Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from southwestern Australia estimated from tag-recapture data

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Abstract—Tagged neonate and small juvenile *Carcharhinus obscurus* were released between March 1994 and June 1996 in southwestern Australia. Length and time-at-liberty data from 304 usable recapture data were used to examine growth rates of male, female, oxytetracycline injected, noninjected, and all individuals combined. Recaptures were made up to 4.7 years after release. Four methods of analysis were employed: Gulland and Holt, Fabens, Francis, and length-at-age. Length-at-age analysis was possible because the majority of the animals released had open umbilical scars and so were of known age. The four methods produced varying results. One method was not able to estimate growth parameters, another produced inaccurate estimates of von Bertalanffy growth parameters, and two methods indicated that a linear growth model described growth better than the von Bertalanffy model. Although each produced different results, the three successful methods estimated that the growth rate up to age 5 ranged from 8 cm/year to 11 cm/year. These growth rates agreed closely with those reported for young *C. obscurus*. Length-at-age analysis indicated significant differences in the growth rates between males and females, and between oxytetracycline-injected and noninjected males. Results from the Francis method did not show significant differences between males and females, or injected and noninjected animals. The coefficient of variation of growth variability ranged from 0.24 to 0.40, mean measurement error ranged from 0.0 cm to 0.94 cm, and the standard deviation of measurement error ranged form 2.1 cm to 2.4 cm. The usefulness of each of the methods is discussed—the more detailed methods providing a better understanding of tag-recapture data.

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Tag-recapture data are a useful source of information on the growth of animals. The simplest form of analysis is to estimate an average growth rate, normally for a specific size range, from the period at liberty and the growth increment. This approach has been used in studies examining elasmobranch growth. For example, Thorson and Lacy (1982) estimated the average growth rate of adult sawfish (*Pristis perotteti*), Pratt and Casey (1983) provided average growth rates for shortfin mako sharks (*Isurus oxyrinchus*) in 20-cm size groups, and Casey et al. (1985) provided estimates of growth rates for sandbar sharks (*Carcharhinus plumbeus*) in 20-cm size groups. Although this approach provides information on growth rates that can be compared with those predicted by other techniques, it does not provide estimates of parameters for growth functions (e.g. the von Bertalanffy growth function).

A more useful approach is to fit growth functions to tag-recapture data. A range of techniques have been developed to undertake this type of analysis. Early techniques used relatively simple approaches (e.g. Walford, 1946; Gulland and Holt, 1959; Fabens, 1965) to estimate parameters of the von Bertalanffy growth function. Species of elasmobranchs for which these types of techniques have been used include three species of *Raja* (Holden, 1972), *C. plumbeus* (Wass, 1973; Casey and Natanson, 1992), *Galeorhinus galeus* (Grant et al., 1979), *Squatina californica* (Cailliet et al., 1992) and *Galeocerdo cuvier* (Natanson et al., 1999). With the advent and proliferation of powerful computers, more sophisticated techniques have been developed to deal with tag-recapture data and to allow the fitting of a range of growth functions and the estimation of confidence intervals (Francis, 1988). These growth functions have included both the widely used von Bertalanffy curve, as well as other forms (e.g. Schnute, 1981; Francis, 1995). In addition, functions that allow for the estimation of seasonal growth patterns (e.g. Francis, 1988), growth variability (e.g. Francis, 1988, Wang et al., 1995), and measurement error (e.g. Francis, 1988) have been developed. These more complex functions allow researchers to extract more information from tag-recapture data, as well as identify factors that may be important in determining the growth of individual animals. These types of analysis have not been widely used in elasmobranch studies to date. However, Francis and Francis (1992) and Francis and Mulligan (1998) used the Francis (1988) method for *Mustelus lenticulatus* and *G. galeus*, respectively.

Tagging studies of elasmobranch populations have also been used to validate age data based on vertebrae. Individuals are injected with a marker that is incorporated into calcifying structures so that the number of bands laid down between tagging and recapture can be determined, and the periodicity of band formation validated (Cailliet, 1990). The most commonly used marker in these studies is oxytetracycline (OTC) at dose rates of approximately 25 mg/kg (Gelsleichter et al., 1998). OTC is also a powerful antibiotic with recommended daily doses of 10mg/kg for elasmobranchs (Stoskopf, 1993). Despite its antibiotic properties it has been demonstrated to have toxic effects on some teleosts (e.g. Marking et al., 1988). Although widely used, the impact of OTC injection on the growth of elasmobranchs has been poorly studied. Tanaka (1990) demonstrated that injection of OTC did not affect the growth of juvenile *Orectolobus japonicus* at normal dosages. Gelsleichter et al. (1998) reported that OTC injection did not affect the growth of nurse sharks (*Ginglymostoma cirratum*), but that it may have some level of hepatotoxicity. In the only reported study of a wild elasmobranchs, Natanson et al. (1999) reported that four *Galeocerdo cuvier* specimens injected with OTC did not have growth rates different from those not injected with OTC.

