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Growth of Lesser Spotted Dogfish *Scyliorhinus canicula* (L., 1758) in the Cantabrian Sea, Based on Tag-return Data (Elasmobranch Fisheries – Poster)

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Abstract

Tag-recapture data of lesser spotted dogfish (*Scyliorhinus canicula*, L., 1758) have been 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 VBGF parameters for sex combined (L ∞ closer to observed data), although all the models underestimate the L ∞ . Estimates of the asymptotic length and the growth coefficient for both sexes are 69.3 cm and 0.21 year⁻¹ respectively. According to the different models growth rate is slight higher in males than females.

Key words: Scyliorhinus canicula, growth, tag, Cantabrian Sea.

Introduction

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 of a bony structure. However, many techniques have been developed attempting to age these species (Prince and Pulos, 1983; Caillet, 1990), which have given good results in some sharks and rays. Some vertebrae procedures applied to this species have not provided satisfactory results for age determination (Lyle, 1981), nevertheless Correia and Figuereido (1997) developed a decalcification technique for enhancing growth bands which has been used with relative success to this species (Machado, 1996; Henderson and Casey, 2001).

Length frequency analysis is one of the methods suggested to estimate age in elasmobranchs (Anon, 1995). Regardless the difficulties associated to this procedure, it has been recently 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 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, probably being 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 is one of the most important methods for estimating growth parameters (K and L ∞) especially for species than 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 or the tag or the tagging procedure has a significant effect on growth.

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Despite a wide series of criticisms the growth model in length most commonly used in fisheries is the three parameter equation developed by von Bertalanffy (1938). In this paper growth parameter estimates for *Scyliorhinus canicula* were calculated by using tag-recapture data 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 have been applied.

Materials and Methods

A tagging program has been carried out since 1993 during the bottom trawl surveys carried out in the north of Spain by Spanish Institute of Oceanography (Table 1). A total of 7 644 dogfish have been tagged, comprising a size range from 16 to 74 cm (Fig. 1). The dogfish were tagged with a T-bar anchor tag using a Mark II regular tagging gun. For each specimen total length was measured at the inferior centimetre and sex was noted. From 200 recaptures received up to date (June 2002), a total of 156 have been used in growth analysis (95 males and 61 females). Only fish that were measured both at tagging and recaptured and were at liberty for at least three months were included in the analysis. The choice of three months was to allow some time for fish to grow and to avoid noise of possible error measurement. The computation involve was carried out by using a Solver-based spreadsheet in MS Excel.

Description of models

Seven models were fitted to estimate the growth parameters, all based on the von Bertalanffy (1938) growth equation from tag-recaptured 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 (7) Sainsbury with model error. Models 5 and 6 incorporate model error following analysis 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 VBGF, growth rate declines linearly with length, reaching zero at L ∞ . The function is a linear regression between the ratio $\nabla L/\nabla T$ and L'.

$$\nabla L/\nabla T = a + b * L'$$

where ∇L = Length increment ∇T = Time interval in years L' = Mean length

Model 2. Munro (1982): Similar to the previous one, it tests different values of L^{∞} and the one which produces the lowest value of the coefficient of variation it is assumed to provide the best value of K. The function minimises the coefficient of variation:

ratio = $(\ln (L\infty-li) - \ln (L\infty-lr)) / (\nabla T)$

where L = asymptotic lengthli = Length at tagging lr = Length at recapture ∇T = Time interval in years

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

 $(\delta i) = (L \infty - li) x (1 - e^{(-K ti)})$

where $\delta li = length$ increment

li = length at tagging

ti = time interval in years

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

$$LL = -\ln L = \frac{n}{2}\ln(2ps_e^2) + \frac{\sum_{i=1}^{n} [dli - E(dli)]^2}{2s_e^2}$$

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

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

and variance,

$$\operatorname{var}\left(\delta \mathbf{i}\right) = \sigma_{\mathrm{L}^{\infty}}^{2} (1 - \mathrm{e}^{-\mathrm{K} \mathrm{t} \mathrm{i}})$$

