

AGE ESTIMATION AND GROWTH OF SOME DEEP-SEA FISH FROM THE NORTHEAST ATLANTIC OCEAN

by

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ABSTRACT. Age is a necessary parameter used in population dynamics to assess the state of exploited resources. This parameter is poorly known for most deep-sea species (depth > 400 m). This work focused on age estimation from otoliths of *Alepocephalus bairdii* (Alepocephalidae), *Coryphaenoides rupestris* (Macrouridae), *Helicolenus dactylopterus* (Sebastidae) and *Hoplostethus atlanticus* (Trachichthyidae), which French fishery exploitation, off the west coasts of the British Isles, began the late 1980's. Considering otolith growth zones as annual, the four species all show high longevity: 38, 54, 43 and 130 years, respectively, together with slow growth. The differences in growth between sex were estimated and difficulties in accurately estimating the age were highlighted and showed the need to standardise and validate age estimation. The ages currently estimated for deep-sea fish must be used with caution.

RÉSUMÉ. Estimation de l'âge et de la croissance de quelques poissons profonds de l'Atlantique du Nord-Est.

L'âge est un paramètre indispensable de la dynamique des populations pour l'évaluation de l'état des ressources exploitées. Il est mal connu pour la plupart des espèces profondes (profondeur > 400 m). Le présent travail porte sur l'estimation de l'âge à partir des otolithes de *Alepocephalus bairdii* (Alepocephalidae), *Coryphaenoides rupestris* (Macrouridae), *Helicolenus dactylopterus* (Sebastidae) et *Hoplostethus atlanticus* (Trachichthyidae) dont l'exploitation halieutique française, à l'Ouest des îles Britanniques, a commencé à la fin des années 80. En considérant les zones d'accroissement des otolithes comme annuelles, ces espèces présentent toutes de fortes longévités: 38, 54, 43 et 130 ans respectivement et des croissances lentes. Les écarts de croissance entre les sexes ont été estimés et les problèmes liés à l'estimation de l'âge ont été mis en évidence. Ils ont montré le besoin de standardiser et de valider l'estimation de l'âge. Il convient donc d'être prudent sur l'utilisation des âges actuellement estimés chez les poissons profonds.

Key words. *Alepocephalus bairdii* - *Coryphaenoides rupestris* - *Helicolenus dactylopterus* - *Hoplostethus atlanticus* - ANE - Slope fish - Age estimation - Otoliths.

Commercial deep-sea fisheries began in the mid 1960's in northwest Atlantic (Atkinson, 1995) and in the late 1960's in southwest Pacific around New-Zealand (Clark and King, 1989). In the northeast Atlantic, although the French deep water fishery started in 1973 with the exploitation of blue ling: *Molva dypterygia* (Pennant, 1784) (Lotidae), the deeper-water species dealt with here were not exploited until the late 1980's (Charuau *et al.*, 1995).

Although crucial for stock assessment and fisheries management, data on the age structure of deep water species are still limited, and studies dealing with the age and growth of deep-sea fish are scattered and usually incomplete (Bergstad, 1995). Despite the initial

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hypothesis of large-scale temporal and spatial homogeneity in environmental factors below 500m depth and hence a great constancy in deep ecosystem (Gage and Tyler, 1991), calcified structures of deep-sea fish display growth increments (Geistdoerfer, 1982). Validation of this annual periodicity was obtained by Gordon and Swan (1996) for juveniles of the macrourid *Coryphaenoides rupestris* and by Mace *et al.* (1990) for the trachichthyid *Hoplostethus atlanticus*. There is as yet no reason to believe that the growth increments observed in adult fish are not annual and may be related to some seasonal abiotic and biotic factors (Bergstad, 1990). This study focused on the age of three commercially exploited species in the northeast Atlantic: the roundnose grenadier, *C. rupestris*, the bluemouth, *Helicolenus dactylopterus* (Sebasteidae) and the orange roughy, *H. atlanticus*, as well as that of the dominant discarded species, the Baird's smooth-head *Alepocephalus bairdii* (Alepocephalidae). Only preliminary results were published on the age of *A. bairdii* by Kelly *et al.* (1998). Several studies have been conducted on *C. rupestris* since 1971 (Savvatimsky, 1971; Bridger, 1978; Bergstad, 1990; Kelly *et al.*, 1998; Draganik *et al.*, 1998) and *H. dactylopterus* was the subject of two recent papers (White *et al.*, 1998; Kelly *et al.*, 1999), but for those two species variable ages were obtained. Several studies of the age and otolith structure of *H. atlanticus* from South Pacific populations have been published (Gauldie, 1990; Mace *et al.*, 1990; Fenton *et al.*, 1991; Smith *et al.*, 1995; Francis and Horn, 1997; Gauldie and Cremer, 1998; Horn *et al.*, 1998). The aim of this paper is to improve knowledge about the age structure, longevity and growth of these poorly known exploited species.