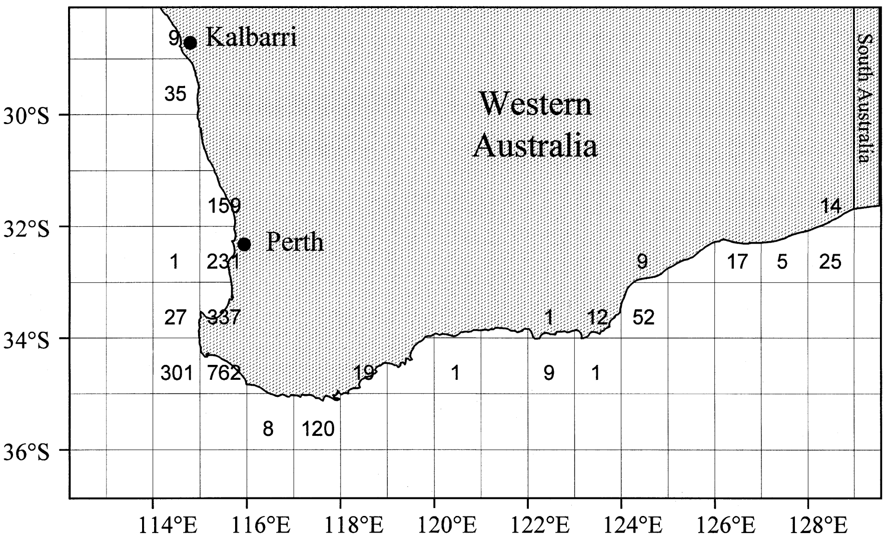

Figure 1

Numbers of juvenile *Carcharhinus obscurus* released in one-degree geographic blocks off southwestern Australia.

The dusky shark, *Carcharhinus obscurus*, is a large species of coastal shark that occurs in tropical, subtropical, and temperate oceans world-wide (Compagno, 1984). They are born at 70–100 cm total length (TL), mature at approximately 280 cm TL, and grow to at least 365 cm TL (Last and Stevens, 1994). Natanson et al. (1995) provided estimates of growth parameters for *C. obscurus* from the western North Atlantic, using length-at-age data and length-frequency data. These data indicate that *C. obscurus* is slow growing, reaches maturity at approximately 19–21 years, and possibly lives to 45 years. Natanson and Kohler (1996) estimated growth parameters for *C. obscurus* from the southwest Indian Ocean, using length-at-age data that indicated growth similar to that from the western North Atlantic.

A demersal gillnet fishery in southwestern Australia targets neonate and small juvenile *C. obscurus*, mostly from February to June. The fishery has operated since the 1940s, but significant catches of *C. obscurus* were not taken until the mid 1970s (Simpfendorfer and Donohue, 1998). Increasing fishing effort in the 1980s lead to concerns about the status of this resource and prompted a research project that included a tag and release study to estimate mortality (Simpfendorfer, 1999), movement, and growth parameters for *C. obscurus*. The aims of this paper are 1) to estimate growth rates and growth parameters for *C. obscurus* based on tag-recapture data using four different methods, 2) to investigate differences in growth due to sex or injection with OTC, and 3) to estimate growth variability and measurement error.

Materials and methods

Tagging

Neonate and juvenile *C. obscurus* were caught between March 1994 and June 1996 by commercial demersal gillnet vessels operating in southwestern Australia. These vessels operate in continental shelf waters in depths of 7–100 m. The gill nets are constructed of 16.5-cm and 17.8-cm (stretched) mesh monofilament netting that is 1.5 m to 2.0 m deep. Nets are 3–7 km in length and are set on the sea floor for periods of 7–24 hours.

Individual *C. obscurus* were measured (fork length [FL]: the distance from the tip of the snout to the caudal fork measured as a straight line) to the nearest centimeter, the sex of each fish was determined, and each fish was examined for the presence of an open umbilical scar, and tagged with an individually numbered Jumbo Rototag (Dalton Supplies, Woolgoolga, New South Wales, Australia) in the first dorsal fin. Approximately one in every three animals was injected with OTC (25 mg/kg) to mark the vertebral centra for age validation studies.

A total of 2199 juvenile *C. obscurus* were released from March 1994 to June 1996 between the Western Australian and South Australian border (129°E) and Kalbarri (29°S) (Fig. 1). Tagged sharks ranged in size from 53 cm FL to 108 cm FL but most were 70–81 cm FL (Fig. 2). One thousand seven hundred and thirty (78.7%) had open umbilical scars; 1062 were female, 1100 were male, and 37 were of unknown sex; 879 were injected with OTC and 1320 were not injected. Information on tag-recaptures, including date and location of recapture, and length were reported by commercial fishermen and research observers operating in the demersal gillnet fishery. Fishermen were provided with tape measures and trained to measure fork length in an attempt to improve the accuracy of recapture data.

Analysis

Growth rates of five groups of juvenile *C. obscurus*—males, females, OTC injected, non–OTC-injected, and all recaptures combined—were estimated by using four different

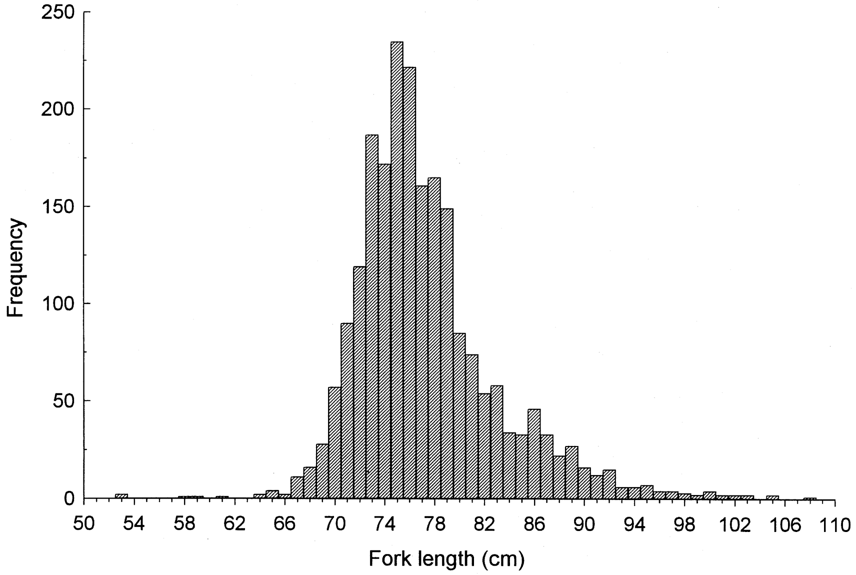

Figure 2

Size at release for 2199 juvenile *Carcharhinus obscurus* tagged off southwestern Australia,

methods. Only recaptures with data that included the date of recapture and accurate length at release and recapture were used in the analyses.

