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## Size and age compositions and reproductive biology of the nervous shark *Carcharhinus cautus* in a large subtropical embayment, including an analysis of growth during pre- and postnatal life

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**Abstract** The lengths-at-age of individuals of the nervous shark *Carcharhinus cautus* in Shark Bay, Western Australia, have been determined and used to explore the types of situation when it might be advisable to shift from employing a von Bertalanffy equation to a more complex equation for describing the growth of this species and of elasmobranchs in general. The reproductive biology of *C. cautus* was also examined in order to construct curves for describing growth throughout life from conception as well as from parturition. The presence, in November and early December, of fresh bite marks on the sides of mature females and of a very high proportion of spent individuals among mature males indicate that *C. cautus* copulates in late October/early November. Ovulation and conception occur in late November/early December and parturition takes place approximately 11 months later. Since mature non-pregnant females contain vitellogenic ova for 12–13 months, i.e. from November or December to the following December, and mature pregnant females contain embryos for 11 months, i.e. from December to October, *C. cautus* has a biennial reproductive cycle. By parturition, the females and males of *C. cautus* had reached ~28% and 32% of their lengths at their maximum observed ages, respectively. The maximum recorded total lengths and ages of females and males of *C. cautus* were 133 cm and 16 years and 111 cm and 12 years, respectively. Females and males reached maturity at ~101 and ~91 cm, respectively, and at least 50% of females and males had become mature by the

end of their sixth and fourth years of life after parturition, respectively. The three-parameter, von Bertalanffy growth curves provided reasonably good fits to the lengths-at-age of females and males of *C. cautus* during just postnatal life and throughout the whole of pre- and postnatal life. While the four-parameter, Schnute growth curve significantly improved the fit to these data for both females and males from conception and for females from parturition, it was recognised that the likelihood ratio test is very sensitive when, as in these cases, there are a large number of data points. A number of interrelated factors were thus taken into account when discussing circumstances when it might be appropriate to switch from using a von Bertalanffy growth curve to the more complex Schnute growth curve.

### Introduction

The Carcharhinidae (requiem or whaler sharks) contains 49 species, which makes it one of the largest shark families (Last and Stevens 1994). More than half of these species belong to the genus *Carcharhinus*, the vast majority of which are found in Australian waters (Garrick 1982). The members of this genus, which range in length from 0.7 to 3.7 m, are the dominant shark species in tropical and subtropical waters (Last and Stevens 1994).

Although *Carcharhinus* is a speciose and widely distributed genus, there have been few studies of the age compositions and growth of its various species. However, the ages of individuals of *C. tilstoni* and *C. sorrah* in northern Australian waters have been determined, and the resultant length-at-age data have been used to construct von Bertalanffy growth curves (Davenport and Stevens 1988). Although the ages at length 0 of these species, i.e.  $t_0$ , were  $<0$  in the von Bertalanffy growth equations, as would be expected when the age at parturition was set as age 0, they were still, in most cases, appreciably greater than the duration of embryonic life. This implies that the rate of growth in the

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period prior to birth, when a considerable amount of growth occurs, was more rapid than could be accommodated by the von Bertalanffy growth equation that was fitted to the length-at-age data during postnatal life.

Recent studies have demonstrated that the mean size (disc width) at parturition of individuals of another group of elasmobranchs, namely the myliobatiforms *Urolophus lobatus*, *Trygonoptera personata* and *T. mucosa*, represented between 33% and 52% of their asymptotic disc widths (White et al. 2001, 2002). Thus, in the case of the two *Trygonoptera* species, it was decided to ascertain whether it was possible to use a single, smooth curve to describe the pattern of growth of the females and males of these species throughout the whole of their prenatal and postnatal life. Although the von Bertalanffy growth curve fitted most of the latter data well, it passed below the points for the lengths-at-age of the very largest females. This slight deficiency was overcome by using the Schnute growth curve (Schnute 1981), which incorporates four parameters rather than the three that are present in the von Bertalanffy growth equation.

The objectives of the present study were: (1) to determine the age compositions of the females and males of the nervous shark *Carcharhinus cautus*, (2) to elucidate the timing of reproductive events and the sizes attained by embryos at regular intervals, and (3) to use the resultant length-at-age data to construct growth curves for both sexes of this species. Since this species gives birth at a relatively large size (Lyle 1987), the pattern of growth throughout their entire life from conception, as well as throughout just postnatal life, has been determined. Growth was initially analysed using the von Bertalanffy growth equation, as is typically employed for describing growth in elasmobranchs (e.g. Branstetter 1987a; Simpfendorfer 1993; Lessa et al. 1999). Although the resultant growth curves for females fitted most of the lengths-at-age well, they passed below the points for larger fish, as was also the case with the two *Trygonoptera* species referred to earlier (White et al. 2002). The Schnute growth equation has thus likewise been used to ascertain whether it provided a significantly better fit to the lengths-at-age of this species. However, since the likelihood-ratio test, which is used to compare growth curves, is very sensitive when, as in the current study, the number of points for the lengths-at-age are large, the question of whether it is desirable to shift to a more complex and far less widely used equation has been explored.

Emphasis was placed initially on elucidating the timing of reproductive events and the sizes attained by embryos at regular intervals in order to determine accurately the pattern of growth of female and male *C. cautus* throughout the whole of life after conception. Since the timing of reproductive events is likely to be influenced by water temperature, our data on the reproductive biology have been compared with those of Lyle (1987), who studied *C. cautus* in a far more northern and thus warmer part of Australia.

## Materials and methods

### Sampling location and regime

*Carcharhinus cautus* was collected from waters surrounding the central and large Peron Peninsula of Shark Bay, and mainly from the region of Herald Bight (25°40'S; 113°32'E) on the north-eastern tip of this peninsula (see Fig. 1 in Walker et al. 1988). The samples at Herald Bight were obtained from one site containing moderately dense mangroves, another with sparse mangroves and a third where no mangroves were present nearby. These three sites, which were located near the shore and in water depths <1.8 m, were sampled using gill nets in at least bimonthly intervals between January 1999 and September 2001. The waters over seagrass (*Amphibolis antarctica* and *Posidonia australis*) at Herald Bight, where the depth was 2–3 m, were also sampled by gill netting on four occasions. The nets were set at night for ~3 h around the time of high tide. Further samples were obtained from Herald Bight and other regions along the Peron Peninsula by rod and line, using fish fillets as bait, and by opportunistic haul and seine netting. The haul and seine nets were used in unvegetated areas near the shore, with the latter catching the small individuals of *C. cautus* soon after they had been born. Water temperatures and salinity were recorded at each site on each sampling occasion.

The composite monofilament gill nets, which were 2.5 m high, comprised three 30-m-long panels containing either 10, 15 or 17.5 cm mesh. The meshes in the 60-m-long haul net and in the bunt of the 21.5 m seine net were 100 and 3 mm, respectively.

The total length (to the nearest 1 mm and 1 cm for sharks less than and greater than 60 cm, respectively), total body weight (to the nearest 1 g) and sex of each shark were recorded in the field. The entire reproductive tract of each mature female was removed and frozen for subsequent examination in the laboratory. In the case of males, a note was kept as to whether their claspers were calcified and, if so, to what extent. The lengths of claspers were recorded to the nearest 1 mm. A stretch of six vertebrae was removed from that part of the vertebral column that was located in the region of the first dorsal fin and then frozen.

