Life-history traits of a small-bodied coastal shark

Adrian N. Gutteridge[A,B,F], *Charlie Huveneers*[C,D], *Lindsay J. Marshall*[E],
Ian R. Tibbetts[A] *and Mike B. Bennett*[B]

[A]School of Biological Sciences, University of Queensland, St Lucia, Brisbane,
 Qld 4072, Australia.
[B]School of Biomedical Sciences, University of Queensland, St Lucia, Brisbane,
 Qld 4072, Australia.
[C]School of Biological Sciences, Flinders University, Sturt Road, Bedford Park,
 Adelaide, SA 5042, Australia.
[D]Threatened, Protected and Endangered Species Program, South Australia Research
 and Development Institute − Aquatic Sciences, West Beach, Adelaide,
 SA 5024, Australia.
[E]Stickfigurefish Biological Illustrations, 47 Hunter Street, Everton Park, Brisbane,
 Qld 4053, Australia.
[F]Corresponding author. Email: gutteridge.adrian@gmail.com

Abstract. The life histories of small-bodied coastal sharks, particularly carcharhinids, are generally less conservative than those of large-bodied species. The present study investigated the life history of the small-bodied slit-eye shark, *Loxodon macrorhinus*, from subtropical Hervey Bay, Queensland, and compared this species' biology to that of other coastal carcharhinids. The best-fit age model provided parameters of $L_\infty = 895$ mm total length (TL), $k = 0.18$ and $t_0 = -6.3$ for females, and $L_\infty = 832$ mm TL, $k = 0.44$ and $t_0 = -2.6$ for males. For sex-combined data, a logistic function provided the best fit, with $L_\infty = 842$ mm TL, $k = 0.41$ and $\alpha = -2.2$. Length and age at which 50% of the population was mature was 680 mm TL and 1.4 years for females, and 733 mm TL and 1.9 years for males. Within Hervey Bay, *L. macrorhinus* exhibited an annual seasonal reproductive cycle, producing an average litter of 1.9 ± 0.3 s.d. With the exception of the low fecundity and large size-at-birth relative to maximum maternal TL, the life-history traits of *L. macrorhinus* are comparable to other small-bodied coastal carcharhinids, and its apparent fast growth and early maturation contrasts that of large-bodied carcharhinids.

Additional keywords: age and growth, Australia, Carcharhinidae, elasmobranch, *Loxodon macrorhinus*, reproductive biology, slit-eye shark, subtropical.

Introduction

The collection of life-history information for exploited species is extremely important in a fisheries-biology context (Cailliet and Goldmann 2004). Such information can determine parameters such as length and age at maturity, growth rates, mortality estimates, reproductive output and life span (Ricker 1975; Cailliet and Goldmann 2004; Goldmann 2005; Walker 2005b). Combined, these parameters provide information that is required for the production of accurate stock assessments (Quinn and Deriso 1999), as well assessing a species' susceptibility to exploitation and rebound potential following over-harvest (Stevens et al. 2000; Walker 2005a).

Carcharhiniform sharks, in particular the Carcharhinidae, are among the most species-diverse and abundant groups of elasmobranchs within tropical and subtropical neritic waters (Compagno et al. 2005; Last and Stevens 2009). As such,

carcharhinids form a major component of the targeted commercial catch of elasmobranchs within these waters (Henderson et al. 2007; White 2007; Harry et al. 2011b). Life-history parameters such as maximum total length, growth rates and length and age at maturity show considerable variation within the Carcharhinidae (Stevens and McLoughlin 1991; Last and Stevens 2009). Because the aforementioned parameters are implicitly linked to the susceptibility of individual species (Smith et al. 1998), the resilience to exploitation is therefore not uniform among carcharhinid sharks. Additionally, because life-history parameters can show spatial variation among stocks (Lombardi-Carlson et al. 2003), it is of paramount importance that regionally specific data are determined for exploited species.

In comparison with large-bodied carcharhinids (maximum total length (TL) of >1000 mm), many small-bodied

carcharhinids (maximum TL of <1000 mm) display fast growth rates, early maturation, short life spans and aseasonal reproductive cycles (Stevens and McLoughlin 1991; Smith *et al.* 1998; Last and Stevens 2009). For example, the Australian sharpnose shark, *Rhizoprionodon taylori*, matures at approximately 1 year of age and has one of the fastest known growth rates of any species of shark ($k = 1.33 \, \text{year}^{-1}$ for males; Simpfendorfer 1993). Similarly, for the Atlantic sharpnose shark, *R. terraenovae*, initial growth is rapid, with maturity for both sexes being reached after 3 years (Loefer and Sedberry 2003). Such growth characteristics contrast those of large-bodied species, such as the dusky shark, *C. obscurus*, which matures at ~20 years and exhibits slower growth rates ($k = 0.043 \, \text{year}^{-1}$; (Simpfendorfer *et al.* 2002). For reproductive seasonality, particularly from tropical waters, small-bodied carcharhinids generally produce an annual litter, with breeding occurring seasonally or aseasonally (Stevens and McLoughlin 1991). Larger-bodied species, however, typically display seasonal breeding cycles and produce annual, biennial or triennial litters (Dudley and Cliff 1993; Allen and Cliff 2000; Last and Stevens 2009). Although large-bodied carcharhinids typically display higher fecundity than do small-bodied species (Stevens and McLoughlin 1991; White 2007; Last and Stevens 2009), the overall life-history traits of small-bodied species generally lead to a higher biological productivity (Frisk *et al.* 2001).

The slit-eye shark, *Loxodon macrorhinus*, is a small-bodied carcharhinid that occurs throughout the Indo-western Pacific (Compagno 1988; Last and Stevens 2009). It has been reported in moderate numbers from commercial and artisanal shark fisheries from Indonesia (White 2007), the Maldives (Anderson and Ahmed 1993), Oman (Henderson *et al.* 2007) and eastern Australia (Harry *et al.* 2011*b*). Although limited research has been conducted on the biology of the species, *L. macrorhinus* has demonstrated regional variations in reproductive characteristics, with length at maturity ~600 mm TL in northern Australia (Stevens and McLoughlin 1991) and ~820 mm TL in Indonesia (White 2007). Similarly, size-at-birth varies geographically, ranging from 400–460 mm TL in northern Australia (Stevens and McLoughlin 1991) to 540–550 mm TL in Indonesia (White 2007). Currently, no age or growth data are available for this species.

The present study examines the life history of *L. macrorhinus* from subtropical Hervey Bay, Queensland, Australia. Hervey Bay supports several recreational and commercial fisheries, including the East Coast Inshore Fin Fish Fishery (ECIFFF), a commercial fishery that targets sharks. Although *L. macrorhinus* forms a component of the shark catch within this fishery, local biological data are lacking. We describe the life history of this species, compare these data to other carcharhinid sharks and test the hypothesis that the life history of *L. macrorhinus* conforms to that of other small-bodied carcharhinids.

Materials and methods

Sample collection

Sharks were collected from Hervey Bay, Queensland, during monthly fisheries-independent sampling between May 2008 and October 2010 (Fig. 1). Sharks were captured in a bottom-set gillnet ($n = 36$) of $150 \, \text{m} \times 2 \, \text{m}$ drop, 89-mm stretch
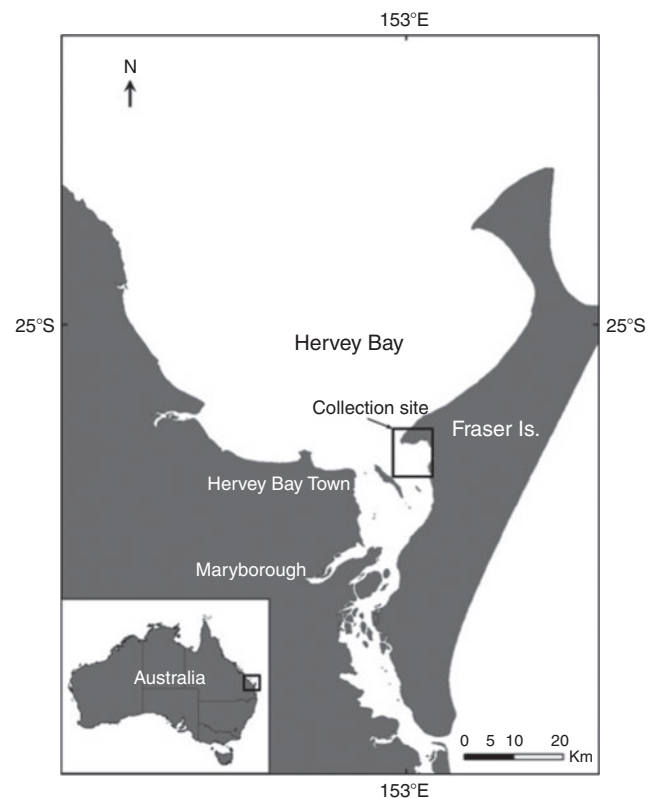

Fig. 1. Schematic map of Hervey Bay, Queensland, Australia, demonstrating the site of *Loxodon macrorhinus* collection.