Gulland and Holt (1959) The first method used for estimating growth rates was that of constructing plots of growth rate by average fork length (Gulland and Holt, 1959). The average fork length was calculated as the average of the fork length at release and recapture. Von Bertalanffy growth parameters were estimated by fitting a line through the data. The slope of the line was equal to $-K$, and the intercept with the x-axis was equal to L_∞.

Fabens (1965) The Fabens (1965) method involved fitting the nonlinear function:

$$L_R = L + (L_\infty - L)\,(1 - e^{-Kd}), \tag{1}$$

where L_R = the length at recapture;
L = the length at release; and
d = the period at liberty.

This function was fitted to the data by using the nonlinear estimation module in STATISTICA (Statsoft, 1998). The value of t_0 was estimated by solving the function for the value of T

$$L_T = L_0 + (L_\infty - L_0)\,(1 - e^{-KT}), \tag{2}$$

where the value of L_0 = the mean size at birth; and
L_T = 0 cm.

The mean size at birth of *C. obscurus* from southwestern Australia was estimated by fitting a normal probability function to a size-frequency distribution of tagged individuals that had an open umbilical scar (Fig. 3). From these data the mean size at birth was 75.3 cm FL.

Francis (1988) method This method uses a maximum likelihood approach to fitting a growth function that includes estimated growth rates (g_α and g_β) at two selected lengths (α=75 cm FL and β=100 cm FL), the coefficient of variation of growth variability (v), measurement error (assumed to be normally distributed with a mean, m, and standard deviation, s), and outlier probability (p). The estimated growth increment for an individual, i, is given by

$$\Delta L_i = \left[\frac{\beta \cdot g_\alpha - \alpha \cdot g_\beta}{g_\alpha - g_\beta} - L_i\right]\left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta}\right)^{\Delta T_i}\right],$$

where L_i = the length at release; and
ΔT_i = the period at liberty.

Francis (1988) suggested several methods of incorporating growth variability into the model.

The likelihood function is

$$\lambda = \sum_i \log\left[(1-p)\lambda_i + p / R\right],$$

where $\lambda_i = \dfrac{\exp\left(-0.5(\Delta L_i - \mu_i - m)^2 / (\sigma_i^2 + s^2)\right)}{\left[2\pi(\sigma_i^2 + s^2)\right]^{0.5}}$;

R = the range of the observed growth increments;

μ_i = the expected value of growth increment of the ith individual; and

σ_i = the standard deviation of the growth variability.

In the present study σ_i was assumed to be proportional to predicted growth increment (i.e. $\sigma_i = v\mu_i$).

The solver function in Microsoft Excel (Microsoft, 1999) was used to maximize the likelihood value of the model. Although the growth model allowed the use of six parameters, the number of parameters used for each of the groups was determined by using the likelihood ratio test (LRT). In its simplest form growth was assumed to be linear ($g_\alpha = g_\beta$) and to include s. The addition of more parameters (nonlinear growth [$g_\alpha \neq g_\beta$], v, m, and p) was significant if the likelihood increased by more than 1.92 per parameter (Francis, 1988). The final model used for each group was the one with the least number of significant parameters.

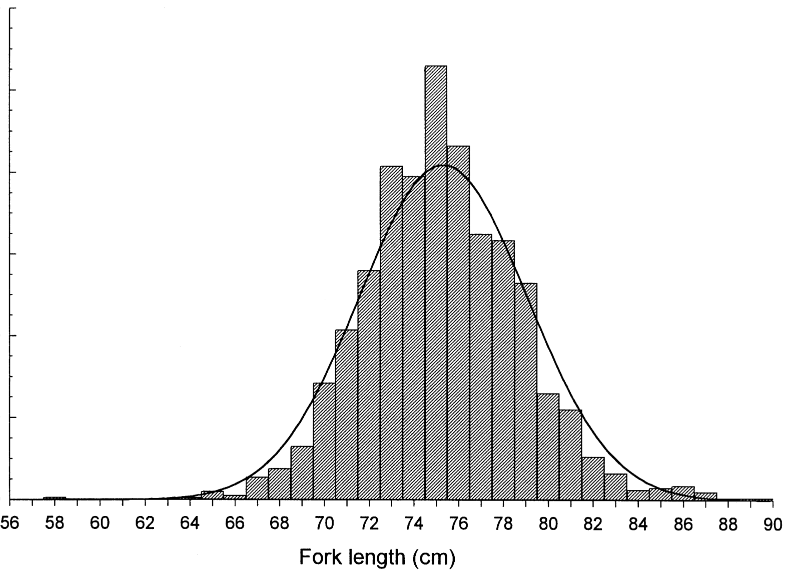

Figure 3

Size-frequency distribution of 1537 neonate *Carcharhinus obscurus* from southwestern Australia with open umbilical scars. The line represents a normal distribution with a mean of 75.3 cm and a standard deviation of 3.75 cm.

