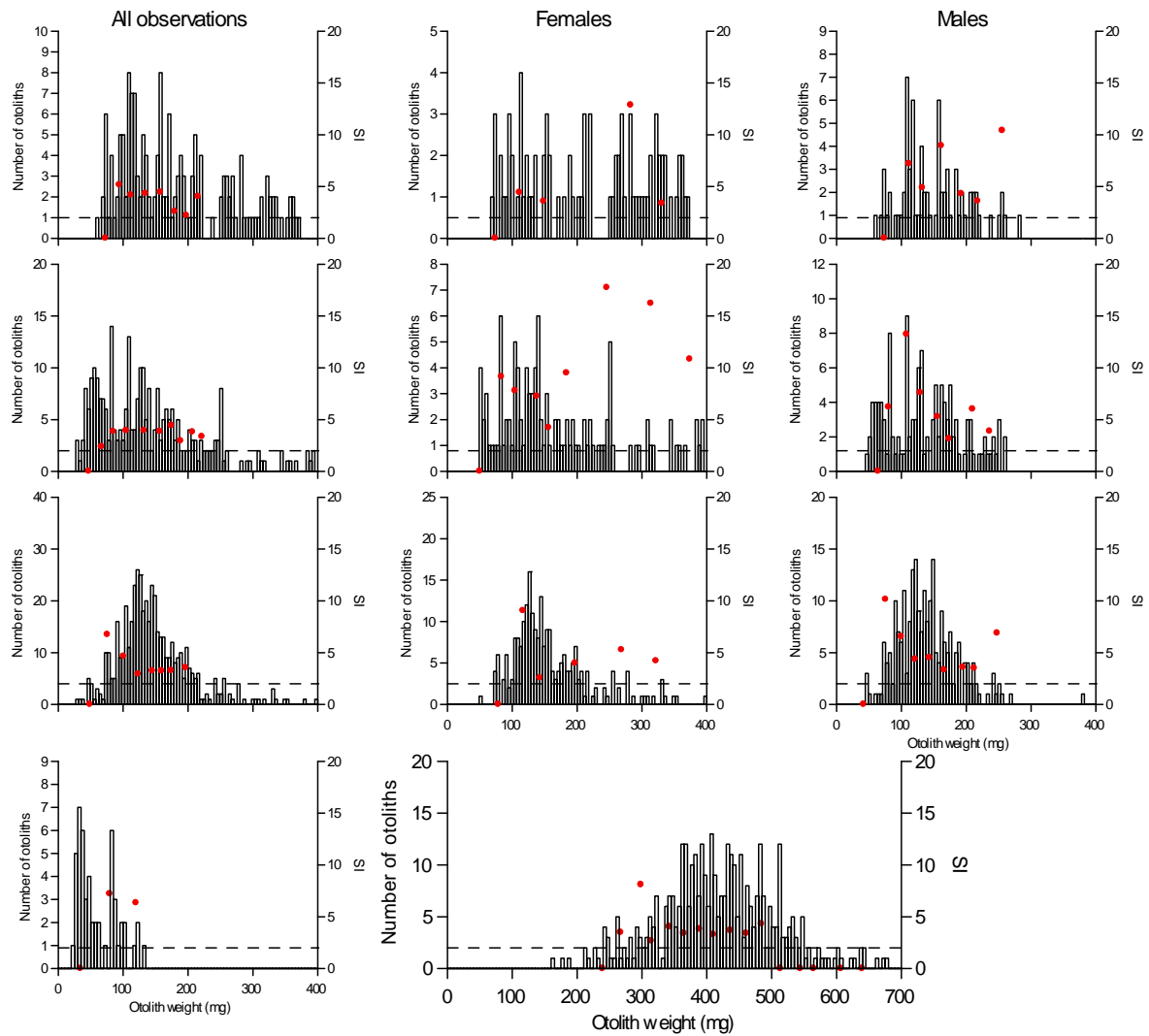


Figure 4 Frequency distributions of otolith weight from different surveys. From top: west Greenland September 2003, underneath east Greenland June 2004, west Greenland October/November 2004. Left to right: All data, females, and males. At the bottom left: Rockall Trough 2005 all data, in the middle females from MAR 2004. Estimated mean values of modes from the MAP analysis is included and plotted against the separation index S.I. on the second y-axis. The horizontal lines included in the figures indicate S.I. values of 2. For the MAR longline data the last 5 S.I. values are given the value 0, determined in a second MPA due to limitations in Fisat II (Gayaniilo *et al.*, 2002).