### Reproductive biology

The maturity stage of each individual shark was recorded. Females that contained large, yolked ova in their right ovary and possessed well-developed uteri, but which were not pregnant, were recorded as mature, non-pregnant, while those with either intrauterine eggs or embryos were recorded as mature, pregnant. Females possessing enlarged but flaccid and empty uteri were termed post-partum. All other females, including those containing ova undergoing vitellogenesis and uteri that were not yet fully developed, and which were thus not yet capable of reproduction, were recorded as immature. Males were considered mature when their claspers were enlarged and fully calcified. Recently born sharks could be distinguished by the presence of an umbilical scar on their ventral body surface in the region between the pectoral fins.

The presence of any bruised claspers on males and fresh bite marks on the sides of females was taken as indicating that mating had recently occurred. Males were recorded as spent when their testes were enlarged but flaccid and their seminal vesicles were enlarged but empty. Data for the above variables were used to determine the approximate time of copulation.

The diameter of the single largest ovum in the ovary of each mature female, i.e. the maximum ovum diameter (MOD), was measured to the nearest 0.1 mm, while the length of each intrauterine embryo was measured to the nearest 1 mm. The intrauterine embryos could generally be sexed once they were 1–2 months old and ~10 cm in length.

The lengths at which 50% of both females and males of *C. cautus* attain maturity (i.e. the  $L_{50}$  at first maturity) were derived by fitting the logistic function:

$$p_L = \frac{1}{1 + \exp\left[-\ln(19) \frac{(L-L_{50})}{(L_{95}-L_{50})}\right]}$$

to the proportion,  $p_L$ , of those sharks that were mature at length  $L$ , where  $L_{50}$  and  $L_{95}$  are constants and  $\ln$  is the natural logarithm. Maximum-likelihood estimates of the parameters were obtained using the routine SOLVER in Microsoft Excel and calculating the likelihood of immature and mature individuals as  $1-p_L$  and  $p_L$ , respectively. The reported estimates of the parameters were determined as the median values derived from 200 sets of the randomly resampled data, with the same sample size drawn from the data on observed maturity status at length for female and male sharks, respectively. The approximate 95% confidence intervals were estimated as the 2.5 and 97.5 percentiles of the 200 estimates resulting from the resampled data.

### Age and growth

Two adjacent vertebral centra were separated from the extracted part of the vertebral column of each *C. catus*, and their cartilaginous processes and surrounding connective tissue removed. They were then soaked in 5% sodium hypochlorite for 5–20 min, depending on their size (Simpfendorfer 1993; White et al. 2001), washed and allowed to dry. Each centrum was mounted in clear epoxy resin and cut into 0.3–0.4 mm sections using a low-speed Isomet diamond saw. The sections were moistened with distilled water to enhance the definition of the opaque zones and, using a dissecting microscope, then examined against a black background under reflected light. The opaque zones in the two adjacent centra selected from each vertebral column were counted to confirm that the number of opaque zones visible in each centra was the same, after which one of these centra was selected for future use. The sections were stored by mounting on glass slides using DePeX mounting medium.

The distance between the outer edge of the outermost opaque zone and the periphery of each centrum, i.e. the marginal increment, was measured. When only one opaque zone was present, the distance between the nucleus and the outer edge of that zone was measured. In contrast, when more than one opaque zone was present, the distance between the outer edges of the two outermost zones was measured. All measurements were made to the nearest 0.05 mm along the vertical axis of the centrum and thus perpendicular to the opaque zone(s). The marginal increment on each centrum was then expressed as a proportion of the distance between the nucleus of the centrum and the outer edge of the opaque zone, when only one such zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more such zones were present.

Von Bertalanffy growth curves were fitted to the individual lengths of each female and male at their estimated age at capture, firstly by including only the lengths of postnatal individuals and employing the date of parturition as age 0, and then by including those of both embryos and postnatal individuals and using the conception date as age 0 and thus encompassing growth during both prenatal and postnatal life. The data were fitted by minimising the sum of squared deviations between observed and predicted lengths using a non-linear regression in SPSS (SPSS 1999) and the routine SOLVER in Microsoft Excel. The von Bertalanffy growth equation is:

$$L_t = L_{\infty} \left(1 - e^{-k(t-t_0)}\right)$$

where  $L_t$  is the length at age  $t$ ,  $L_{\infty}$  is the mean asymptotic length,  $k$  is the growth coefficient and  $t_0$  is the age at which the estimated length is zero.

The Schnute growth equation (see below) was fitted to the same length-at-age data as the von Bertalanffy growth equation:

$$L_t = \left[ L_1^b + (L_2^b - L_1^b) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{1/b}$$

(Schnute 1981, Eq. 15), where  $L_1$  and  $L_2$  are the estimated lengths at selected reference ages  $\tau_1$  and  $\tau_2$  (years) and  $a$  and  $b$  are constants (both  $\neq 0$ ). From this equation, the asymptotic length can be calculated using the equation:

$$L_{\infty} = \left[ \frac{e^{a\tau_2} L_2^b - e^{a\tau_1} L_1^b}{e^{a\tau_2} - e^{a\tau_1}} \right]^{1/b}$$

(Schnute 1981).

The theoretical age at which the estimated length is zero, i.e.  $t_0$ , was determined from:

$$t_0 = \tau_1 - \frac{1}{a} \ln \left\{ 1 + \frac{L_1^b (1 - e^{-a(\tau_2-\tau_1)})}{L_2^b - L_1^b} \right\}$$

It was assumed that, when fitting all growth curves,  $L_t = 0$  if the age of an individual lay below  $t_0$ .

A runs test was applied using SPSS to the residuals from each of the analyses to determine whether the growth curves deviated systematically from the observed data. Before applying this test, the lengths-at-age were sorted by age and then randomly within age.

The von Bertalanffy and Schnute growth curves derived for female and male *C. catus*, using firstly the lengths-at-age for postnatal fish and then the combined lengths-at-age for embryos and postnatal fish, were compared using a likelihood-ratio test to determine whether there were significant differences between the curves derived for each sex using the different growth equations and between the curves derived for both sexes using the same growth equations (Kimura 1980). The null hypothesis,  $\omega$ , that the growth curves could be described by equations with  $q$  linear constraints on the parameters was compared with the alternative hypothesis,  $\Omega$ , that the parameters for the two curves were distinct. The log-likelihood was determined for the null hypothesis and for the alternative hypothesis as  $\lambda_{\omega}$  and  $\lambda_{\Omega}$ , respectively, where each was calculated, ignoring constant terms, from the associated sum of squared deviations (SS) over the  $n$  observations, as:

$$\lambda = -\frac{n}{2} \ln \left( \frac{SS}{n} \right)$$

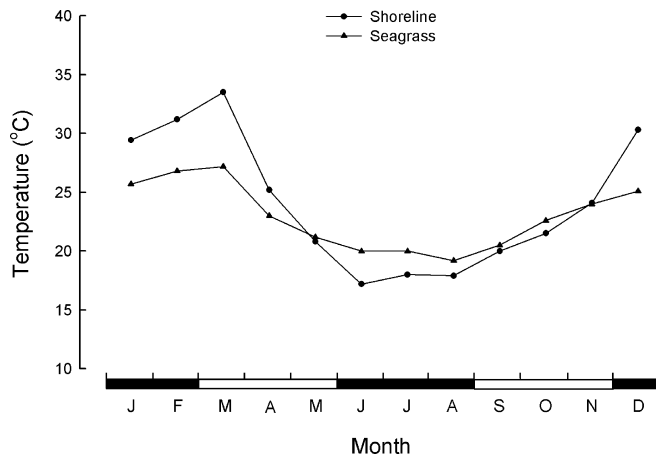
Next, the test statistic for the likelihood-ratio test was calculated as  $2(\lambda_{\Omega} - \lambda_{\omega})$ . The null hypothesis was rejected at the  $\alpha = 0.05$  level of significance when the test statistic exceeded  $\chi^2_{\alpha}(q)$  (e.g. Cerrato 1990).

