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Northwest Atlantic Fisheries Organization

Serial No. N4511 **NAFO SCR Doc. 01/123**

SCIENTIFIC COUNCIL MEETING – SEPTEMBER 2001
(Deep-sea Fisheries Symposium – Oral)

Age Estimation of the Roundnose Grenadier (*Coryphaenoides rupestris*), Effects of Uncertainties on Ages

by

P. Lorance[1], F. Garren[1], J. Vigneau[2]

1. IFREMER, 150 quai Gambetta, BP 699, 62321 Boulogne-sur-mer, France
e-mail: pascal.lorance@ifremer.fr
2. IFREMER, av. du Général de Gaulle, BP 32, 14520 Port-en Bessin, France

Abstract

The estimation of the age composition of the catch is a prerequisite for the analytical assessment of exploited fish resources. However, most deep-water fish stocks are assessed or managed in the lack of age structure, which would often be of little help and subject to debate. In the case of the roundnose grenadier, the larger macrourid species exploited at the upper and mid-slope depth in the North Atlantic, the reading scheme of the otoliths is quite easily agreed upon between different readers, and they are in acceptable agreement with age validation formerly obtained on the juveniles. In the North East Atlantic, the fishery operates over large areas and does not target fish concentration of pure adult fish like for some other deep-water species. Then, the changes of the age compositions of the exploited populations are likely to appear in the catch and changes in the length distribution of the landings appeared since the onset of target fishing, which is hardly the case for aggregating species such as orange roughy or blue ling.

However, the uncertainties on the age estimated are probably wide, growth parameters from the Von Bertalanffy growth model were estimated, the effects of the age uncertainties on these parameters were investigated showing that they cannot be disregarded and the usefulness of such parameters for assessment purposes is discussed. The relationships between length, age and otolith weight were analysed and the otolith weight appeared as a possible alternative solution to estimate the age of the roundnose grenadier.

Introduction

The roundnose grenadier is one of the major deep-water species exploited in the northeast Atlantic. Although the potential interest for fisheries of this species was noticed more than 20 years ago (Bridger, 1978; Ehrich, 1983) the exploitation did not start before the late 1980s when French trawlers began to fish deeper along the slope to the west of the British isles and south of Faeroe islands (Charuau*, et al.*, 1995). The roundnose grenadier is now the first species in the landings of the French deep-water fleet. The French exploitation is mainly developed to the west of Scotland (ICES sub-area VI). In the ICES area, it is also exploited by Denmark and Norway in the Skagerrak (ICES sub-area III) and, to a lesser extent by Iceland and Faeroe Islands mainly in their respective surrounding waters and by Scotland in ICES sub-area VI. Lastly the catch strongly increased over recent year in ICES sub area XII due to a developing exploitation from Spanish trawlers.

Before exploitation in the northeast Atlantic, the species was exploited in the northwest Atlantic and on the mid-Atlantic ridge from the late 1960s (Atkinson, 1995; Troyanovsky and Lisovsky, 1995). The biology of the species is quite well described; its reproduction was the subject of several studies as well as its distribution and some aspect of its ecology (Allain, 1999; Allain, 2001; Atkinson, 1995; Bergstad, 1990; Gordon, 1979; Haedrich and Merrett, 1988; Kelly*, et al.*, 1996, 1997; Mauchline and Gordon, 1984). However, the stocks and populations identity are as yet unknown and the areas used as stock units for stock assessment purposes are based upon hydrological hypothesis (Anon., 2000).

The most recent assessment of the species in the ICES area was based upon commercial catch CPUE using surplus production and modified DeLury models (Large et al, this symposium, Anon., 2000). Preliminary aged-based assessment was also tried (Anon., 1998; Lorance*, et al.*, 2001) and growth and mortality parameters were used for the calculation of maximum sustainable yield (MSY) from the Beddington and Cooke procedure (Beddington and Cooke, 1983). Such assessment requires age distribution of the catch and the roundnose grenadier is probably one deep-sea species for which reasonably reliable aged distributions can be estimated. Age structures were formerly estimated for the (assumed) population of the Skagerrak, in the North Sea (Bergstad, 1990) and for the west of the British Isles (Kelly*, et al.*, 1997; Lorance*, et al.*, 2001). Lastly, the annual periodicity of the annuli read on otoliths was validated for juveniles up to the age of 8 (Gordon and Swan, 1996). Although the validation does not apply to the adult fish, the growth rate of the juveniles in the range of the validated ages is consistent with that inferred from otoliths reading of larger fish and the growth increments counted on large individuals appear as a continuation of the deposition of the validated few first annual rings. In the present paper the growth of the roundnose grenadier is investigated from age readings of otoliths collected in 1996 and 1999. The observed growth is adjusted to the Von Bertalanffy growth model (VBGM) and the difference in the estimated growth parameters according to the method used to fit the model is explored. The sexual dimorphism in growth is investigated and the implications of the uncertainties in growth and age estimations for the assessment of this species are discussed.

Material and Method

Sampling

The otoliths were collected during two deep-water trawling cruises of the French R/V Thalassa in 1996 and 1999. On board, both sagital otoliths were removed and stored in paper envelopes. The pre anal fin length (PAFL), from the tip of the snout to the first anal fin spine, was recorded at the lowest ½ cm together with the sex and total weight at the nearest 10 g of the fish.

Most of the otoliths (n=725) used here were collected in 1999 from the catch of a large otter bottom trawl of commercial type by depths of 1000 to 1300 m in two sampling areas:(i) the West of Brittany by about 48°N and 8°30'W and (ii) the West of the British Isles from 54°30'N to 56°40'N to the East of the Rockall Trough by 9°30'W to 11°25'W. A further set of 228 otoliths was taken from the collection of a cruise carried out in 1996. These were mainly otoliths of juvenile individuals (n=195) of less than 10 cm PAFL, which number in the 1999 sampling was low. The sampling area was the same as in 1999 to the West of the British Isles and the depth range was slightly larger from 990 m to 1400 m. Some small fish were taken from a 6 m beam trawl used to sample the benthic fauna (Godart, 1997). Due to this combination two different years, the data may not be suitable for constructing an age-length key to be used for assessment but this is not a problem for growth estimation.

The otolith readings were carried out in late 2000 and 2001 (i.e. after a much sufficient time for the otolith to be dry in the ambient conditions of the laboratory). One otoliths of each of 953 individuals was read. The weight of one otolith of 698 individuals was estimated from the half weight of the pair of otoliths weighted at 0.1 mg except in a few cases where one single otolith in good condition was available.