MATERIALS AND METHODS

Samples of *Alepocephalus bairdii* Goode & Bean, 1879, *Coryphaenoides rupestris* (Gunnerus, 1765) and *Helicolenus dactylopterus* (Delaroche, 1809) were collected by French highsea trawlers from ports of Southern Brittany, between December 1995 and September 1997, in depth ranges of 800-1300m, 780-1300m and 100-1100m, respectively. For *Hoplostethus atlanticus* Collett, 1889 some samples were collected from landings at Boulogne-sur-mer (France) and may include fish caught at greater depths. All fish were caught between 47 and 59°N and 7 and 16°W by trawlers exploiting the deep water resources to the west of the British Isles using trawls fitted with 100mm meshsize codend. Though the sampling area was large, the fish were considered to belong to a unique population.

The sex and maturity stage of the fish were determined by macroscopic examination of the gonads. The standard length (SL) was then measured on *A. bairdii* and *H. dactylopterus*, whereas the pre-anal fin length (Lpa), from the tip of the snout to the first ray of the anal fin, was recorded for *C. rupestris* and the total length (TL) for *H. atlanticus*. The length distributions of the catch of the first three species were established from random sampling on board commercial trawlers. Otoliths were extracted and stored in dry paper bags: 1,391 otoliths of *A. bairdii* (765 females, 593 males, 33 unsexed), 1,602 otoliths of *C. rupestris* (850 females, 734 males, 18 unsexed), 1,210 otoliths of *H. dactylopterus* (716 females, 453 males, 41 unsexed) and 198 of *H. atlanticus*, this last figure is the number of otoliths that could be read successfully as several thin slices appeared unreadable. As most of *H. atlanticus* material either referred to small individuals or came from sampling of commercial landings, the sex were not taken into account.

Beamish and McFarlane (1987) highlighted the inaccuracy of age estimates derived from readings of whole older otoliths of several species, due to both the increasing thickness of otoliths and tightness of growth increments with age. In our study, depending on the aspect

of the otoliths, different reading methods were applied as described in the literature. The flat and thin otoliths of *Alepocephalus tairdii* were read under transmitted light immersed in a 50% ethanol/50% glycerine mixture. The preferential reading axis was from the nucleus towards the anterior part along the rostrum on the distal side. The thick otoliths of *C. tpestris* were embedded in polyester black resin; transverse 0.4mm sections passing through the nucleus were cut with a high-speed diamond-saw as for the related shelf gadoids (Bedford, 1983). These sections were covered with the ethanol/glycerine mixture and read under transmitted light. The preferential axis of reading was from the nucleus towards the proximal side (Kelly *et al.*, 1997). Two methods were successively applied to the same otoliths of *H. taylori*. First, whole otoliths immersed in the mixture were observed under reflected light and read from the nucleus towards the anterior part along the rostrum on the distal side. Second, the same otoliths were prepared like those of *C. tpestris*, and the transverse sections were read from the nucleus towards the dorsal side (1,179 of the 1,210 otoliths could be sliced). *Hoplostethus atlanticus* otoliths that become thick with age have a complex shape and the aspect of growth increments are different according to the cutting axis. Whole otoliths of immature fish (<30mm TL) were read under transmitted light (n=159). For mature fish, 400-700µm-thick slices were prepared and observed under transmitted light (n=39).

All otoliths were read under microscope at magnification varying from x4 to x50. Growth increments were defined as structures that comprise an opaque zone and a translucent zone. Although the annual periodicity of these increments is as yet not validated for adult deep-sea fish, counts were converted in number of years. The results are expressed in terms of age groups, which are not absolute age because neither deposition periods of opaque and translucent zones nor the birth date of the fish are known.

Radiometric age estimation, according to the $^{210}\text{Pb}/^{226}\text{Ra}$ disequilibrium, was carried out on four samples of *H. atlanticus*. As this method requires 1µg of otolith material, otoliths of several fish of the same sex and size were pooled when necessary: sample n°1 includes ten 25-cm-unsexed fish, n°2 three 58-cm-males, n°3 one 64-cm-female and n°4 one 69-cm-female. This method allows estimations to be made of the average age of the material deposited, which can be converted to the actual age of the fish under assumptions on the growth rate of the otolith in term of rate of deposition of the otolith material (Fenton *et al.*, 1991).

Table 1. Models used to test the differences between Von Bertalanffy growth curves of males and females.