Bootstrapping was used to estimate 95% confidence intervals for parameter estimates. New growth increment values were generated by adding randomly selected points from two normal distributions. The first distribution had a mean of the predicted growth increment with a standard deviation equal to $v\mu$ and represented growth and growth variability. The second distribution represented the measurement error and had a mean of m and a standard deviation of s. Five hundred bootstrapped data sets were created by using each method and fitted by using the technique described above. Ninety-five percent confidence intervals were calculated from the 2.5th percentile and the 97.5th percentile of the resulting parameter distributions.

Length-at-age for neonate releases The use of length-at-age data is normally associated with aging studies where the age of an individual shark is estimated from the number of bands on the vertebrae. Because most animals tagged in the current study had open umbilical scars, it was possible to estimate the age of each of the recaptured animals directly from the time at liberty and the rate of healing of the umbilical scar. There is limited information available on the time that it takes for the umbilical scar to close, but most estimates range from 4 to 6 weeks (Bass et al., 1973). If it is assumed that a shark with an open scar was tagged at an age of three weeks (the assumed age at release), the age at recapture is the time at liberty plus three weeks. Preliminary data analysis showed that a linear growth function ($L_t = bL + a$, where b is the growth rate and a is a constant) provided a better fit to the data than a von Bertalanffy function. Thus a linear model was fitted to the length-at-age data. Growth rates (b values) were compared between males and females, and between injected and noninjected animals, using the homogeneity-of-slopes model within the visual general linear model module of STATISTICA. Significant differences in growth rates existed when the interaction term (age×sex or age×injection status) was significant. If there were significant differences in the growth rates for sexes then differences in the growth rates between injected and noninjected animals were assessed separately for males and females, otherwise they were assessed for males and females combined.

Results

A total of 473 recaptures of juvenile *C. obscurus* were reported to September 1998. Recaptured animals were at liberty between 0 and 1716 days (4.7 years); seven were at liberty for more than three years. Tag-recapture data from all individuals with usable data were included in the Francis (1988) method, whereas only those with times at liberty greater than 60 days were used in the other methods of analysis. Individuals at liberty less than 60 days were excluded because many individuals had growth rates that were beyond those considered reasonable because of the short period at liberty (Fig. 4). The size at recapture ranged from 68.5 to 147 cm FL. There were 304 recaptured sharks with usable data, and 274 recaptured sharks with times at liberty greater than 60 days. These recaptured sharks included 153 males (137 at liberty >60 days), 143 females (130 at liberty >60 days), 118 individuals injected

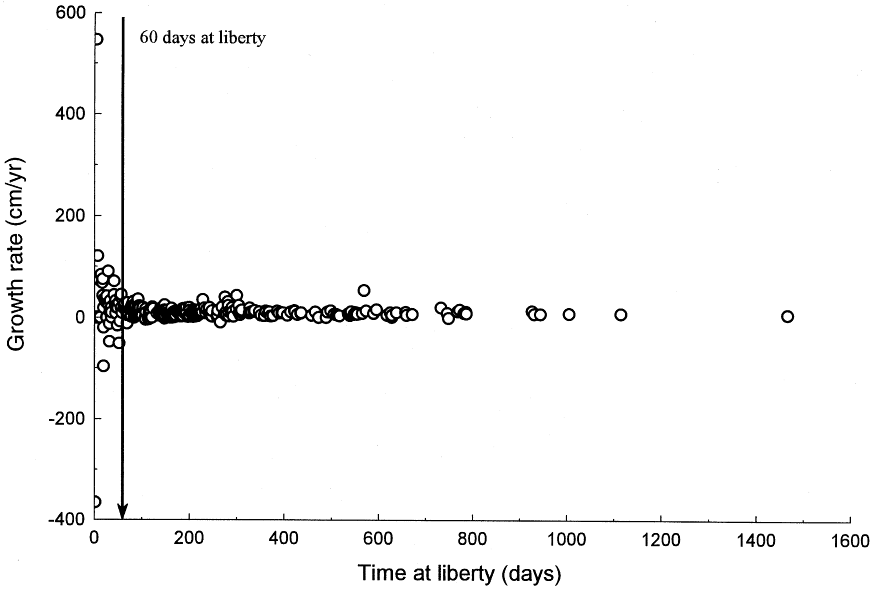

Figure 4

Growth rates of recaptured juvenile *Carcharhinus obscurus* from southwestern Australia as a function of time at liberty. The line indicates 60 days at liberty, the time below which individuals were excluded from analysis.

with OTC (111 at liberty >60 days), and 179 individuals not injected with OTC (160 at liberty >60 days).

Gulland and Holt (1959) method

Linear regressions fitted to the growth rate versus average fork length had positive slopes for all groups examined. As a result estimates of K were negative, and L_∞ was unsolvable. These results indicate that this method was unable to estimate growth parameters for juvenile *C. obscurus*.

Fabens (1965) method

Von Bertalanffy growth parameters estimated by the Fabens (1965) method varied widely (Table 1). All the groups, except the noninjected individuals, produced estimates of K between 0.092/year and 0.187/year, and estimates of L_∞ between 142 cm FL and 194 cm FL. For the noninjected individuals the estimate of K was 0.031/year and L_∞ was 379 cm FL. Values of r^2 for all groups were relatively high, indicating that the von Bertalanffy parameters explained most of the variation in the data.

Francis (1988) method

The likelihood ratio tests for each of the five groups of *C. obscurus* indicated that the appropriate models were relatively simple, containing linear growth ($g_\alpha = g_\beta$), v, s, and sometimes m (Table 2). Contamination probability (p) and g_β were not included in the final models for any of the groups. The value of m was assumed to be zero for models in which it was not included.