Preparation and reading of otoliths

Two reading methods were applied to two sets of otoliths. A large set of 848 otoliths from fish measuring 1.5 to 25 cm PAFL was embedded in translucent polyester resin, cut in thin slices on a BUELHERT ISOMET low speed diamond saw in their dorso-ventral axis. The slices were made as thin as possible but the slices of the larger otoliths became very fragile and difficult to handle without damage when they were made too thin. Two or three slices per otolith were cut. The thickness of a set of 30 slices was measured on a MITUTOYO comparator. The thin slices were read under transmitted light on a LEITZ LABOVERT reverted microscope fitted with a black and white video camera connected to a SONY TRINITRON monitor of 21". The counting of the otoliths annuli was mainly done on the monitor screen but direct vision from the microscope oculars was used to clearly identify the thinner ones using magnifications up to 125x.

An extra set of 105 otoliths from fish measuring 2 to 6 cm PAFL were read in whole under reflected light on a LEICA MZ6 binocular microscope fitted to the same video camera and monitor as above. The magnification used on the microscope was 8x to 16x when the image was read on the Sony Monitor and up to 40x when reading in the microscope oculars.

The interpretation scheme of the whole otoliths was quite straightforward as they displayed very clear rings that could be follow almost along all around the otolith (Figure 1a). These rings correspond to the hyaline zones seen on the thin slices and similar to the growth zones of gadoids species as described by Bergstad (1990)(Figure 1b). From a size of the fish above about 6 cm PAFL whole otoliths were difficult to read due to their increasing thickness, all the larger individuals were read in thin slices. The readings of the thin slices were carried out as described by Kelly et al. (1997). Usually, 6 to 8 rings were counted in the dorso-ventral axis (Figures 1b, 2) and correspond to the pre-collar growth of Kelly et al., (1997) and the further zones were counted in the post-collar growth zone (Figure 2; see also Figure 5 in Kelly et al., 1997).

Fitting of the Von Bertalanffy Growth model

The Von bertalanffy growth model was used to estimate the growth of the species and to compare the growth of males and females. As usual, the model expresses as:

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

where: L_t: is the size at time t
L_∞ is the asymptotic length of the species
K is the growth coefficient
t_0 is a parameter which interpretation is variable among authors some considering it as mathematical artefact and other allocating it an actual biological time: the theoretical time at which the fish would have a length of 0.

Two adjustment methods were used for the Von Bertalanffy model.

1. Based on the hypothesis of normality of residuals, Kimura (1980) proposed to calculate the parameters from a likehood function of the normal distribution function associated to the residuals. Under the hypothesis of constant variance the function to minimize is:

$$\sum \left(L_{ti} - L_\infty \left(1 - \exp(-k(t_i - t_0)\right)\right)^2 \text{ i=1,….n} \qquad \text{(Model 1)}$$

where: $L_\infty, k \text{ and } t_0$ are the parameter to estimate;
L_{ti} is the length of the *i*th individual of age t_i.

2. In the case where the variance of L_{ti} varies with t_i, Kimura (1980) propose a weighted model where the function to minimize is:

$$\sum \frac{n_t}{\hat{\sigma}t^2} \left(\overline{L}_t - L_\infty \left(1 - \exp(-k(t_i - t_0)\right)\right)^2 \qquad \text{(Model 2)}$$

In order to do this fit, the observed length of each individual was transformed to:

$$y_{ti} = \frac{1}{\hat{\sigma}_t} L_{ti} \quad \text{(i=1,…n)}$$

and the parameters were estimated from a regression on y:

$$y = \left(\frac{1}{\hat{\sigma}_t}\right)\left[L_\infty\left(1-\exp(-k(t-t_0))\right)\right]$$

The estimation of the growth parameters from males and females and the significance of the difference between the two sexes were estimated from the weighted model (model 2). The differences in k and L_∞ between sexes were introduced as extra parameters in the model. It was decided not to include a parameter for the deviation in t_0. Considering t_0 as the hypothetical age at length 0 (Kimura, 1980) there is no biological reason that it would be different between males and females. If it is a model parameter without biological meaning (Pauly, 1997) there is no more reason to make it different between males and females. Lastly, a unique t_0 keeps the analysis simpler.

In other word, indexing the parameters of males and females by *m* and *f*, the model to adjust is:

$$y = \left(\frac{1}{\hat{\sigma}_t}\right)\left[\left(L_{\infty m} + \Delta L_\infty\right)\left(1-\exp\left(-(k_{\mathrm{m}} + \Delta k)(t-t_0)\right)\right)\right] \qquad \text{(Model 3)}$$

where ΔL_∞ and Δk are the differences in L_∞ and k between females and males. These differences were arbitrarily set as $L_{\infty f}$ - $L_{\infty m}$ and $k_f - k_m$.

To assess these parameters, the Gauss-Newton iteration algorithm was used with S+ software. Kimura (1980) used the maximum likelihood method to have the best properties of the estimation: consistency, smallest possible variance and asymptotic normality. Antoniadis et *al.*, (1992) shown that when the errors are normally distributed the model is said non-linear gaussian and then, the maximum likelihood estimators and the mean square estimators are the same.

In a former study, the growth of the species was estimated with the model 1 on another set of age estimates from fish sampled on board commercial trawler in 1996-97 (Allain & Lorance, 2000). The difference parameters were included in the model 1 and the difference between sexes was tested from nested model taking into account differences in L_∞, k and t_0. It was concluded that only the parameter L_∞ was different between males and females (Allain & Lorance, 2000).

In order to improve the estimated growth parameters and to compare the results obtained from two sets of otoliths read by two different readers this data set was re used here and the parameters were estimated from the model 3. The main data set in this study, from fish collected from cruises is referred to below as 1999 data set, the other one as 1997 data set.

Construction of confidence bounds and confidence region

The confidence bounds of each parameter are calculated with the "profile" function of S+ software. This method for a given parameter, θ_p, uses a function that is equivalent to the studentized parameter $\delta(\theta_p)$ (S-plus 2000 Guide to statistics, vol 1, 2000):

$$\delta(\theta_p) = \frac{\theta_p - \hat{\theta}_p}{\sigma(\hat{\theta}_p)}$$

where $\hat{\theta}_p$ is the model estimate of θ_p.

Then a confidence interval can be constructed as follows :

$$-t_{(N-p,\alpha/2)} \le \delta(\theta_p) \le t_{(N-p,\alpha/2)}$$

The comparison between the two sets of growth parameters for males and females was carried out by constructing the confidence region of the pair of parameters $\theta = \begin{bmatrix} L_\infty \\ K \end{bmatrix}$ for each set. The confidence region for a vector of estimated parameters $\hat{\theta}$ is defined as the θ values such as (Rooney & Biegler, 1999):

$$\left(\theta - \hat{\theta}\right)^{'} X^{'} X \left(\theta - \hat{\theta}\right) \leq \hat{\sigma}^2 p F^{-1}_{p,n-p}(1-\alpha)$$

Due to the correlations between the parameters in θ, these areas have an ellipsoidal shape.

