

Similar life history traits in bull (*Carcharhinus leucas*) and pig-eye (*C. amboinensis*) sharks

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Abstract. Appropriate management strategies for coastal regions require an understanding of how ecological similarities and differences among species shape ecosystem processes. Here, we tested whether morphological similarity equated to similar age and growth patterns in two common coastal sharks in northern Australia. Vertebrae of 199 pig-eye (*Carcharhinus amboinensis*) and 94 bull (*C. leucas*) sharks were sourced principally from commercial fisheries operating along the Northern Territory coastline during 2007–2009. We sectioned vertebrae to provide estimates of age of these animals. Model averaging results indicated female pig-eye sharks matured at 13 years and lived >30 years. Theoretical asymptotic length (L_{∞}) (\pm s.e.) was estimated to be 2672 (\pm 11.94) mm with a growth coefficient (k) of 0.145 year⁻¹. Male pig-eye sharks matured slightly earlier than females (12 years) and survived >26 years. Theoretical asymptotic length for males (L_{∞}) (\pm s.e.) was also smaller (2540 \pm 13.056) mm and they grew faster ($k = 0.161$ year⁻¹) than females. Bull sharks matured at 9.5 years and reached a maximum theoretical size (L_{∞}) (\pm s.e.) of 3119 mm (\pm 9.803) with a similar growth coefficient ($k = 0.158$ year⁻¹) to pig-eye sharks. Longevity of bull sharks was estimated to be more than 27 years. Our results indicate that these patterns of high longevity and slow growth are indicative of low resilience and high susceptibility to over-exploitation of these coastal sharks.

Additional keywords: bomb-radiocarbon, *Carcharhinus* sp., Indo-Pacific, resilience.

Introduction

Growing global populations and unsustainable fishing practices threaten species diversity in tropical ecosystems. Appropriate ecosystem-based management requires an understanding of how species' ecological similarities and differences shape ecological function. Age structure and growth dynamics (longevity, age at maturity and growth rate) are important factors shaping species' ecological function and provide estimates of species resilience and susceptibility to over-exploitation (Simpfendorfer *et al.* 2002; Cailliet and Goldman 2004; Cailliet *et al.* 2006). Furthermore, quantifying these parameters enables management agencies to identify the contribution of different cohorts to species persistence and ensure that dominant cohorts

receive special emphasis or protection, reducing the risk of over-exploitation (Campana 2001; Cortes 2002; Otway *et al.* 2004). Age structures and survival of key cohorts can also be monitored over time, with any evidence of change used as an indicator of the impact of increased exploitation pressure (Stevens 2002; Bradshaw *et al.* 2007; Field *et al.* 2009).

Here, we compare the age structures and growth dynamics of two sympatric and morphologically similar carcharhinids, bull (*Carcharhinus leucas*) and pig-eye (*C. amboinensis*) sharks, both common apex predators in shallow tropical and subtropical coastal waters (Last and Stevens 2009). The proximity of many of their habitats to human influences (coastal development, runoff sources) and their susceptibility to fishing (via