Table 1

Estimates of von Bertalanffy growth parameters with the Fabens (1965) method for juvenile *Carcharhinus obscurus* from southwestern Australia.

Group	L_∞ (cm)	K (per year)	r^2
All	177	0.111	0.74
Male	195	0.092	0.80
Female	142	0.187	0.67
Injected	156	0.167	0.73
Noninjected	379	0.031	0.72

The Francis (1988) method estimated that the linear growth rate for all juvenile *C. obscurus* was 9.23 cm/year (Table 3). The growth rate of males was 1.1 cm/year higher than that for females, and 2.2 cm/year higher for OTC-injected than for noninjected animals. The 95% confidence intervals (CI), however, indicated that differences in growth rate were not significant between any of the five groups. Estimates of v and s were similar for all groups examined, ranging from 0.24 to 0.40 and from 2.09 cm FL to 2.54 cm FL, respectively. The 95% CIs indicated no significant differences in v or s between groups. The values of m, for models in which it was calculated, ranged from 0.69 cm FL to 0.94 cm FL. There were no significant differences in m between the all, females, and noninjected groups.

Table 2

Likelihood values from the Francis (1988) method for different combinations of parameters. Values in bold indicate the final model used in the analysis for each of the five groups of *Carcharhinus obscurus*. Significance of additional parameters was tested with the likelihood ratio test (see text for details).

Model	All	Male	Female	Injected	Noninjected
g_{75}, s	–807.23	–396.19	–386.90	–305.04	–470.90
g_{75}, v, s	–778.69	**–382.17**	–372.77	**–296.24**	–456.65
g_{75}, v, s, m	**–774.73**	–381.57	**–369.53**	–295.69	**–453.42**
g_{75}, v, s, m, p	–774.73	–381.57	–369.47	–295.69	–452.26
g_{75}, g_{100}, s	–806.76	–395.98	–386.81	–304.90	–497.58
g_{75}, g_{100}, v, s	–778.51	–382.16	–372.62	–295.83	–480.47
g_{75}, g_{100}, v, s, m	–774.69	–381.56	–369.46	–295.52	–476.73
$g_{75}, g_{100}, v, s, m, p$	–774.69	–381.56	–369.39	–295.52	–476.06

Table 3

Growth parameter estimates for five groups of *Carcharhinus obscurus* from southwestern Australia with the Francis (1988) method for the best models determined in Table 2. Numbers in parentheses after estimates are 95% confidence intervals calculated by bootstrapping.

Parameter	All	Male	Female	Injected	Noninjected
g_{75} (cm/year)	9.23	10.24	9.14	10.84	8.69
	(8.24–10.11)	(9.41–11.17)	(7.73–10.49)	(9.68–11.63)	(7.43–10.01)
v	0.34	0.34	0.33	0.24	0.40
	(0.26–0.42)	(0.24–0.43)	(0.21–0.45)	(0.23–0.37)	(0.28–0.52)
s	2.35	2.09	2.54	2.43	2.33
	(2.03–2.63)	(1.69–2.46)	(2.09–2.93)	(1.91–2.74)	(1.94–2.73)
m (cm)	0.69	—	0.94	—	0.83
	(0.22–1.17)		(0.23–1.67)		(0.12–1.49)

As a comparison to estimates of m and s from the Francis (1988) method, differences in the size at release and recapture for animals at liberty less than 30 days were determined. If it is assumed than these animals grew a negligible amount over this period, and the animals were measured perfectly by research staff at release, then the mean and standard deviation of the differences should provide an independent estimate of m and s. The mean difference in size for 38 *C. obscurus* at liberty less than 30 days was 1.17 cm FL, and the standard deviation was 2.09 cm FL (Fig. 5). These values are similar to those estimated from the model for most of the groups

Length-at-age for neonate releases

A total of 241 released neonates (with open umbilical scars) were recaptured, including 117 males, 120 females, four of unknown sex, 92 OTC-injected animals, and 149 noninjected animals. The linear growth rate based on all neonate recaptures was 9.4 cm/year. The growth rate was higher for males than for females, and higher for injected animals than for noninjected animals (Table 4). Comparison of growth rates with the homogeneity-of-slopes models (Fig. 6, Table 5) indicated that there were significant differences between males and females, and between injected and noninjected males. However, there was no significant difference between injected and noninjected females (Table 5).

Discussion

Shark growth studies have typically used the von Bertalanffy growth function to describe how sharks grow, including previous work on *C. obscurus* (e.g. Natanson et al., 1995; Natanson and Kohler, 1996). However, in the current study the results indicated that a linear growth curve more accurately describes the growth of juvenile *C. obscurus* up to five years of age. Pratt and Casey (1990) suggested that for some slow growing sharks (e.g. *Carcharhinus plumbeus*) a linear growth function might provide a better predictive model than the von Bertalanffy growth function. Although linear growth functions have been rarely used in fish growth studies, Bayliff (1988) reported that this type of function provided the best fit to

