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Growth of Lesser Spotted Dogfish (*Scyliorhinus canicula* L., 1758) in the Cantabrian Sea, Based on Tag-recapture Data

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Abstract

Tag-recapture data of lesser spotted dogfish (*Scyliorhinus canicula,* L., 1758) were analysed to estimate the von Bertalanffy growth parameters of this species in the Cantabrian Sea. Seven models were applied including those incorporating variability in growth among individuals and model error. Similar results were obtained among them. The Gulland and Holt (1959) method produced the most convincing estimates of von Bertalanffy growth parameters for sexes combined (L_∞ or the asymptotic length closer to observed data), although all the models underestimated L_∞ . Estimates of the asymptotic length and the growth coefficient for both sexes combined were 69.3 cm and 0.21 per year, respectively. According to the different models, growth rate was slightly higher in males than females.

Key words: Cantabrian Sea, growth, length, *Scyliorhinus canicula*, spotted dogfish, tag

Introduction

Lesser spotted dogfish (*Scyliorhinus canicula*) is one of the most abundant elasmobranchs in the Cantabrian sea (ICES Division VIIIc). Although it has a low commercial value it is commonly landed in many fishing ports along the Cantabrian coast (Rodríguez-Cabello *et al*., 2004). Despite a lot of studies carried out with this species there are not many regarding age and growth. One of the main objectives of DELASS project (Development of Elasmobranch Assessments, CFP 99/055) was to provided preliminary assessments for a number of elasmobranch species which included the lesser spotted dogfish. The knowledge of the age or growth pattern of a species is one of the main requirements for the applications of any age-structured models.

One of the most common ways of estimating growth in fishes, is studying the hard parts (otoliths, spines, vertebrae, etc.). In elasmobranchs this is not so easy since they lack a bony structure (Ørvig, 1951; Moss, 1977), and the amount and pattern of calcification may vary considerably among species (Ridewood, 1921). Recently the evidence of the presence of osseous tissue in dogfish vertebrae has been reported (Peignoux-Deville *et al*., 1982; Bordat, 1986), while many techniques have been developed attempting to age these species (Prince and Pulos, 1983; Caillet, 1990), which have given reliable results in some sharks and rays.

The identification of growth zones deposited in vertebral centra of elasmobranchs suggested that these zones could be used in age determination studies. Several authors then developed and used various techniques to enhance these zones. Some vertebrae procedures applied to this species have not yielded satisfactory results for age determination (Lyle, 1981); nevertheless, Correia and Figueiredo (1997) developed a decalcification technique for enhancing growth bands which has been used with relative success in this species (Machado, 1996; Henderson and Casey, 2001).

Length frequency analysis is one of the methods suggested to estimate age in elasmobranchs (Anon, 1995). Despite the difficulties associated with this procedure, it has recently been used successfully in many species. The fact that this species has an extended egg-laying season (Ford, 1921, Capapé *et al*., 1991; Ellis and Shackley, 1997) makes it difficult to clearly identify age classes in the data. Estimates of growth parameters based on length frequency data have been given by Zupanovic (1961) from specimens caught in the Adriatic sea; this study was the first attempt to apply the modal class progression and Petersen method to this species. Later Rodríguez-Cabello *et al.,* (1998) provided growth estimates based on Bhattacharya's method for the population in the Cantabrian Sea.

Tag-recapture data, besides other applications, (Jones, 1976; Thorsteinsson, 2002) is one of the most important methods for estimating growth parameters (K and L_∞) especially for species that cannot be aged directly. However, some problems are associated with this method as well if: accurate measurements are not taken both at tagging or recapture, time at liberty is not enough for fish to grow, recaptures are size dependent, and the tag or the tagging procedure has a significant effect on growth.

Despite a wide series of criticisms, the model for growth in length most commonly used in fisheries is the three parameter equation developed by von Bertalanffy (1938). In this paper growth parameter estimates were calculated by using tag-recapture data from fishers harvesting lesser spotted dogfish (*Scyliorhinus canicula*) for the population in the Cantabrian Sea. Different growth models were examined; all based on the von Bertalanffy growth equation. Standard growth models and those incorporating individual variability in growth were applied.

TABLE 1. Summary of spotted dogfish tagging and recapture data from 1993 to 2001.