Fitting of the Age – Otolith weight relation

A linear regression was used to fit the relation between the age of the individual and its otolith weight. In order to investigate the differences between male, female and immature, a covariance analysis was carried out.

The model can be written as:

$$y_{is} = (a + \alpha_s) + (b + \beta_s) x_{is} + \varepsilon_{is}$$

where y_{is} and x_{is} are the age and the otolith weight of the individual i and sex s

α_s, β_s are the additive sex effect on the intercept and the slope of the regression

and ε_{is} is the error between the measure and the prediction

F tests were used to quantify the probability of a sex effect on the relation between age and otolith weight.

Results

Ranges of size, age and otolith weight in the samples

Age estimates were attributed to all of the 105 otoliths read in whole. These ages ranged from 2 to 8 years old.

The average thickness of the thin slices was 0.24 mm. Over the total 848 otoliths read in thin slices, 30 were judged unreadable so that a total 923 age estimates were available. The global range of ages was 2 to 45 years. Constructing an age length key, 4 individuals appeared to be outliers as very old relative to their size. The otoliths of these individual had also inconsistent otolith weights relative to the size of the fish and were excluded from further analysis.

The otolith weight varied from 13 mg in 2 immature individuals measuring 2 cm PAFL to 865 mg in one large female measuring 24 cm PAFL.

VBGM

The distribution of the residuals from the model 1 where normally distributed (Figure 3a). However, there was a clear trend of increasing residuals with age (Figure 3c). In other words, the variance increases with t_i. This trend in the residual disappeared with the models 2 and 3 (Figure 3d) while the global normal distribution of the residual was kept (Figure 3b). Then, the parameters were further estimated from the model 2. It can be noted, however, that the growth curve obtained from the two models substantially diverge only for the older ages (Figure 4) and the estimates of L_∞ and k have large overlapping confidence intervals (Table 3).

In the complete model (model 3), the parameters for the difference between females and males are significant, the model indicates that females grow more slowly (Δk is negative) but reach a larger size (ΔL_∞ is positive).

The estimated parameters from the data set for 1997 were different (Table 4). For both males and females L_∞ was lower and k was higher from the 1997 data set. For males, the confidence intervals from the two samples overlapped strongly while for females the overlaps was less important but for both parameters the confidence intervals indicate that the differences between the two data set are not significant.

Considering the confidence areas of the parameters, the difference between males and females clearly appears and the results from the 1997 and 1999 sampling appear as significantly different (Figure 5). The females have a higher L_∞ and a lower k and the difference between the two data sets are small but significant for males and larger for females.

Relationship between otolith weight and fish length and age

The weight of otoliths increased with the fish length and the estimated age. Expectedly, as a relationship between a weight estimate and a length estimate, the scatter plot of otolith weight *vs* PAFL showed a curvilinear relation (Figure 6).
The global linear regression between the estimated ages and the otolith weights appeared to have a clear structure in the residuals. This structure disappeared in the model including a sex effect and the covariance analysis showed that the slopes were significantly different ($p<0.01$) for the 3 categories, the intercept for males and females was not significantly different but was different from that of juveniles (Table 1). As some outliers (such as large unsexed individual) were included in the computation, the relationships were recomputed over more restricted ranges of otolith weights with minor reduction in the number of individuals included in the regressions (Table 2). The coefficients were only slightly different and the covariance analysis results were the same. However the variance of age increased with otolith weight, the age of a fish can be predicted from its otolith weight (Figure 7).

Discussion

Dealing with unvalidated age estimates

A complete validation of age estimates of the roundnose grenadier as been obtained for juvenile fishes up to age 8 (Gordon and Swan, 1996). The reading scheme adopted here and by previous authors (Bergstad, 1990; Kelly*, et al.*, 1997) considers that the periodicity of deposition of the fine growth increments seen in the post-collar zone is annual. Indeed, the validation obtained by Gordon and Swan (1996) roughly applies to the pre-collar growth. The thin layer of material deposited all around the otolith prevented them to follow up the seasonal changes in the aspect of the otolith margin after age 8. The age *vs* otolith weight relationship suggests that the change in the growth pattern of the otolith from the pre-collar to the post-collar zone coincides with an increase in the apparent weight of material deposited each year. Then, the age estimated here should be regarded as not validated beyond about 8 years old fish. However, this reading scheme seems consistent, explanations for an annual cycle of the food available to roundnose grenadier were proposed (Gordon and Swan, 1996) and, as Bergstad (1990) developed, the hypothesis that the growth marks read are annual is the most likely.

Comparing VBGM parameters

Comparison of growth based upon the parameters L_∞ and k of the VBGM can be fallacious (Pauly, 1997). This is due to the strong colinearity between the two parameters and also to the available samples. Here, it is likely that the higher L_∞ obtained here from the 1999 sample comes from a lower proportion of larger individuals in this sample than in that from 1996-97. In these later samples these larger individuals force the model fit toward the plateau of the observed PAFL/age scatter plot. This is indeed a property of any regression fit that predicted values out the range of the observed value are very poor. Estimating L_∞ from a VBGM amounts to estimate predicted value at the right end of the scatter plot of observed value. This cannot be done accurately unless the sample contains a sufficient number of large individuals which growth has levelled of. Although accurate modelling, such as the weighted models 2 and 3, can improve the estimated parameters, lacking of large individuals cannot be balanced. The sizes predicted by the model 3 for the oldest female (45 years) and male (42 years) are respectively 24 and 20.5 cm PAFL in agreement with observed values. A size of 0.9 x L_∞ would be reached at 75 years for females, well beyond the known longevity of the species, and at 52 years for males which is more realistic suggesting than our estimates are more reliable for males.

The absence of large individuals may result from several sampling factors. The main one is probably that the sample was collected from trawling by about 1250 m in an area, the West of Scotland that has been exploited from the fishery for more than 10 years. The time series of the length distribution of the French landings suggests that the fishery impacted the demographical structure of the population by reducing the proportion of larger individuals (Anon., 2000). In addition to this, in the depth range sampled during the surveys from which otolith came from, the proportion of large individuals tend to be lower than at shallower depths (Gordon, 1979; Mauchline and Gordon, 1984). It may be also that the size reached by the roundnose grenadier does not clearly levels off before the natural death of most individuals in the study area. In this later case, the estimation of L_∞ from a VBGM would be a helpless question, however, this is very hypothetical and does not occur in the Skagerrak where Bergstad (1990) did observe a very clear and long plateau in the length at ages, but in this area the species reaches smaller sizes.