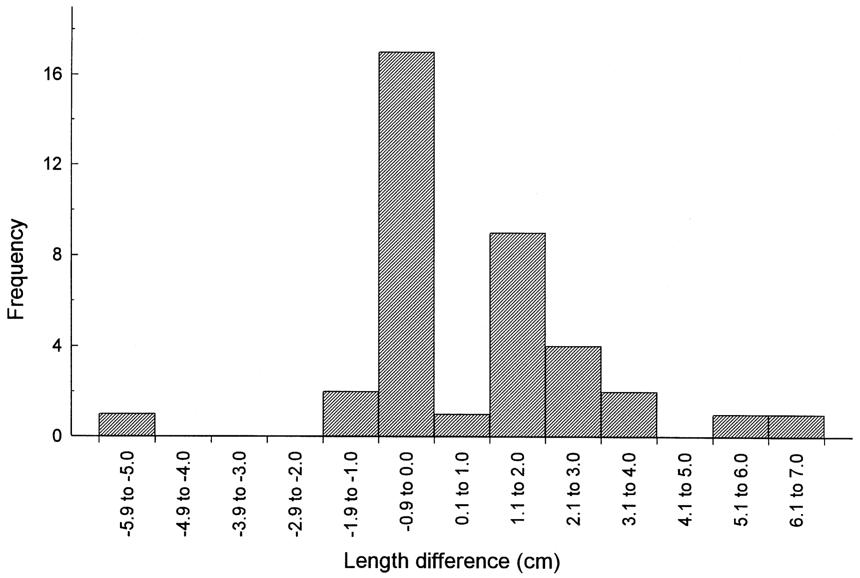

Figure 5

Differences between release and recapture lengths for 38 juvenile *Carcharhinus obscurus* at liberty less than 30 days off southwestern Australia.

growth data from tagged yellowfin tuna (*Thunnus albacares*) up to 100 cm long. Because the current study used only data from individuals up to five years old, which is a short period in relation to the estimated longevity of this species (45 years, Natanson et al., 1995), there was no information in the data on the rate at which the length reaches its asymptote (equivalent to the rate of decrease in the growth rate with increasing age). As a result the von Bertalanffy growth function cannot adequately describe the data. If recapture data were available for individuals from older age classes, it is likely that a decrease in growth rate with increasing age may have been observed and thus a von Bertalanffy growth function (or the Francis (1988) model with $g_\alpha \neq g_\beta$) may have provided the best fit to the data.

The Gulland and Holt (1959) method relies on a decrease in growth rates with increasing age to estimate both L_∞ (x-intercept) and K (slope). Thus, because the tag-recapture data for *C. obscurus* did not contain this information, the method was not able to estimate von Bertalanffy growth parameters. The inability to produce results, while other methods did, illustrates that the Gulland and Holt (1959) method fails in some situations where the periods at liberty are short in relation to the maximum age and where the recaptured individuals cover only a small proportion of the age classes present in the population. The lack of information in the data on the decrease in growth rate with increasing age also caused problems for the estimation of parameters in the Fabens (1965) method. In all cases, except for the noninjected group, this method provided substantially lower values of L_∞ than expected from observations of the maximum length of *C. obscurus* in Western Australian waters (280 cm FL, Simpfendorfer et al., unpubl. data[1]) and from previous growth studies (Natanson et al., 1995; Natanson and Kohler, 1996). Similarly, values of K were substantially higher than literature values (0.034 to 0.062, Natanson et al., 1995; 0.047, Natanson and Kohler, 1996) for each of the groups except the noninjected animals. The von Bertalanffy growth parameters estimated for the noninjected group by the Fabens (1965) method were similar to those estimated by Natanson et al. (1995) and Natanson and Kohler (1996).

Table 4

Linear growth rates (b) of juvenile *Carcharhinus obscurus* based on length-at-age data for neonate releases. Values in parentheses are standard errors of b.

Group	n	b (cm/yr)	r^2
All	241	9.39 (0.38)	0.706
Male	117	10.58 (0.48)	0.787
Female	120	8.46 (0.56)	0.644
Injected	92	10.05 (0.53)	0.773
Noninjected	149	8.54 (0.53)	0.633

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[1] Simpfendorfer, C. A., R. McAuley, J. Chidlow, R. Lenanton, and N. Hall. 1999. Biology and stock assessment of Western Australia's commercially important shark species. Unpubl. report. Western Australian Marine Research Laboratories, PO Box 20, North Beach, Western Australia 6020, Australia.

