

Growth of white anglerfish (*Lophius piscatorius*) tagged in the Northeast Atlantic, and a review of age studies on anglerfish

Jorge Landa, Rafael Duarte, and Iñaki Quincoces

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Growth of white anglerfish was estimated from the results of a tagging study in south European waters. In all, 1326 fish, caught by bottom trawl and gillnet commercial vessels and on trawl surveys, were tagged from 1995 to 2004; 50 were recovered, and a growth rate of 13.6 cm year⁻¹ was estimated from the four fish at liberty long enough to allow extrapolation of the growth rate to an annual period. Growth patterns were reviewed based on available studies of growth verification of white anglerfish in Atlantic waters, including another tag-recapture study, length-frequency of catches, and microstructure analysis of hard parts. The growth rate estimated from these studies showed many similarities, and an overall growth pattern was estimated: growth rate = 18.24e^{-0.015length}. A von Bertalanffy growth curve fitted to all data yielded the parameter values $L_{\infty} = 140$ cm and $k = 0.11$. This growth rate is faster than estimated recently using illicia for age estimation, but similar to that found in the first studies that used illicia and sectioned otoliths. Current estimates of growth based on illicia, which are used in assessing the northern European stock of white anglerfish, seem to be underestimated.

Keywords: age estimation, anglerfish, growth, illicia, *Lophius piscatorius*, otoliths, tagging.

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J. Landa: Instituto Español de Oceanografía, Apartado 240, 39080 Santander, Spain. R. Duarte: Instituto de Investigação das Pescas e do Mar, Avenida de Brasília, 1400 Lisboa, Portugal. I. Quincoces: AZTI Tecnalia, Txatxarramendi ugarte a z/g, 48395 Sukarrieta, Spain. Correspondence to J. Landa: tel: 34 942291060; fax: +34 942275072; e-mail: jorge.landa@st.ieo.es

Introduction

White anglerfish (*Lophius piscatorius*) are found from the Barents Sea to the Straits of Gibraltar, and in the Mediterranean and Black Seas (Caruso, 1986). They are commercially important to European fisheries, and caught by trawl and artisanal fleets using fixed nets. Many studies of the biology of the species have been conducted during the past 20 years (Afonso-Dias and Hislop, 1996; Duarte *et al.*, 2001; Hislop *et al.*, 2001; Quincoces, 2002; Laurenson *et al.*, 2005; Charrier *et al.*, 2006). Studies on growth have focused on age estimation using different calcified structures, such as illicia (Dupouy *et al.*, 1986; Peronnet *et al.*, 1992; Duarte *et al.*, 1997; Landa *et al.*, 2001), otoliths (Tsimenidis and Ondrias, 1980; Crozier, 1989; Wright *et al.*, 2002; Woodroffe *et al.*, 2003), and analyses of the length frequency distributions of commercial and research catches (Fulton, 1903; Dupouy *et al.*, 1986; Jónsson, 2007).

Annuli formation has been verified as annual for illicia (Dupouy *et al.*, 1986; Woodroffe *et al.*, 2003) and sectioned otoliths (Crozier, 1989; Woodroffe *et al.*, 2003). In both, an annual cycle of growth consists of one wide opaque zone (WOZ) and one wide translucent zone (WTZ), the latter formed in winter. The pattern of laying down of these zones throughout the year seems to be similar in both structures (Woodroffe *et al.*, 2003). However, reliable age estimation based on *Lophius* otoliths has been scarce (Tsimenidis and Ondrias, 1980; Griffiths and Hecht, 1986; Crozier, 1989; Armstrong *et al.*, 1992; Maartens *et al.*, 1999; Duarte *et al.*, 2005), mainly because of the presence of confusing secondary structures or

multichecks (Woodroffe *et al.*, 2003), and an increase in the opacity of otoliths with age, which makes it difficult to discern the translucent zone. Crozier (1989) and Woodroffe *et al.* (2003) found valid and consistent age readings from sectioned otoliths only up to ages 6 and 7. Such difficulties in interpreting otoliths are common to most *Lophius* species, so many recent studies have been based on other hard parts: illicia in *L. budegassa* (Duarte *et al.*, 1997; Landa *et al.*, 2001; García-Rodríguez *et al.*, 2005), *L. vomerinus* (Maartens *et al.*, 1999; Walmsley *et al.*, 2005), and *L. americanus* (Cullen *et al.*, 2007); and vertebrae in *L. litulon* (Yoneda *et al.*, 1997; Cha *et al.*, 1998) and *L. americanus* (Armstrong *et al.*, 1992; Cullen *et al.*, 2007). The illicia of white anglerfish exhibit fewer secondary structures (Dupouy *et al.*, 1986; Quincoces, 2002) and a wider WOZ relative to WTZ than otoliths (Woodroffe *et al.*, 2003), suggesting that the growth pattern may be easier to distinguish in the former. Since 1991, age estimation workshops, involving age readers from several European countries, have taken place with the aim of comparing illicia and otoliths, and attempting to standardize reading criteria (Anon., 1997, 1999; Landa *et al.*, 2002). Woodroffe *et al.* (2003) showed that the correlation between illicia and otolith readings from the same fish was >90%, and that length-at-age relationships based on the two structures were not significantly different. They also found better agreement and precision in otoliths than in illicia. However, precision and agreement in age estimation among readers are related to the experience and familiarity of the reader with each structure. At the last anglerfish age workshop