Year	Number tagged			Recaptures	
tagged	Total	Males	Females	Males	Females
1993	903	428	475	11	14
1994	783	357	426	14	8
1995	468	244	224	14	11
1996	828	374	454	20	11
1997	1 250	650	600	20	18
1998	784	394	390	10	8
1999	523	290	233	12	7
2000	1 083	660	423	12	5
2001	1 022	533	489	4	1
n = 9	7 644	3 930	3 714	117	83

Materials and Methods

A tagging program has been carried out since 1993 during the bottom trawl surveys in the north of Spain by Spanish Institute of Oceanography (Table 1). A total of 7644 spotted dogfish have been tagged, comprising a size range from 16 to 74 cm (Fig. 1). They were tagged with a T-bar anchor tag using a Mark II regular tagging gun. For each specimen total length was measured to the nearest cm and sex was noted. From 200 recoveries received up to June 2002, a total of 156 was used in growth analysis (95 males and 61 females). Only fish that were at liberty for at least three months were included in the analysis. The choice of three months was to allow time for fish to grow and to avoid noise of possible errors in measurement. The computation involved was carried out by using a Solver-based spreadsheet in MS Excel.

Description of models

Growth parameter estimates were derived from tag-recovery data using seven models, all based on the von Bertalanffy (1938) growth equation data: 1) the classical method of Gulland and Holt (1959) 2) Munro (1982) derived equation 3) the standard method described by Fabens (1965) 4) Kirkwood and Sommers (1984) model and 5) Kirkwood and Sommers incorporating model error 6) Sainsbury (1980) model and 7) Sainsbury with model error. Models 5 and 7 incorporate model error following analyses done by Hampton (1991).

Model 1. Gulland and Holt (1959): this method provides an estimation of growth parameters from growth increments based on the fact that under the von Bertalanffy equation, growth rate declines linearly with length, reaching zero at L_∞ .The function is a linear regression between the ratio $\nabla L/\nabla T$ and $\bar{L}$.

$$\nabla L/\nabla T = a + b * \bar{L}$$

where ∇L is the length increment
∇T is the time interval in years
$\bar{L}$ is the mean length

Model 2. Munro (1982): similar Model 1, this approach tests different values of L_∞, and the one which produces the lowest value of the coefficient of variation is assumed to provide the best value of *K*. The function minimises the coefficient of variation

$$ratio = \left(ln(L_\infty - l_i) - ln(L_\infty - l_r)\right)/(\Delta T)$$

where L_∞ is the asymptotic length
l_i is the length at tagging
l_r is the length at recapture
∇T is the time interval in years

Model 3. Fabens (1965): the non-linear model is described as:

$$(\delta l_i) = (\ L_\infty - l_i\ ) \times (\ 1 - e^{\ (-K\ t_i)})$$

where δl_i is length increment
l_i is length at tagging
t_i time interval in years

Estimates of L_∞, K and σ_e^2 can be obtained by non-linear ordinary least squares or by minimizing the log-likelihood function (Kimura, 1980):

$$LL = -LnL = \frac{n}{2} ln(2\pi\sigma_e^{\ 2}) + \frac{\sum_{i=1}^{n}\left[\delta l_i - E\delta l_i\right]^2}{2\sigma_e^{\ 2}}$$

Model 4. Kirkwood and Sommers (1984): Kirkwood and Sommers described a model that allowed for individual variation in growth through an individually variable L_∞:

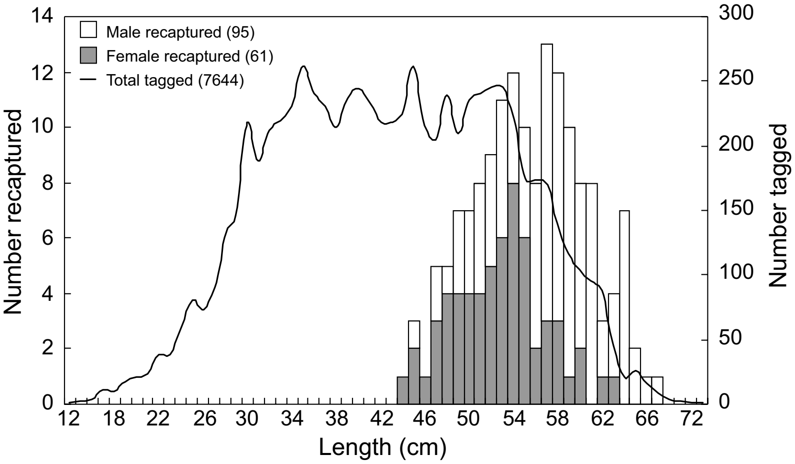

Fig. 1. Length distribution of the total number by sex of dogfish tagged from 1993 to 2001 and recaptured used in the growth analysis.