The negative log-likelihood in this case is:

$$LL = \sum_{i=1}^{n} \frac{\ln \left[2\mathbf{p} \operatorname{var}(\mathbf{d}li) \right]}{2} + \frac{\left[\mathbf{d}li - E(\mathbf{d}li) \right]^{2}}{2 \operatorname{var}(\mathbf{d}li)}$$

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

$$\operatorname{var}(\boldsymbol{s}li) = \boldsymbol{s}L_{\infty}^{2} \left(1 - e^{-Kti}\right)^{2} + \boldsymbol{s}_{e}^{2}$$

Model 6. Sainsbury (1980) described a model that recognised 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. He also assumed that, as an approximation, δi is normally distributed for given li and ti:

$$\operatorname{var}(\boldsymbol{d}li) = C_1 \boldsymbol{s}_{L^{\infty}}^2 + C_2 (\boldsymbol{m}_{L^{\infty}} - li)^2$$

and

$$E(\mathbf{d}li) = [\mathbf{m}_{L\infty} - li] * \left[1 - \left[1 + \frac{\mathbf{s}_k^2 ti}{\mathbf{m}_k} \right]^{-\frac{\mathbf{m}_k^2}{\mathbf{s}_k^2}} \right]$$

where,

$$C_{1} = 1 - 2 \left[1 + \frac{\boldsymbol{s}_{k}^{2} ti}{\boldsymbol{m}_{k}} \right]^{-\frac{\boldsymbol{m}_{k}^{2}}{\boldsymbol{s}_{k}^{2}}} + \left[1 + \frac{2\boldsymbol{s}_{k}^{2} ti}{\boldsymbol{m}_{k}} \right]^{-\frac{\boldsymbol{m}_{k}^{2}}{\boldsymbol{s}_{k}^{2}}} \quad \text{and} \quad C_{2} = \left[1 + \frac{2\boldsymbol{s}_{k}^{2} ti}{\boldsymbol{m}_{k}} \right]^{-\frac{\boldsymbol{m}_{k}^{2}}{\boldsymbol{s}_{k}^{2}}} - \left[1 + \frac{\boldsymbol{s}_{k}^{2} ti}{\boldsymbol{m}_{k}} \right]^{-\frac{2\boldsymbol{m}_{k}^{2}}{\boldsymbol{s}_{k}^{2}}}$$

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

$$\operatorname{var}(\mathbf{s}li) = C_1 \mathbf{s} L_{\infty}^{2} + C_2 (\mathbf{m} L_{\infty} - li)^{2} + \mathbf{s}_{e}^{2}$$

Parameter t_{θ}

The parameter t_0 defined as the hypothetical age at which the species has zero length cannot be estimated from tagging data alone, rather it requires an estimate of absolute size at age, such as size at birth, and was calculated from VBGF solving:

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

Model selection

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

$$AIC = -2\log[L(\boldsymbol{q})] + 2K$$

where L (θ) is the maximised likelihood of the parameter vector θ and K is the number of parameters to estimate.

Results

A preliminary analysis of growth increments against mean length done by sex revealed that some points where outliers. Only those which were thoughtfully unreasonable and its standardised residual was greater than 4.099 in males and 3.0243 in females were removed, further exploration of the data showed some doubtfully points but *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 fitted models are shown in Table 2. Results are quite similar across models. In the case of sex combined, the Gulland and Holt (1959) method (model 1) produces the highest L ∞ values and lowest K being more realistic although the coefficient of determination is 0.39. Munro's (model 2) estimates are very close to the previous model. According to the AIC estimates for models 3 to 7 the best one would be model 5 with a L ∞ = 64.5 cm and K=0.27 cm/year, models 4 and 6 produce similar results and are 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 said for males. In this case the highest L ∞ values and lowest K is achieved with model 2 followed by model 1. For models 3 to 7 the best fit is attained with Sainsbury with model error (model 7) given a L ∞ = 63.8 cm and K= 0.34 cm/year. Fig. 5 and 6 show the same pattern as figures 4 and 5 for sex combined.