Model	Number of parameters		Growth curve(s)	Constraint
1	6	♂ ♀	$L_1 = L_{\infty 1} [1 - \exp(-k_1(t - t_{01}))]$ $L_1 = L_{\infty 2} [1 - \exp(-k_2(t - t_{02}))]$	None (L_{∞} , k , t_0 different for males and females)
2	5	♂ ♀	$L_1 = L_{\infty 1} [1 - \exp(-k_1(t - t_0))]$ $L_1 = L_{\infty 2} [1 - \exp(-k_2(t - t_0))]$	Same t_0
3	4	♂ ♀	$L_1 = L_{\infty 1} [1 - \exp(-k(t - t_0))]$ $L_1 = L_{\infty 2} [1 - \exp(-k_1(t - t_{01}))]$	Same k , t_0
4	4	♂ ♀	$L_1 = L_{\infty} [1 - \exp(-k_1(t - t_0))]$ $L_1 = L_{\infty} [1 - \exp(-k_1(t - t_0))]$	Same L_{∞} , t_0
5	3	Sexes combined	$L_1 = L_{\infty} [1 - \exp(-k(t - t_0))]$	Same L_{∞} , k , t_0 (one single growth curve)

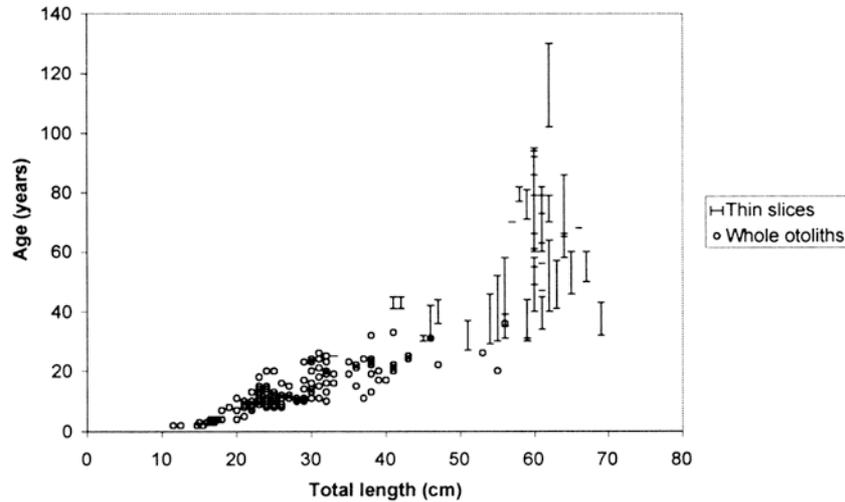


Fig. 1. Age estimated for *Hoplostethus atlanticus* from whole and sliced otoliths.

The age-length keys obtained from these age estimations allow length structures to be converted into age structures except for *H. atlanticus*, for which the low number of samples did not allow establishment of an accurate age-length key and growth curves. For other species, the growth model of Von Bertalanffy fit the data using a non-linear least square regression model. The difference between the growth curves of males and females were investigated by fitting five models for each species and testing the significance of the parameters added when shifting from one single growth curve for both sexes to complete independence of the fits for males and females (Table 1).

RESULTS

Sampled *A. bairdii*, *C. rupestris*, *H. dactylopterus* and *H. atlanticus* show high maximum age: 38, 54, 43 and 130 years, respectively (Table 1). The scatter plots of lengths at age from the two methods used for *H. dactylopterus* overlap widely. However, from whole otoliths the oldest age estimated was 17 while 60 fish (in the n=1,179 sample) were ascribed older ages from the sliced otolith method. This clearly indicates the inaccuracy of the whole

Table 1. Age range estimated for *A. bairdii*, *C. rupestris*, *H. dactylopterus* and *H. atlanticus*.

Species	Age estimation technique	Length range (cm)	Age range (year)
<i>A. bairdii</i>	Whole otoliths	11-93	3-38
<i>C. rupestris</i>	Sliced otoliths	3-29.5	1-54
<i>H. dactylopterus</i>	Whole otoliths	6.5-32.5	1-17
	Sliced otoliths	6.5-32.5	1-43
<i>H. atlanticus</i>	Whole otoliths	18-43	5-33
	Sliced otoliths	54-67	30-130

otolith method from which the inferred growth curve does not level off, resulting in a poor estimate of L_{∞} . As a consequence only the sliced otolith method was used to estimate growth parameters.

For *H. atlanticus*, the ages up to 36 years were estimated from whole otoliths. The thin slices of larger otoliths were often difficult to read and the results are expressed in term of the range of growth zones counted after several readings (Fig. 1). Radiometric age estimation provided high mean ages: 29 years for the 25-cm-fish, 71 years for the 58-cm-males and the 64-cm-female and 80 years for the 69-cm-female. The actual ages estimated from this method are by far higher than the ages obtained from optical readings (Lorance, unpubl.).