$$E(\delta l_i) = (\mu_{L_\infty} - l_i)(1 - e^{-Kt_i})$$

and variance,

$$var(\delta l_i) = \sigma_{L_\infty}^{2}(1 - e^{-Kt_i})^2$$

The negative log-likelihood in this case is:

$$LL = \sum_{i=1}^{n} \frac{ln[2\pi var(\delta l_i)]}{2} + \frac{[\delta l_i - E(\delta l_i)]^2}{2var(\delta l_i)}$$

Model 5. Kirkwood and Sommers with model error: In this case $E(\delta l_i)$ is the same as the previous model but now the variance becomes:

$$var(\sigma l_i) = \sigma_{L_\infty}^{2}(1 - e^{-Kt_i})^2 + \sigma_e^2$$

Model 6. Sainsbury (1980): Sainsbury described a model that recognized individual variation in K, as well as in L_∞, assuming both as independent random variables with K following a gamma distribution and L_∞ being normally distributed. Sainsbury (1980) also assumed that, as an approximation,is normally distributed for given l_i and t_i. Sainsbury (1980) also assumed that, as an approximation, δl_i is normally distributed for given l_i and t_i.

$$E(\delta l_i) = [\mu_{L_\infty} - l_i] * \left[1 - \left[1 + \frac{\sigma_k^{2} t_i}{\mu_k}\right]^{-\frac{\mu_k^2}{\sigma_k^2}}\right]$$

and

$$var(\delta l_i) = C_1\sigma_{L_\infty}^{2} + C_2(\mu_{L_\infty} - l_i)^2$$

where,

$$C_1 = 1 - 2\left[1 + \frac{\sigma_k^{2} t_i}{\mu_k}\right]^{-\frac{\mu_k^2}{\sigma^2_k}} + \left[1 + \frac{2\sigma_k^{2} t_i}{\mu_k}\right]^{-\frac{\mu_i}{\sigma_i}}$$

and

$$C_2 = \left[1 + \frac{2\sigma_k^{2} t_i}{\mu_k}\right]^{-\frac{\mu_k^2}{\sigma^2_k}} - \left[1 + \frac{\sigma_k^{2} t_i}{\mu_k}\right]^{-\frac{2\mu_k^2}{\sigma_k^2}}$$

Model 7. Sainsbury with model error: In this case $E(\delta l_i)$ is the same as the previous model but now the variance becomes:

$$var(\delta l_i) = C_1\sigma_{L_\infty}^{2} + C_2(\mu_{L_\infty} - l_i)^2 + \sigma_e^{2}$$

Parameter t_0: The parameter t_0 defined as the hypothetical age at which the species has zero length cannot be estimated from tagging data alone. It requires an estimate of absolute size at age, such as size at birth, and this was calculated from the von Bertalanffy equation and solving for each model:

$$t_0 = t + \frac{1}{K}\left[ln\frac{(L_\infty - L_t)}{L_\infty}\right]$$

The selection of the most appropriate model was done using the Akaike information criterion, AIC (Akaike, 1981; Anderson *et al.*, 1998):

$$AIC = -2log[L(\theta)] + 2K$$

where $L(\theta)$, is the maximized likelihood of the parameter vector and K is the number of estimated parameters.

Results and Discussion

A preliminary analysis of growth increments against mean length done by sex revealed that some points were outliers. Only those which were unreasonable with standardized residual greater than 4.099 in males and 3.0243 in females were removed. Further exploration of the data showed some doubtful points, however, *a priori* there was no reason to eliminate them, so they were included in the analysis, resulting in 93 recaptures for males and 58 for females (Fig. 2).

Estimates of growth parameters and maximum likelihood estimates for all models are shown in Table 2. Results are quite similar across models. In the case of sexes combined, the Gulland and Holt (1959) method (Model 1) produced the highest L_∞ values and lowest K, as being more realistic, although the coefficient of determination was 0.39. Munro's (Model 2) estimates were very close to the previous Model 1. According to the AIC estimates for Models 3 to 7, the best one would be Model 5 with $L_\infty = 64.5$ cm and $K = 0.27$ cm/year, Models 4 and 6 produced similar results and were very close to Model 5. The predicted recaptured length *versus* the observed recapture length for Model 5 is shown in Fig. 3. Examination of residuals against the recaptured length reveals that the distribution is quite uniform (Fig. 4).