The absolute differences between the lengths-at-age, estimated from the von Bertalanffy and Schnute growth curves for the fish throughout all ages from age 0, were determined and expressed as a percentage of the length calculated for each age using the von Bertalanffy equation. Our considerations regarding the potential value of using the Schnute curve rather than the von Bertalanffy curve took into account the extent of the maximum difference between the curves, whether the runs test revealed any structural problems with either growth curve and other comparisons between the curves, such as the values for the coefficient of determination,  $t_0$ , and  $L_{\infty}$ .

## Results

### Environmental data

Mean monthly temperatures at the three gill net sites along the shore at Herald Bight increased from 29.4°C in January to a maximum of 33.5°C in March, and then declined to a minimum of 17.2°C in June and remained below 20°C for the next 2 months, before increasing progressively to 30.3°C in December (Fig. 1). Although mean monthly water temperatures in the shallow sea-grass meadows at Herald Bight, in which gill nets were



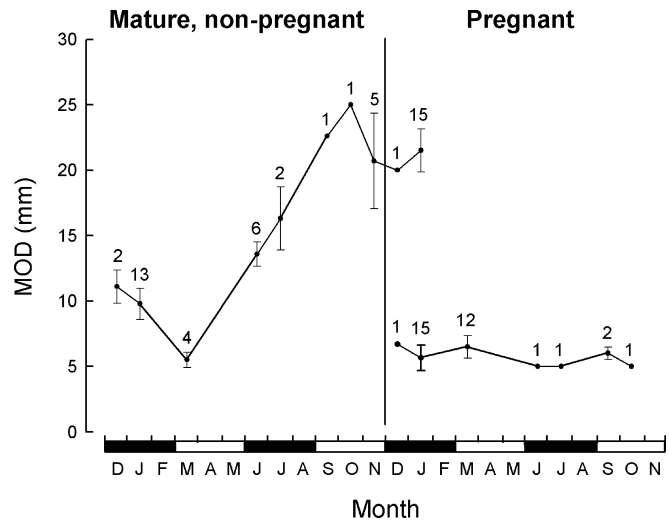
**Fig. 1** Mean monthly water temperatures at sites along the shoreline and in the seagrass where gill netting was conducted in Shark Bay between January 1999 and September 2001. In this and subsequent figures, the data for the corresponding months of the different years have been pooled. On the x-axis, filled bars refer to summer and winter months; open bars to autumn and spring months

also set, followed a similar trend to that along the shore, they did not vary to the same extent. Thus, the maximum and minimum mean monthly temperatures recorded for these sites differed by only 8.0°C, compared with 16.3°C along the shoreline (Fig. 1).

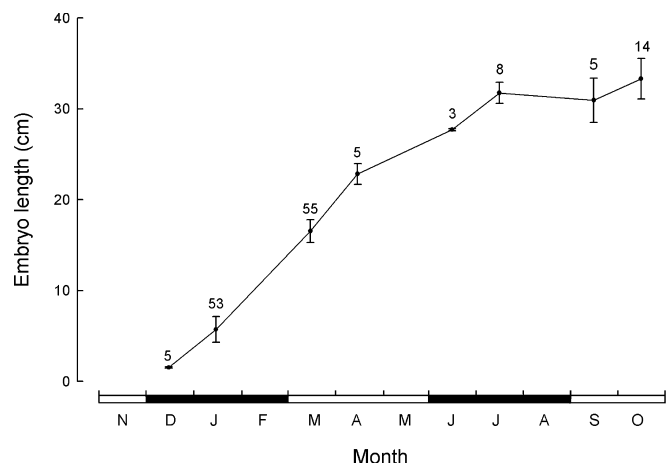
The salinity at each of the sampling sites at Herald Bight lay within the narrow range of 39.1–41.6‰.

### Reproductive biology

Although only a small number of mature, non-pregnant females were caught, the mean monthly MODs in the right ovary of such females still showed a clear trend throughout the year, with values declining from 10–11 mm in December and January to ~5 mm in March, before rising to >20.5 mm in September, October and November (Fig. 2). While the majority of large, yolked ova had already been ovulated by December, one or two residual large ova, with diameters  $\geq 20.0$  mm, were retained in both that month and also January by those females that had recently become pregnant (Fig. 2). Since large ova were not present in pregnant females in subsequent months, the few large ova found in pregnant females in mid- to late summer would presumably have been destined to soon become either expelled or resorbed. The mean monthly MODs of the second and quite distinct cohort of small ova present in the right ovary of females in December and January were much lower, i.e. 6.7 and 5.7 mm, respectively. The MODs of pregnant females were 6.5 mm in March and remained low in all subsequent months. Thus, since the majority of ova in mature, non-pregnant females had been ovulated by late November and recently pregnant females with very small embryos were first caught in December (Fig. 3), 1 December was assigned as the date of both



**Fig. 2** *Carcharhinus cautus*. Mean monthly maximum ovum diameters (MOD  $\pm 1$  SE) in the ovary of mature, non-pregnant and pregnant females. Sample size for each month is given above each monthly mean. Symbols see Fig. 1



**Fig. 3** *Carcharhinus cautus*. Mean monthly total lengths ( $\pm 1$  SE) of in utero embryos. Number of embryos measured in each month is given above each monthly mean. Symbols see Fig. 1

ovulation and conception. This date was used as age 0 for calculating the lengths-at-age of female and male fish for constructing the growth curves that encompassed the whole of pre- and postnatal life in both sexes.

During November and early December, some of the mature females bore fresh bite marks on their sides and the majority of the mature males were spent and had bruised claspers. This provides strong circumstantial evidence that this species copulates mainly in late October/early November and thus just prior to ovulation.

The mean lengths of embryos increased from 1.5 cm in December, when embryos were first found, to 22.8 cm in April and then to a maximum of 33.3 cm in October (Fig. 3). The attainment by embryos of their maximum size in October and the absence of embryos in utero in November, strongly indicates that parturition typically

occurs in late October and early November. Therefore, 1 November was assigned as the date of parturition (age 0) for calculating von Bertalanffy growth curves during postnatal growth. This estimate of the time of parturition is consistent with the presence of large numbers of small juvenile *C. cautus* in the shallow waters of Herald Bight in November and December and the fact that the lengths of these in a subsample from the latter month, i.e. 42–45 cm, were only about 10 cm greater than the maximum mean monthly length of the embryos.