None of the models that assumed a difference in growth parameters between male and female *A. bairdii*, provided significantly better fits than a simple growth model for sexes combined (Table 1). In consequence, a unique growth curve can be used: $Lst = 35.3 \left[1 - e^{-0.077 \left(\frac{age}{1.45} \right)} \right]$ (Fig. 2A).

For *C. rupestris*, models 1, 2 and 3 indicate a difference in L_{∞} . When L_{∞} is set as identical for both sexes (model 4), the different lengths at ages imply that different k parameters are estimated (Table 1). As models 1 and 2 consistently ascribe the difference to L_{∞} and the residual standard error is lower in model 3 than in model 4, model 3 is retained for this species and the growth curves are estimated as: $Lp_{males} = 20.7 \left[1 - e^{-0.059 \left(\frac{age+0.29}{0.29} \right)} \right]$ and $Lp_{females} = 33.9 \left[1 - e^{-0.059 \left(\frac{age+0.29}{0.29} \right)} \right]$ (Fig. 2B). Females reach larger sizes than males.

For *H. dactylopterus* only models 3 and 4 are better than model 5. This means that there are differences in the fits but they are small enough so that when several parameters are fitted, the differences distributed over them are not significant. Model 3 returns a lower L_{∞} for females (28.31 vs 29.35) and model 4 a lower k (0.095 vs 0.102). As the residual standard errors of model 3 and 4 are very similar, it is difficult to decide which is best. Lastly, the estimated difference in these parameters being low and the residual error of model 5 not being substantially higher, model 5 is kept in this rather preliminary study. The growth equation is then expressed as $Lst = 29.0 \left[1 - e^{-0.098 \left(\frac{age \times \text{iced} \times \text{otolith} + 2.79}{\text{iced} \times \text{otolith} + 2.79} \right)} \right]$ (Fig. 2C).

The age structure of *C. rupestris* was computed for each sex from the age-length keys and length distribution by sex from on-board sampling and then summed up. For the two other species the age structures were derived from the global age-length keys and length distributions (Fig. 3). The main distribution mode are around 15-19 years for *A. bairdii*, 18-22 years for *C. rupestris* while the age distribution of *H. dactylopterus* is strongly asymmetrical with a mode at 5-6 years.

Table 1. Comparison of growth parameters by sex for *A. bairdii*, *C. rupestris* and *H. dactylopterus*, critical probabilities of the differences in the growth parameters (-: not significant).

Model	Tested difference	Probability under null hypothesis		
		<i>A. bairdii</i>	<i>C. rupestris</i>	<i>H. dactylopterus</i>
1	L_{∞}	-	p = 0.042	-
	k	-	-	-
	t_0	-	-	-
2	L_{∞}	-	p = 0.00001	-
	k	-	-	-
3	L_{∞}	-	p < 0.00001	p < 0.00001
4	k	-	p < 0.00001	p = 0.00001