Similar remarks can be made for males. In this case the highest L_∞ values and lowest K was achieved with Model 2 followed by Model 1. For Models 3 to 7 the best fit was attained with Sainsbury with model error (Model 7) giving $L_\infty = 63.8$ cm and $K = 0.34$ cm/year. Figures 5 and 6 show the same pattern as Fig. 4 and 5 for sexes combined.

In females large differences were found between Model 1 estimates and the rest of the models, however the regression coefficient was rather low ($r^2 = 0.183$). On the

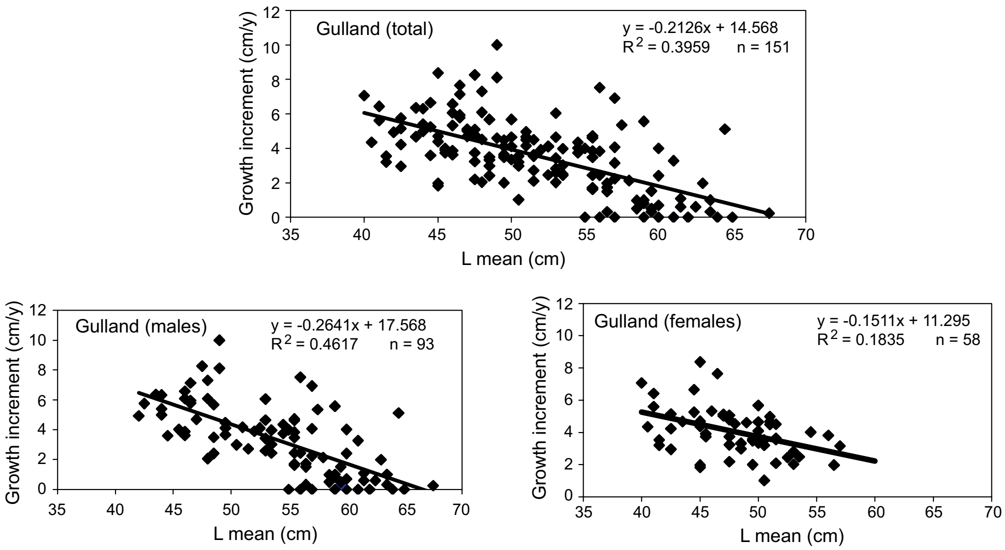

Fig. 2. Plots of mean length against growth increment of spotted dogfish following Gulland and Holt (1959) method.

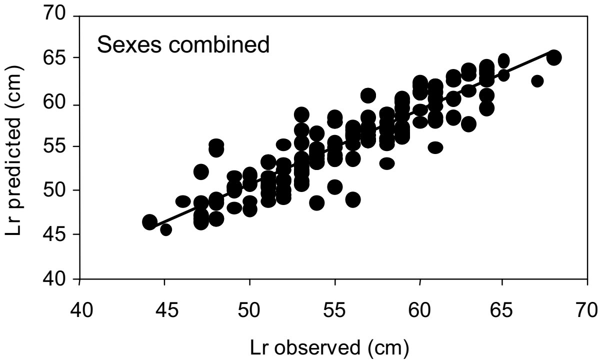

Fig. 3. Observed length *versus* predicted length of recaptured (Lr) spotted dogfish based on the fit of Model 5 for sexes combined.

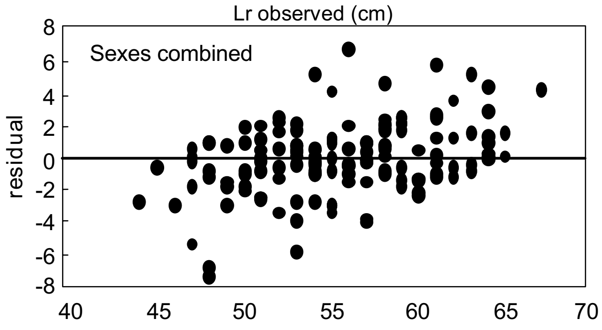

Fig. 4. Plot of residuals against observed recapture length (Lr) following the fit of Model 5 for sexes combined.