(Duarte *et al.*, 2005), although no sectioned otoliths were analysed, reader agreement, accuracy and precision reached a good level for illicia but remained low for whole otoliths, for both experienced and inexperienced readers. Because of the aforementioned benefits, the illicium has become the standard structure for anglerfish age estimation in several European countries (France, Ireland, Portugal, Spain), and the one used as a basis for stock assessment. For this last purpose, ICES defines three geographically differentiated stocks (Figure 1). The northern shelf stock (Divisions IIIa, IV, VI) is not assessed because of the lack of reliable fishery data. The northern stock on the southern shelf (Divisions VIIb, c, e–k, and VIIIa, b, d) is assessed using an age-structured model, with age information derived from illicia. The southern stock on the southern shelf (Divisions VIIIc and IXa) is assessed using stock production models.

There has been a tendency to forget the need to validate fish growth, and this has led to serious misunderstanding of population dynamics and management strategies (Beamish and McFarlane, 1983). Given the importance of age reading to current assessment practices, and the uncertainty concerning the annual nature of illicia increments, growth validation studies for white anglerfish are of great importance. Until recently, there was no validation or verification of age that could provide an indication of the accuracy of age estimates. The objective of the present study is therefore twofold; first, to analyse the growth estimated from the first tagging experiment in southern European waters; and second, to review all information on growth verification of white anglerfish in Atlantic waters obtained from other tag-recapture studies, microstructure analyses of hard parts, and length frequency distributions of catches. The data from these