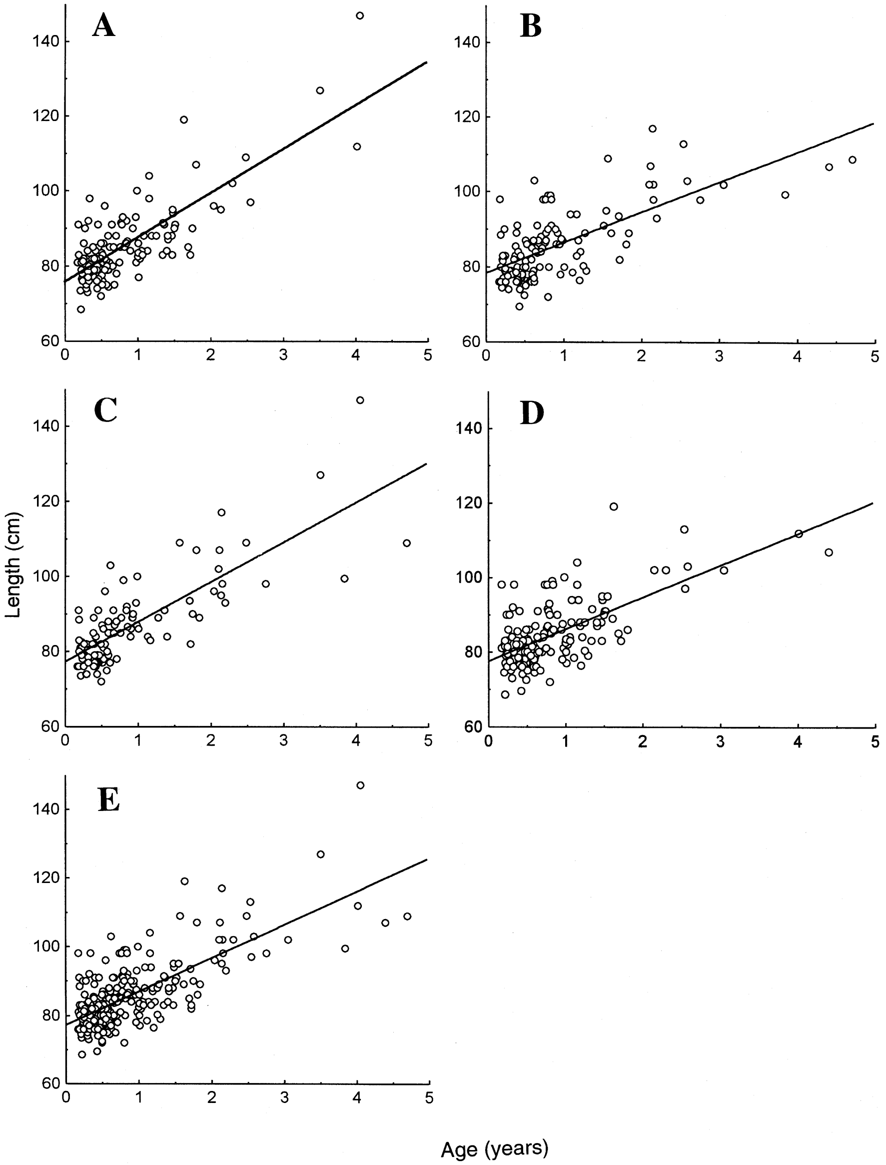

Figure 6

Length-at-age plots for (**A**) male, (**B**) female, (**C**) injected, (**D**) noninjected, and (**E**) all *Carcharhinus obscurus* from southwestern Australia. Lines represent linear growth functions based on parameters given in Table 4.

Despite the difficulties in obtaining von Bertalanffy growth parameters with the Fabens (1965) method, the growth rates from age zero to 5 years were similar to those from the linear growth function from the Francis (1988) and length-at-age methods (Fig. 7). Each of the methods indicates that on average juvenile *C. obscurus* grow 8–11 cm/year. The results from the current study (for all methods) were also similar to those from previous studies for *C. obscurus* in the western North Atlantic and southwestern Indian Ocean by Natanson et al. (1995) and Natanson and Kohler (1996), respectively (Fig. 7). However, the growth rates were lower than those suggested by Branstetter (1990) who used data from Schwartz (1983) to estimate the growth rate of *C. obscurus* pups from the western North Atlantic to be approximately 15 cm/year. At ages greater than five years, the growth rates estimated by the current study corresponded poorly to observed results in other studies. This is a result of the linear growth of the juveniles that does not predict the decrease of growth rates as individuals age. Extrapolation of the results to ages greater than five years is thus invalid and should be avoided.

The results of the Francis (1988) method indicate a relatively high level of growth variation in juvenile *C. obscu-*

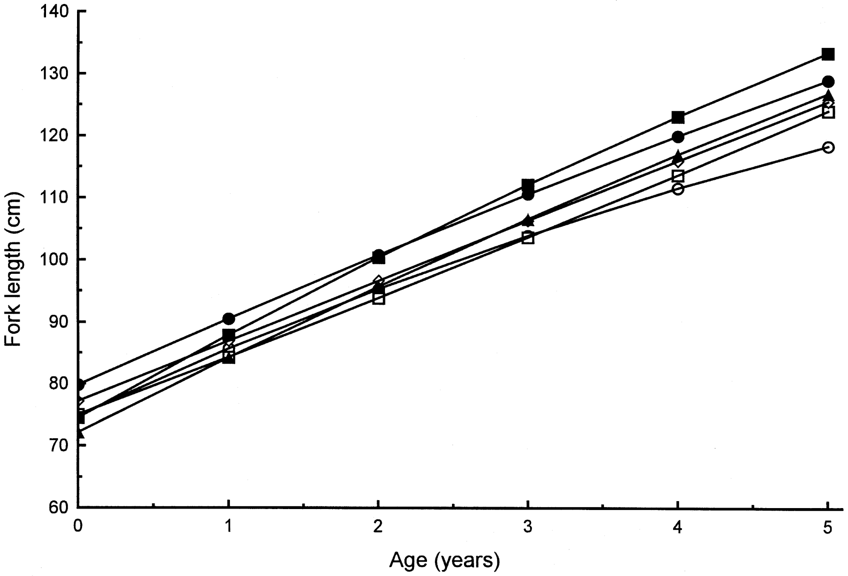

Figure 7

Comparison of growth rates from three methods used in the current study (open symbols: circle = Fabens [1965] method; square = Francis [1988] method; diamond = length-at-age method) and previous research (solid symbols: circle = length-at-age from vertebrae; square = tag-recapture data from Natanson et al. [1995]; triangle = Natanson and Kohler [1996]).

Table 5

Results of homogeneity-of-slopes models in which growth rates between male and female, and injected and noninjected *Carcharhinus obscurus* were compared. ** indicates significant effects. SS = sum of squares.