TABLE 2. Lesser spotted dogfish growth estimates derived from the models. Parameters are as follow: L_∞ is asymptotic average maximum length (cm), K is growth rate (cm/yr), σL_∞ is standard deviation of L_∞, σ K is error standard deviation of model error, to hypothetical age (years) at which fish length is zero, r^2 is coefficient of determination, *LL* is value of the log-likelihood function, *AIC* is Akaike information criterion.

No.	Model	L_∞	K	σL_∞	σK	σe	t_0	r^2	*LL*	*AIC*
	Sexes Combined (n = 151)									
1	Gulland and Holt	69.3	0.21	_	_	_	-0.76	0.395		
2	Munro	68.0	0.23	_	_	_	-0.69	_	_	_
3	Fabens	64.5	0.27	_	_	2.232	-0.62	_	335.5	675.1
4	Kirkwood and Sommers	64.4	0.30	5.748	_	2.271	-0.57	_	329.9	665.9
5	Kirkwood and Sommers with model error	64.5	0.27	2.196	_	2.233	-0.62	_	326.6	661.2
6	Sainsbury	64.4	0.30	4.930	0.070	2.259	-0.51	_	328.6	665.2
7	Sainbury with model error	64.6	0.28	0.000	0.055	2.225	-0.61	_	331.2	672.4
	Male (n = 93)									
1	Gulland and Holt	66.5	0.26	_	_	_	-0.62	0.461	–	–
2	Munro	68.0	0.24	_	_	_	-0.66	_	_	_
3	Fabens	63.7	0.33	_	_	2.118	-0.52	_	201.8	407.5
4	Kirkwood and Sommers	63.6	0.37	4.896	_	2.181	-0.46	_	201.8	409.5
5	Kirkwood and Sommers with model error	63.8	0.33	2.008	_	2.118	-0.52	_	197.2	402.4
6	Sainsbury	63.6	0.38	4.284	0.095	2.165	-0.45	_	200.8	409.6
7	Sainbury with model error	63.8	0.34	2.030	0.085	2.108	-0.50	_	195.4	400.7
	Females (n = 58)									
1	Gulland and Holt	74.8	0.15	_	_	_	-0.95	0.183	–	–
2	Munro	63.0	0.30	_	_	_	-0.58	_	_	_
3	Fabens	66.6	0.22	_	_	2.188	-0.74	_	127.7	259.4
4.	Kirkwood and Sommers	63.9	0.27	5.260	_	2.206	-0.63	_	118.0	242.0
5	Kirkwood and Sommers with model error	66.4	0.22	2.339	_	2.189	-0.74	_	123.7	255.4
6	Sainsbury	66.2	0.23	2.421	0.072	2.172	-0.71	_	116.3	240.6
7	Sainbury with model error	67.5	0.22	0.000	0.051	2.179	-0.73	_	121.3	252.6

contrary, Model 2 estimates produced the highest growth rate K = 0.30. Higher differences are found in the AIC values than for males or sexes combined, however, the K and L_∞ estimates were quite similar among all the models. The best fit was obtained with Model 6 giving L_∞ = 66.2 cm and K = 0.23 cm/year. The distribution of residuals was not remarkable, although it showed a slight tendency to underestimate the recaptured size for small sizes and overestimate the length at recapture for larger sizes. Most of the recaptures were from specimens of 45 to 60 cm, whereas in males, besides the larger data set, most were mainly from specimens 50 to 65 cm (Fig. 7 and 8).

Summarizing, the asymptotic length obtained with Model 1 was always slightly larger than with the other models particularly for females and sexes combined. Consequently the growth coefficient was lower. Model 2 estimates were close to Model 1 for males and both sexes

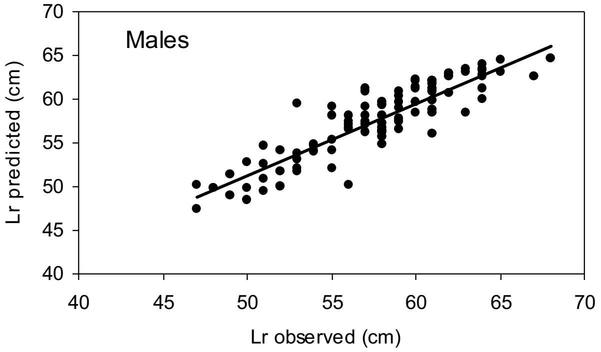

Fig. 5. Observed length *versus* predicted length of recaptured (Lr) spotted dogfish based on the fit of Model 7 for males.