monofilament mesh, or on a 400-m set-line ($n = 129$) of 8-mm braided polyester rope) consisting of 30 hooks baited with teleost fishes. Soak times and deployment details are outlined in Gutteridge *et al.* (2011). On capture, sharks were either retained for life-history examinations, or injected with the fluorochrome marker calcein (5 mg (kg body mass)$^{-1}$), tagged (plastic type PDA, Hallprint, Hindmarsh Valley, SA) and released as part of a mark–recapture study. Fish kept for life-history examinations were pithed, retained on ice while at sea and subsequently frozen for later dissection. In addition, 13 *L. macrorhinus* were obtained from commercial fishermen operating in Hervey Bay using bottom-set gillnets fitted with 100-mm stretch monofilament mesh. These specimens were collected at various times throughout the study period. Sex, TL and fork length (FL) (± 1 mm) were recorded for all specimens, whereas body mass (M) (± 1 g) was recorded for only those specimens that were retained. TL was determined by allowing the caudal fin to take a natural position, then placing the top caudal lobe in line with the body axis. A chi-square goodness-of-fit test was used to examine whether the sample was sex-biased (R Development Core Team 2010, The R Foundation, Vienna), with significance accepted at $P < 0.05$. A Shapiro–Wilk test for normality was conducted to determine whether the size-frequency distribution of either sex was skewed. The regression relationships among TL, FL and M were determined using SigmaPlot 11.0 (Systat Software Inc., Chicago, IL).
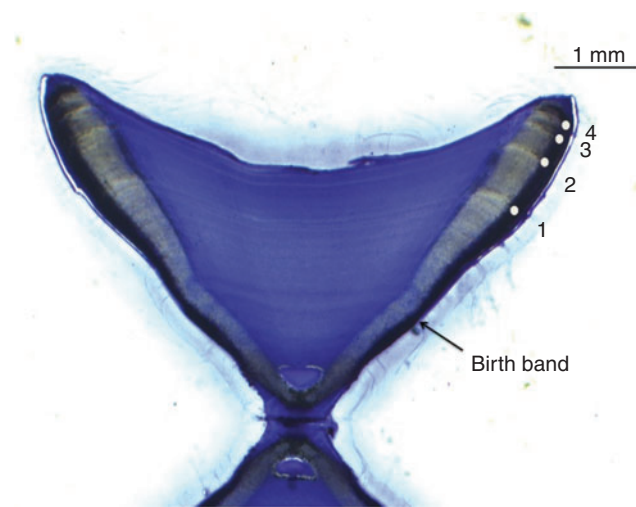
Fig. 2. Photograph of sectioned vertebrae taken from an 810-mm mature male captured on 5 December 2008. This individual was aged 4 years by the primary and secondary reader, with a partial age assigned as 4.9 years. The birth band was recognisable from a change in the angle on the *corpus calcareum*.

Growth estimates

For each retained specimen, a section of four vertebrae was removed from directly under the first dorsal fin. A single centrum from each vertebral section was cleaned of excess connective tissue and the neural and haemal arches were removed. Each centrum was immersed in 10% sodium hypochlorite solution for 20 min, distilled water for 20 min, air-dried and embedded in a clear polyester resin (Diggers, Reochem, Brisbane). A sagittal-plane 150-μm-thick section was taken through the focus of the centrum with a precision diamond wafering saw (Leco VC-50, St. Joseph, MI, USA; (Cailliet and Goldmann 2004). This thickness was chosen because it had the highest readability for a trial that comprised 150-μm-, 300-μm-, 450-μm- and 600-μm-thick sections. Two training counts were then performed on all centra (Pierce and Bennett 2009). Because the banding remained indistinct in a large proportion of these, crystal violet staining was used to enhance the banding on the *corpus calcareum*. Band enhancement was greatest following immersion of the section in 0.01% crystal violet solution for 30 min (Johnson 1979; Schwartz 1983). Excess stain was removed by washing in distilled water, with each section subsequently dehydrated in a series of ethanol solutions (70%, 90% and 100%, for 30 s each), placed in xylene for 1 min, then air-dried and mounted on glass slides.

Each individual section was viewed under transmitted light with a dissecting microscope (Olympus ZH10, Center Valley, PA, USA) and photographed (QImaging MicroPublisher 3.3RTV, Surrey, BC, Canada). Prior to assigning age counts, each centrum was allocated a qualitative measure of readability, from 1 (high readability) to 5 (unreadable or not readily distinguished) (Officer *et al.* 1996; Smith *et al.* 2007). Age estimates were determined only from centra with scores of 1–4 (Smith *et al.* 2007). The age of each individual was determined to the nearest whole year by counting growth bands on the *corpus calcareum*. Each growth band comprised one opaque and one

translucent band (Cailliet *et al.* 2006), with the birth band recognisable by an angle change on the *corpus calcareum* (Fig. 2). To define when the first growth band was laid down, all centra were compared with a reference sample taken from the largest late-term embryo.

Ages were estimated from two independent counts performed by the primary author (A. N. Gutteridge) and a secondary reader (L. J. Marshall). Using data obtained from investigating the reproductive cycle of the species, partial ages were assigned, assuming a date-of-birth of 1 January, with final ages determined from comparison between the second count of each reader. If age estimates differed between reads, these were recounted in the presence of both readers (Goldmann 2005; Piercy *et al.* 2007). If consensus could not be reached, these were removed from the sample (Goldmann 2005; Piercy *et al.* 2007). Last, age-band counts were assessed for precision and bias. The precision between the two final counts of both readers was tested by percentage agreement (PA; Goldmann 2005; Cailliet *et al.* 2006), the coefficient of variation (CV; Chang 1982) and the average percentage error (APE; Beamish and Fournier 1981). An age-bias plot was constructed to test for bias between the second counts of the two readers (Cailliet *et al.* 2006).

Periodicity of growth-band formation

A mark–recapture study of *L. macrorhinus* was undertaken to validate the assumption of annual band-pair deposition. Centra of a recaptured shark were prepared as described above and the number of band pairs formed distal to the fluorochrome label were counted and compared with time at liberty (Pierce and Bennett 2009). Additionally, centrum-edge analysis (CEA) was conducted to qualitatively verify the timing of band formation by observing the translucency or opacity of the centrum edge (Cailliet and Goldmann 2004). This was then compared with the time of year when each individual was caught (Cailliet and Goldmann 2004).

Age and growth models

Five growth models were fitted to length-at-age data by using least-squares non-linear regression (PASW Statistics, ver. 18, 2009, IBM, New York). These were, the three-parameter von Bertalanffy growth function (3VBGF; von Bertalanffy 1938; Beverton and Holt 1957), the two-parameter modified von Bertalanffy growth function (2VBGF; Fabens 1965), the three-parameter Gompertz growth function (3GGF; Ricker 1979), the two-parameter Gompertz growth function (2GGF; Ricker 1975), and the logistic growth function (LGF; Ricker 1979) (Table 1). Fixed size at birth for the 2VBGF and 2GGF was taken from the largest near-term embryo from the study (TL = 425 mm). To test for significant differences between the growth curves of females and males, the results were tested for equality by using a log-likelihood ratio test (Kimura 1980). However, because of the small sample size, growth models were also fitted to sex-combined data.

Akaike's information criterion (AIC) was determined using the small-sample, bias-adjusted AIC (AIC$_c$) (Harry *et al.* 2011*a*) and calculated as

$$AIC_c = AIC + 2K \times (K + 1) \times (n - K - 1)^{-1},$$

where K is the number of parameters $+1$, n is the sample size, and

$$AIC = n\ln(\sigma^2) + 2p,$$

where p is the number of parameters and σ is the sum of residual squares divided by n. Models were then ranked, on the basis of the lowest AIC_c differences (Δ_i) calculated as

$$\Delta_i = AIC_i - AIC_{min},$$

where $AIC_i = AIC$ of the ith model, and $AIC_{min} = AIC$ of the best-candidate model (Burnham and Anderson 2002). Models can show varying support from substantial, $\Delta_i = 0$–2, to essentially no support, $\Delta_i \geq 10$ (Burnham and Anderson 2002). Akaike's weights (ω_i) were then calculated to determine the weight of evidence in favour of a particular model being the best fit to the data (Burnham and Anderson 2002).