Lastly, the confidence areas allow to compare the growth parameters much more accurately than the nested model formerly used (Allain and Lorance, 2000), which does not account for the colinearity between the parameters.

Effects of uncertainties on ages

Due to these problems with estimation of the growth parameters, several authors have proposed methods to compare the growth performance of populations. Zivkov et al. (1999) listed 19 methods. Such comparison may be of interest for deep-water species as the presence of individual of different growth on different grounds would be an indication of non-mixing groups, i.e. of demographically separated populations. Such comparisons over time would also be useful to investigate the possible reaction of the populations to depleted fish density due to fishery (Anon., 2000; Lorance and Dupouy, 2001). The method proposed by Zivkov (1999) was tried here. However, in our case we only have one length at age per fish while Zivkov (1999) used back calculation to estimate the length at several age of each fish (he estimated the average yearly growth increment in length over age 1 to 10). Using the mean length at ages for roundnose grenadier lead to some negative yearly increments due to both the slow growth of the species and the dispersion of individual length at ages. The back-calculation is probably hardly applicable to this species beyond the few first years (pre-collar growth) due to the narrowness of the growth increments on the otoliths and use of two different reading axes (Figure 2).

Then due to intrinsic problem with the growth of this species, the estimates of growth cannot be considered as very reliable, the problem is probably more serious the for the index of size (L_∞) than for that of growth (k) according to Francis (1996) definition. The implications of these for population assessment purpose are relatively important. First, however a large confidence is attached to the consensus hypothesis that the growth increments seen on roundnose grenadier otolith are yearly marks, the age estimated of the fish of commercial size are still not validated. Although, age composition of the catch can be constructed from age length keys like that used here (Lorance*, et al.*, 2001) the results should still be regarded with much caution.

It is likely that the large dispersion of individual lengths at ages come from a combination of the individual variability in growth and age reading errors. These also apply to the relationships between ages and otolith weights. Then the use of the L_∞ and k parameter should be cautious. However, as the k parameter appeared here as less sensitive to sampling problems its use in the Beddington and Cooke procedure (Beddington and Cooke, 1983) may still be of help for future assessment of the stocks.

Notwithstanding the reservations given here, the roundnose grenadier is believed to be one species for which age-based assessment may soon become possible (Large et al., this symposium; Lorance et al., 2001). In this perspective, the possibility to estimate the age composition of the population from the weight distribution of the otoliths in the catch seems attractive. To our knowledge this as been so far seldom used. In the case of the deep-water species, it may be of serious help due to the cost (in term of staff time) of optical age reading. It is also possible that more reliable age compositions would be derived from this method than from optically read yearly age-length keys. It is indeed clear that for deep-water species changes in readers may be more critical than for shelf species and calibration workshop between national readers may be of little help due to the small number of countries involved in the exploitation of these species. In addition to this, it should be considered that measuring the length of this species might not be a very reliable process. Actually, the use of the PAFL allows to sample this species more accurately that the total length due to the frequently damaged tail of the species during the catch and its cutting out in commercially landed fish. However, when stored in ice, the roundnose grenadier losses water, in particular in its head and snout parts. Indeed, the measurement of PAFL in eviscerated individuals from commercial landing may be poorly reliable due to variable time spent in ice and evisceration methods. These may change from year to year and are clearly different between commercially landed fish (iced and eviscerated) and the freshly caught fish sampled during surveys. Then a direct sampling of ages may allow skipping one source of bias. Moreover, it would allow estimating the ages of a much larger sample of individuals and could indeed improve the accuracy of the age composition estimated for the population or the landings. A further work is now to test this hypothesis by building an age length key from optical reading on a sample taken from the fishery and comparing the derived age composition to that estimated from the otolith weights.

Further perspectives

The deep-water species in general offer the possibility to investigate how fish populations react to fishery exploitation because some data prior to exploitation are available. Although these data are often limited, this opportunity should not be disregarded, as it is quite unique in fishery-exploited species. In term of growth, change over time due to depleted density may occur. The VBGM is probably not a good candidate to study this point as large individuals would be more depleted by the fishery and the accuracy of the parameters would decline with increasing depletion. However, the present study show that accurate modelling (here the use of the weighted model) improves the accuracy of the estimated growth parameters and the k parameters estimated here can be used for assessment purposes (e.g. the Beddington and Cooke procedure).

Alternative methods need then to be investigated and may lie with back-calculation (Zivkov, 1999; Jones, 2000). The method from zivkov was used here on the mean length at age with poor success. Back-calculated length at ages would be more efficient but their application to the reading scheme for roundnose grenadier is not straightforward.

Attractive too is the use of the regression of age vs otolith weight, which may allow avoiding some sampling problems. This approach needs further studies but the present work provide estimated parameters that can be applied to further samples (e.g. collected from the landings) to compare the age-length keys from optical reading and age-otolith weight regression.

References

ALLAIN, V. 1999. Ecologie, biologie et exploitation des populations de poissons profonds de l'Atlantique du nord-est., Océanologie Biologique, Université de Bretagne Occidentale, Brest, 376p.

ALLAIN, V. 2001. Reproductive strategies of three deep-water benthopelagic fishes from the northeast Atlantic Ocean. *Fish. Res.*, **51** (2-3): 165-176.

ANONYMOUS, 1998. Report of the study group on the biology and assessment of deep-sea fisheries resources. ICES, Copenhagen, ICES CM 1998/ACFM:12, 172 p.

ANONYMOUS, 2000. Report of the study group on the biology and assessment of deep-sea fisheries resources. Copenhagen, ICES CM 2000/ACFM:8, 205 p.

ANTONIADIS, A., J. BERRRUYER and R. CARAMONA. 1992. Régression non linéaire. Coll. "Economie et statistiques avancées". Economica, Paris, 275 p.

ATKINSON, D. B. 1995. The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the north west Atlantic. In: Hopper A. G., Deep-water fisheries of the north Atlantic oceanic slope, 296. Kluwer Academic Publishers, Dordrecht/Boston/London, pp. 51-111.

BEDDINGTON, J. R. and J. G. COOKE. 1983. The potential yield of fish stocks. FAO, Rome,242, FAO Fisheries Technical Paper, 242, 47 p.

BERGSTAD, O. A. 1990. Distribution, population structure, growth and reproduction of the roundnose grenadier *Coryphaenoides rupestris* (Pisces: Macrouridae) in the deep waters of the Skagerrak. *Mar. Biol.*, **107**, 25-39.