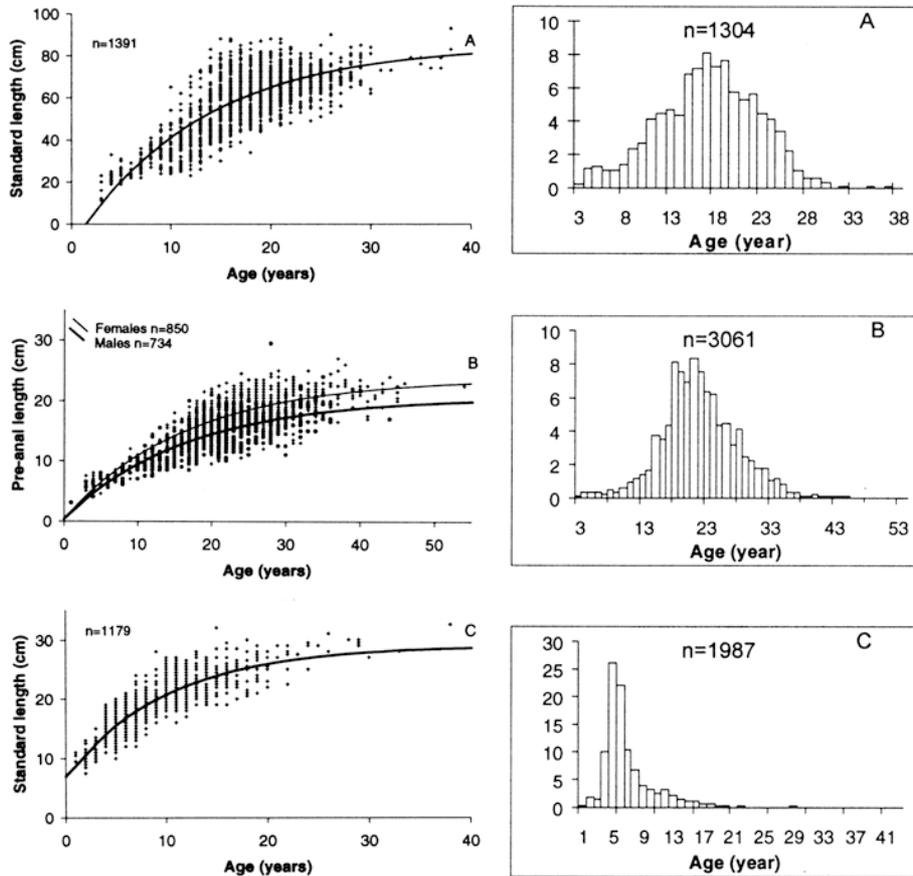


Fig. 2. Growth curves on Bertalanffy growth curves. A: *Alepocephalus bairdii*; B: *Toryphaenoides rupestris*; C: *Ellicolenus dactylopterus*.

Fig. 3. Age structure of total catch. A: *Alepocephalus bairdii*; B: *Toryphaenoides rupestris*; C: *Ellicolenus dactylopterus*.

DISCUSSION

Little age validation work relevant to the species dealt with here are available and are restricted to juvenile fish (Mace *et al.*, 1990; Gordon and Swan, 1996), i.e., not in the size range of the fish, which age were estimated in this study. Despite the acceptable agreement between these validated ages and that estimated here (Lorance *et al.*, 1998) or the method validation that they bring (Mace *et al.*, 1990; Fenton *et al.*, 1991) age estimation from this study should be regarded with caution.

Very few data in relation with age and growth of *A. bairdii* are available in the literature. Bridger (1978) and Gordon (1979) mentioned the lack of visible growth increments structures on their otoliths. Kelly *et al.* (1998) estimated ages from sliced otoliths between 8 and 28 years, which is in the same range as our results.

The age and growth literature for *C. t. pestris* can be split into two sets according to the maximum age reported (Allain, 1999): (i) the references in which maximal age is >27 years (Bridger, 1978; Gordon, 1978; Bergstad, 1990; Kelly *et al.*, 1997; Draganik *et al.*, 1998; this study), and (ii) the references in which maximal age is ≤ 20 years (Savvatimsky, 1971; Eliassen, 1986; Kosswig, 1987; Magnusson and Magnusson, 1995). In these two sets, ages were estimated by different methods: sliced, broken or polished otolith for the former and scales for the later. The lower age estimates of Draganik *et al.* (1998) are probably due to their use of sagittal section. As otoliths of old individuals grow mainly in thickness, sagittal sections tend to return lower age estimates than the transverse sections used in the other studies. Although the samples were caught in the same area and year and the methods were similar, the growth curves of Kelly *et al.* (1997) differ from ours. This difference may come from different interpretation of increments. Conversely, the growth curves of Bridger (1978) and Gordon (1978) before the start of the fishery look similar to ours.

The better accuracy of the sliced otolith method found here for *H. t. actylopterus* is not surprising in light of results on others species including some Sebastidae (Beamish and McFarlane, 1987; Maceina and Betsill 1987). Although they are inaccurate in terms of absolute ages, studies from whole otoliths suggest that fish from the Azores (Isidro, 1987; Esteves *et al.*, 1997; Krug *et al.*, 1998) grow faster than that from the Mediterranean and northeast Atlantic (Ragonese, 1989; D'Onghia *et al.*, 1994; this study). No difference was noticed between the data from Northwest Atlantic (White *et al.*, 1998) and those from Northeast Atlantic (this study). Kelly *et al.* (1999) reported on growth slower than ours though fish came from the Northeast Atlantic; such discrepancy probably results from differences in age estimation and increment identification.