Table 1. Growth models used to fit estimated length-at-age data for *Loxodon macrorhinus* from Hervey Bay

3VBGF, three-parameter von Bertalanffy growth function; 2VBGF, two-parameter von Bertalanffy growth function; 3GGF, three-parameter Gompertz growth function; 2GGF, two-parameter Gompertz growth function; LGF, logistic growth function; L_t, mean length at time t; L_∞, mean length at age infinity; L_0, length at birth; k, growth coefficient; t_0, theoretical age at zero length; α, time at which the absolute rate of increase in length begins to decrease. The Gompertz growth functions from Ricker (1975, 1979) provided mass in the equation instead of total length (TL). In the present study, TL was substituted for mass, similarly to previous ageing studies of elasmobranchs (e.g. Carlson and Baremore 2005; Jacobsen and Bennett 2010; Harry *et al.* 2011*a*)

Model	Equation
3VBGF	$L_t = L_\infty(1 - e^{-k(t-t_0)})$
2VBGF	$L_t = L_\infty(1 - be^{-kt}), b = (L_\infty - L_0)/L_\infty$
3GGF	$L_t = L_\infty e^{-e[-k(t-t_0)]}$
2GGF	$L_t = L_0(e^{G(1-e^{(-kt)})}), G = \ln(L_\infty/L_0)$
LGF	$L_t = L_\infty/1 + e^{-k(t-\alpha)}$

Reproductive biology

The reproductive stage of females was determined only from retained specimens. Females were deemed mature if eggs or embryos were present in the uterus or if the oviducal gland was enlarged and heart-shaped (Walker 2005*b*). If mature, the ovary was removed and weighed (± 0.1 g) and the mean maximum ovum diameter derived from the three largest oocytes (± 0.1 mm) and plotted against Julian day. Eggs *in utero* were weighed (± 0.1 g) and macroscopically visible embryos were measured (TL), weighed and sexed by noting the presence or absence of claspers. The overall ratio of male to female embryos was tested for significant variation from a ratio of $1:1$ (chi-square goodness-of-fit test). To aid in determining the timing and duration of gestation, embryo TL was regressed against Julian day (Systat Software Inc.).

For males, maturity was determined following external examination of the claspers for all specimens (Bass *et al.* 1973; Walker 2005*b*), with specimens deemed mature if the claspers were rigid and fully calcified (Walker 2005*b*). If mature, the testes were removed and weighed (± 0.1 g).

The length and age at which the 50% of the population was mature (L_{50} and A_{50}, respectively) were determined separately for each sex. The proportion of mature animals was determined from 30-mm TL classes and 0.5-year age classes. Parameters were determined by least-squares non-linear regression (PASW Statistics), using the logistic function

$$P(l) = 1 \cdot \left(1 - e^{-\ln(19)\left(\frac{l-L_{50}}{L_{95}-L_{50}}\right)}\right)^{-1} \text{ (Walker 2005}b\text{),}$$

where $P(l)$ is the proportion of mature animals at TL l, and L_{50} and L_{95} correspond to the lengths at which 50% and 95% of the population are mature. For A_{50}, the proportion of mature animals in each age class (a) was substituted for l, with A_{50} and A_{95} substituted for L_{50} and L_{95}.

To determine the changes in reproductive condition, the gonadosomatic index (GSI) was calculated for mature female (including pregnant animals) and male specimens by using the equation GSI $= 100 \times$ gonad mass (g) $\times$ (whole body mass (g) $-$ gonad mass (g))$^{-1}$ (van der Velde *et al.* 2010). For pregnant sharks, embryo mass was excluded from total body mass. One-way analysis of variance (ANOVA) was then used to determine whether significant differences existed for GSI among months (PASW Statistics). For both sexes, GSI data were visually assessed for the assumptions underlying ANOVAs, with a $\log_{10}$ transformation substantially improving normality and heteroscedasticity. As such, a one-way ANOVA was conducted on transformed data for both sexes. If a significant difference was found, a Tukey *post hoc* test was used to examine among-month variations. If a month contained only a single sample, this was excluded from these analyses.

Results

Samples collected

In total, 178 *L. macrorhinus* specimens were measured, comprising 66 females (571–878 mm TL) and 112 males (571–855 mm TL). Of these, nine females of between 610 and 700 mm TL and 12 males of between 615 and 850 mm TL were calcein-injected, tagged and released. The size-frequency of retained specimens is represented in Fig. 3. The overall female size-frequency distribution was normal ($W = 0.98$, $n = 66$, $P > 0.05$), whereas the overall male size-frequency distribution was positively skewed ($W = 0.83$, $n = 112$, $P < 0.05$). A sex-ratio bias of $1.00 : 1.65$ towards males was present in the sampled population ($\chi^2 = 11.9$, d.f. $= 1$, $P < 0.05$). The relationships among TL, FL and M for sexes combined are given by the following equations:
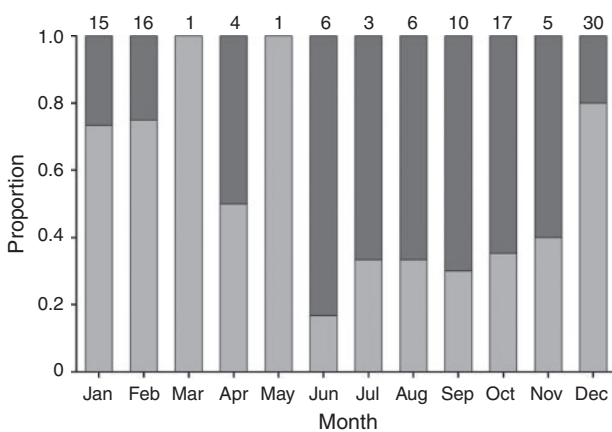
$$TL \text{ (mm)} = 70.195 + (1.134 \times FL \text{ (mm)}) \ (R^2 = 0.98, P < 0.05),$$

$$M \text{ (g)} = 3.93 \times 10^{-7} (FL)^{3.410 \pm 0.101} \ (R^2 = 0.87, P < 0.05), \text{ and}$$

$$M \text{ (g)} = 2.50 \times 10^{-8} (TL)^{3.709 \pm 0.110} \ (R^2 = 0.88, P < 0.05).$$
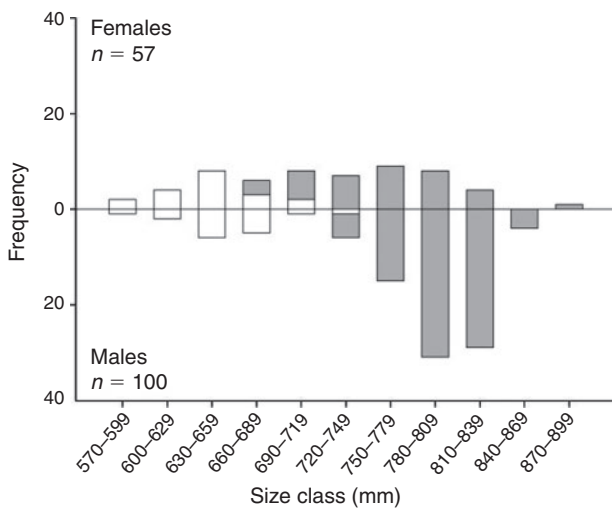
Fig. 3. Size-frequency of retained immature (white) and mature (grey) *Loxodon macrorhinus* individuals. Tagged and released specimens are not included in this plot.


Fig. 4. Centrum-edge analysis (CEA) for *Loxodon macrorhinus*, showing the proportion of opaque (light grey) and translucent (dark grey) bands at the centrum edge for each month. Sample sizes for each month are given above columns.

Age validation and verification

Of the 21 *L. macrorhinus* calcein-injected, tagged and released specimens, a single female with an estimated age of 1.3 years at time of recapture was recaptured after 336 days at liberty, and had grown from 610 mm to 664 mm TL. This individual formed a near complete growth band distal to the calcein mark, supporting the assumption of annual band-pair formation. Annual-band formation was also qualitatively verified, because CEA indicated that the highest proportion of opaque bands at the edge of the centrum occurred during the Austral summer and early autumn, excluding those months with low sample sizes (e.g. March; Fig. 4).

Age counts

Fifteen centra were excluded from the analysis because of a readability score of 5. Ages were determined from 114 centra
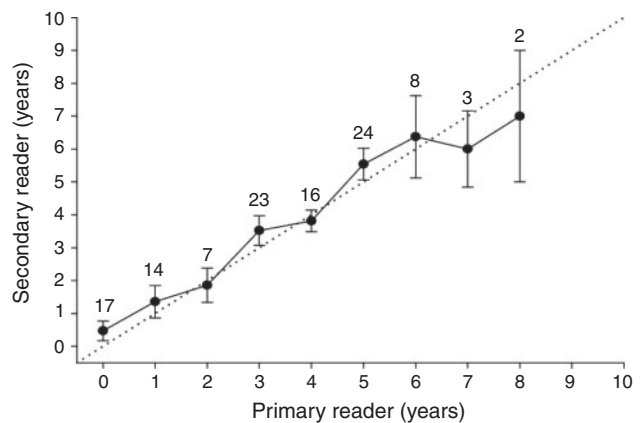
Fig. 5. Age-bias plot between the second count of the primary reader (A. N. Gutteridge) and the second count of the secondary reader (L. J. Marshall). Counts are plotted relative to a line of equivalence, with error bars representing two standard errors. Numbers above data points indicate sample sizes.

(38 females and 76 males). For all counts, between-reader APE and CV were 17.1% and 24.2%, respectively. PA for age estimates ±1 year between readers was 85.1%. The age-bias plot showed that the secondary reader produced higher age estimates for younger specimens, and that the highest variability came from age estimates derived from older animals (Fig. 5).