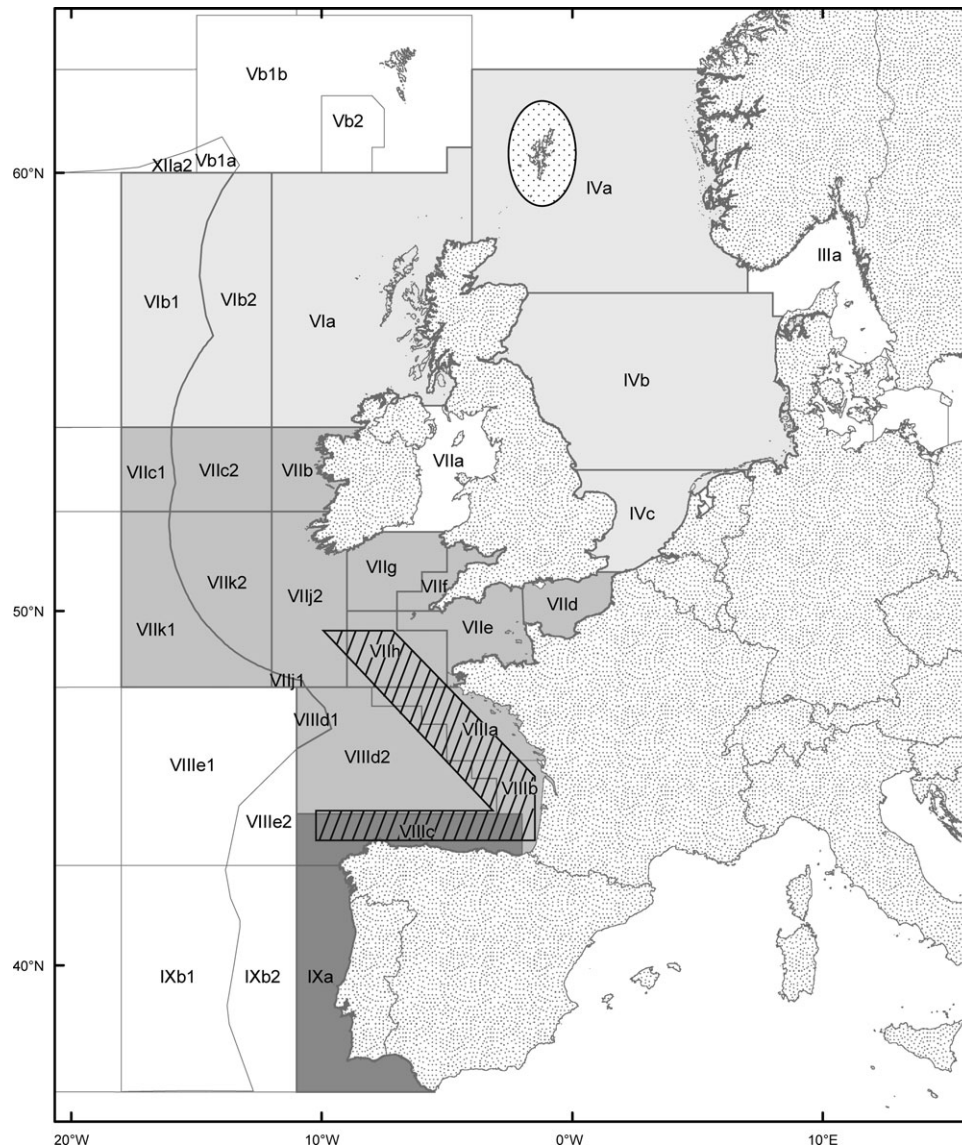


Figure 1. Stock units defined by ICES for white anglerfish: southern stock in Divisions VIIIc and IXa, northern stock in Divisions VIIb–k and VIIIa, b, d, northern shelf stock in Division IIIa, Subarea IV and Subarea VI. Tag-recapture areas with information on growth: present study (striped); Laurenson *et al.* (2005) (dotted).

studies are combined, an overall growth function is estimated, and the results obtained from illicia and otoliths are compared.

Methods

Tag-recapture

Tagging experiments have been conducted in southern European Atlantic waters since 1995, covering ICES Divisions VIIIb–k, VIIIa–d, and IXa (Figure 1). Fish were caught by commercial fishing vessels in bottom trawls and gillnets, and during scientific bottom-trawl surveys. Healthy fish >15 cm total length were measured to the centimetre below and a tag was inserted in the tail muscle, between the two dorsal fins. External tags were spaghetti T-bar anchor, 4 cm long, and yellow or red in colour. Tags contained a unique code, and the name and contact information of the Institute deploying the tag. Fish were always released in the same area as they were caught, and the release location was recorded. Information about the tag-recapture experiments, rewards, and information about the recovery was advertised internationally.

Growth by length

All available data on growth rates from Atlantic waters based on direct or indirect growth validation or verification methods (Panfili *et al.*, 2002) were analysed. Growth rates by length were estimated from recaptured fish with ~1 year (or more) at liberty, from the current tagging experiment (Table 1) and from that of Laurenson *et al.* (2005). Growth rates were also estimated as the difference in length between the modes clearly identified in the length frequency distributions of commercial landings and scientific surveys, from the studies of Fulton (1903), Dupouy *et al.* (1986), Landa (2004), and Jónsson (2007) (Table 2). Estimated length-specific growth rates from those studies were fitted using several functional relationships (linear, logarithmic, inverse, quadratic, cube, power, compound, S-curve, logistic, growth, and exponential), and the function providing the best fit and residual distribution was selected as the overall growth rate.

Growth-at-age

White anglerfish growth-at-age was estimated from the von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938):

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

where Lt is the length at age class t , L_{∞} the maximum attainable length, k the instantaneous growth coefficient, t the age, and t_0 the point at which the von Bertalanffy curve intersects the x -axis.

Table 1. The lengths at tagging and recapture of four white anglerfish, the differences between these two lengths, the number of days at liberty, and the annual growth rates.

Specimen	Length (cm) at tagging	Length (cm) at recapture	Difference (cm)	Days at liberty	Growth rate (cm year ⁻¹)
1	25	45	20	300	23.7
2	41	62	21	465	16.5
3	60	67	7	327	7.8
4	78	83	5	282	6.5

The growth expected for a given period, for instance the time elapsed between tagging and recapture, can be derived from Equation (1) as follows (Fabens, 1965):

$$L_2 - L_1 = (L_{\infty} - L_1)(1 - e^{-k(t_2-t_1)}), \quad (2)$$

where L_2 and L_1 are the lengths at recapture and tagging, respectively, or the lengths of two modal lengths in the catches, and t_2-t_1 is the interval between both observations (e.g. tagging and recapture, or between two modal lengths). Equation (2) was used to compute the growth predicted by the VBGF (L_{∞} and k) as previously published, so allowing a comparison between the observed and the predicted growth. Growth parameters were determined by non-linear least-squares regression.

Results

Tag-recapture

In all, 1326 white anglerfish were tagged and released in southern European waters between 1995 and 2004 (298 between 1995 and 1999, 262 in 2000, 395 in 2001, 239 in 2002, 97 in 2003, and 35 in 2004). Their total length ranged from 15 to 135 cm, covering the range of commercial landings (Figure 2).