Hoplostethus atlanticus appears as one of the oldest fish exploited. Growth increments on otoliths have been shown to form annually for juveniles (Mace *et al.*, 1990). Their regularity up to about 30 years suggests that reading should be accurate up to this age. However, adults display much thinner layers at the outer part of the otoliths and the ages estimated are then very sensitive to the reading scheme, resulting in the ranges of ages estimated from most of the large otoliths (Fig. 1). The ages estimated for small fish (whole otoliths) and large fish (sections) are relatively consistent. However, the scatter plot suggests that the former method tends to underestimate ages above 30 years. Nevertheless, this fish is long-lived and the first 30 strong rings probably correspond to the immature phase (Francis and Horn, 1997); a total longevity on the order of one century is the most likely hypothesis. Applied to Tasman fish, radiometric ageing provided ages consistent with optical readings (Fenton *et al.*, 1991) while in this study the ages were much higher than the optical readings. Both the radiometric measurement itself, which as a measure of very low radio-activity may be sensitive to methodological problem, and the need to assume a growth model of the otolith to infer the age of the fish from the "mean" radiometric age measure may account for this. Moreover, the use of this method is still subject of debates (Gauldie and Cremer, 1998). The high longevity and slow growth of the species should be considered as not validated. However, the environmental conditions in the depth range (800–1,800 m) of this top predator fish (Koslow, 1997) are unlikely to support fast growth; its discrete and short spawning period (Pankhurst *et al.*, 1987; Du Buit and Lorange, unpubl.) proves that *H. t. atlanticus* is sensitive to one annual signal and it is likely that the major increments seen on otoliths are annual. In other respects, the rapid stock depletion due to fisheries (Clark, 1995; Clark, 1998; Lorange and Dupouy, 1998; Clark *et al.*, 2000; Koslow *et al.*, 2000) are consistent with what is still an hypothesis.

Comparisons of our results with other studies highlighted several problems related to deep-sea fish age estimation and the imperious need for standardisation and its validation.

First, the use of different calcified structures does not allow the comparison of age reading. As a rule, otolith-estimated age is considered more reliable than scale-estimated age because of the existence of regenerated scales (Bergstad, 1995), and this problem is likely to increase with species longevity. As shown for *H. actylopterus*, otolith preparation and reading techniques are also important. However, despite the use of the same techniques, difficulties are encountered in identification and interpretation of growth increments leading to discordance between readers (Bergstad *et al.*, 1998; Allain, 1999). In general, the legibility and the reproducibility of the readings decrease for large fish. Moreover interpretation of growth increments can vary. For instance, for *H. actylopterus*, Morales-Nin (1998) considered that the first annulus observable after the nucleus is not an annual ring, but is instead related to benthic settlement.

Independent from difficulties in reading of increments observed on deep-sea fish calcified structure, a major problem is the validation of age estimation. Indeed, all the authors agree to consider growth increments as annual rings, but very few validations have been conducted, because they are especially difficult on deep-sea fish. Tests have been made on the analysis of the edge of otoliths, tagging, daily growth increment and radiometry (Gordon and Swan, 1996; Merrett and Haedrich, 1997; Morales-Nin, 1998). They sometimes allowed one to validate age, but usually it was proved to be imperfect and only valid on a short age range. One should be cautious in the use of the ages currently estimated for deep-sea fish, and while continuing to collect data on age estimation is important, validation should be the main objective of the next studies on deep-sea fish age estimation.

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REFERENCES

- ALLAIN V., 1999. **Écologie, biologie et exploitation des populations de poissons profonds de l'Atlantique du Nord-Est.** Thèse Doctorat. 376p. Univ. de Bretagne Occidentale, Brest.
- ATKINSON D.B., 1995. **The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the north west Atlantic.** In: Deep-Water Fisheries of the North Atlantic oceanic Slope (Hopper A.G., ed.), pp. 91-111. Netherlands: Kluwer Academic Publishers.
- BEAMISH R.J. & G.A. MCFARLANE, 1987. **Current trends in age determination methodology.** In: Age and Growth of Fish (Summerfelt R.C. & G.E. Hall, eds), pp. 35-42. Ames: Iowa State Univ. Press.
- BEDFORD B.C., 1983. **A method for preparing sections of large numbers of otoliths embedded in black polyester resin.** *J. Cons. Expl. Mer.*, 41: 4-12.
- 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.
- BERGSTAD O.A., 1995. **Age determination of deep-water fishes: experiences, status and challenges for the future.** In: Deep-Water Fisheries of the North Atlantic oceanic Slope (Hopper A.G., ed.), pp. 267-283. Netherlands: Kluwer Academic Publishers.