Growth estimates varied significantly between females and males ($\chi^2 = 16.9$, d.f. $= 3$, $P < 0.01$); thus, growth models were fitted separately to each sex. Of all growth models fitted to age estimates, the 3VBGF provided the best fit for both females and males (Table 2, Fig. 6). The 3GGF and LGF, however, also showed relatively high support on the basis of ω_i for both sexes. For females, estimated ages ranged from 0.3 to 8.9 years, corresponding to the smallest (571 mm TL) and largest (878 mm TL) specimens. For males, estimated ages ranged from 0.5 to 7.1 years, with the smallest (571 mm TL) and largest (855 mm TL) specimens being aged 0.6 and 6.0 years, respectively. The 2VBGF and 2GGF fitted through a fixed size-at-birth provided the lowest support of the five models fitted to age estimates. For both sexes, the 3VBGF provided the highest estimate of L_∞, with the 2VBGF and 2GGF providing the highest estimates of k (Table 2).

Although there was a significant difference between the growth curves of the two sexes, because of low sample sizes, growth models were fitted to sex-combined data. The LGF provided the best fit for sex-combined data, with the 3VBGF and 3GGF demonstrating strong support for model fitting to age estimates (Table 2).

Reproductive biology

Females ($n = 57$) ranged between 571 and 878 mm TL and 470 and 2300 g. Length and time at which 50% of the population was mature for females was 680 mm TL (95% CI: 674 mm, 686 mm) and 1.4 years (95% CI: 0.8, 1.9). Of all mature females ($n = 38$), 84.2% were pregnant and the smallest pregnant *L. macrorhinus* specimen was 664 mm TL. Pregnant sharks were caught in all months, excluding May (Fig. 7).
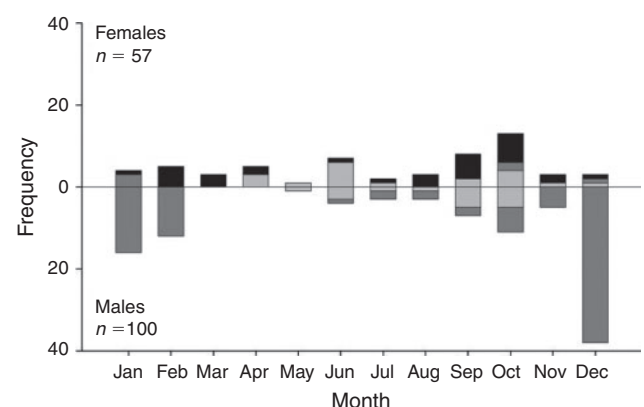
Table 2. Growth model parameters for *Loxodon macrorhinus* from Hervey Bay

3VBGF, three-parameter von Bertalanffy growth function; 2VBGF, two-parameter von Bertalanffy growth function; 3GGF, three-parameter Gompertz growth function; 2GGF, two-parameter Gompertz growth function; LGF, logistic growth function; L_∞, mean total length at age infinity; k, growth coefficient; t_0, theoretical age at zero length; α, time at which the absolute rate of increase in length begins to decrease; L_0, total length at birth; Δ_i, Akaike differences; ω_i, Akaike weights

| Sex	Model	L_∞ (95% CI)	k (95% CI)	t_0 (95% CI)	L_0 (mm)	α (95% CI)	Δ_i	ω_i
Combined	3VBGF	853 (823, 882)	0.32 (0.22, 0.41)	−3.7 (−4.9, −2.6)	–	–	0.6	0.28
	2VBGF	798 (789, 807)	1.01 (0.89, 1.13)	–	425	–	168.9	0.00
	3GGF	847 (821, 873)	0.36 (0.26, 0.46)	−2.9 (−3.7, −2.1)	–	–	0.2	0.34
	2GGF	795 (786, 804)	1.24 (1.09, 1.36)	–	425	–	194.2	0.00
	LGF	842 (819, 866)	0.41 (0.30, 0.51)	–	–	−2.2 (−2.7, −1.6)	0.0	0.38
Female	3VBGF	895 (791, 999)	0.18 (0.05, 0.31)	−6.3 (−9.9, −2.8)	–	–	0.0	0.37
	2VBGF	781 (754, 807)	1.03 (0.75, 1.32)	–	425	–	99.8	0.00
	3GGF	883 (797, 967)	0.22 (0.09, 0.35)	1.0 (0.8, 1.2)	–	–	0.3	0.33
	2GGF	776 (750, 802)	1.27 (0.93, 1.61)	–	425	–	108.4	0.00
	LGF	874 (799, 946)	0.26 (0.12, 0.39)	–	–	−3.4 (−4.6, −2.1)	0.6	0.29
Male	3VBGF	832 (809, 855)	0.44 (0.29, 0.60)	−2.6 (−3.7, −1.6)	–	–	0.0	0.43
	2VBGF	802 (795, 810)	1.09 (0.96, 1.22)	–	425	–	47.9	0.00
	3GGF	830 (808, 850)	0.49 (0.33, 0.65)	−2.1 (−2.9, −1.3)	–	–	0.6	0.33
	2GGF	800 (792, 808)	1.36 (1.20, 1.52)	–	425	–	59.9	0.00
	LGF	827 (808, 847)	0.53 (0.37, 0.70)	–	–	−1.6 (−2.3, −1.0)	1.2	0.24
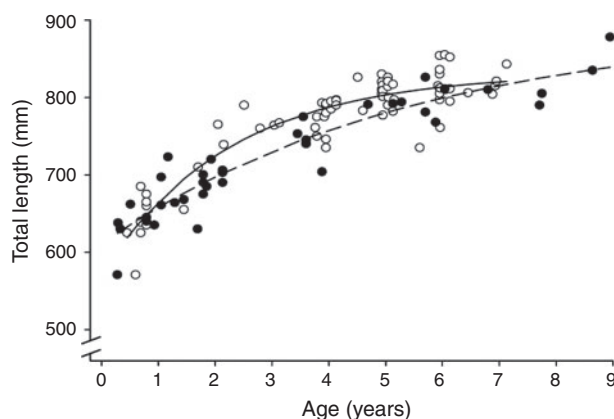
Fig. 6. von Bertalanffy growth model curves for female (closed circles, dashed line) and male (open circles, full line) *Loxodon macrorhinus* individuals from Hervey Bay.

Fig. 7. Number of female and male *Loxodon macrorhinus* individuals caught by month in Hervey Bay, including immature individuals (light grey bars), mature males and non-pregnant mature females (dark grey bars) and pregnant females (black bars). Tagged and released specimens are not included in this plot.

Mean GSI for female *L. macrorhinus* individuals peaked in mid-summer and late spring (November–January; Fig. 8*a*), with values being significantly higher in January than in February, August and September (one-way ANOVA: d.f. = 8, $P < 0.05$). Mean fecundity was 1.9 ± 0.3 s.d. ($n = 31$ litters) and ranged from one to two pups. Uterine eggs were observed from January to April. A positive correlation ($R^2 = 0.89$) existed between embryo development and increasing Julian day, with macroscopic embryos first observed in February (the smallest embryo 50 mm TL), developing through to December (Fig. 9*a*). The largest full-term embryo was 425 mm TL and 208.7 g, with this length assumed to be the size at birth for this species within Hervey Bay. The overall body size of the largest full-term pup was ∼48% of maternal TL and ∼10% of maternal body mass.

Sex was determined for 27 embryos, with no significant sex bias between females and males ($\chi^2 = 1.82$, d.f. = 1, $P > 0.05$). Vitellogenic oocytes were observed between November and April, with the largest mean oocyte diameters found between November and February (Fig. 9*b*). The largest mean ovarian oocyte diameter was recorded from a pregnant shark carrying late-term embryos in December. Overall, results are consistent with an annual and seasonal reproductive cycle for *L. macrorhinus* within Hervey Bay.