In all, 50 anglerfish were recovered (2.6%), 32 with information on length-at-recapture. The length range of recaptured specimens covered the length range of tagged fish (Figure 2), although a greater proportion of large fish was recaptured (70–90 cm), most tagged by the gillnet fleet, where they are handled individually before tagging, possibly giving them a better chance of survival.

Some 80% of the recaptured specimens were at liberty for less than 1 month. Only seven were at liberty for more than 9 months (Figure 3), and information on length-at-recapture was only available for four fish (Table 1). The remainder were at liberty for less than 6 months. The annual growth rate was only estimated for fish at liberty for more than 9 months, so allowing reliable extrapolation of the growth rate to an annual period (Table 1). The mean growth rate determined from these four fish was 13.6 cm year⁻¹.

Growth verification at early age

To achieve better knowledge of the growth of white anglerfish in Atlantic waters during its first year, the following information was considered (Table 2): micro-increments (Wright *et al.*, 2002), tag-recapture (Laurenson *et al.*, 2005; this study), and

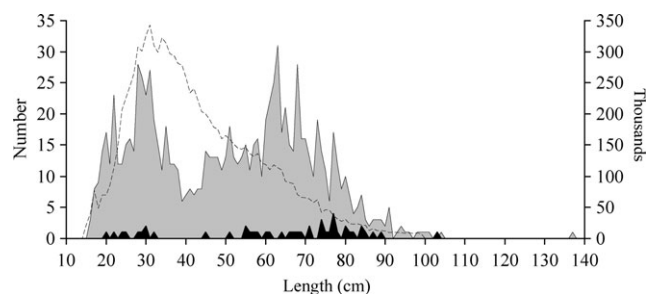


Figure 2. Length frequency distribution white anglerfish tagged (grey) and recaptured (black). The length frequency distribution from commercial landings is shown as a dotted line and the right y-axis values.

length frequency (Fulton, 1903; Dupouy *et al.*, 1986; Thangstad *et al.*, 2002; Landa, 2004; Jónsson, 2007). Dupouy *et al.* (1986) and Landa (2004) considered that the first modal length (21 and 18 cm, respectively) could be age 1, but provided no evidence to validate the allocation of those lengths to that age. However, these modal lengths are age 0 according to the verification of the first age by Wright *et al.* (2002) and other evidence. Therefore, all the modal lengths given by Dupouy *et al.* (1986) and Landa (2004) are placed in a younger age class in Table 2.

There are indications that the mean length-at-age at the end of the first year may be ~ 20 cm. However, this mean length is dependent on the season of hatch, which differs among areas (Table 2). In areas where spawning takes place around the second quarter of the year, as in the Iberian Peninsula (Duarte *et al.*, 2001) or in Icelandic waters (Jónsson, 2007), mean length may reach ~ 10 cm in the third quarter (Jónsson, 2007) and around 20 cm at the end of the first year (Table 2). If the spawning season is earlier, say in the first quarter, as in waters north of Scotland (Afonso-Dias and Hislop, 1996), then the growth period is longer and a mean length > 20 cm would be reached by the end of the first year (Wright *et al.*, 2002). If spawning is in summer or autumn (Wright *et al.*, 2002), the mean length reached by the end of the first year is likely to be < 20 cm (Table 2).

Length at age class 1 is similar among studies (Table 2), with modal lengths of ~ 25 cm in the second quarter, ~ 29 cm in the third quarter, and ~ 32 cm in the fourth quarter (Fulton, 1903; Dupouy *et al.*, 1986; Thangstad *et al.*, 2002; Landa, 2004; Jónsson, 2007). In general, therefore, if hatching takes place around the middle of the year, the growth rate might be around 27 cm year^{-1} during the first year of life (Table 2). Growth during this first year of life is faster than subsequently.

Length at age class 2 is ~ 40 cm in the middle of the year (Table 2), which implies a growth rate of around 12 cm year^{-1} during the second year of life. This is corroborated by the recaptures made by Laurenson *et al.* (2005) that spent more than a year at liberty after tagging; they were 29–33 cm long when released (all in August) and grew at $10.2 \text{ cm year}^{-1}$. This means that they would reach a length of ~ 41 cm a year later. The value of ~ 40 cm also agrees with lengths observed by Fulton (1903) in

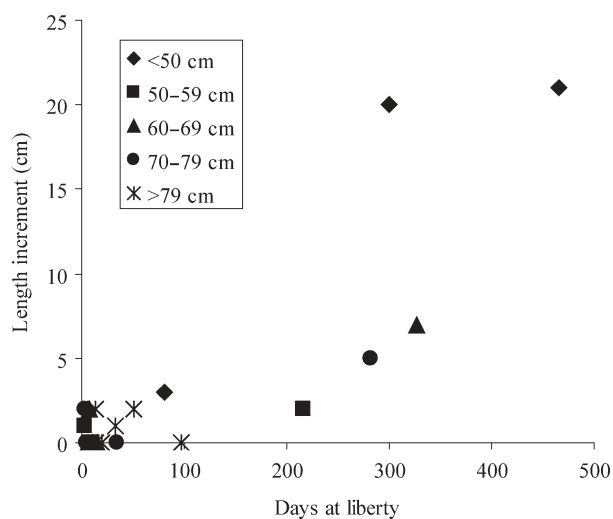


Figure 3. Length increment of recaptured white anglerfish, shown by length range at tagging, plotted against time at liberty.