The mean litter size of *C. cautus* is 4.2, i.e. 2.1 per uterus, with the number of young in females ranging from two to six. There was no obvious relationship between the number of embryos and the total body length of *C. cautus*.

Although the percentage of females amongst mature individuals was much greater than that of males in most months of the year, this percentage was close to parity in spring when this species copulates. This indicates that, when copulation is not occurring, the mature males move to different areas than mature females, in which context it appears relevant that only mature males were caught in seagrass on the four occasions that this habitat type was sampled.

#### Validation of the ageing procedure

The mean monthly marginal increments on vertebral centra of *C. cautus* with either two or three opaque zones increased from ~0.45 in January to their maxima of 0.55–0.75 in July–September and then fell to their minima of ~0.3 in October (Fig. 4). The mean monthly marginal increments on centra with four or more opaque zones followed the same trend, increasing from ~0.5 in January to reach a peak of ~0.9 in September, before declining precipitously to ~0.1 in October and then increasing to ~0.5 in December (Fig. 4). Although individuals with vertebral centra possessing only one opaque zone were not found in some months and were in low numbers in some other months, the mean monthly marginal increments of such centra were still clearly greatest in winter and least in mid-spring and thus apparently followed the same trends as those on centra in which there were two or more opaque zones. Since the marginal increments on vertebral centra with two or more opaque zones, and probably also on those with a single opaque zone, declined precipitously only once during the year and then rose progressively to reach a peak in winter, only one opaque zone becomes delineated annually on the centra of *C. cautus*. Thus, the number of such opaque zones on these centra can be used to help determine the age of the individuals of this species.

#### Size and age compositions

Since *C. cautus* undergoes considerable growth in the 11 months between conception and parturition, it was

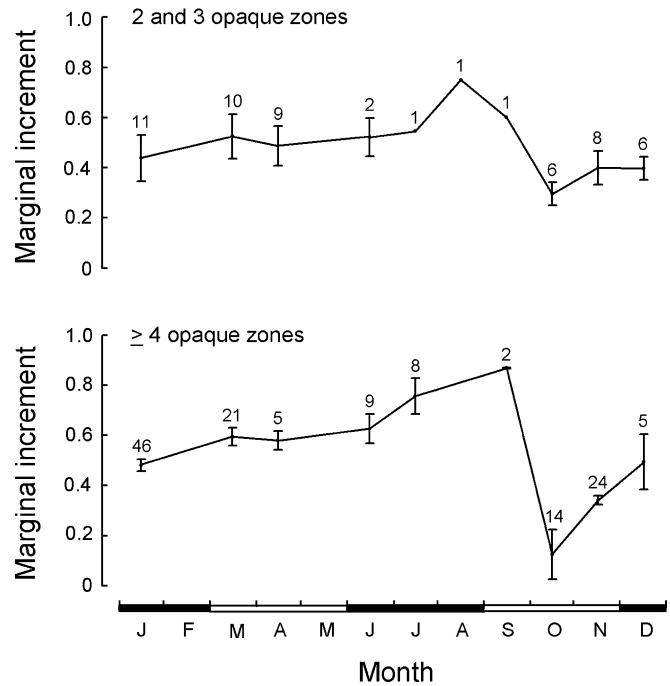


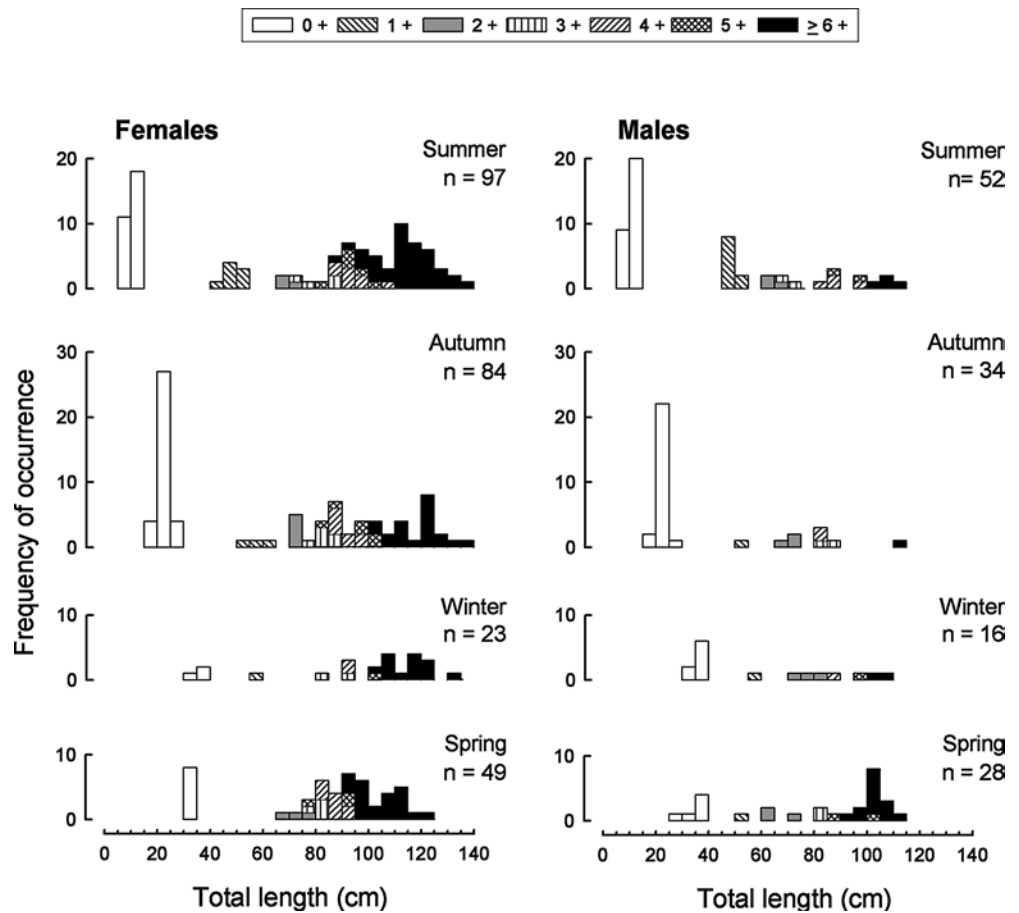
Fig. 4 *Carcharhinus cautus*. Mean monthly marginal increments ( $\pm 1$  SE) for vertebral centra, with either 2 or 3 or  $\geq 4$  opaque zones. Sample size for each month is given above each monthly mean. Note that marginal increments are recorded as a proportional value (see "Materials and methods"). Symbols see Fig. 1

decided, in the following account of the length distributions of the different age classes of this species, to regard the 0+ age class as commencing at conception. Thus, since gestation lasts for 11 months, the 0+ age class corresponds to in utero individuals in all but the last month of the first year of life.

The 0+ age class of *C. cautus* was first found in summer, when its modal length class was only 10.0–14.9 cm (Fig. 5). The modal length of the females and males of this cohort increased to 20.0–24.9 cm in autumn and to 30.0–34.9 and 35.0–39.9 cm, respectively, in spring. In summer, the early 1+ females and males of *C. cautus*, i.e. the recently born juveniles, were represented by a modal length class of 45.0–49.9 cm, and their length distributions were discrete from those of subsequent age classes (Fig. 5). The absence of an opaque zone in the vertebral centra of these fish shows that no opaque zone was laid down during the preceding winter when this species was still an embryo. However, a single opaque zone was clearly present in those fish that, in summer, were slightly larger than the 1+ age class. Thus, the first zone is laid down in the first winter after parturition.