Males ($n = 100$) ranged from 571 to 855 mm TL and from 500 to 1900 g. In all, 84% of all males in the sample were mature, with L_{50} of 733 mm TL (95% CI: 733 mm, 733 mm) and A_{50} of
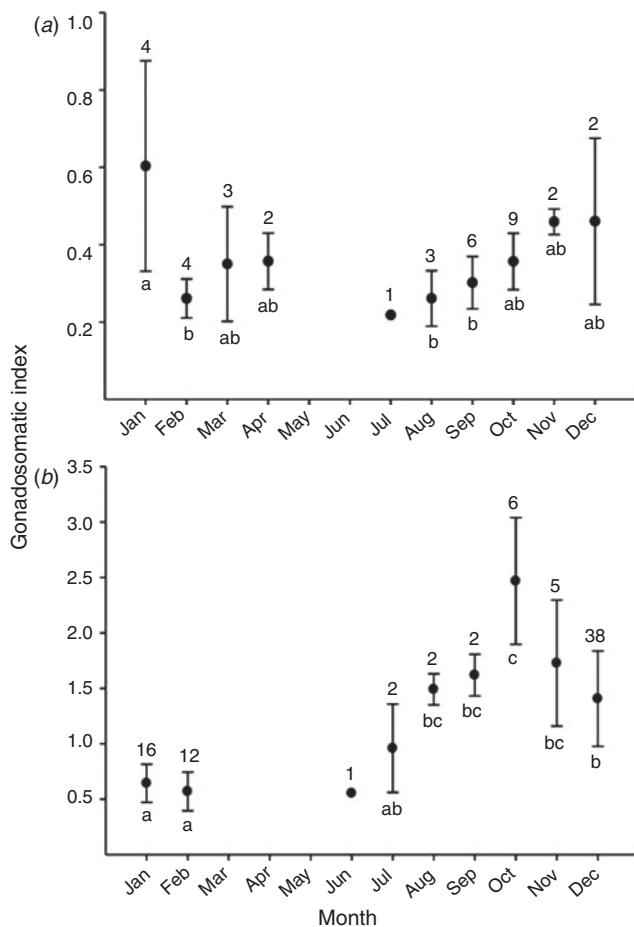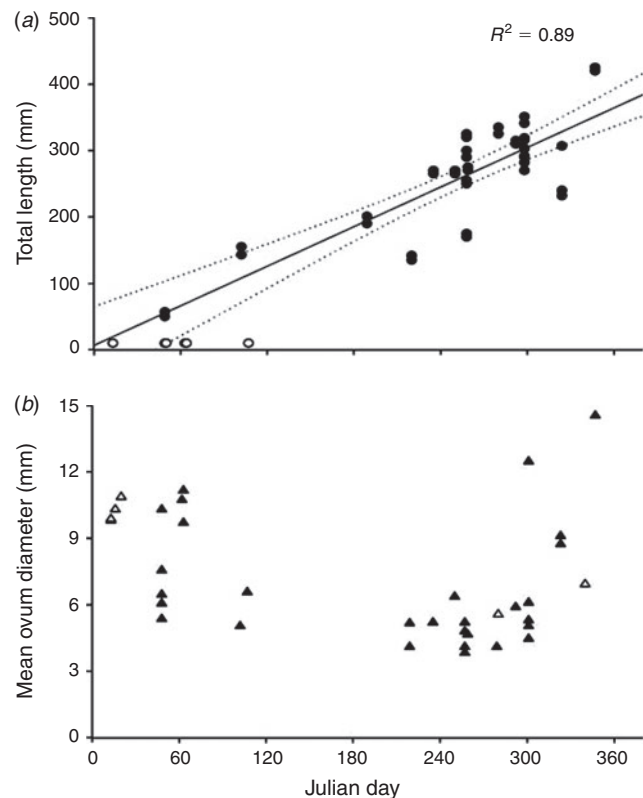
Fig. 8. Mean (±s.d.) monthly gonadosomatic index (GSI) for mature (*a*) female and (*b*) male *Loxodon macrorhinus*. Values above bars indicate monthly sample sizes. Months that are significantly different ($P < 0.05$) do not share a common letter.

Fig. 9. Julian day against (*a*) total length (TL) of embryos and (*b*) mean maximum ovum diameter (mm) from mature females. Embryos with measurable TL (solid circles); and uterine eggs, given an arbitrary value of 10 mm TL for visual representation (open circles). Only embryos with measurable TLs were included in the regression analysis. Mature pregnant females (solid triangles); and mature non-pregnant females (open triangles).

1.9 years (95% CI: 1.9, 1.9) years. For mature males, mean GSI peaked in October, with values varying significantly among months (one-way ANOVA: d.f. = 7, $P < 0.05$; Fig. 8*b*).

Discussion

Loxodon macrorhinus is a relatively fast-growing shark that exhibits a synchronous, annual reproductive cycle within Hervey Bay. In terms of age and growth, the *k* values and estimated maximum ages were comparable to those estimated for other small-bodied coastal carcharhinids (maximum TL of <1000 mm; Table 3). As with age and growth, the reproductive biology of *L. macrorhinus* was similar to that of other small-bodied coastal carcharhinids. An exception to this was the observed fecundity, with the production of one or two pups per litter being among the lowest for any carcharhinid (Stevens and McLoughlin 1991; Last and Stevens 2009). Excluding fecundity and the relatively large size at birth, the hypothesis that the life history of *L. macrorhinus* conformed to that of other small-bodied carcharhinids was supported.

The present study provided the first age and growth estimates for *L. macrorhinus*. Annual band formation was validated from

a flurochrome-labelled shark, recaptured after almost 1 year at liberty, and estimated to be 1.3 years at the time of recapture. Such annual band validation is consistent with reports from other coastal carcharhiniform sharks (Simpfendorfer *et al.* 2002; McAuley *et al.* 2006; Harry *et al.* 2011*a*) and inshore elasmobranchs (Pierce and Bennett 2009). Annual band formation was further verified across all ages from centrum-edge analysis, with opaque bands forming during the Austral summer. The growth coefficients (*k*) from the best-fit models for males and sex-combined data were comparable to those for other small-bodied carcharhinid species (Table 3). For females, however, the observed *k* value from the best-fit model (0.18 year⁻¹) was the lowest recorded for this group of species (Table 3), suggesting that females grow relatively slowly. However, low sample size was likely to have influenced this result, as witnessed by the high error associated with model parameters. Given this large error, in the absence of more robust age and growth data, it is recommended that the parameters generated from the sex-combined data be used for population assessments. Additionally, because plotted age estimates indicated that the initial growth of *L. macrorhinus* was rapid, the *k* values generated by the 2GGF and 2VBGF (between ~1.00 and 1.30 year⁻¹) may provide a more biologically realistic estimate for growth. Notwithstanding, the *k* values from all growth models were

Table 3. Growth-model variations for small-bodied carcharhinid sharks

L_∞, mean length at age infinity; k, growth coefficient; Max. age, maximum reported age for each species from the given study. Measurements are given as total length (TL), stretched total length (STL), and pre-caudal length (PCL)

Species	Sex	L_∞ (mm)	k	Age at maturity	Max. age	Study
Slit-eye shark, *Loxodon macrorhinus*	Female	895 TL	0.18	1.4[C]	8.9	Present study
	Male	832 TL	0.44	1.9[C]	7.1	
Spadenose shark, *Scoliodon laticaudus*	Combined	842 TL	0.41	–	–	(Prabhakaran Nair 1976)
	Combined	715 TL	0.358	–	5+	
Milk shark, *Rhizoprionodon acutus*	Female	861 STL	0.63	1.8[C]	8.1	(Harry *et al.* 2010)
	Male	821 STL	0.94	1.1[C]	4.5	
Australian sharpnose shark, *R. taylori*	Female	732.5 TL	1.013	1	6.9	(Simpfendorfer 1993)
	Male	652.2 TL	1.337	1	5.7	
Atlantic sharpnose shark, *R. terraenovae*	Female	749 PCL	0.49	–	11+	(Loefer and Sedberry 2003)
	Male	745 PCL	0.5	–	–	
	Combined[A]	1100.8 TL	0.39	2.3 (both sexes)[C]	9.5+ female	(Carlson and Baremore 2003)
	Combined[B]	940 TL	0.73	1.6 females, 1.3 males[C]	9.5+ female	

[A]Parameter values from samples obtained in 1984;
[B]Parameter values from samples obtained between 1998 and 2001 (Carlson and Baremore 2003);
[C]Age at which 50% of the population was mature (A_{50}).

consistent with those reported for other small-bodied species, and were relatively high when compared with those for large-bodied carcharhinids and coastal elasmobranchs (Cailliet and Goldmann 2004).

The values of APE (17.1%) and CV (24.2%) were high in comparison with those in other ageing studies of elasmobranchs (e.g. McAuley *et al.* 2006; Jacobsen and Bennett 2010; Harry *et al.* 2011*a*), thus indicating that there was a bias associated with assigning age estimates. The secondary reader generally produced higher age estimates, with the highest variability between readers occurring on older specimens (Fig. 5). The variability associated with these larger animals stemmed from the banding becoming increasingly narrow and difficult to discriminate towards to the edge of each centrum. Because the PA between all reads ±1 year was 85.1%, and the CV was similar to age estimates for *R. acutus* (Harry *et al.* 2010), age estimates were considered valid.

Although numerous large-bodied chondricthyans reach maximum estimated ages in excess of 20 years (McAuley *et al.* 2006; Piercy *et al.* 2007; Cerna and Licandeo 2009), smaller inshore species of shark, particularly carcharhinids, often have a maximum age of <10 years (Table 3). Therefore, the maximum ages of *L. macrorhinus* reported in the present study were within an expected range. For many small-bodied carcharhinids, initial growth is extremely rapid and slows markedly on obtaining sexual maturity, e.g. for *R. taylori* (Simpfendorfer 1993). Although male *L. macrorhinus* demonstrated a similar trend, the best-fit age model (3VBGF) for females did not reach an asymptote. This was possibly due to age underestimations for larger specimens, resulting from the aforementioned tight banding at the edge of the centrum. Alternatively, the lack of asymptote and potential underestimation of the k values in the 3VBGF growth curve could be an artefact of low sample size or the absence of neonate sharks in the sample.