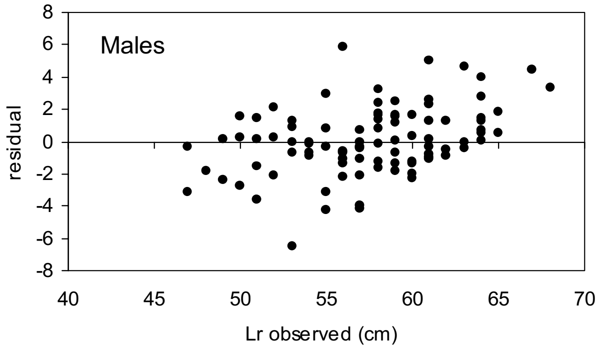

Fig. 6. Plot of residuals against observed recapture length (Lr) following the fit of Model 7 for males.

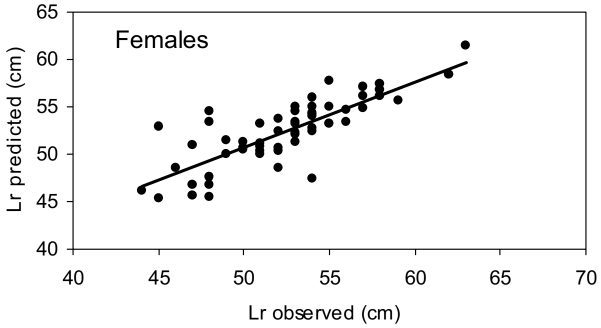

Fig. 7. Observed length *versus* predicted length of recaptured (Lr) spotted dogfish based on the fit of Model 6 for females.

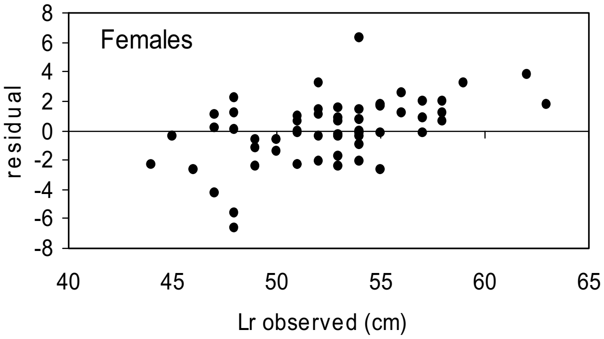

Fig. 8. Plot of residuals against observed recapture length (Lr) following the fit of Model 6 for females.

combined, but were rather different for females with the highest growth rate value. In Fabens family of models, the objective function minimized was lower for those incorporating variability in growth and maximum length as was the case of males and females and for Model 5 in the case of sexes combined. According to the standard deviation of L_∞ and K there was more variability attributed to individual estimates of L_∞ than to K.

Maximum observed lengths were always larger in males than females. This would mean that males should have L_∞ values higher than females. However estimated L_∞ values for males (Table 2) were lower than for females for most models. This could be explained by a number of male recaptures with no growth increments (13%) which would force the estimates downward. This phenomenon was not evident for females which had some growth increments in all lengths recorded (Fig. 2). Also there were more recaptures for males than females, which could also contribute to the lower Lr estimates obtained in the case of sexes combined.

The parameter t_o cannot be estimated from tagging data alone. Rather it requires an estimate of absolute size at age, in addition to tag-recapture data. Kirkwood (1983) described a maximum likelihood method for determining t_o, along with L_∞ and K if additional age-length data were available. Length at birth for lesser spotted dogfish has been reported to be between 9 to 11 cm (Ford, 1921; Collenot, 1966; Leloup and Oliverau, 1951; Mellinger and Wrisez, 1984; Ellis and Shackley, 1997). According to this, values of t_o were estimated for each model, which led to different values according to the predicted growth parameters (Table 2). Growth curves for the seven models are shown in Fig. 9.

The longevity of this species is unknown; the longest times at liberty recorded was 8.6 years for a male, and 7 years for a female, both specimens at time of tagging were adults of 57 cm and 43 cm, respectively. Based on growth estimates presented in this study a male of 57 cm will be 7–8 years old. The longevity estimate is therefore at least 17 years.