BRIDGER, J. P. 1978. New deep-water trawling grounds to the West of Britain. Lab. Leaf., MAFF Direct., Lowestoft. (41), 40 p.

CHARUAU, A., H. DUPOUY, and P. LORANCE, 1995. French exploitation of the deep-water fisheries of the North Atlantic. In: Hopper A. G., Deep-water fisheries of the North Atlantic oceanic slope, 296. Kluwer Academic Publishers, Dordrecht/Boston/London, pp. 337-356.

EHRICH, S. 1983. On the occurrence of some fish species at the slopes of the Rockall Trough. *Archiv fur Fischereiwissenschaft*, **33** (3): 105-150.

FRANCIS, R. I. C. C. 1996. Do herring grow faster than orange roughy? *Fish. Bull.*, **94** (4): 783-786.

GODART, G. 1997. Contribution à l'étude des peuplements de la mégafaune en domaine benthique abyssal au large de l'irlande et de l'Ecosse. IFREMER, unpublished report, 95 pp.

GORDON, J. D. M. 1979. Lifestyle and phenology in deep sea Anacanthine Teleosts. *Symp. Zool. Soc. London*, **44**: 327-359.

GORDON, J. D. M., and S. C. SWAN, 1996. Validation of age readings from otoliths of juvenile roundnose grenadier, *Coryphaenoides rupestris*, a deep-water macrourid fish. *J. Fish Biol.*, 49 (Suppl. A): 289-297.

HAEDRICH, R. L., and N. R. MERRETT, 1988. Summary atlas of deep-living demersal fishes in the North Atlantic Basin. *Journal of Natural History*, **22**: 1325-1362.

JONES, C. 2000. Fitting growth curves to retrospective size-at-age data. Fish. Res., **46**: 123-129.

KELLY, C. J., P. L. CONNOLLY, and J. J. BRACKEN, 1996. Maturity, oocyte dynamics and fecundity of the roundnose grenadier from the Rockall Trough. *J. Fish Biol.*, **49** (Supplement A): 5-17.

KELLY, C. J., P. L. CONNOLLY, and J. J. BRACKEN, 1997. Age estimation, growth, maturity and distribution of the roundnose grenadier from the Rockall Trough. *J. Fish Biol.*, **50**: 1-17.

KIMURA, D. K. 1980. Likelihood methods for the Von Bertalanffy growth curve. *Fish. Bull.*, **77** (4): 765-776.

LORANCE, P., and H. DUPOUY. 2001. CPUE abundance indices of the main target species of the French deep-water fishery in ICES Sub-areas V-VII. *Fish. Res.*, **51** (2-3): 137-149.

LORANCE, P., H. DUPOUY, and V. ALLAIN. 2001. Assessment of the roundnose grenadier (Coryphaenoides rupestris) stock in the Rockall Trough and neighbouring areas (ICES Sub-areas V-VII). *Fish. Res.*, **51** (2-3): 151-163.

MAUCHLINE, J. and J. D. M. GORDON, 1984. Diets and bathymetric distributions of the macrourid fish of the Rockall Trough, northeastern Atlantic Ocean. *Mar. Biol.*, **81**: 107-121.

PAULY, D., 1997. Méthodes pour l'évaluation des ressources halieutiques. CEPADUES - éditions, adaptation française de J. Moreau., 288p.

ROONEY, W., and L. BIEGLER. 1999. Incorporating joint confidence regions into design under uncertainty. *Computers and Chemical Engineering* **23**: 1563-1575.

S-Plus 2000. Guide to Statistics. Vol. 1, 1999. data analysis products division, MathSoft Inc. Seatle, Washington. 638 p.

TROYANOVSKY, F. M., and S. F. LISOVSKY. 1995. Russian (USSR) fisheries research in deep waters (below 500 m.) in the North Atlantic. In: Hopper A. G., Deep-water fisheries of the North Atlantic oceanic slope, 296. Kluwer Academic Publishers, Dordrecht/Boston/London, pp. 357-365.

ZIVKOV, M. T., T. A. TRICHKOVA, and G. N. RAIKOVA PETROVA, 1999. Biological reasons for the unsuitability of growth parameters and indices for comparing fish growth. *Environmental Biology of Fishes*, **54** (1): 67-76.

Table 1. Parameters and determination coefficient of the regressions of age *vs* otolith weight together with the number of individuals (N) and the range of otolith weight and fish size used in the regressions.

	Slope	Intercept	R^2	N	Ranges Oto. weight	PAFL
Males	0.047	5.61	0.75	392	74 - 694	5 - 23
Females	0.040	7.08	0.72	205	90 - 865	6 - 25
Immat./Unsexed	0.067	1.05	0.94	83	13 - 403	1.5 – 19.5

Table 2. Parameters and determination coefficient of the regressions of age *vs* otolith weight on restricted ranges of otolith weights.