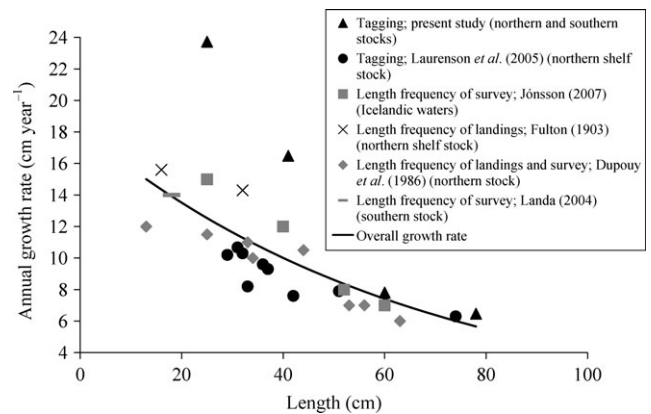


Figure 4. Annual growth rate at length determined from tagged-recaptured white anglerfish and from length frequency distributions of catches. The overall growth rate is based on these values. The x-axis shows the length at release of tagged fish or the modal length from length frequency distributions.

the same area (ICES Divisions IVa, b) as the later tag-recapture experiment took place, and it also agrees with the slightly longer values observed by Dupouy *et al.* (1986) and Fulton (1903) for the fourth quarter (42 and 46 cm, respectively; Table 2).

Overall growth verification

The verified results of growth (tagging and length frequency) reveal decreasing growth rates with increasing length, and the growth rates for lengths > 50 cm were similar in all studies (Figure 4). Comparing the growth rates in detail, Figure 4 shows general agreement in growth rates over the length ranges studied from two different sources: the tagging data of Laurenson *et al.* (2005) from waters around the Shetland Islands, and the length frequency of the catches given by Dupouy *et al.* (1986) for the Celtic Sea and the northern Bay of Biscay. The annual growth rate decreased from 12 to 10 cm year^{-1} over the range 15–40 cm, and to $6\text{--}7 \text{ cm year}^{-1}$ for fish of 50–60 cm. Fulton (1903) found an annual growth rate of $\sim 15 \text{ cm year}^{-1}$ based on the length frequency of catches in the North Sea, similar to that of Jónsson (2007), who found an annual growth rate of $\sim 15 \text{ cm year}^{-1}$ for his assumed 1-year-olds and $\sim 12 \text{ cm year}^{-1}$ for 2-year-olds (Figure 4). The rate is also similar to the estimate of 14 cm year^{-1} given by Landa (2004), who analysed the first two modal lengths of bottom-trawl surveys north of Spain. The growth rates of the two larger anglerfish in the present study are similar to the rates documented by others, but the rates of the two smaller fish are rather different (Figure 4).

An overall growth-rate curve (exponential model) was estimated (Figure 4) based only on the rates available to us, namely those on the rates of tagging (Laurenson *et al.*, 2005; this study) and length frequency (Fulton, 1903; Dupouy *et al.*, 1986; Landa, 2004; Jónsson, 2007). The overall relationship for growth rate is $18.24e^{-0.015\text{length}}$ ($r^2 = 0.58$).

Growth-at-age of hard parts

An overall VBGF was adjusted to all growth data from tagging and length frequency according to Equation (2), with a non-linear regression model resulting in estimates of $L_\infty = 105.3 \text{ cm}$ and $k = 0.174 \text{ year}^{-1}$. These parameters are close to those of Crozier (1989), who used sectioned otoliths (Table 3). However, the

Table 3. Annual mean lengths-at-age and von Bertalanffy growth parameters estimated in the current study and literature ones based on sectioned otoliths and illicia. Global differences in age classes between the present study and previous ones are marked by arrows.