In the case of females large differences are found between model 1 estimates and the rest of the models, however the regression coefficient is rather low $r^2 = 0.183$. On the contrary, model 2 estimates produces the highest growth rate K= 0.30. Higher differences are found in the AIC values than for males or sex combined however, the K and L ∞ estimates are quite similar among all the models. The best fit is obtained with model 6 given L $\infty = 66.2$ cm and K= 0.23 cm/year. The residuals distribution is unremarkable, although it shows a slight tendency to underestimate the recaptured size for small sizes and overestimate the length at recapture for larger sizes. It is also evident that most of the recaptures are from specimens of 45 to 60 cm while in the case of males, besides the higher number of data, these are from specimens mainly from 50 to 65 cm (Fig. 7 and 8).

Summarising the asymptotic length obtained with model 1 is always a little bit higher than with the other models particularly for females and sex combined, consequently the growth coefficient is lower. Model 2 estimates are close to model 1 for males and both sexes combined, but are rather different in the case of females with the highest growth rate value. In the case of Fabens family models, the objective function minimised is lower for those incorporating variability in growth and maximum length as is the case of males and females and for model 5 in the case of sex combined. According to the standard deviation of I_{∞} and K there is more variability attributed to individual estimates of L ∞ than to K.

Maximum observed lengths are always larger in males than females, this would mean that males have L ∞ values higher than females. In the case of males the bias in L ∞ could be explained by certain number of recaptures with no growth increment (13 %) which would force the L ∞ estimates downward. This phenomenon is not accounted for females which present some growth increment in all lengths recorded (Fig. 2). Since there are more recaptures for males than females this circumstance could also contribute to the low L ∞ estimates obtained in the case of sex 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 are available. This species has the advantage as other elasmobranchs, that length at birth can be determined. Length at birth is assumed to be between 9 to 11 cm (Ford, 1951; Collenot, 1966; Leloup *et al.*, 1951; Mellinger and Wrisez, 1984; Ellis and Shackley, 1997). According to this, values of to were estimated for each model, which lead 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 specimen which more time at liberty recorded has been 8.6 years for a male, and 7 years for a female, both specimens were adults of and 57 cm and 43 cm at time of tagging, respectively. Based on growth estimates presented in this study a male of 57 cm will have 7-8 years old. The longevity estimate is therefore at least 17 years.

Discussion

In general all the asymptotic length estimates are underestimated, compared to those expected. Despite Wheeler (1978) determines an asymptotic length for this species in 100 cm, a value more than 80 cm is rarely observed (ETI, 1996; Ford, 1921; Capape *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 maximum length-asymptotic length (Lmax / 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 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 of underestimate the L ∞ and overestimate the K. Same results are found in the tiger shark (*Galeocerdo cuvier*) by Natanson *et al.*, (1999). Cailliet *et al.*, (1992) obtained better results with Gulland and Holt method than Fabens 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, appears to be more appropriated 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 with dogfish however some data suggests a decrease in growth specially in the case of males, but if this is true this effect its supposed to affect both males and females. It is likely that growth declines as fish reaches the asymptotic or maximum size however some male recaptures show no growth increment in fish of medium size. It is expected that the initial or release length error cannot always be measured exactly (particular for large specimens which have a great capacity of shrink themselves) and this additional source of error should be considered.

Another important assumption 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 has not a high commercial value and most of the catch is discarded. For this reason, the specimens kept on board are frequently of large size and that increases 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, although 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 its advisable to use a pragmatic decision based on previous study 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 no advisable to make such comparisons since growth rate may differ not only among species but also within itself. A summary of growth parameters and maximum observed length for this species is presented in table 3. Despite the extensive literature and experiments carried out with this species, growth studies are very limited. More documentation exists regarding maximum observed lengths and other biological parameters (Table 3). Recently the development of new techniques for improving the lecture of vertebrae has drawn the attention to determine the age of this species.