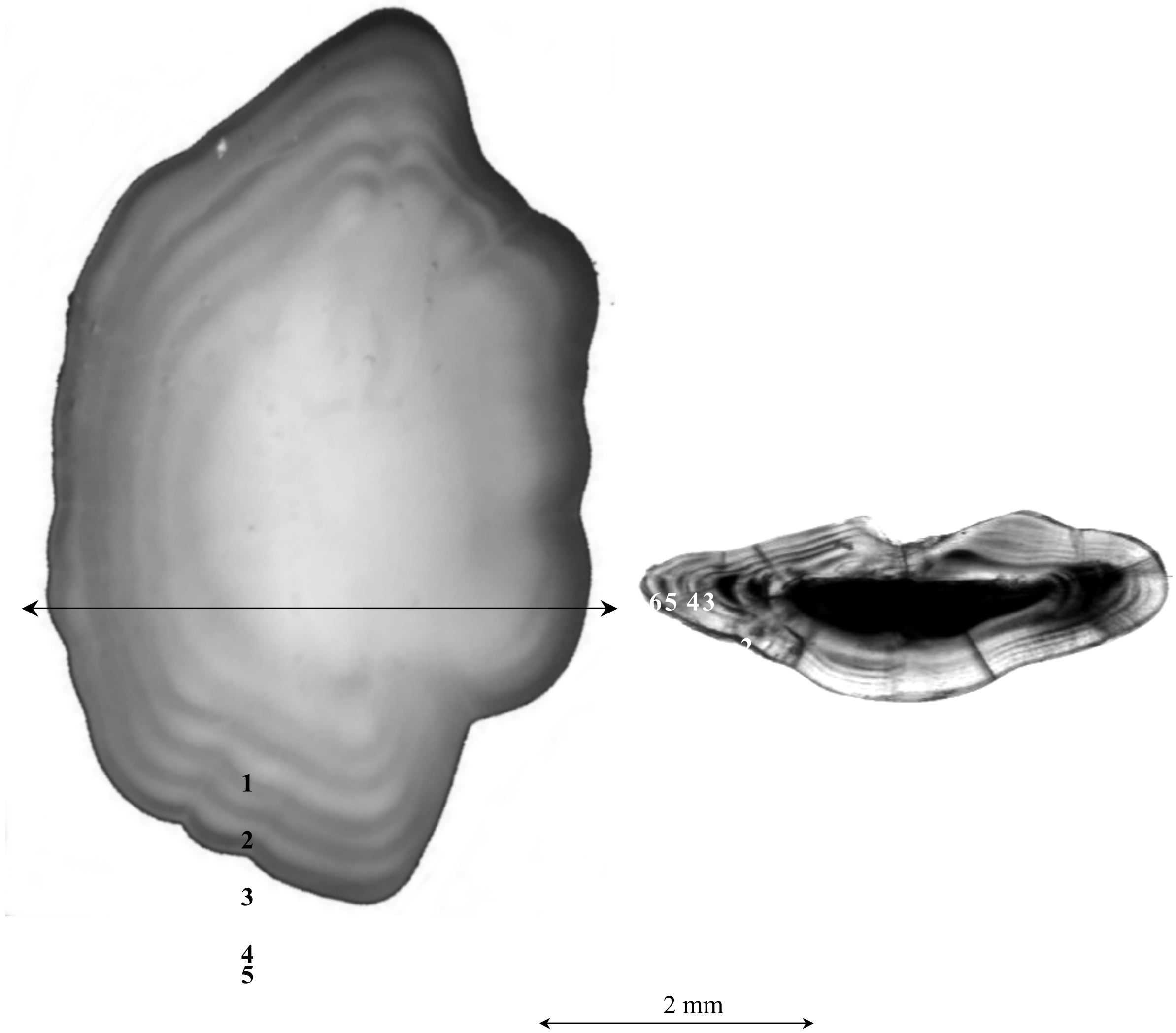
	Slope	Intercept	R^2	N	Ranges Oto. weight	PAFL
Males	0.045	6.30	0.70	380	140 - 694	7 - 23
Females	0.039	7.75	0.69	201	140 - 865	8 - 25
Immat./Unsexed	0.073	0.61	0.88	81	13 - 175	1.5 - 9.5

Table 3. Parameters of models 1, 2 and 3 with their 95% confidence intervals.

Model	L_∞	ΔL_∞	k	Δk	t_0
1	28.9 (27.0–31.3)		0.035 (0.031–0.040)		-0.03 (-0.5–0.4)
2	32.4 (29.3–36.7)		0.029 (0.024–0.034)		-0.4 (-0.7–-0.2)
3	24.9 (23.1–27.2)	6.9 (3.2–11.2)	0.042 (0.037v0.047)	-0.011 (-0.018–-0.0039)	-0.4 (-0.7–-0.2)

Table 4. Comparison of estimates growth parameters for males and females from the 1997 and 1999 samples.

	Males		Females		t_0
Sample	L_∞	k	L_∞	k	
1997	23.2 (21.8–24.7)	0.044 (0.039–0.045)	28.2 (27.0–29.7)	0.038 (0.03–0.042)	-2.2 (-3.2–-1.4)
1999	24.9 (23.1–27.2)	0.042 (0.037–0.047)	31.9 (28.8–35.9)	0.031 (0.026–0.036)	-0.4 (-0.7–-0.2)



a b

Figure 1. Correspondence of (a) annuli read on the outer face of a whole sagittal otoliths seen under reflected light and (b) those on the dorso-ventral axis of a transverse section of the same otolith under transmitted light. The cutting axis is represented on the whole otolith.