Methodology	Sectioned otoliths		Tagging, length frequency		Illicia				
	Woodroffe <i>et al.</i> (2003)	Crozier (1989)	Present study		Dupouy <i>et al.</i> (1986)	Landa and Pereda (1997)	Duarte <i>et al.</i> (1997)	Quincoces <i>et al.</i> (1998, 2002)	Landa <i>et al.</i> (2001)
Stock	Northern shelf		All		Northern	Southern	Southern	Northern	Southern
Sex	Combined		Combined		Females	Combined	Combined	Combined	Combined
L_{∞}		105.55	105.31	140.00	166.60	132.05	137.00	147.58	163.50
k		0.176	0.174	0.110	0.077	0.110	0.090	0.078	0.065
t_0		0.380			0.395	0.660	0.190	-0.446	-0.385
n		3357			1028	514	209	1747	844
Age (years)	Mean length (cm)								
1	~20	22.5	24.1	21.3	13.2	18.9	17.5	20.0	19.0
2	~27	36.5	37.1	33.7	24.2	30.9	30.1	27.2	27.0
3	~34	50.0	48.0	44.8	35.0	37.8	36.5	33.7	33.7
4	~41	55.0	57.1	54.7	42.7	44.0	42.9	41.7	39.8
5	~51	62.5	64.8	63.6	53.2	53.6	50.5	50.2	46.5
6	~61	72.5	71.2	71.6	63.5	63.2	58.0	58.1	53.0
7	~77		76.7	78.7	71.9	69.7	64.6	65.4	59.8
8			81.2	85.1	81.1	79.2	71.5	73.0	66.7
9					85.7	86.0		78.1	72.2
10					89.3			87.4	80.4
11					94.5			91.8	87.7
12								93.6	90.7
13									93.9
Differences in age classes compared with the present study	+ 1 age class	Similar	Reference growth		+ 1 age class		+ 2 age class		+ 3 age classes

estimated L_{∞} is much lower than the maximum lengths sampled during surveys and commercial landings. Therefore, to obtain a better estimate of k , we set $L_{\infty} = 140$ cm, closer to the maximum length present in the landings, which is the same value used by Laurenson *et al.* (2005) and the ICES Working Group on the Assessment of Northern Shelf Demersal Stocks (WGNSDS) (ICES, 2004), and very close to the value of Landa and Pereda (1997), Duarte *et al.* (1997), and Quincoces (2002). Table 3 shows the VBGF parameters of previous studies based on illicia and the overall growth curve obtained in our study. To compare growth parameters among different studies, it was necessary to take into account the fact that L_{∞} and k are inversely related. Therefore, a comparison of the value of k with that of studies estimating age from illicia with a similar value of L_{∞} showed that the value of k in the present study (0.11 year^{-1}) is similar to those of

Laurenson *et al.* (2005; $k = 0.104 \text{ year}^{-1}$), Landa and Pereda (1997; $k = 0.11 \text{ year}^{-1}$), and Duarte *et al.* (1997; $k = 0.09 \text{ year}^{-1}$).

Estimating growth parameters is not just dependent on the observed lengths-at-age, but also on the available length/age ranges and the number of observations (Landa *et al.*, 2001), so the difference in observed lengths-at-age between studies is not always adequately reflected by the parameters. Therefore, by analysing both the estimated growth parameters and the mean lengths-at-age from the verified overall growth, and comparing them with those based on the age determination from sectioned otoliths (Table 3), our values are similar to those of Crozier (1989), and there is an approximately one-age-class difference between our mean lengths at early ages and those estimated by Woodroffe *et al.* (2003; Table 3; Figure 5). A one-age-class difference in the first three ages is also clear when one compared the

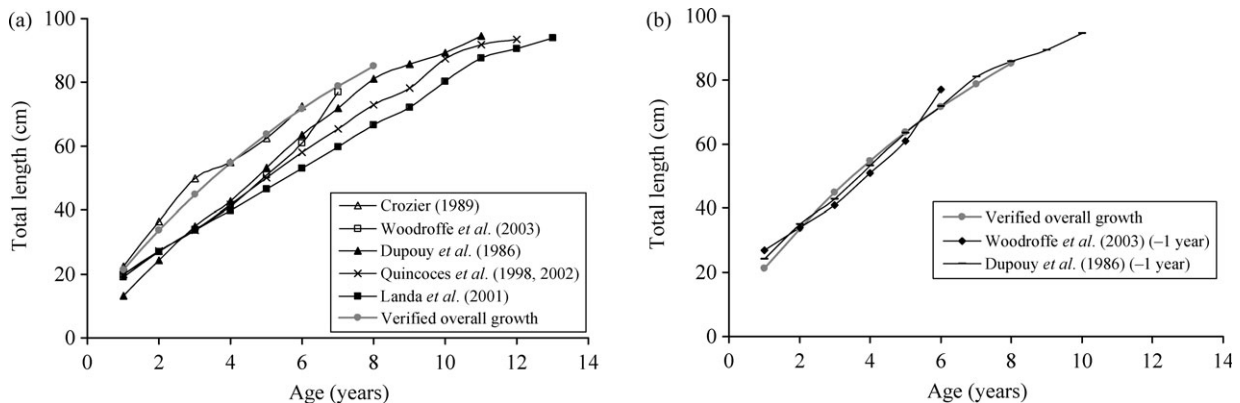


Figure 5. Comparison of mean lengths-at-age determined from verified overall growth rates with those of (a) age estimates from sectioned otoliths (Crozier, 1989; Woodroffe *et al.*, 2003) and illicia (Dupouy *et al.*, 1986; Quincoces *et al.*, 1998, 2002; Landa *et al.*, 2001), and (b) age estimates from Woodroffe *et al.* (2003) on sectioned otoliths and Dupouy *et al.* (1986) on illicia, but subtracting 1 year (the putative false annual increment).