- BERGSTAD O.A., MAGNUSSON J.V., MAGNUSSON J., HAREIDE N.-R. & J. REINERT, 1998. \square -Intercalibration of age readings of ling (*Molva molva* L.) blue ling (*Molva dipterygia* Pennant, 1784) and tusk (*Brosme brosme* L.). *ICES J. Mar. Sci.*, 55: 309-318.
- BRIDGER J.P., 1978. \square New deep-water trawling grounds to the West of Britain. *Lab. Leaf.*, 41: 1-41.
- CHARUAU A., DUPOUY H. & P. LORANCE, 1995. \square French exploitation of the deep-water fisheries of the north Atlantic. In: Deep-Water Fisheries of the North Atlantic oceanic Slope (Hopper A.G., ed.), pp. \square 37-356. Netherlands: Kluwer Academic Publishers.
- CLARK M.R. & K.J. KING, 1989. \square Deepwater fish resources off the North Island, New Zealand: Results of a trawl survey, May 1985 to June 1986. *N.-Z. Fish. Tech. Rep.*, 11: 1-56.
- CLARK M.R., 1995. \square Experience with the management of orange roughy (*Hoplostethus atlanticus*) in New Zealand, and the effects of commercial fishing on stocks over the period 1980-1993. In: Deep-Water Fisheries of the North Atlantic oceanic Slope (Hopper A.G., ed.), pp. 251-266. Netherlands: Kluwer Academic Publishers.
- CLARK M.R., 1998. \square Are deepwater fisheries sustainable? - The example of orange roughy in New Zealand. *ICES CM 1998/*, O: 14.
- CLARK M.R., ANDERSON O.F., FRANCIS R.I.C.C. & D.M. TRACEY, 2000. \square The effects of commercial exploitation on orange roughy (*Hoplostethus atlanticus*) from the continental slope of the Chatham Rise, New Zealand, from 1979 to 1997. *Fish. Res.*, 45: 217-238.
- D'ONGHIA G., MASTROTOTARO F. & M. PANZA, 1994. \square On the growth and mortality of rockfish, *Helicolenus dactylopterus* (Delaroche, 1809), from the Ionian Sea. *FAO Fish. Rep.*, 533, suppl.: 143-152.
- DRAGANIK B., PSUTY-LIPSKA I. & J. JANUSZ, 1998. \square Ageing of roundnose grenadier (*Coryphaenoides rupestris* Gunn.) from otoliths. *ICES CM 1998/*, O: \square 9, 21 \square .
- ELIASSEN J.E., 1986. \square Investigations on the distribution, occurrence and population structure of the roundnose grenadier (*Coryphaenoides rupestris* Gunnerus) in the coastal waters off Trondelag, Norway. *Fisk. og Hav.*, 1: 1-19.
- ESTEVEZ E., ANIBAL J., KRUG H. & H. MARQUES DA SILVA, 1997. \square Aspects of age and growth of bluemouth, *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809) from the Azores. *Arq. Life Mar. Sci.*, 15A: 83-95.
- FENTON G.E., SHORT S.A. & D.A. RITZ, 1991. \square Age determination of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) using ^{210}Pb : ^{226}Ra disequilibria. *Mar. Biol.*, 109: 197-202.
- FRANCIS R.I.C.C. & P.L. HORN, 1997. \square Transition zone in otoliths of orange roughy (*Hoplostethus atlanticus*) and its relationship to the onset of maturity. *Mar. Biol.*, 129: 681-687.
- GAGE J.D. & P.A. TYLER, 1991. \square Deep-Sea Biology. A natural History of Organisms at the Deep-Sea Floor. Great Britain: Cambridge Univ. Press.
- GAULDIE R.W., 1990. \square Phase differences between check ring locations in the orange roughy otolith (*Hoplostethus atlanticus*). *Can. J. Fish. Aquat. Sci.*, 47(4): 760-765.
- GAULDIE R.W. & M.D. CREMER, 1998. \square Loss of ^{222}Rn from otoliths of orange roughy, *Hoplostethus atlanticus*, invalidates old ages. *Fish. Sci.*, 64(4): 543-546.
- GEISTDOERFER P., 1982. \square Rythmes biologiques et croissance des poissons dans les grandes profondeurs marines. *Oceanis*, 8: 599-609.
- GORDON J.D.M., 1978. \square Some notes on the biology of the roundnose grenadier *Coryphaenoides rupestris* to the west of Scotland. *ICES C.M. 1978/*, G: \square 0, 13 \square .
- GORDON J.D.M., 1979. \square Lifestyle and phenology in deep sea Anacanthine Teleosts. *Symp. Zool. Soc. Lond.*, 44: 327-359.
- GORDON J.D.M. & S.C. SWAN, 1996. \square Validation of age readings from otoliths of juvenile roundnose grenadier, *Coryphaenoides rupestris*, a deep-water macrourid fish. *J. Fish Biol.*, 49: 289-297.
- HORN P.L., TRACEY D.M. & M.R. CLARK, 1998. \square Between-area differences in age and length at first maturity on the orange roughy *Hoplostethus atlanticus*. *Mar. Biol.*, 132: 187-194.
- ISIDRO E.J., 1987. \square Age and growth of the bluemouth, *Helicolenus dactylopterus dactylopterus* (De la Roche, 1809) off the Azores. *ICES CM 1987/*, G: \square 3: 15 \square .
- KELLY C.J., CONNOLLY P.L. & J.J. BRACKEN, 1997. \square Age estimation, growth, maturity and distribution of the roundnose grenadier from the Rockall Trough. *J. Fish Biol.*, 50: 1-17.