The distribution of the lengths of age classes 2 and above overlapped (Fig. 5). The length-frequency distributions demonstrated that, amongst the older fish, i.e.  $\geq 6$  years, the females were both more abundant and attained larger sizes. The maximum observed lengths were 133 cm for a female of 16.4 years and 111 cm for a male of 9.0 years.

**Fig. 5** *Carcharhinus cautus*. Length-frequency histograms for different age classes of females and males in the four seasons using data for the whole sampling period ( $n$  = number of fish caught). Ages are recorded from conception



### Growth curves

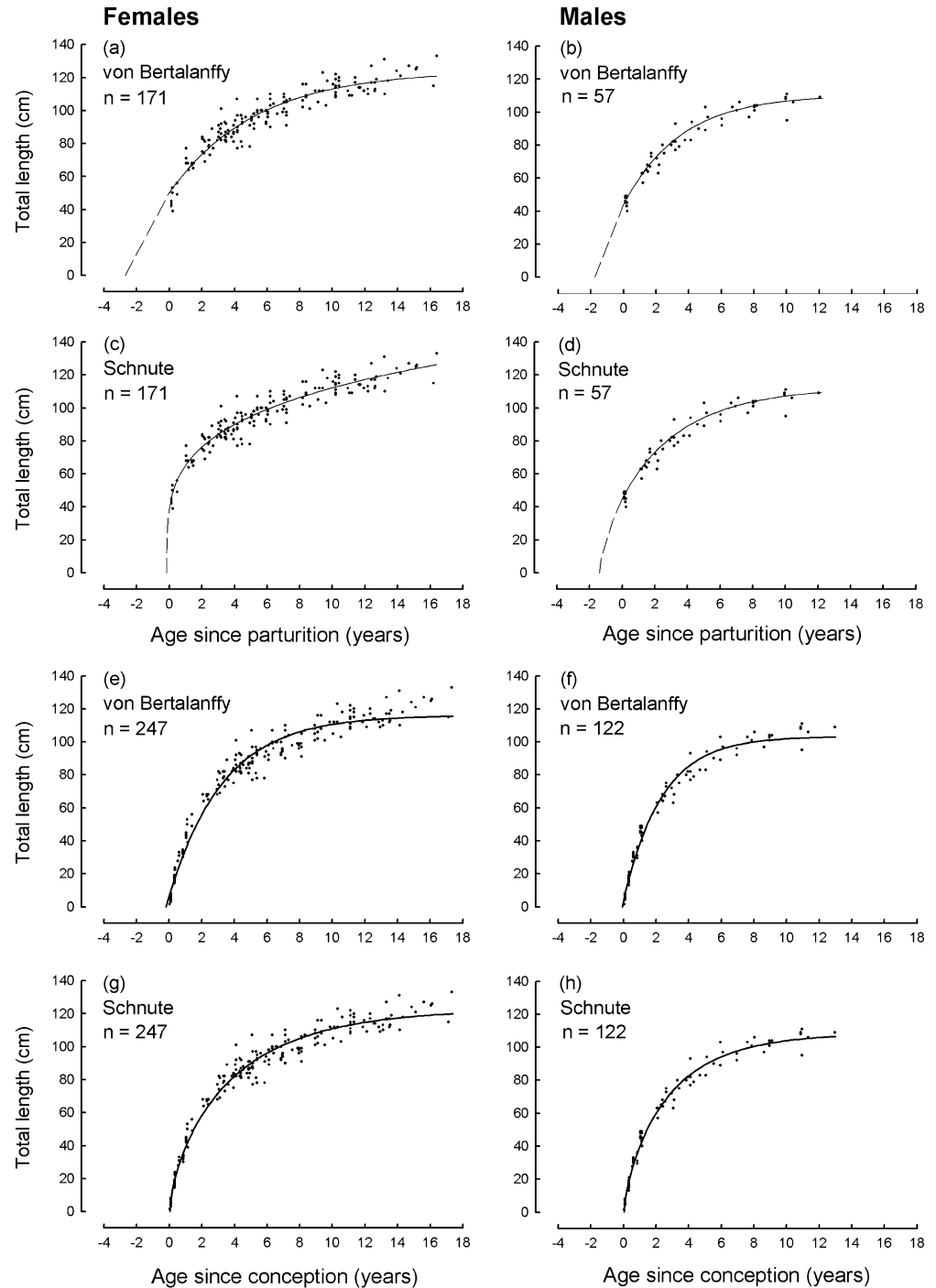
The runs test failed to detect a structural deficiency in the von Bertalanffy growth curve fitted to the lengths-at-age of postnatal females of *C. cautus* ( $P > 0.05$ ), which is consistent with the visual observation that this curve provided a good fit to the lengths-at-age throughout most of the age range of these fish (Fig. 6a). However, the curve did tend to pass above the lengths-at-age of recently born fish and below the lengths-at-age of the very oldest fish (Fig. 6a), which would help account for the coefficient of determination ( $R^2$ ) being  $< 0.910$ . The poor fit at the extreme lower end of the age range and the fact that the lengths of prenatal individuals were not included also account for the age at length 0 ( $t_0$ ) being  $-30.2$  months rather than  $-11$  months, the value that would be expected on the basis of the duration of the gestation period. The likelihood-ratio test demonstrated that the Schnute growth curve significantly improved ( $P < 0.001$ ) the fit to the length-at-age data for postnatal females from that obtained using the von Bertalanffy equation (cf. Fig. 6a, c). Furthermore, the runs test failed to detect any major structural problems with the Schnute growth curve for these data ( $P > 0.05$ ). The Schnute growth curve overcame the deficiencies at the very upper and very lower ends of the age range (cf. Fig. 6a, c). The improvement in the fit by using the Schnute growth curve is emphasised by the fact that

the coefficient of determination increased from 0.906 to 0.919 (Tables 1, 2). It also resulted in a very marked increase in the  $L_\infty$  from 123.8 to 223.8 cm (cf. Tables 1, 2). The Schnute growth curve passed upwards towards the von Bertalanffy growth curve but still differed by 25.8% at age 0. It subsequently passed over the von Bertalanffy growth curve to produce a maximum difference of 5.0% at 1.3 years, before passing back below that curve to produce a maximum difference of only 1.9% at 7.3 years and then rising again above that curve to produce a maximum difference of 4.5% at 16.4 years.

In contrast to the situation for females, the fits to the lengths-at-age of postnatal males by the von Bertalanffy and Schnute growth curves were visually almost indistinguishable and had the same coefficients of determination and very similar  $L_\infty$  values (Tables 1, 2). This point is emphasised by the fact that the maximum difference between the lengths at any age estimated from the two growth equations never exceeded 0.83%. Furthermore, the runs test demonstrated that the structure of the von Bertalanffy growth curve was appropriate ( $P > 0.05$ ). Thus, as would be expected, the curves were not significantly different ( $P > 0.05$ ) (Fig. 6b, d), and there would thus be no advantage in using the Schnute growth curve rather than the von Bertalanffy growth curve.