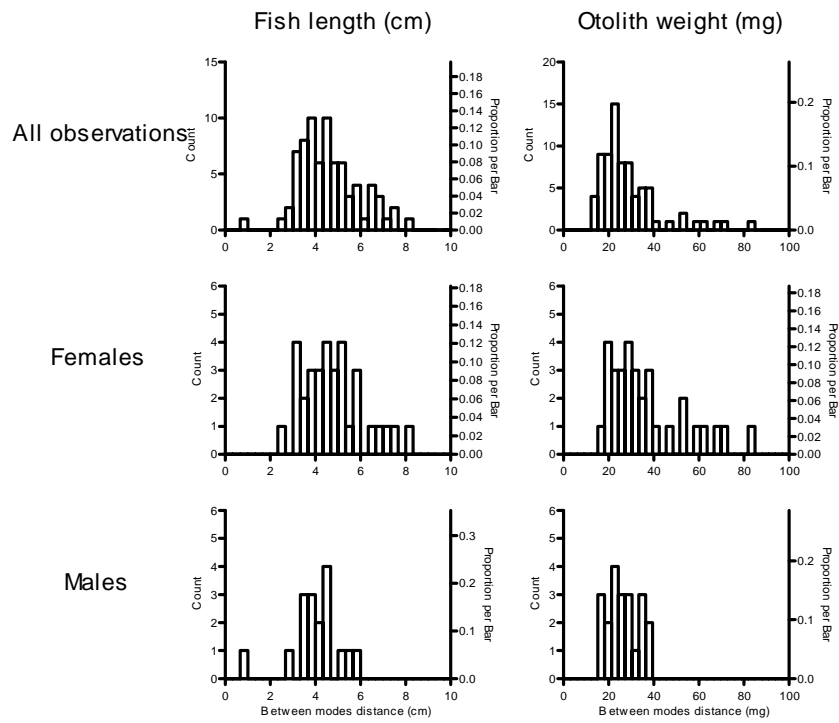


Figure 5 Histograms of between mode distance from modal progression analysis within distributions of total length and otolith weight. Data from Greenland and the MAR.

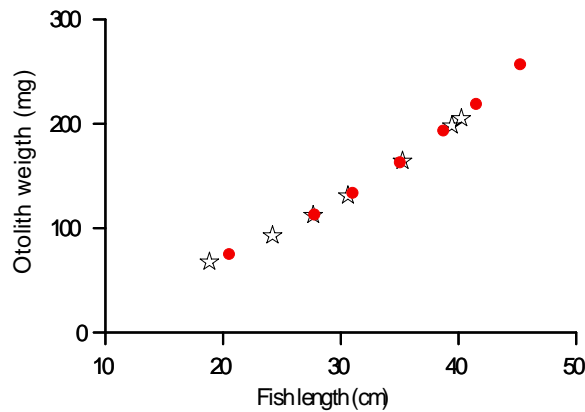


Figure 6 Estimated modal averages within fish length (star) and otolith weight (filled circle) distributions plotted against corresponding values of fish length and otolith weight respectively. Data from male *A. rostrata* collected off the west coast of Greenland, September 2003.

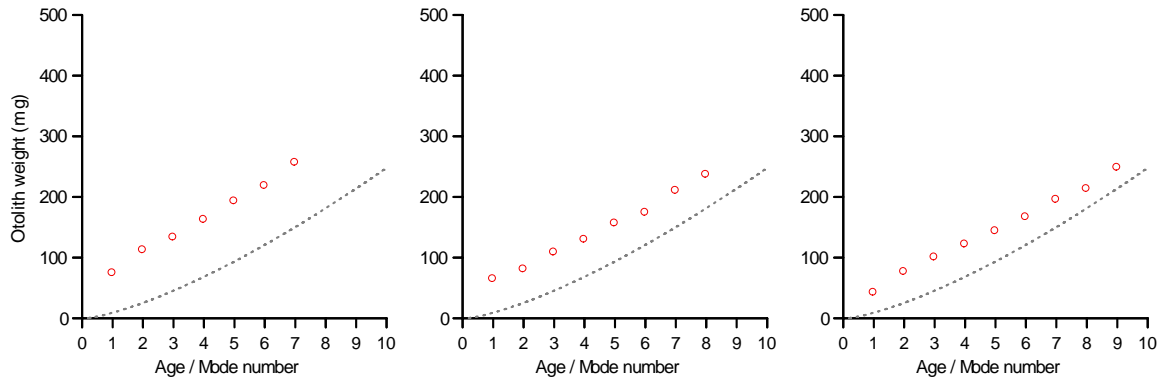


Figure 7 Relationship between otolith weight and age from experimental age determination of zonation pattern (dotted line, $OW=10.009 \cdot X^{1.3956}$, $N=108$, $r^2=0.804$; data from Greenland 2004 with readability < 4 (Fossen & Bergstad, 2006)), and mean otolith weight against mode number determined in the MPA (open circles). Data for males from the three Greenland surveys, from left to right: West-Greenland September 2003, East Grl. June 2004, and west Grl. November 2004. The first mode found in otolith weight within each distribution was given the x-value 1 and so on.