verified overall growth with those of the illicia studies (Table 3). The verified overall growth indicates that observed (Table 2) and estimated mean lengths-at-age 1 (Table 3) ranged between 21 and 27 cm, and for age 2 between 33 and 40 cm. The studies based on illicia age estimation of the northern and southern stocks of the southern shelf (Dupouy *et al.*, 1986; Quincoces *et al.*, 1998; Landa *et al.*, 2001) showed the mean length-at-age 1 to lie between 13 and 20 cm, and that at age 2 to be between 24 and 27 cm. Therefore, age 3 estimated by illicia could be actually age 2, age 2 from illicia interpretation age 1, and age 1 could be actually age 0.

Discussion

Tag-recapture

Tagging is a direct method of validating the growth of a fish during its time at liberty. It is therefore an important source of information to validate age readings (Beamish and McFarlane, 1983). Two tagging studies have been undertaken for white anglerfish, the present work on northern and southern stocks of the southern shelf, and that of Laurenson *et al.* (2005) on the northern shelf stock. Taking into account only those fish recaptured after a period at liberty of >9 months (long enough to be able to use the growth rate as an annual estimate), the rate of 9.3 cm year⁻¹ of Laurenson *et al.* (2005) is slower than that found in the present study (13.6 cm year⁻¹). The two largest recaptures in the present study had similar growth rates to the recaptures of Laurenson *et al.* (2005). Nevertheless, the two smallest fish of our recaptures grew faster than those of similar size in the Laurenson *et al.* (2005) dataset (Figure 4). This result should, however, be treated with caution because our data are for just two fish and individual growth may be highly variable. Geographical differences may also have had a bearing on the results because, in general, anglerfish from warmer regions tend to grow faster.

Growth-at-age of hard parts

The verified overall growth pattern is based on studies undertaken in different geographical areas, and the differences between them may be a consequence of these differences. Also, only parts of the size/age distribution were covered (mainly up to 60 cm). However, we can draw some information too by comparing the pattern with the results of growth studies based on hard parts.

In sectioned otoliths, growth up to age 6 was shown by Crozier (1989) to be similar to the overall growth pattern described here (Table 3; Figure 5). The growth pattern for whole otoliths is particularly difficult to interpret (Crozier, 1989). In the Anglerfish Illicia/Otoliths Ageing Workshop (Duarte *et al.*, 2005), the readings from both structures were compared, and the between-reader agreement was better for illicia than for whole otoliths (for both experienced and non-experienced readers). Although illicium readings were more precise and less biased than whole otolith readings (Duarte *et al.*, 2005), Woodroffe *et al.* (2003) showed that sectioned otoliths can also provide precise age estimates up to ages 6 or 7. Nevertheless, the increase in growth rate with age (from 7 cm year⁻¹ at the youngest age to >10 cm year⁻¹ in older fish) shown by Woodroffe *et al.* (2003) is surprising when it is compared with other studies (Table 3). Crozier (1989) seems to document a more realistic growth pattern (Table 3), but he did not recommend the use of sectioned otoliths age analysis in anglerfish older than 6 years, because the multi-ring

appearance of the annulus is compacted as the annuli become progressively closer together. Therefore, although the utility of age estimation using sectioned otoliths seems to be appropriate for young anglerfish, more research in the age determination methodology for ages >6 years is necessary.

The growth based on illicia is underestimated in comparison with that of verified ages, overestimating by between one and three age classes (Table 3). It seems that two or three illicia increments can be counted that are not true annual ones. This is the case in particular for lengths <60 cm. For lengths >60 cm, the growth rate seems to be regular and similar in all illicia studies (20 cm in four age classes; Table 3). Wright *et al.* (2002) showed that the first supposed annual increment in illicia does not correspond to an annual period and suggests subtracting 1 year from ages determined by this method. If this was the case, it would at least partially explain the discrepancies observed between readings of illicia and the verified overall growth. If the first assumed annual increment is considered a false one, the growth rates in Dupouy *et al.* (1986) and Landa and Pereda (1997) would be similar to the overall growth pattern estimated here. Another 1 or 2 false annuli could have been counted as true ones between age classes 3 and 5 in the studies of Duarte *et al.* (1997), Quincoces *et al.* (1998), and Landa *et al.* (2001), showing that a slight drift in estimates of young ages could have taken place over time since Dupouy *et al.* (1986) carried out their analyses. Such an interpretational drift can be explained by the known improvement in illicia processing over time. Both tools and method have improved, allowing thinner slices of illicia to be made and greater magnification of the structures within achieved. This could have led to the identification of more increments close to the core of the illicium. We conclude that more research on optimal sectioning methods and magnifications could help to improve age estimation criteria and the identification of true annuli.