The von Bertalanffy growth curve provided a good fit to the lengths-at-age for females throughout the vast

**Fig. 6a–h** *Carcharhinus catus*. Von Bertalanffy and Schnute growth curves fitted to lengths-at-age of females and males, using: **a–d** data solely from the time of parturition, i.e. during just postnatal life and **e–h** data from the time of conception, i.e. throughout both prenatal and postnatal life. The parameters for the von Bertalanffy and Schnute growth equations for females and males are provided in Tables 1 and 2, respectively. Note: age 0 corresponds to the date of parturition in a–d and to the date of conception in e–h



majority of their pre- and postnatal life, i.e. from conception (Fig. 6e), which is consistent with the relatively high  $R^2$  of 0.978 (Table 1). However, the runs test showed that this curve had some structural deficiencies ( $P < 0.001$ ), which could be explained, at least partly, by the fact that this curve passed below most of the lengths of the very oldest fish. The use of the Schnute rather than the von Bertalanffy growth equation significantly improved ( $P < 0.001$ ) the description of the growth of females during the whole of their pre- and postnatal life,  $R^2 = 0.983$  (Fig. 6g), and the runs test suggested that this curve was

appropriate for these fish ( $P > 0.05$ ). The changes brought about by the use of a Schnute rather than a von Bertalanffy growth equation were reflected in an increase in the  $L_\infty$  from 116.5 to 130.8 cm (Tables 1, 2). The estimated lengths-at-age derived from the Schnute growth curve increased rapidly from a length of zero at 0.2 years and passed upwards and over the von Bertalanffy growth curve to yield a percentage difference between the two curves of 27.2% at 0.7 years. The curve then passed back below the von Bertalanffy curve to produce a maximum percentage difference of 3.1% at 6.1 years, before rising



**Table 1** *Carcharhinus cautus*. Von Bertalanffy growth parameters for females and males, including upper and lower 95% confidence limits, derived from lengths-at-age of individuals during just postnatal life and using the parturition date as age 0, and for those throughout pre- and postnatal life and employing the conception date as age 0 ( $L_{\infty}$  asymptotic length;  $k$  growth coefficient;  $t_0$  hypothetical age at length 0;  $R^2$  coefficient of determination;  $n$  sample size)

Von Bertalanffy parameters						
		$k$ (year <sup>-1</sup> )	$L_{\infty}$ (cm)	$t_0$ (years)	$R^2$	$n$
Postnatal life						
Females	Estimate	0.198	123.8	-2.52	0.906	171
	Upper	0.226	127.6	-2.04		
	Lower	0.170	119.9	-2.99		
Males	Estimate	0.287	110.5	-1.75	0.953	57
	Upper	0.345	115.5	-1.36		
	Lower	0.229	105.5	-2.15		
Pre- and postnatal life						
Females	Estimate	0.298	116.5	-0.187	0.978	247
	Upper	0.317	118.5	-0.132		
	Lower	0.280	114.5	-0.242		
Males	Estimate	0.427	103.3	-0.081	0.986	122
	Upper	0.459	105.6	-0.043		
	Lower	0.395	101.0	-0.118		

**Table 2** *Carcharhinus cautus*. Schnute growth parameters for females and males, including upper and lower 95% confidence limits, derived from lengths-at-age of individuals during just postnatal life and using the parturition date as age 0, and for those throughout pre- and postnatal life and employing the conception date as age 0 [ $L_1$  and  $L_2$  lengths at selected reference ages  $\tau_1$  (3 years) and  $\tau_2$  (12 years);  $a$  and  $b$  constants (both  $\neq 0$ );  $L_{\infty}$  asymptotic length;  $R^2$  coefficient of determination;  $n$  sample size]

Schnute parameters								
		$L_1$ (cm)	$L_2$ (cm)	$a$	$b$	$L_\infty$ (cm)	$R^2$	$n$
Postnatal fish								
Females	Estimate	83.9	117.2	0.007	3.99	223.8	0.919	171
	Upper	85.2	118.8	0.079	5.12			
	Lower	82.7	115.7	-0.067	2.85			
Males	Estimate	82.2	109.3	0.229	1.57	112.9	0.953	57
	Upper	84.2	114.5	0.436	3.53			
	Lower	80.2	104.1	0.023	-0.40			
Pre- and postnatal fish								
Females	Estimate	73.1	115.1	0.121	2.16	130.8	0.983	247
	Upper	74.3	116.4	0.156	2.44			
	Lower	71.9	113.8	0.085	1.88			
Males	Estimate	73.0	106.6	0.261	1.53	109.8	0.991	122
	Upper	74.3	108.9	0.304	1.66			
	Lower	71.7	104.4	0.218	1.40			

again above that curve to produce a maximum difference of 6.0% at 17.3 years.

Although the runs test suggested that there were structural deficiencies in both the von Bertalanffy and Schnute growth curves fitted to the lengths-at-ages of individual male fish throughout life (both  $P < 0.01$ ), the  $R^2$  for both of these two growth curves were high, i.e. 0.986 and 0.991, respectively (Tables 1, 2). The Schnute growth curve provided a slightly better fit than the von Bertalanffy growth curve ( $P < 0.001$ ), by bringing about, in particular, a slight reduction in the location of the curve for the middle part of the age range and an elevation in its position for the very oldest fish (cf. Fig. 6f, h). From its  $t_0$  of 0.068 years, the Schnute growth curve rose rapidly and passed upwards and over the von Bertalanffy growth curve to reach a maximum percentage difference between the two curves of 12.9% at 0.4 years. It then passed back below the von Bertalanffy curve to produce a maximum percentage difference of 3.6% at 3.6 years and subsequently rose again above that curve to produce a maximum difference of 4.3% at 13 years.

Irrespective of whether the von Bertalanffy or Schnute growth equations were used, the four corresponding growth curves for females and males shown in Fig. 6 were always significantly different ( $P < 0.001$ ).

## Size and age at maturity

The smallest mature female and male of *C. cautus* were 91 and 89 cm length, respectively. Maturity was attained by virtually all females by the time they had reached a length of 105 cm and by all males by the time they had reached a length of 95 cm. The  $L_{50}$  values (and 95% confidence intervals) for first maturity of females and males were 100.7 cm (98.2–102.5) and 91.3 cm (87.3–93.9), respectively (Fig. 7).