As with maximum estimated age, the A_{50} values for *L. macrorhinus* females (1.4 years) and males (1.9 years) were similar to those reported for other small-bodied carcharhinids, e.g. for *R. acutus* females (1.8 years) and males (1.1 years)

(Table 3). In all the aforementioned cases, ages-at-maturity represent a small proportion of the maximum reported ages. Such early maturation contrasts with that of many large-bodied shark species that typically undergo maturation at much older ages, and at a greater proportion of their maximum age (Simpfendorfer *et al.* 2002; Bishop *et al.* 2006; Harry *et al.* 2011*a*). Thus, the results of the present study indicate that for *L. macrorhinus*, the time to reach theoretical maximum length and the early maturation contrasts with that of large-bodied species. Such traits are likely to be an adaptive response to the possible high natural mortality across all ages for *L. macrorhinus* (Harry *et al.* 2010).

Analysis of the reproductive biology of *L. macrorhinus* indicated a seasonal annual cycle within Hervey Bay. This was largely due to the fact that oocytes developed simultaneously to embryos and that vitellogenic oocytes were largest around the time of parturition. An increase in embryo size from February to December and the presence of eggs *in utero* from January to April indicated that parturition likely occurred in December and January. Because the largest ova were observed from December to March and *in utero* eggs were observed from January to April, ovulation is estimated to have occurred from December until March. The protracted time over which ovulation took place led to an estimated gestation of 9–12 months. Male GSI peaked in October and remained high until December. This is consistent with the proposed mating period, because sperm development can lag behind the highest GSI values by a few months (Kyne and Bennett 2002). Additionally, the proposed mating period of December to February coincided with an influx of mature males into the study area. However, to fully confirm this interpretation, the cycle of spermatogenesis in *L. macrorhinus* should be investigated by the histological analysis of testes. Additionally, because there was a lag between the proposed mating period and the presence of eggs *in utero*, histological examinations of the oviducal gland are recommended to identify the possibility of sperm storage before ovulation (Pratt 1993; Driggers *et al.* 2004*b*).

Table 4. Regional variation of the reproductive biological parameters for *Loxodon macrorhinus*

All lengths are given as total length (TL, mm) with values for females (♀) and males (♂) given separately where appropriate. The table is sorted according to the maximum reported size of male *L. macrorhinus*

Location	*n*	Size at birth	No. of pups	Length at maturity, ♀	Length at maturity, ♂	Max. TL, ♀	Max. TL, ♂	Study
Great Barrier Reef	332	–	–	–	–	–	990	(Harry *et al.* 2011*b*)
Indonesia	117	540–550	2	–	819[A]	989	974	(White 2007)
Republic of Maldives	321	–	–	–	–	–	940	(Anderson and Ahmed 1993)
Tanzania	4	–	2	–	<780	850	905	(Wheeler 1959)
Hervey Bay	157	425	1 or 2	680[A]	733[A]	878	855	Present Study
Oman	250	–	–	–	–	870	850	(Henderson *et al.* 2007)
South Africa	14	400	2	–	730–750	900	850	(Bass *et al.* 1975)
Northern Australia	279	400–430	1 or 2	560–600	590–680	880	800	(Stevens and McLoughlin 1991)

[A]Length at which 50% of the population was mature (L_{50}).

Sampled populations of *L. macrorhinus* exhibit regional variations in life-history parameters (Table 4). Of note is the considerably larger size at birth, size at maturity and maximum TL from the Indonesian population (White 2007). Variations in length at maturity and maximum TL among geographic regions have been reported in sharks and have been linked to differences in water temperature (Menni and Lessa 1998) that correlate to latitude (Yamaguchi *et al.* 2000; Lombardi-Carlson *et al.* 2003). For example, Colonello *et al.* (2007) reported an increased size-at-maturity with increasing latitude for the angular angel shark, *Squatina guggenheim*. This increased length at maturity was hypothesised to occur because animals at a higher latitude needed to store more energy during seasons of low productivity and low water temperature (Blackburn *et al.* 1999). Counter-intuitively, for *L. macrorhinus*, size-at-maturity and maximum TL in Hervey Bay were smaller than those for the Indonesian population. Within Australian waters, however, *L. macrorhinus* conformed to the trend observed in *S. guggenheim*, with sharks from northern Australia (Stevens and McLoughlin 1991) having a smaller maximum TL and size-at-maturity than for individuals in the present study (Table 4). This suggests a possible segregation between the Indonesian and Australian populations, with latitudinal effects on length at maturity within the Australian population of *L. macrorhinus*.

As with length at maturity and maximum total length, regional differences have been observed in the reproductive biology of elasmobranchs (Yamaguchi *et al.* 2000). The seasonal, annual cycle observed in the present study differed from that of a northern Australian population of *L. macrorhinus*. In the northern Australian population, monthly GSI, maximum ova diameter (MOD) and embryo development showed no obvious seasonality, indicating an asynchronous cycle with year-round breeding (Stevens and McLoughlin 1991). For another small-bodied species, *R. acutus*, variations in the reproductive cycle occur throughout its range (Bass *et al.* 1975; Henderson *et al.* 2006), ranging from an annual and seasonal reproductive cycle off Senegal (Capapé *et al.* 2006), to an aseasonal reproductive cycle in the northern Australian population (Stevens and McLoughlin 1991). Because the differences in reproductive seasonality are likely to be related to local environmental conditions, particularly water temperature (Walker 2007), it is possible that the subtropical environment of Hervey Bay influenced the reproductive biology of *L. macrorhinus*.

Female *L. macrorhinus* within Hervey Bay had a lower age and length at maturity than did males. Although a smaller length at maturity for females has been observed in some elasmobranchs, e.g. Colclough's shark, *Brachaelurus colcloughi* (Kyne *et al.* 2011), and the eastern shovelnose ray, *Aptychotrema rostrata* (Kyne and Bennett 2002), this is atypical of most viviparous elasmobranchs, including carcharhinids (Stevens and McLoughlin 1991; Last and Stevens 2009). In northern Australia, female *L. macrorhinus* also underwent maturation at sizes smaller than those of males (Stevens and McLoughlin 1991) (Table 4), suggesting that this trend is not exclusive to the Hervey Bay population. Although the reasons underlying this observation are unknown, it may be linked to the proportion of mature males in the sample or the reproductive strategy exhibited by *L. macrorhinus*. The high proportion of mature males may have influenced the L_{50} calculations, thus inflating the differences between estimates of male and female maturity. Excluding this sample bias, however, the reproductive strategy of *L. macrorhinus* may inherently drive a lower L_{50} in females. Small-bodied carcharhinids are likely to have high natural mortality as a result of predation across all age classes (Branstetter 1990). As such, their life history may be driven by the need to undergo early maturity so as to produce as many litters as possible throughout their life (Simpfendorfer 1992). Therefore, it is possible that female *L. macrorhinus* individuals undergo maturity at a smaller TL than do males, so as to maximise the number of litters they produce throughout their lifecycle, thus offsetting their low fecundity and potentially high natural mortality.

Across all studied regions, including the present study, the litter size of *L. macrorhinus* was one or two pups, with a mean of about two pups (Stevens and McLoughlin 1991; White 2007). This low fecundity is balanced by a relatively large size-at-birth in comparison with the maximum maternal TL. *L. macrorhinus* from Hervey Bay, northern Australia (Stevens and McLoughlin 1991) and Indonesia (White 2007) were born at 48–55% of the maximum-recorded TL. Small-bodied carcharhinids vary in life history, from species that demonstrate low fecundity and pro-portionally large size at birth, such as e.g. the hardnose shark, *C. macloti*, with a mean litter size of two pups at 42% of maximum maternal TL (Stevens and McLoughlin 1991), to those that demonstrate high fecundity and proportionally low size at birth, such as *R. taylori*, with a mean litter size of 4.5 at 33% of

maximum TL (Simpfendorfer 1992). Of these two strategies, the former has the higher maternal investment per pup (Hussey *et al.* 2010), which, presumably, increases the chance of survival of each offspring into adulthood. In contrast, the latter divides maternal investment more broadly to produce a larger number of smaller young, such that, even with potentially higher rates of mortality, some will survive into adulthood. When placed in a fisheries biology context, species that produce low numbers of well developed young, such as *L. macrorhinus*, may have a comparatively protracted recovery time following exploitation, as regeneration of subsequent generations would be low (Smith *et al.* 1998).

Low sample sizes, particularly for females, reduced the robustness of life-history estimates in the present study. For females, the high amount of error around the age and growth estimates suggests that the data should be treated as preliminary. The reasons underlying the low sample size for females remain unknown; however, it is possible that segregation of larger animals occurred in areas outside the sampling location. Although gear selectivity may have led to under-representation of smaller individuals, previous estimates of gill-net selectivity for *R. terraenovae* suggest that the probability of capture for larger *L. macrorhinus* would have been high (Carlson and Cortes 2003). Rather, the low number of females was possibly because of habitat segregation. This segregation may be linked to gestation, because 84.2% of females in the present study were pregnant. As such, it is possible that the sampling area was a pupping and mating ground and that immature and non-pregnant mature females occur in higher proportions within habitats not sampled in the present study. By occupying the shallow waters sampled by the study, pregnant females may increase the proficiency of their gestation (Jirik and Lowe 2012) or limit their interactions with mature males (Knip *et al.* 2012).