- KELLY C.J., CONNOLLY P.L. & J.J. BRACKEN, 1999. **LA**ge estimation, growth, maturity, and distribution of the bluemouth rockfish *Helicolenus d. dactylopterus* (Delaroche, 1809) from the Rockall Trough. *ICES J. Mar. Sci.*, 56: 61-74.
- KELLY C.J., CONNOLLY P.L. & M.W. CLARKE, 1998. **LI**the deep water fisheries of the Rockall trough; some insights gleaned from Irish survey data. *ICES CM 1998/*, O: **20**, 22**LI**.
- KOSLOW J.A., 1997. **LS**eamounts and the ecology of deep-sea fisheries. *Am. Sci.*, 85: **168**-176.
- KOSLOW J.A., BOEHLERT G., GORDON J.D.M., HAEDRICH R.L., LORANCE P. & N. PARIN, 2000. **LI**ontinental slope and deep-sea fisheries: Implications for a fragile ecosystem. *ICES J. Mar. Sci.*, 57(3): **548**-557.
- KOSSWIG K., 1987. **LI**vestigations on grenadierfish (*Macrourus berglax* and *Coryphaenoides rupestris*) by the Federal Republic of Germany in 1986 and 1987. *Mitt. Inst. Seefisch.*, 44: 67-70.
- KRUG H., ROSA D., MENEZES G. & M. PINHO, 1998. **LA**ge and growth of some demersal species of the Azores. *ICES CM 1998/*, O: 84, 11**LI**.
- LORANCE P. & H. DUPOUY, 1998. **LI**.P.U.E. abundance indices of the main target species of the French deep-water fishery in ICES sub-areas V, VI and VII. *ICES CM 1998/*, O: 19, 17**LI**.
- LORANCE P., DUPOUY H., & V. ALLAIN, 1998. **LA**ssessment of the roundnose grenadier (*Coryphaenoides rupestris*) stock in the Rockall Trough and neighbouring areas (ICES sub-areas V, VI and VII). *ICES CM 1998/*, O: 60, 16**LI**.
- MACE P.M., FENAUGHTY J.M., COBURN R.P. & I.J. DOONAN, 1990. **LI**rowth and productivity of orange roughy (*Hoplostethus atlanticus*) on the north Chatham Rise. *N.-Z. J. Mar. Freshw. Res.*, 24: 105-119.
- MACEINA M.J. & R.K. BETSILL, 1987. **LI**verification and use of whole otoliths to age white crappie. *In: Age and Growth of Fish* (Summerfelt R.C. & G.E. Hall, eds), pp. **267**-278. Ames: Iowa State Univ. Press.
- MAGNUSSON J.V. & J. MAGNUSSON, 1995. **LI**the distribution, relative abundance, and biology of the deep-sea fish of the Icelandic slope and Reykjanes ridge. *In: Deep-Water Fisheries of the North Atlantic oceanic Slope* (Hopper A.G., ed.), pp. **161**-199. Netherlands: Kluwer Academic Publishers.
- MERRETT N.R. & R.L. HAEDRICH, 1997. **LI**Deep-Sea demersal Fish and Fisheries. London: Chapman & Hall.
- MORALES-NIN B., 1998. **LI**Mediterranean deep-water fish age determination and age validation: The state of the art. *ICES CM 1998/*, O: 8, 9**LI**.
- PANKHURST N.W., McMILLAN P.J. & D.M. TRACEY, 1987. **LS**easonal reproductive cycles in three commercially exploited fishes from the slope waters off New Zealand. *J. Fish. Biol.*, 30: 193-211.
- RAGONESE S., 1989. **LI**on the application of the generalized Von Bertalanffy growth formula: The case of northern Tyrrhenian rockfish (*Helicolenus dactylopterus*) (Delar.) (Pisces: Scorpaenidae). *Oebalia*, XV: 753-762.
- SAVVATIMSKY P.I., 1971. **LI**etermination of the age of grenadiers (Order Macrouriformes). *J. Ichthyol.*, 11: 397-403.
- SMITH D.C., FENTON G.E., ROBERTSON S.G. & S.A. SHORT, 1995. **LA**ge determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric ageing. *Can. J. Fish. Aquat. Sci.*, 52: 391-401.
- WHITE D.B., WYANSKI D.M. & G.R. SEDBERRY, 1998. **LA**ge, growth, and reproductive biology of the blackbelly rosefish from the Carolinas, USA. *J. Fish Biol.*, 53: 1274-1291.

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