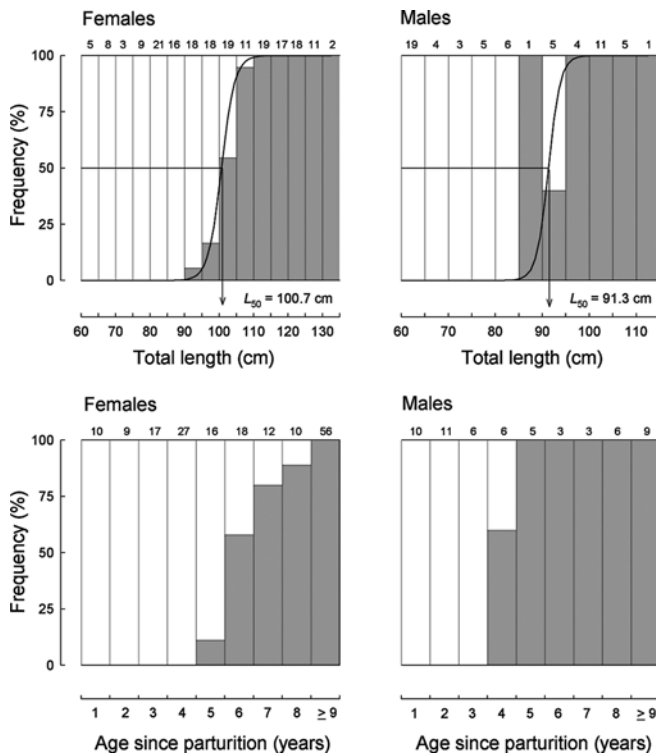
Females and males first reached maturity after 5 and 4 years of life after parturition, respectively (Fig. 7). While a few females did not attain maturity until they were 9 years old, all of the males had become mature by the time they were 5 years old.

## Discussion

### Reproductive biology

The data presented in this paper demonstrate that, i Shark Bay, *Carcharhinus cautus* copulates in late October/early November and ovulates and conceives in late November/early December, i.e. approximately





**Fig. 7** *Carcharhinus cautus*. Percentage frequency of occurrence of immature (open boxes) and mature (closed boxes) sharks in each sequential 5 cm length class and each sequential age class of females and males. Logistic curves for the length data were derived from the percentage contributions of mature sharks in sequential size classes. Arrows indicate position of  $L_{50}$ . Number of fish examined are given above each size and age class.

4 weeks later. This implies that sperm is stored in the oviducal gland for about 4 weeks until ovulation occurs, as is the case with certain other shark species, e.g. *C. tilstoni* and *Prionace glauca* (Pratt 1979; Stevens and Wiley 1986). Since *C. cautus* subsequently gives birth in late October/early November, gestation lasts for approximately 11 months in Shark Bay. Although the individuals of *C. cautus* in Darwin Harbour give birth at a similar time of the year as in Shark Bay, i.e. November, they ovulate at a different time, i.e. February and March versus late November/early December (Lyle 1987). This species thus has a shorter gestation period in Darwin Harbour, i.e. 8–9 versus 11 months, which is presumably related to the warmer temperatures found in that environment, which is located at 12°30'S, i.e. ~1460 km north of Shark Bay. The latter conclusion would be consistent with the observation that the gestation period of the clearnose skate *Raja eglanteria* lasts for about 3 months in Delaware Bay, where water temperatures are 12–23°C, but for only 2 months in Florida, where they are consistently above 24°C (Libby and Gilbert 1960).

The fact that mature, non-pregnant females contained ova undergoing vitellogenesis for 12–13 months, i.e. from November or December to the beginning of the following December and mature, pregnant females contain embryos for 11 months, i.e. from December to

October, demonstrates that *C. cautus* has a biennial reproductive cycle. This parallels the situation recorded for certain other carcharhinid sharks, e.g. the finetooth shark *Carcharhinus isodon*, the Galapagos shark *Carcharhinus galapagensis* and the sandbar shark *Carcharhinus plumbeus* (Castro 1993; Joung and Chen 1995; Wetherbee et al. 1996).

The estimated length at first maturity ( $L_{50}$ ) and maximum length attained by *C. cautus* in Shark Bay were greater for females than males, i.e. 100.7 and 133 cm, respectively, versus 91.3 and 111 cm, respectively. Although these trends parallel those recorded for *C. cautus* in Darwin Harbour, the above values are each approximately 10 cm greater than those recorded by Lyle (1987) in that more northern environment.

### Age composition and growth rates

This present study demonstrated that, by the time they are born, the females and males of *C. cautus* have attained ~28% and 32%, respectively, of their lengths at their maximum observed age, as estimated from the Schnute growth equations for postnatal fish. The relatively large amount of growth undergone by this species prior to birth parallels the situation recorded for *C. amblyrhynchos*, *C. brevipinna*, *C. falciformis*, *C. melanopterus* and *C. plumbeus*, amongst which their lengths at the time of parturition are between 25% and 38% of their maximum lengths (Lyle 1987; Stevens and McLoughlin 1991; Joung and Chen 1995; Wetherbee et al. 1997). It also parallels the values recorded for the myliobatiforms *Urolophus lobatus*, *Trygonoptera personata* and *T. mucosa* (White et al. 2001, 2002).

Virtually every fishery paper concerned with growth uses the von Bertalanffy growth equation, even when it does not provide a particularly good fit (Haddon 2001). Recent work on two species of rays belonging to the genus *Trygonoptera* showed that the Schnute growth equation produced a significantly better fit to the width-at-age of discs for these particular elasmobranchs than the von Bertalanffy growth equation (White et al. 2002). During the present study of *C. cautus*, the use of the Schnute rather than von Bertalanffy growth equation significantly improved the fit for females during both postnatal life (Fig. 6a vs. c) and the whole of life (Fig. 6e vs. g) and for males during the whole of life (Fig. 6f vs. h), but not for males during postnatal life (Fig. 6b vs. d). Whenever possible, it is desirable to use the von Bertalanffy rather than the Schnute equation to describe growth in elasmobranchs, as it is both a simpler equation and the one that has almost invariably been used for this purpose with other members of this subclass (e.g. Branstetter 1987b; Davenport and Stevens 1988; Simpfendorfer 1993; Simpfendorfer et al. 2000) and which consequently facilitates comparisons with the estimates recorded for the von Bertalanffy growth parameters of other elasmobranch species. The fitting of an appropriate growth curve is important both for enabling a

reliable estimate of the range of lengths of fish of a given age to be calculated and for yielding reliable parameters for the growth equation employed.

When a statistically significant difference is found between the curves produced by two different growth equations, it is important to recognise that the likelihood-ratio test is extremely sensitive to small differences in these growth curves, when those curves have been fitted to a large number of size-at-age points, as is the situation both in our present study and in that which we conducted on two *Trygonoptera* species (White et al. 2002). The importance that has been placed on the von Bertalanffy growth parameters is exemplified by the fact that, for example, two of these parameters ( $k$  and  $L_{\infty}$ ) are used in the Pauly (1980a) equation for estimating the natural mortality of species. Thus, the poor values for these two parameters, which would result from a particularly bad fit at the bottom or top end of the curve, would generate poor estimates for natural mortality. The results of our analyses have thus been examined closely in an attempt to ascertain whether it would always be desirable to change from the von Bertalanffy to Schnute growth equations, when it significantly improved the fit from a statistical point of view but, from a biological perspective, might have limited relevance.

The coefficient of determination for the von Bertalanffy and Schnute growth curves for postnatal males of *C. cautilus* were identical (0.953), and the quality of the fit was not significantly improved by using the more complex Schnute growth curve. There was thus no point in using the Schnute rather than the von Bertalanffy growth to describe the growth of postnatal males. However, the values for  $t_0$  in the von Bertalanffy and Schnute growth equations for postnatal males, i.e. -21 and -17 months, respectively, exceeded the -11 months that would be expected from the duration of gestation. This reflects, in part, the tendency for both curves to pass slightly above the points for the lengths-at-age of the youngest fish.