We also have to consider the fact that assessment of the northern white anglerfish stock (ICES, 2006) is based on age-structured models and age readings from illicia. Currently, there are also age series available that can be used in the assessment of the southern stock (ICES, 2007). Therefore, using a biased age estimation criterion may have important consequences for stock assessment and management. In particular, underestimating growth is likely to result also in an underestimate of a stock's productivity; a stock with a fast growth rate might recover faster from low biomass than would otherwise be expected. A similar problem of growth-rate underestimation has been reported recently for hake (de Pontual *et al.*, 2003, 2006), another important demersal stock in the Northeast Atlantic and for which the implications of incorrect age determination on stock assessment have been analysed (Bertignac and de Pontual, 2007).

There are two main conditions for a calcified structure being accepted for sclerochronological studies: (i) the structure on which the age determination is based has to exhibit a consistent interpretable pattern of increments; and (ii) the increments must be laid down with a periodicity that can be related to a regular time-scale (Panfili *et al.*, 2002). Until now, estimation of the age of anglerfish from illicia has fulfilled the first condition. Considerable effort has been made to improve the precision of age data through successive international workshops on ageing, and the growth estimates obtained from illicia seem to be consistent over years (Figure 6), and similar to the results obtained in previous studies using illicia (Landa *et al.*, 2001). Using illicia provides

other benefits too, such as a standardized methodology for their preparation and age reading, and that sampling can be performed at fish markets without damaging or manipulating the fish, so precluding the necessity to purchase the fish to obtain data. The first steps conducted to fulfil the second condition have been accomplished as well. Panfili *et al.* (2002) grouped the different age validation/verification methodologies available: direct, semi-direct, and indirect. Growth based on illicia was verified semi-directly by Dupouy *et al.* (1986) and Woodroffe *et al.* (2003), who confirmed the seasonal nature of annual increment formation. The current study is a step towards direct (tagging) and indirect (length frequency) growth verification. Recently, Jónsson (2007) also verified age estimation through comparing the modal lengths of abundant year classes in Icelandic waters with the modal lengths of illicia readings. This may also be a sign that interpreting illicia is easier in some areas, probably because of a lesser prevalence of false annual increments, and therefore that they show more clearly the true pattern of growth. It seems that illicia can be considered valid calcified structures for age estimation after validating annual increments. The analysis of growth rates from different studies and areas performed here is a step forward because it provides and highlights basic information that should help to establish better ageing criteria. Another way ahead could be to re-introduce the Dupouy *et al.* (1986) age estimation criterion, but disregarding the first annual increment, as shown in Figure 6. Then, the mean lengths-at-age are similar to those of the verified overall growth.

However, the main issue should be to enhance our knowledge of the true growth of white anglerfish by developing and using methodologies that allow validation. It is unproductive to go further in estimating white anglerfish growth patterns and age without progress being made in age validation (Duarte *et al.*, 2005). Improving the precision in the absence of accuracy cannot, under any account, guarantee data quality (de Pontual *et al.*, 2006). Therefore, although the discussion and analyses here have covered only the lower part of the length range of white anglerfish in certain areas, it is the first necessary overall step. Definitive conclusions on the true growth of white anglerfish can only be drawn, however, when evidence is available covering all size/age classes in the different areas of the species' distribution. In this respect, tagging results show promise.

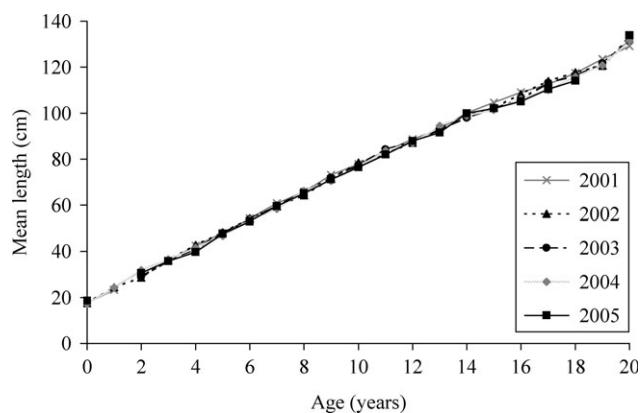


Figure 6. Mean lengths-at-age obtained from readings of illicia of white anglerfish for the period 2001–2005.

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