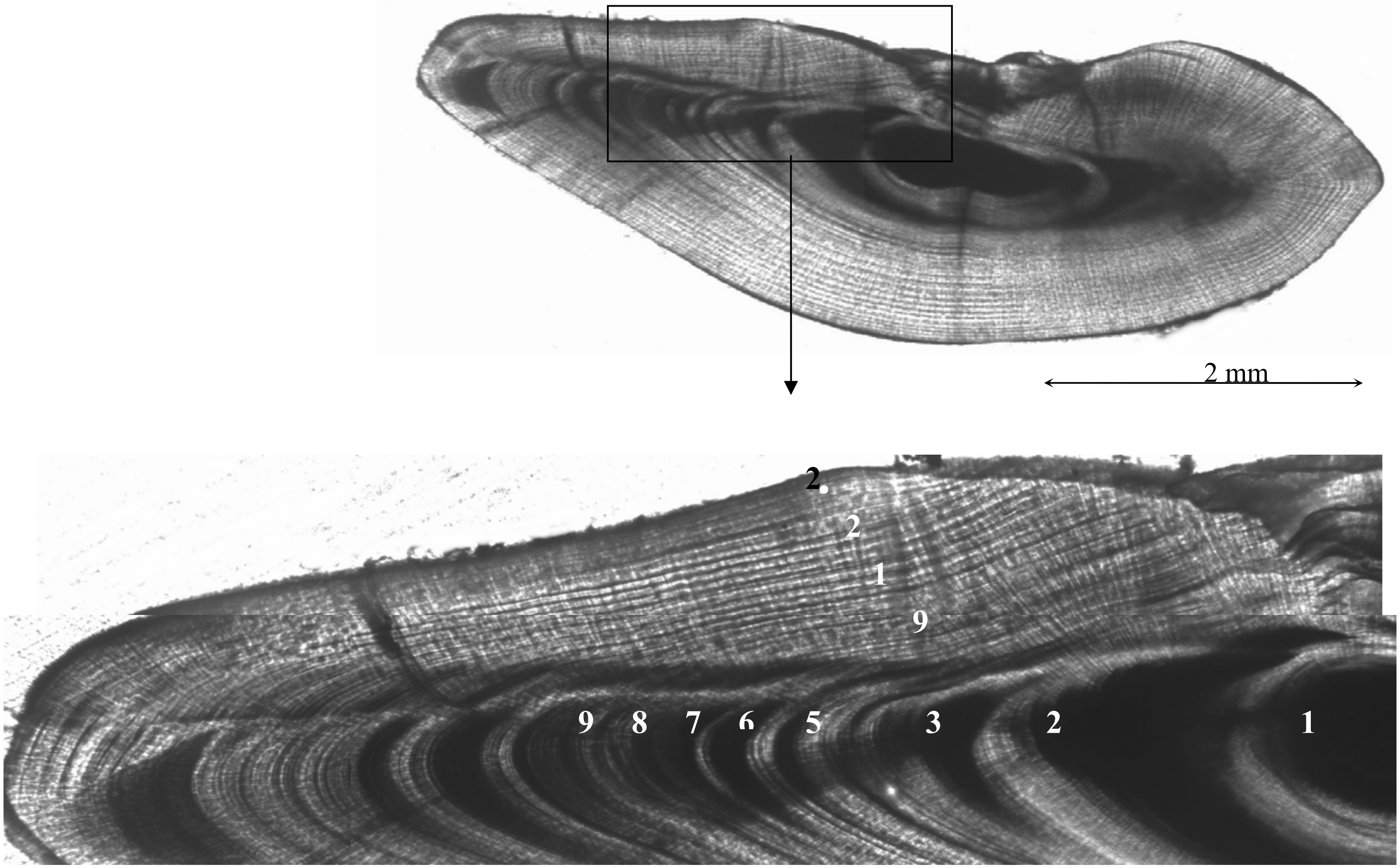


Figure2. Reading axis of a transversal section of an otolith seen under transmitted light.

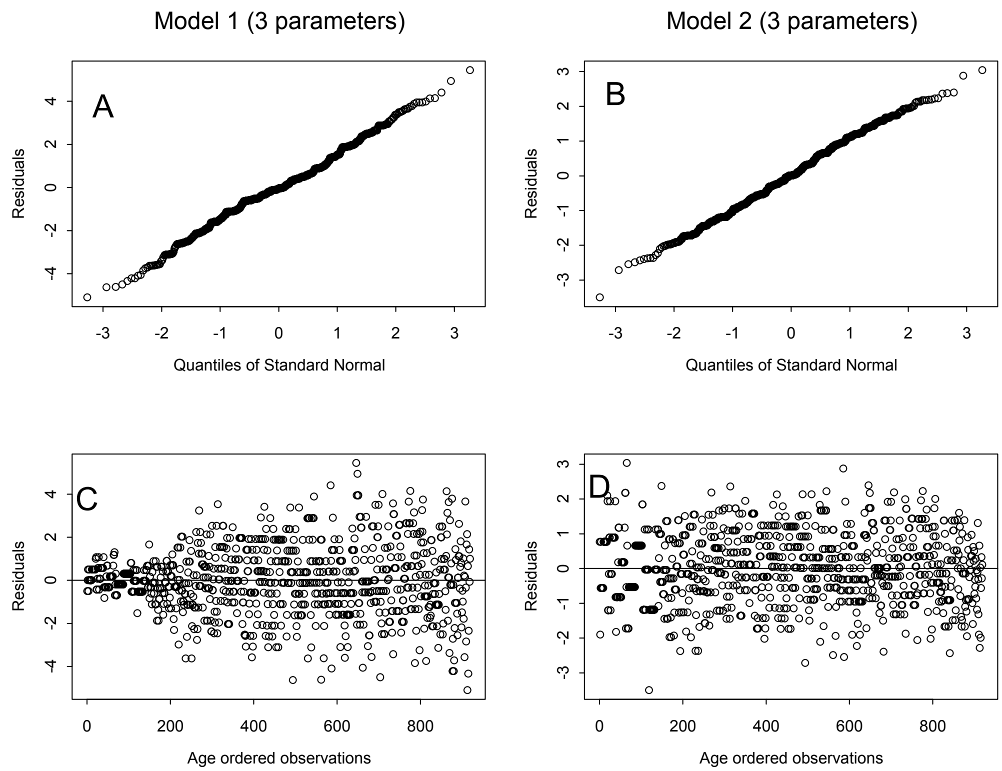


Figure 3. Residuals of the models 1 and 2 vs the quantiles of the normal distribution and distribution of the residuals according to the estimated age.

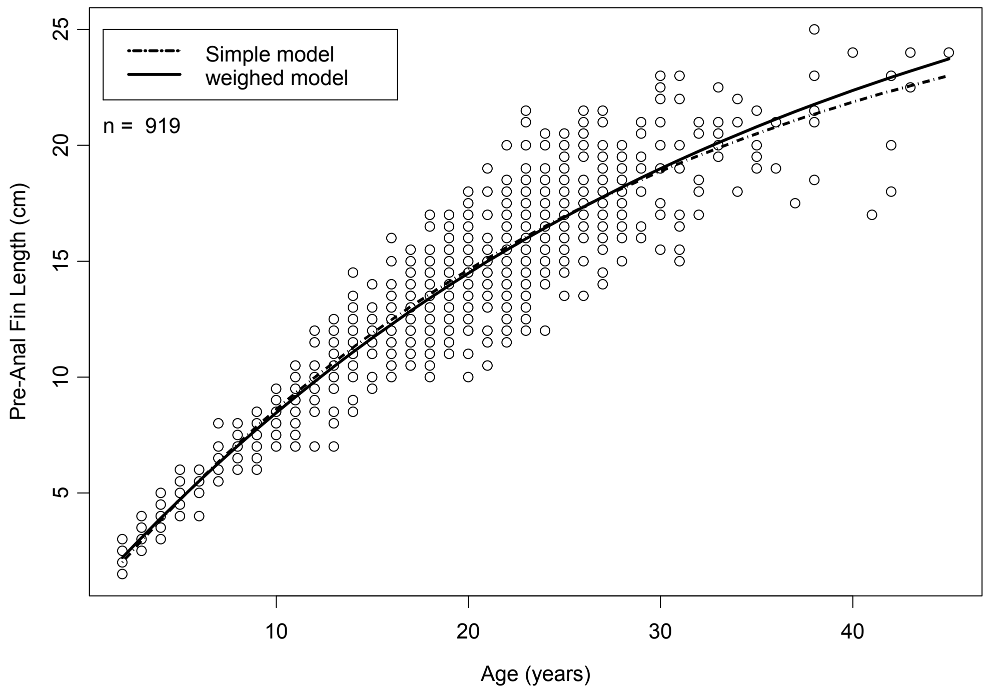


Figure 4. Fitting of the simple model (model 1) and the weighted model (model 2) to all the age estimates.