Comparison	Effect	SS	df	*F*	*P*
Male with female	sex	107.60	1	5.31	0.022**
	age	12997.64	1	641.44	0.000**
	sex × age	161.69	1	7.98	0.005**[1]
Male					
Injected with noninjected	injection status	7.72	1	2.99	0.086
	age	7012.62	1	555.84	0.000**
	injection status × age	224.323	1	17.78	0.000**
Female					
Injected with noninjected	injection status	18.02	1	0.68	0.411
	age	5720.07	1	216.34	0.000**
	injection status × age	0.34	1	0.013	0.910

[1] Because *age* × *sex* interaction is significant, comparisons of injected and noninjected groups must be conducted for males and females separately.

rus. The value of v in the present study (0.24–0.40) was higher than that estimated for *Galeorhinus galeus* (0.06) (Francis and Mulligan, 1998), but lower than for *Mustelus antarcticus* (0.58) (Francis and Francis, 1992). Francis and Mulligan (1998) suggested that their data might not contain enough information to distinguish between measurement error and growth variability. Francis (1997) and Francis et al. (1999) reported similar levels of growth variability for elephantfish (*Callorhinchus milii*) and hapuku (*Polyprion oxygeneios*), respectively. Growth variability therefore appears consistently to be relatively high across a range of elasmobranch, chimaerid, and teleost fishes.

The observed growth variability in juvenile *C. obscurus* may in part have been due to seasonal growth variation, migrations between warmer waters on the west coast of Western Australia, and cooler waters on the south coast. Either of these factors could possibly have produced substantial variation in growth rates. Further research on the influence of temperature on growth of *C. obscurus* would prove useful in isolating the causes of growth variability in this species.

The estimated measurement error parameters from the Francis (1988) method were similar but slightly lower than those from the differences in length for individuals at liberty less than 30 days. The close agreement between these results indicates that the Francis (1988) method provides accurate estimates of measurement error and that the confounding of measurement error and growth variability reported by Francis and Mulligan (1998) was not a problem in the current study. The magnitude of the mean measurement error was small (0–0.94 cm) in relation to the length of the sharks examined (55–140 cm). Previous studies using the Francis (1988) method have indicated that including m in the model does not improve the result, whereas values of s have included 1.2 cm (*C. milii,* Francis, 1997), 1.5 cm (*P. oxygeneios*, Francis et al., 1999), 1.6 cm (*Mustelus lenticulatus*, Francis and Francis, 1992) and 7.2 cm (*G. galeus*, Francis and Mulligan, 1998).

The length-at-age analysis indicated that male juvenile *C. obscurus* have significantly higher growth rates than females. This result, however, was not supported by the results from the Francis (1988) method that showed overlap in the 95% confidence intervals derived from bootstrapping. Differences in growth rates do occur between the sexes in sharks, but these differences are most commonly observed at ages close to maturity (approximately 20 years in *C. obscurus*) (e.g. Simpfendorfer, 1993; Simpfendorfer et al., 2000). Thus the lack of significant differences in the growth rate between young male and female *C. obscurus* was not unexpected. The difference in the results between the two methods may be due to the simple linear model fitted to the length-at-age data not being able to account for growth variability and measurement error. This demonstrates the improvement in understanding that the more complex Francis (1988) model can provide over more simplistic approaches.

The results of the length-at-age analysis in the current study indicate that male *C. obscurus* injected with OTC have significantly higher growth rates than noninjected males. However, females showed no significant difference between injection and noninjection with OTC. The parameter estimates from the Francis (1988) model indicated that injected animals grow 2.2 cm/year faster than noninjected animals. However the 95% confidence intervals overlapped slightly (injected, 9.68–11.63; noninjected, 7.43–10.01) indicating that there were no significant differences in growth rates. Although the significance of growth rate differences varied between analysis methods and sexes, suggesting that differences may have been the result of biased data, there is sufficient evidence to warrant further investigation of the effect of OTC injection on juvenile *C. obscurus*. Previous studies of elasmobranchs have not found significant differences in growth rates between injected and noninjected animals (Tanaka, 1990; Gelsleichter et al., 1998; Natanson et al., 1999). However, only one of these studies (Natanson et al., 1999) was carried out on sharks in the wild. This study was based on four OTC-injected *G. cuvier* specimens and no statistical comparison of growth rates between injected and noninjected individuals was undertaken.

If growth differences between OTC-injected and noninjected *C. obscurus* do occur, they may result from the antibiotic properties of OTC. It is likely that injections of OTC would not increase growth rates; rather, the growth of noninjected animals may be lower after tagging. The capture and tagging process is likely to present a significant source of stress for sharks—one that may increase their chances of microbial infection and slow their growth (e.g. Olsen, 1953; Davies and Joubert, 1967; Manire and Gruber, 1991). Animals injected with OTC would be more likely to overcome these infections quickly and thus grow at rates indicative of untagged individuals. If this scenario can be proven, then the faster growth rates predicted by the Francis (1988) method for the injected juvenile *C. obscurus* (10.84 cm/year) are likely to be most representative for this species.

This study indicates that although a range of techniques are available to estimate growth rates and von Bertalanffy growth parameters from tag-recapture data, they can produce variable results. One method, the Gulland and Holt (1959) method, was not able to produce results for juvenile *C. obscurus*. Another, the Fabens (1965) method, produced unrealistic von Bertalanffy growth parameters. Two methods, the Francis (1988) and length-at-age methods, indicated that linear growth functions provided better predictive power for juvenile *C. obscurus* than the nonlinear von Bertalanffy growth function. The use of the Francis (1988) method allowed for a more detailed investigation of the growth of *C. obscurus,* including the investigation of measurement error and growth variability. Estimation of these additional parameters is particularly useful in tag-recapture studies where commercial and recreational fishermen provide the majority of data. Thus, although the more traditional methods are still commonly used for elasmobranchs, researchers should consider the use of more detailed approaches, such as that of Francis (1988), to extract the maximum possible information from their data.

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