As with larger females, there was an under-representation of subadult males and smaller mature males in the sample. This is likely to have influenced the estimated L_{50} and A_{50}, because the proportion of mature animals in the size classes around these parameters underwent a sharp increase. As such, the CI around these estimates was extremely tight. A low representation of subadult and smaller mature males in the sample, and the influx of larger mature males that coincided with the proposed breeding season, further support the hypothesis that the area sampled by the present study was a mating ground. To fully explore this hypothesis, however, acoustic telemetry targeting various life-history stages and additional sampling outside the study area would be required.

Within the ECIFFF of Queensland, a fishery that operates within Hervey Bay waters, onboard-observer data from commercial gill-netting boats indicated that *L. macrorhinus* was captured in moderate to low numbers (Harry *et al.* 2011*b*; Gutteridge 2012). Coupled with its general biology of relatively fast growth, early maturation and an annual reproductive cycle, it is therefore likely that *L. macrorhinus* is resilient to the current exploitative pressures within this fishery. However, the lower fecundity exhibited by this species may result in its susceptibility to exploitation being higher than for other small-bodied species. Quantitative methods to determine mortality and susceptibility, particularly those that incorporate fecundity (Smith *et al.* 1998), are therefore required to determine whether the above assumption is correct. Last, as the biology of *L. macrorhinus* from Hervey Bay differed from that in other locations, it is recommended that further studies be conducted on this species, because regional variations in life history are likely (Driggers *et al.* 2004*a*; Piercy *et al.* 2007). Therefore, research on a local scale should be encouraged and populations of *L. macrorhinus* should be managed with a cautionary approach in the absence of regionally specific life-history data and quantitative mortality assessments.

Acknowledgements

References

Allen, B. R., and Cliff, G. (2000). Sharks caught in the protective gill nets off KwaZulu–Natal, South Africa. 9. The spinner shark *Carcharhinus brevipinna* (Müller and Henle). *South African Journal of Marine Science* **22**, 199–215. doi:10.2989/025776100784125654

Anderson, R. C., and Ahmed, H. (1993). 'The Shark Fisheries of the Maldives.' (FAO Ministry of Fisheries and Agriculture: Rome.)

Bass, A. J., D'Aubrey, J. D., and Kistnasamy, N. (1973). 'Sharks of the East Coast of Southern Africa. l. The Genus *Carcharhinus* (Carcharhinidae).' (The Oceanographic Research Institute: Durban, South Africa.)

Bass, A. J., D'Aubrey, J. D., and Kistnasamy, N. (1975). 'Sharks of the East Coast of Southern Africa. 3. The Families Carcharhinidae (Excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae.' (The Oceanographic Research Institute: Durban, South Africa.)

Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 982–983. doi:10.1139/F81-132

Beverton, R. J. H., and Holt, S. J. (1957). 'On the Dynamics of Exploited Fish Populations.' (Ministry of Agriculture Fisheries, and Food, Fisheries Investigations: UK.)

Bishop, S. D. H., Francis, M. P., Duffy, C., and Montgomery, J. C. (2006). Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters. *Marine and Freshwater Research* **57**, 143–154. doi:10.1071/MF05077

Blackburn, T. M., Gaston, K. J., and Loder, N. (1999). Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity & Distributions* **5**, 165–174. doi:10.1046/J.1472-4642.1999.00046.X

Branstetter, S. (1990). Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries. Vol. 90'. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) pp. 17–28. NOAA Technical Report. (National Marine Fisheries Service.)

Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multi-model Inference – A Practical Information-theoretic Approach.' (Springer: New York.)

Cailliet, G. M., and Goldmann, K. J. (2004). Age determination and validation in chondrichtyan fishes. In 'Biology of Sharks and Their Relatives'. (Eds J. C. Carrier, J. A. Musick and M. R. Heithaus.) pp. 399–447. (CRC Press: Boca Raton, FL.)

Cailliet, G. M., Smith, W. D., Mollet, H. F., and Goldmann, K. J. (2006). Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation and growth function fitting. *Environmental Biology of Fishes* **77**, 211–228. doi:10.1007/S10641-006-9105-5

Capapé, C., Diatta, Y., Diop, M., Guelorget, O., Vergne, Y., and Quignard, J.-P. (2006). Reproduction in the milk shark, *Rhizoprionodon acutus* (Rüppell, 1837) (Chondrichthyes: Carcharhinidae), from the coast of Senegal (eastern tropical Atlantic). *Acta Adriatica* **47**, 111–126.

Carlson, J. K., and Baremore, I. E. (2003). Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity? *Marine and Freshwater Research* **54**, 227–234. doi:10.1071/MF02153

Carlson, J. D., and Baremore, I. E. (2005). Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coasts: a comparison of methods. *Fish Bulletin* **103**, 280–291.

Carlson, J. K., and Cortes, E. (2003). Gillnet selectivity of small coastal sharks off the southeastern United States. *Fisheries Research* **60**, 405–414. doi:10.1016/S0165-7836(02)00135-2

Cerna, F., and Licandeo, R. (2009). Age and growth of the shortfin mako (*Isurus oxyrinchus*) in the south-eastern Pacific off Chile. *Marine and Freshwater Research* **60**, 394–403. doi:10.1071/MF08125

Chang, W. Y. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1208–1210. doi:10.1139/F82-158

Colonello, J. H., Lucifora, L. O., and Massa, A. M. (2007). Reproduction of the angular angel shark (*Squatina guggenheim*): geographic differences, reproductive cycle, and sexual dimorphism. *ICES Journal of Marine Science* **64**, 131–140.

Compagno, L. J. V. (1988). 'Sharks of the Order Carcharhiniformes.' (Princeton University Press: Princeton, NJ.)

Compagno, L. J. V., Dando, M., and Fowler, S. (2005). 'A Field Guide to the Sharks of the World.' (Princeton University Press: Princeton, NJ.)

Driggers, W. B., Carlson, J. K., Cullum, B., Dean, J. M., Oakley, D., and Ulrich, G. (2004*a*). Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth rates. *Environmental Biology of Fishes* **71**, 171–178. doi:10.1007/S10641-004-0105-Z

Driggers, W. B., Oakley, D. A., Ulrich, G., Carlson, J. K., Cullum, B. J., and Dean, J. M. (2004*b*). Reproductive biology of *Carcharhinus acronotus* in the coastal waters of South Carolina. *Journal of Fish Biology* **64**, 1540–1551. doi:10.1111/J.0022-1112.2004.00408.X

Dudley, S. F. J., and Cliff, G. (1993). Sharks caught in the protective gill nets off Natal, South Africa, 7. The blacktip shark, *Carcharhinus limbatus* (Valenciennes). *South African Journal of Marine Science – Suid-Afrikaanse Tydskrif Vir Seewetenskap* **13**, 237–254.

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve *Growth* **29**, 265–289.

Frisk, M. G., Miller, T. J., and Fogarty, M. J. (2001). Estimation and analysis of biological parameters in elasmobranch fishes: a comparitive life history study. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 969–981. doi:10.1139/F01-051

Goldmann, K. J. (2005). Age and growth of elasmobranch fishes. In 'Management Techniques for Elasmobranch Fisheries: FAO Fisheries Technical Paper. Vol. 474'. (Eds J. A. Musick and R. Bonfil.) pp. 76–102. (FAO: Rome.)

Gutteridge, A. N. (2012). Community structure and biology of the elasmobranchs of Hervey Bay, southeast Queensland, Australia. Ph.D. Thesis. University of Queensland, Brisbane.

Gutteridge, A. N., Bennett, M. B., Huveneers, C., and Tibbetts, I. R. (2011). Assessing the overlap between the diet of a coastal shark and the surrounding prey communities in a sub-tropical embayment. *Journal of Fish Biology* **78**, 1405–1422. doi:10.1111/J.1095-8649.2011.02945.X

Harry, A. V., Simpfendorfer, C. A., and Tobin, A. J. (2010). Improving age, growth and maturity estimates for aseasonally reproducing chondrichthyans. *Fisheries Research* **106**, 393–403. doi:10.1016/J.FISHRES.2010.09.010

Harry, A. V., Macbeth, W. G., Gutteridge, A. N., and Simpfendorfer, C. A. (2011*a*). The life histories of endangered hammerhead sharks (Carcharhiniformes, Sphyrnidae) from the east coast of Australia. *Journal of Fish Biology* **78**, 2026–2051. doi:10.1111/J.1095-8649.2011.02992.X

Harry, A. V., Tobin, A. J., Simpfendorfer, C. A., Welch, D. J., Mapleston, A., White, J., Williams, A. J., and Stapley, J. (2011*b*). Evaluating catch and mitigating risk in a multi-species, tropical, inshore shark fishery within the Great Barrier Reef World Heritage Area. *Marine and Freshwater Research* **62**, 710–721. doi:10.1071/MF10155

Henderson, A. C., McIlwain, J. L., Al-Oufi, H. S., and Ambu-Ali, A. (2006). Reproductive biology of the milk shark *Rhizoprionodon acutus* and the bigeye houndshark *Iago omanensis* in the coastal waters of Oman. *Journal of Fish Biology* **68**, 1662–1678. doi:10.1111/J.0022-1112.2006.01011.X

Henderson, A. C., McIlwain, J. L., Al-Soufi, H. S., and Al-Seili, S. (2007). The Sultanate of Oman shark fishery: species composition, seasonality and diversity. *Fisheries Research* **86**, 159–168. doi:10.1016/J.FISHRES.2007.05.012

Hussey, N. E., Wintner, S. P., Dudley, S. F. J., Cliff, G., Cocks, D. T., and MacNeil, M. A. (2010). Maternal investment and size-specific reproductive output in carcharhinid sharks. *Journal of Animal Ecology* **79**, 184–193. doi:10.1111/J.1365-2656.2009.01623.X

Jacobsen, I. P., and Bennett, M. B. (2010). Age and growth of *Neotrygon picta, Neotrygon annotata* and *Neotrygon kuhlii* from north-east Australia, with notes on their reproductive biology. *Journal of Fish Biology* **77**, 2405–2422. doi:10.1111/J.1095-8649.2010.02829.X

Jirik, K. E., and Lowe, C. G. (2012). An elasmobranch maternity ward: female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. *Journal of Fish Biology* **80**, 1227–1245. doi:10.1111/J.1095-8649.2011.03208.X

Johnson, A. G. (1979). A simple method for staining the centra of teleost vertebrae. *Northeast Gulf Science* **3**, 113–115.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* **77**, 765–776.