Accurate age determinations are necessary for both the assessment and management of any species because they are 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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| Year | Nu | Number tagged | | | | | | | | | |
|--------|-------|---------------|---------|------------|--|--|--|--|--|--|--|
| tagged | Total | Males | Females | Recaptures | | | | | | | |
| 1993 | 903 | 428 | 475 | 25 | | | | | | | |
| 1994 | 783 | 357 | 426 | 22 | | | | | | | |
| 1995 | 468 | 244 | 224 | 25 | | | | | | | |
| 1996 | 828 | 374 | 454 | 31 | | | | | | | |
| 1997 | 1250 | 650 | 600 | 38 | | | | | | | |
| 1998 | 784 | 394 | 390 | 18 | | | | | | | |
| 1999 | 523 | 290 | 233 | 19 | | | | | | | |
| 2000 | 1083 | 660 | 423 | 17 | | | | | | | |
| 2001 | 1022 | 533 | 489 | 5 | | | | | | | |
| n =9 | 7644 | 3930 | 3714 | 200 | | | | | | | |

Table 1. Summary of tagging data and recaptures from 1993 to 2001.

Table 2. Lesser spotted dogfish growth estimates derived from the models applied. Parameters are as follow: L ∞ asymptotic average maximum length (cm), K growth rate (cm/y), $\sigma L \infty$ standard deviation of L ∞ , σK standard deviation of K, σ error standard deviation of model error, to hypothetical age (years) at which fish length is zero, r² coefficient of determination, LL value of the log-likelihood function, AIC Akaike information criterion.

SEX COMBINED (n=151)

| N° | Model | L∞ | K | σL∞ | σK | σ_{e} | to | r^2 | LL | AIC |
|----|---------------------------------------|------|------|-------|-------|--------------|-------|-------|-------|-------|
| 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 | Sainsbury with model error | 64.6 | 0.28 | 0.000 | 0.055 | 2.225 | -0.61 | | 331.2 | 672.4 |

MALE (n=93)

| N° | Model | L∞ | К | σL∞ | σK | σe | to | r^2 | LL | AIC |
|----|---------------------------------------|------|------|-------|-------|-------|-------|-------|-------|-------|
| 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 | Sainsbury with model error | 63.8 | 0.34 | 2.030 | 0.085 | 2.108 | -0.50 | | 195.4 | 400.7 |

FEMALES (n=58)

| Nº | Model | L∞ | K | σL∞ | σK | σ_{e} | to | r^2 | LL | AIC |
|----|---------------------------------------|------|------|-------|-------|--------------|-------|-------|-------|-------|
| 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 | Sainsbury with model error | 67.5 | 0.22 | 0.000 | 0.051 | 2.179 | -0.73 | | 121.3 | 252.6 |

Table 3. Summary of growth parameters and maximum observed length for Scyliorhinus canicula.

| | | | L max observed | | | | | |
|----------------------------------|------------------------------|------|----------------|------|--------|--------|--|--|
| Author | Area | Linf | Κ | Male | Female | Method | | |
| Ford (1921) | Atlantic (English Channel) | | | 70 | 70 | | | |
| Fauré-Frémiet (1942) | Atlantic (Roscoff) | | | 66 | 66 | | | |
| Fauré-Frémiet (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 | | | |
| Capapé 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 | | | а | | |
| Jennings et al., (1999) | Atlantic (North Sea) | 88.0 | 0.20 | | | d | | |
| Henderson A.C. and Casey, 2001 | Atlantic (Ireland) | 82.7 | 0.15 | | | с | | |

a) Length Frequency distribution, b) Tag-recapture data c) Vertebra d) Unknown



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



Fig. 2. Plots of mean length against growth increment following Gulland and Holt method.



Fig. 3. Recaptured observed length *versus* recaptured predicted length based on the fit of model 5 for sex combined.



Fig. 5. Recaptured observed length *versus* recaptured predicted length based on the fit of model 7 for males.



Fig. 7. Recaptured observed length *versus* recaptured predicted length based on the fit of model 6 for females.



Fig. 4. Plot of residuals against observed recapture length following the fit of model 5 for sex combined.



Fig. 6. Plot of residuals against observed recapture length following the fit of model 7 for males.



Fig. 8. Plot of residuals against observed recapture length following the fit of model 6 for females.



Fig. 9. Growth curves fitted for each model.