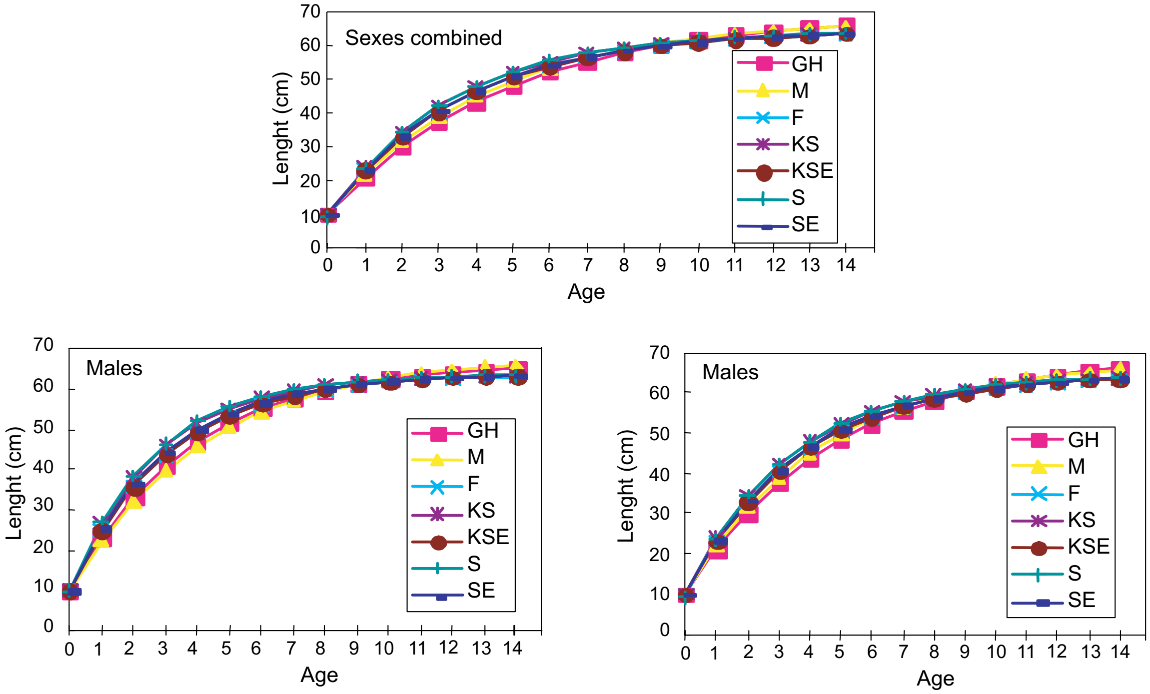

Fig. 9. Growth curves fitted for spotted dogfish for each Model (model names given in Table 2).

TABLE 3. Summary of growth parameters and maximum lengths observed for spotted dogfish.

Author	Area	L_∞	K	L_{max} Observed Male	L_{max} Observed Female	Method
Ford (1921)	Atlantic (English Channel)			70	70	
Faure-Fremiet (1942)	Atlantic (Roscoff)			66	66	
Faure-Fremiet (1942)	Atlantic (Concarneau)			72	72	
Leloup et Olivereau (1951)	Atlantic			68	68	
Leloup et Olivereau (1951)	Mediterranean (south France)			49	49	
Ellis and Shackley (1997)	Atlantic (Bristol Channel)			75	66	
Capape *et al*., (1991)	Mediterranean			55	51	
Rodriguez-Cabello *et al*., (1998)	Atlantic (Cantabrian sea)	88.8	0.13	72	68	a,b
Zupanovic (1961)	Mediterranean (Adriatic sea)	56.8	0.53			a
Jennings *et al*., (1999)	Atlantic (North Sea)	88.0	0.20			d
Henderson and Casey, 2001	Atlantic (Ireland)	82.7	0.15			c

a) Length frequency distribution b) tag-recapture data c) vertebra d) unknown

In general all the asymptotic lengths estimated in this study were underestimated, compared to those expected. Despite Wheeler's (1978) asymptotic length estimate for this species of 100 cm, a value more than 80 cm has been rarely observed (ETI, 1996; Ford, 1921; Capapé *et al*., 1991; Vas, 1991; Rodríguez-Cabello *et al*., 1998) particularly in the Cantabrian Sea (Table 3). As Pauly (1978) pointed out, in large specimens the ratio of maximum length to asymptotic length (L_{max}/L_∞) is about 0.95. Maximum observed lengths for this species in the Cantabrian Sea based on the series of bottom trawl surveys data carried out from 1983 to 2001, are 70 cm for males and 68 cm for females, respectively. Estimations based on Froese and Binohlan (2000) empirical relationships lead to L_∞ values of 74.4 cm (62.8–88.3 cm) for males and 70.4 cm (59.3–83.4 cm) for females. However, as it has been pointed out in many documents, the interpretation of L_∞ is often misleading and should be conceived as the average maximum length that would be attained in the population represented by the data being studied.