Knip, D. M., Heupel, M. R., and Simpfendorfer, C. A. (2012). Habitat use and spatial segregation of adult spottail sharks *Carcharhinus sorrah* in tropical nearshore waters. *Journal of Fish Biology* **80**, 767–784. doi:10.1111/J.1095-8649.2012.03223.X

Kyne, P. M., and Bennett, M. B. (2002). Reproductive biology of the eastern shovelnose ray, *Aptychotrema rostrata* (Shaw and Nodder, 1794), from Moreton Bay, Queensland, Australia. *Marine and Freshwater Research* **53**, 583–589. doi:10.1071/MF01063

Kyne, P. M., Compagno, L. J. V., Stead, J., Jackson, M. V., and Bennett, M. B. (2011). Distribution, habitat and biology of a rare and threatened eastern Australian endemic shark: Colclough's shark, *Brachaelurus colcloughi* Ogilby, 1908. *Marine and Freshwater Research* **62**, 540–547. doi:10.1071/MF10160

Last, P. R., and Stevens, J. D. (2009). 'Sharks and Rays of Australia.' (CSIRO Publishing: Melbourne.)

Loefer, J. K., and Sedberry, G. R. (2003). Life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Richardson, 1836) off the southeastern United States. *Fishery Bulletin* **101**, 75–88.

Lombardi-Carlson, L. A., Cortes, E., Parsons, G. R., and Manire, C. A. (2003). Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo*, (Carcharhiniformes: Sphyrnidae) from the eastern Gulf

of Mexico. *Marine and Freshwater Research* **54**, 875–883. doi:10.1071/MF03023

McAuley, R. B., Simpfendorfer, C. A., Hyndes, G. A., Allison, R. R., Chidlow, J. A., Newman, S. J., and Lenanton, R. C. J. (2006). Validated age and growth of the sandbar shark, *Carcharhinus plumbeus* (Nardo 1827) in the waters off Western Australia. *Environmental Biology of Fishes* **77**, 385–400. doi:10.1007/S10641-006-9126-0

Menni, R.C., and Lessa, R.P. (1998). The chondrichthyan community off Maranhao (northeastern Brazil) II. Biology of species. *Acta Zoologica Lilloana* **44**, 69–89.

Officer, R. A., Gason, A. S., Walker, T. I., and Clement, J. G. (1996). Sources of variation in counts of growth increments in vertebrae from gummy shark, *Mustelus antarcticus,* and school shark, *Galeorhinus galeus:* implications for age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 1765–1777. doi:10.1139/F96-103

Pierce, S. J., and Bennett, M. B. (2009). Validated annual band-pair periodicity and growth parameters of blue-spotted maskray *Neotrygon kuhlii* from south-east Queensland, Australia. *Journal of Fish Biology* **75**, 2490–2508. doi:10.1111/J.1095-8649.2009.02435.X

Piercy, A. N., Carlson, J. K., Sulikowski, J. A., and Burgess, G. H. (2007). Age and growth of the scalloped hammerhead shark, *Sphyrna lewini*, in the north-west Atlantic Ocean and Gulf of Mexico. *Marine and Freshwater Research* **58**, 34–40. doi:10.1071/MF05195

Prabhakaran Nair, K. (1976). Age and growth of the yellow dog shark *Scoliodon laticaudus* Muller and Henle from Bombay waters. *Journal of the Marine Biological Association of India* **18**, 531–539.

Pratt, H. L. (1993). The storage of spermatozoa in the oviducal glands of western North Atlantic sharks. *Environmental Biology of Fishes* **38**, 139–149. doi:10.1007/BF00842910

Quinn, T. J., and Deriso, R. B. (1999). 'Quantitative Fish Dynamics.' (Oxford University Press: New York.)

Ricker, W. E. (1975). 'Computation and Interpretation of Biological Statistics of Fish Populations.' (Department of the Environment Fisheries and Marine Service: Ottawa, Canada.)

Ricker, W. E. (1979). Growth rates and models. In 'Fish Physiology: Bioenergetics and Growth. Vol. VIII'. (Eds W. S. Hoar, D. J. Randall and J. R. Brett.) pp. 677–743. (Academic Press: San Diego, CA.)

Schwartz, F. J. (1983). Shark ageing methods and age estimation of scalloped hammerhead, *Sphyrn lewini,* and dusky, *Carcharhinus obscurus,* sharks based on vertebral ring counts. In 'Proceedings of the International Workshop on Age Determination of Oceanic Fishes: Tunas, Billfishes and Sharks. Vol. NMFS 8'. (Eds E. D. Prince and L. M. Pulos.) pp. 167–174. (NOAA Technical Report: Miami, FL.)

Simpfendorfer, C. A. (1992). Reproductive strategy of the Australian sharpnose shark, *Rhizoprionodon taylori* (Elasmobranchii: Carcharhinidae), from Cleveland Bay, northern Queensland. *Australian Journal of Marine and Freshwater Research* **43**, 67–75. doi:10.1071/MF9920067

Simpfendorfer, C. A. (1993). Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia. *Environmental Biology of Fishes* **36**, 233–241. doi:10.1007/BF00001718

Simpfendorfer, C. A., McAuley, R. B., Chidlow, J. A., and Unsworth, P. (2002). Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. *Marine and Freshwater Research* **53**, 567–573. doi:10.1071/MF01131

Smith, S. E., Au, D. W., and Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **49**, 663–678. doi:10.1071/MF97135

Smith, W. D., Cailliet, G. M., and Melendez, E. M. (2007). Maturity and growth characteristics of a commercially exploited stingray, *Dasyatis dipterura. Marine and Freshwater Research* **58**, 54–66. doi:10.1071/MF06083

Stevens, J. D., and McLoughlin, K. J. (1991). Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. *Australian Journal of Marine and Freshwater Research* **42**, 151–199. doi:10.1071/MF9910151

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**, 476–494. doi:10.1006/JMSC.2000.0724

van der Velde, T. D., Griffiths, S. P., and Fry, G. C. (2010). Reproductive biology of the commercially and recreationally important cobia *Rachycentron canadum* in northeastern Australia. *Fisheries Science* **76**, 33–43. doi:10.1007/S12562-009-0177-Y

von Bertalanffy, L. (1938). A quantitative theory of organic growth, inquiries on growth laws II. *Human Biology* **10**, 181–213.

Walker, T. I. (2005*a*). Management measures. In 'Management Techniques for Elasmobranch Fisheries: FAO Fisheries Technical Paper. Vol. 474'. (Eds J. A. Musick and R. Bonfil.) pp. 216–242. (FAO: Rome.)

Walker, T. I. (2005*b*). Reproduction in fisheries science. In 'Reproductive Biology and Phylogeny of Chondrichthyes. Vol. 3'. (Ed. W. C. Hamlett.) pp. 81–128. (Science Publishers: Enfield, NH.)

Walker, T. I. (2007). Spatial and temporal variation in the reproductive biology of gummy shark *Mustelus antarcticus* (Chondrichthyes: Triakidae) harvested off southern Australia. *Marine and Freshwater Research* **58**, 67–97. doi:10.1071/MF06074

Wheeler, J. F. G. (1959). Sharks of the western Indian Ocean: *Loxodon macrorhinus* M&H. *The East African Agricultural Journal* **25**, 106–109.

White, W. T. (2007). Catch composition and reproductive biology of whaler sharks (Carcharhiniformes: Carcharhinidae) caught by fisheries in Indonesia. *Journal of Fish Biology* **71**, 1512–1540. doi:10.1111/J.1095-8649.2007.01623.X

Yamaguchi, A., Taniuchi, T., and Shimizu, M. (2000). Geographic variations in reproductive parameters of the starspotted dogfish, *Mustelus manazo*, from five localities in Japan and in Taiwan. *Environmental Biology of Fishes* **57**, 221–233. doi:10.1023/A:1007558324902