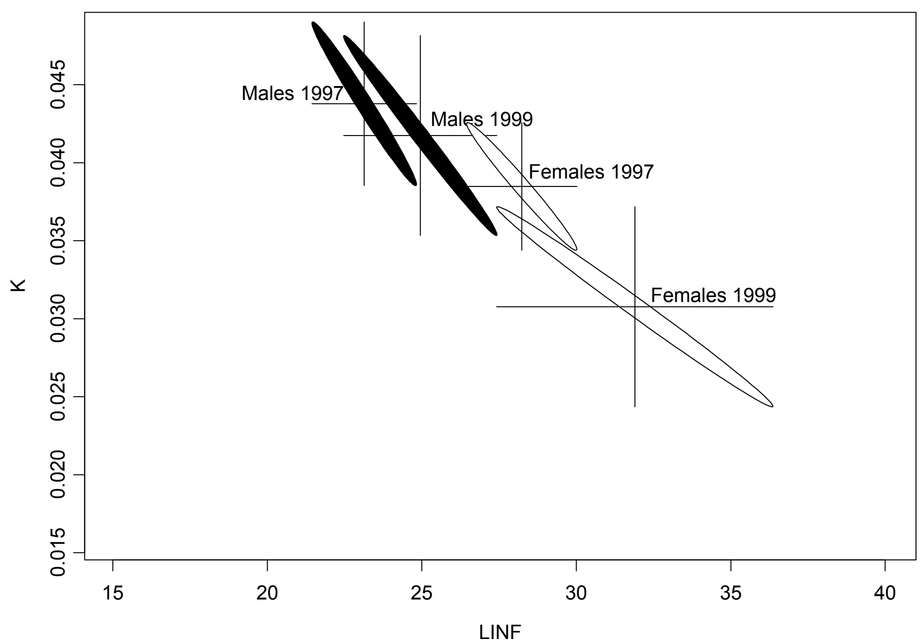


Figure 5. Confidence areas of the couples of growth parameters k and L_∞ for males and females of the two samples.

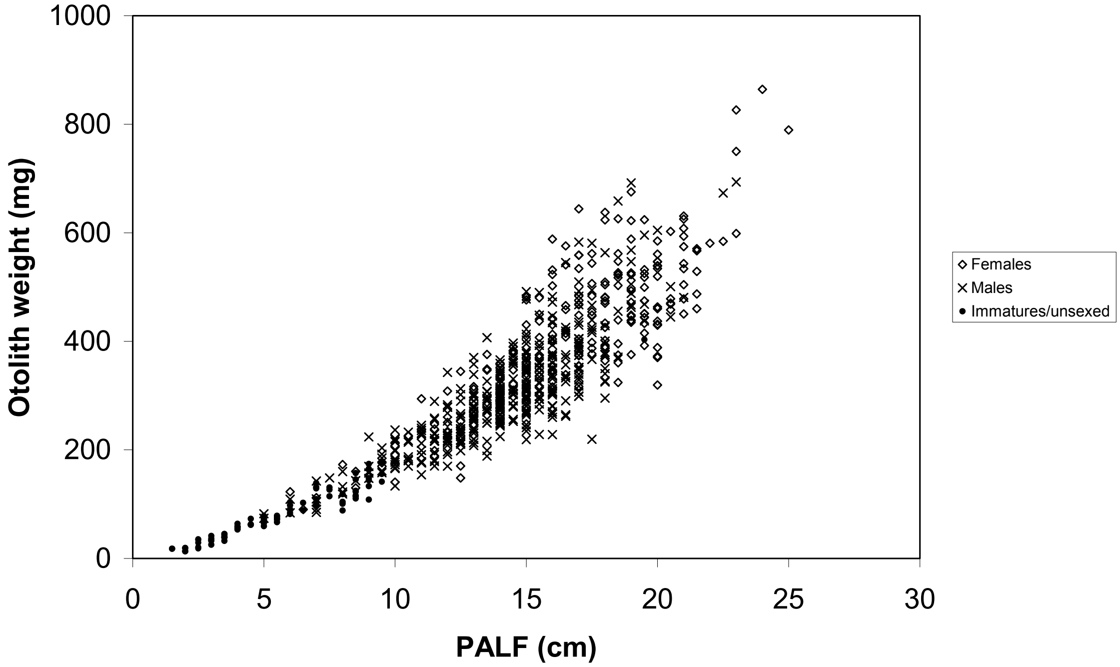


Figure 6. Distribution of otolith weights relative to fish length

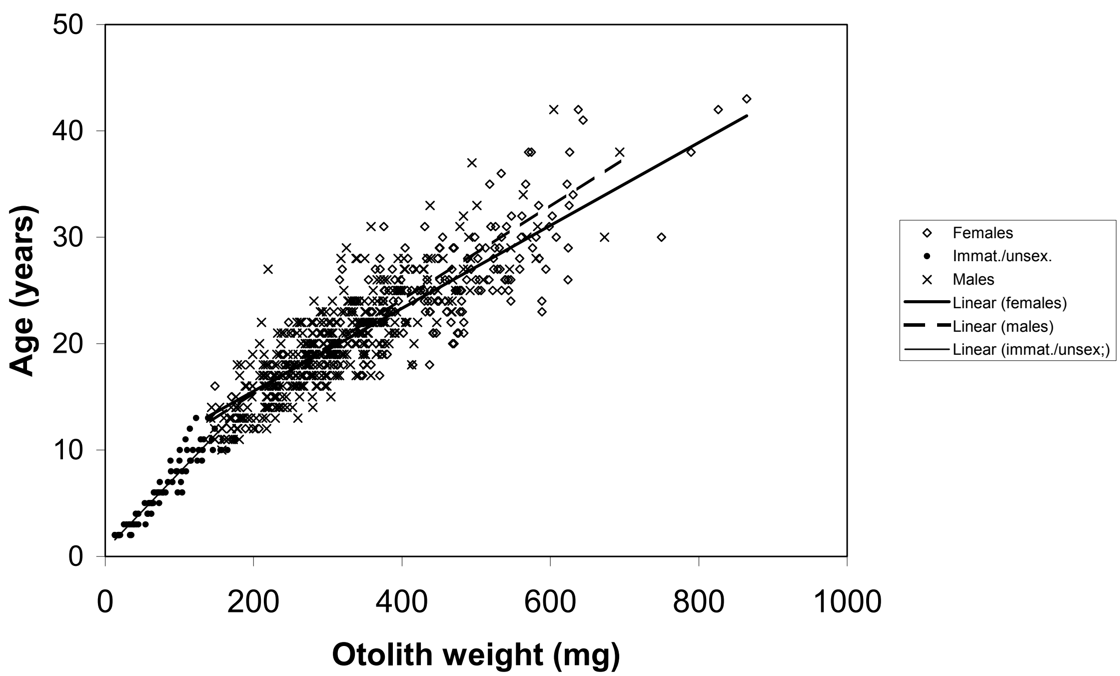


Figure 7. Distribution of estimated ages relative to otolith weight and linear regression for male, female and immature fish.