In contrast to the situation with postnatal males, the use of the Schnute rather than von Bertalanffy growth curve did improve significantly the quality of the fit to the length-at-age data for the males of *C. cautilus* throughout life from conception. Yet, the coefficient of determination for the von Bertalanffy growth curve was still high (0.986) and only slightly less than that for the Schnute growth curve (0.991). In addition, the values for  $t_0$  produced by both growth equations were very close to zero, as would ideally be expected with these data, which employed the age of conception as age 0. The negligible values for  $t_0$  reflect the excellent fit provided by both curves for the lengths-at-age of the youngest fish, i.e. those during the early part of embryonic life. Moreover, the  $L_{\infty}$  values differed by only 6.5 cm, and the percentage difference between the curves at any point after the age of 1.5 years following conception reached a maximum of only 4.3%. The large percentage difference, 12.9%, between the curves at age 0.4 years is attributed to the slight difference between the estimates of  $t_0$  for the

two curves and the magnifying effect of division by the relatively small lengths-at-age estimated for very young *C. cautilus* using the von Bertalanffy growth curve. Thus, while the Schnute growth curve did improve the fit to the length-at-age data, particularly for older fish, the value of using this growth curve rather than the von Bertalanffy growth curve for describing the growth of males throughout life is considered to be limited.

The coefficient of determination for the von Bertalanffy growth equation for female *C. cautilus* during just postnatal life was 0.906, reflecting the reasonably good fit of the curve to the length-at-age data. However, visual comparisons between Fig. 6a and c show that the Schnute growth curve provides a better fit, particularly to the lengths-at-age at the extreme ends of the curves, these differences being reflected in a higher coefficient of determination (0.919), a less negative  $t_0$ , a greater  $L_{\infty}$  and the significant difference between the curves. The very large difference between the values for  $t_0$  are reflected in the marked percentage differences between the lengths at age 0, namely 25.8%. The shift in the  $L_{\infty}$  was particularly marked, with this parameter increasing from 123.8 to 223.8 cm. Moreover, the maximum difference between the curves after age 1 reached 5%. Thus, although the von Bertalanffy growth curves provided a good fit to most of the data, there would be an advantage in using the Schnute growth curve if an accurate estimate of the age of a young or old female of given length was required.

The use of the Schnute growth curve rather than the von Bertalanffy growth curve to describe the growth of females throughout life also resulted in an upwards shift at the upper end to help accommodate the location of the lengths of the older individuals. This resulted in an increase in the  $L_{\infty}$  from 116.5 to 130.8 cm. Furthermore, the difference between the lengths of young female *C. cautilus* derived from the curves was large, reaching a maximum of 27.2% at 0.7 years. The percentage difference between the curves was still 9.4% at age 2 and, following age 3, reached a maximum difference of 6.0%. Thus, although the coefficient of determination was high for the von Bertalanffy growth curve throughout the whole of life (0.978), there would be value in using the Schnute curve ( $R^2=0.983$ ) rather than the von Bertalanffy curve to represent the length-at-age data of female *C. cautilus* throughout life.

Our  $k$  values for postnatal male and female *C. cautilus*, 0.287 and 0.198 year<sup>-1</sup>, respectively, lie towards the upper end of the range for elasmobranchs, as would be expected for this small- to medium-sized shark (Frisk et al. 2001). In the context of asymptotic length, it has been proposed that a value equivalent to about  $L_{\max}/0.95$  would be expected (e.g. Pauly 1980b). More recently, Froese and Binohlan (2000) have used data for a large number of species to develop an empirical relationship between the von Bertalanffy  $L_{\infty}$  and  $L_{\max}$ , which, in the case of the data for male and female *C. cautilus*, would be represented by  $L_{\infty} \approx L_{\max}/0.97$ . The latter relationship yields estimates for  $L_{\infty}$  of 114.0 cm

for males and 136.2 cm for females. The  $L_{\infty}$  values derived for males during postnatal life using the von Bertalanffy growth equation, 110.5 cm, and the Schnute growth equation, 112.9 cm, and for the whole of life using the Schnute equation, 109.8 cm, were all close to the above “hypothetical”  $L_{\infty}$  values, while the  $L_{\infty}$  for males derived for the whole of life using the von Bertalanffy growth equation, 103.3 cm, was slightly below the “hypothetical”  $L_{\infty}$ . The  $L_{\infty}$  derived for females during the whole of life using the Schnute growth equation, 130.8 cm, was closer to the “hypothetical”  $L_{\infty}$  of 136.2 cm for that sex than the  $L_{\infty}$  values of 123.8 cm and, even more distinctly, of 116.5 cm that were both derived employing the von Bertalanffy growth equation for females during postnatal life and the whole of life, respectively. However, the  $L_{\infty}$  of 223.8 cm derived for females during postnatal life using the Schnute equation far exceeded the “hypothetical”  $L_{\infty}$  for females. The fact that the Schnute growth equation for postnatal females produced such a high  $L_{\infty}$ , through accommodating the lengths-at-age of the older fish, emphasises the problems posed by always having a fixed concept as to what constitutes an appropriate value for  $L_{\infty}$ . The derivation of a  $L_{\infty}$  for females during the whole of life, using the von Bertalanffy growth curve, that was appreciably lower than the above “hypothetical”  $L_{\infty}$  emphasises the difficulties in predicting  $L_{\infty}$  on the basis of an empirical equation does not only apply to the use of the Schnute growth equation. The significance of the  $L_{\infty}$  values derived from growth equations thus has to be interpreted with great caution (see also Knight 1968).

Through their addition of a fifth parameter, Schnute and Richards (1990) extended the generalisation of the curve produced by Schnute (1981). While the use of the Schnute and Richards curve significantly improved the fit to the lengths-at-age for both males ( $P < 0.01$ ) and females from conception ( $P < 0.001$ ) (but not for either sex from parturition), the maximum difference between the lengths estimated for any point in the growth curves in either of these first two cases was  $< 3\%$ . Thus, even in these cases, a shift to the more complex growth equation would be of limited value.

We consider that, during this study, the use of the maximum differences at any point along the lines of the two growth curves, in conjunction with statistical tests and comparisons between the values for the coefficient of determination,  $t_0$  and  $L_{\infty}$ , has reduced the subjectivity in assessing when it is appropriate to consider using more complex growth curves, such as those of Schnute (1981) and of Schnute and Richards (1990), for describing the growth of *C. cautus* and of elasmobranchs in general. The growth curves constructed using the lengths-at-age of female and male *C. cautus* during pre- and postnatal life demonstrated that, even though there was a huge shift at birth from obtaining food internally via a placenta to having to forage actively for prey, parturition was not accompanied by an abrupt change in the pattern of growth. Thus, in those cases where there is a shortage of length-at-age data for a shark species in

the period immediately following birth, the inclusion of lengths-at-age of individuals during embryonic life would be likely to increase the quality of the curve representing the growth of fish during postnatal life. The ability to use a smooth, monotonically increasing growth equation to describe the pattern of increase in length-at-age of *C. cautus* throughout the whole of life, and thus commencing at the onset of embryonic growth, parallels the situation recorded using the widths-at-age of discs of two species belonging to the Myliobatiformes, a morphologically very different suborder of elasmobranchs (White et al. 2002).

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