The Gulland and Holt (1959) method produced the most convincing estimates of von Bertalanffy growth parameters (Table 2). Munro's (1982) method has the advantage that it is independent of the sizes of the fish tagged and upon a wide variety of values for the time interval. Estimates based on this model are very close to those of Gulland and Holt (1959) with the exception of females which show a meaningless high growth rate. However, this method is not well established, because it uses a coefficient of variation to derive the best estimates of *K* (Cailliet *et al*., 1992). Models that incorporate individual variability in L_∞ produced the best fit in both sexes, while Sainsbury (1980) model presents the best fits for males and females independently. However, there are not very big differences among the log-likelihood values and the estimated parameters L_∞ and *K* are quite similar between them. A further consideration is that models that incorporate individual variability in growth parameters are very influenced by outliers and therefore a strong criterion in the definition of outlier is required (Hampton, 1991).

The Fabens (1965) analysis has a tendency to underestimate L_∞ and overestimate *K*. Similar results were found in the tiger shark (*Galeocerdo cuvier*) by Natanson *et al*., (1999). Cailliet *et al*., (1992) obtained better results with the Gulland and Holt (1959) method than Fabens (1965) for the Pacific angel shark *(Squatina california*) although in this case *K* was underestimated. The Fabens (1965) method can lead to biased estimates because its basic premise, that tagged individuals are at large for equal time periods, is often violated with sharks (Chien and Condrey, 1987). The Gulland and Holt (1959) method which allows for unequal times at liberty, therefore, appeared to be more appropriate for sharks (Calliet *et al*., 1992).

If tagging is believed to affect growth, a tagging effect should be included in the model. There is evidence that tagging may reduce or halt growth in some sharks such as lemon shark studied by Manire and Gruber, (1991), and it has also been suggested in other sharks by Stevens, (1990), Cailliet *et al*., (1992), Kusher *et al*., (1992) and Natanson *et al*., (1999). There is no evidence that this occurs in the lesser spotted dogfish. Some of our data suggest a decrease in growth in males, particularly in fish of medium size. If this were due to a tagging effect, then tagging should affect both males and females similarly not only males, but more data are needed to verify the effects of tagging on growth for this species. On the other hand, it is expected that the initial or release length error cannot always be measured exactly, particular for large dogfish specimens which have a great capacity to shrink themselves when they are alive (Bone, 1999), and this additional source of error should also be considered (Hampton, 1991).

Another important assumption that we must make when using the parameter estimates obtained from tag-recapture data to describe growth is that the recapture probability is size independent. If larger animals are more likely to be recaptured, growth will be overestimated (Wang, 1999). Probably the recaptures of this species are not totally size independent since it does not have a high commercial value and most of the catch, is discarded. For this reason, the specimens kept on board, are frequently of large size, increasing the possibility of being discovered and reported, nevertheless, small specimens have also been reported.

The AIC is a good criterion for selecting the most parsimonious model, that is, the model which best explains the variation in the data while using the fewest parameters. However, criteria for which is best or worst depends upon the context. As Wang *et al*., (1995) pointed out, the choice of the growth curve is often quite subjective and sometimes it is advisable to use a pragmatic decision based on previous studies and experience than goodness of fit.

The growth rate proposed in this study is comparable to those for other elasmobranch species (Pratt and Casey, 1990). However, it is not advisable to make such comparisons since growth rate may differ not only among species but also within the species. A summary of growth parameters and maximum observed length for the lesser spotted dogfish is presented in Table 3. Despite the extensive literature and the many experiments carried out with this species, growth studies are very limited. Most of the existing documentation are regarding maximum observed lengths and other biological parameters (Table 3). Recently the development of new techniques for improving the reading interpretation of vertebrae has drawn the attention to determine the age of this species.

Accurate age determination is necessary for both the assessment and management of any species because it is the basis for calculations of growth and mortality rates, age at maturity, age at recruitment and longevity. Maybe a better fit on growth estimates of this species could be achieved using other alternative equations proposed by some authors, like the general model of Schnute and Richards (1990) Francis, (1988;1995) or Wang *et al*., (1995).

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