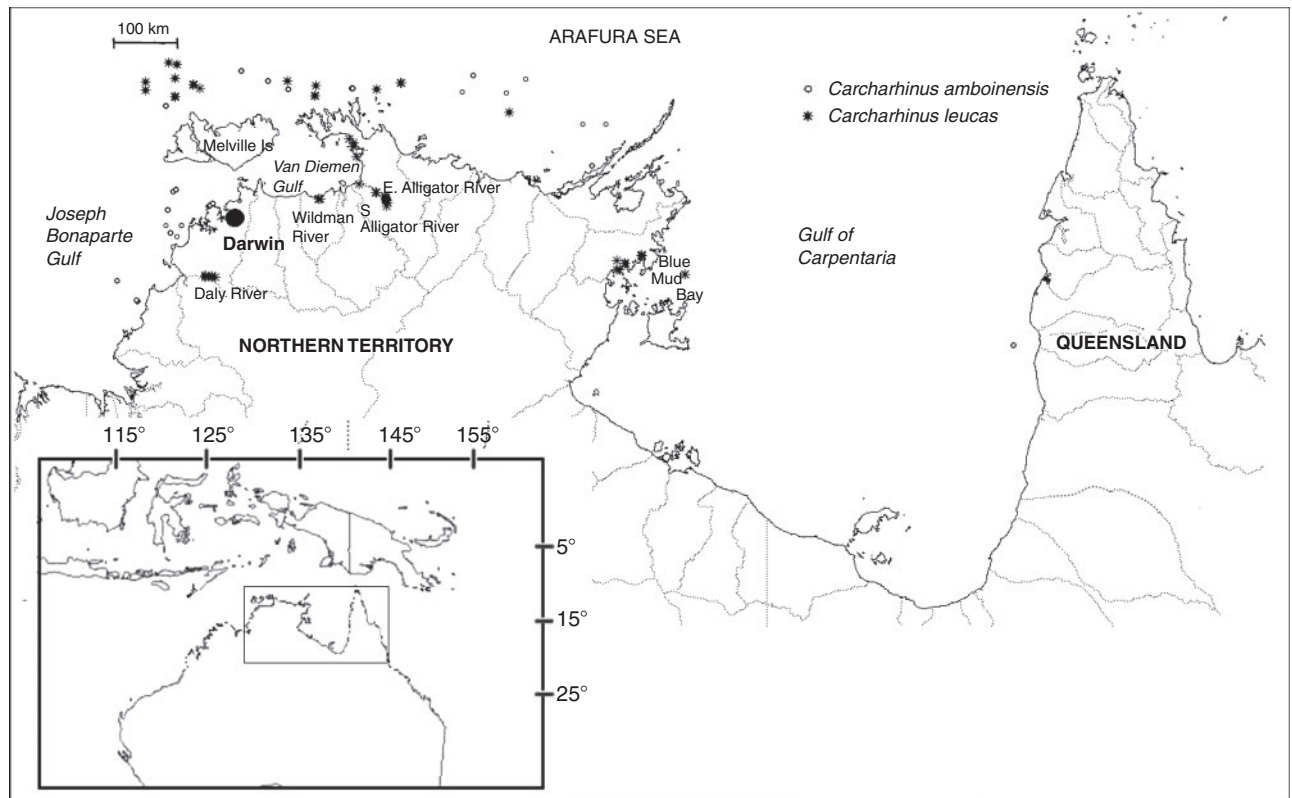


Fig. 1. Capture locations for the pig-eye (*Carcharhinus amboinensis*, $n = 199$) and bull shark (*Carcharhinus leucas*, $n = 94$) across northern Australia.

targeted fisheries or as bycatch) highlights the need for a better understanding of their life history traits. Furthermore, the paucity of good demographic data, combined with the high frequency of human interactions, has led to the listing of the bull shark by the IUCN as Near Threatened (FAO 1999; Salini *et al.* 2007). Although occupying similar habitats, the pig-eye shark is listed by the IUCN as Data Deficient, emphasising the need for a better definition of life history traits to facilitate an accurate assessment of population viability. The pig-eye shark is thought to be common throughout the Indo-west Pacific Oceans, although the full extent of its range is unclear because it might be frequently misidentified in catches (Last and Stevens 2009).

For bull sharks, age and growth estimates are available from South Africa and the northern and southern regions of the Gulf of Mexico (Branstetter and Stiles 1987; Wintner *et al.* 2002; Cruz-Martinez *et al.* 2004; Neer *et al.* 2005). These suggest that bull sharks, like many other carcharhinids, are long-lived, attaining maximum ages from 30 to >50 years. Females typically grow to larger sizes and mature later than males, and growth rates for both sexes are fastest during the juvenile stage. There are, however, differences in maximum age estimates and growth coefficients among locations, suggesting separate stocks within populations. In contrast, there have been no studies estimating age and growth parameters of pig-eye sharks.

The present study is the first to examine the age structure and growth dynamics of bull and pig-eye sharks within Australia. Previous work in the region has provided estimates of ranges of size and fecundity for these species, although sample sizes were

small and based on limited catch data (Stevens and McLoughlin 1991; Stevens 2002). We use the growth increments within vertebrae of 199 pig-eye and 94 bull sharks to: first, estimate and compare age and growth parameters (estimates of longevity, age at maturity and growth rate); second, to verify annual deposition on growth band in pig-eye sharks, third, determine whether variability in birth size influences parameter estimates of age and growth. Finally, we consider our results in the context of the resilience and susceptibility to over-exploitation of these species.

Materials and methods

Vertebral collection

Vertebrae of bull and pig-eye sharks were sourced principally from the catches of the commercial Northern Territory Offshore Net and Line Fishery (NTONL) and from bycatch of the Barramundi Fishery (NTBarr) operating along the Northern Territory coastline during 2007–2009 (Fig. 1). The NTONL Fishery deploys both long-lines and pelagic nets. Long-lines must not exceed 15 nautical miles with no more than 1000 snoods (hooks), and nets must be 1000–2500 m long with a square mesh size of 150–250 mm and a drop of 50–100 meshes. The NTBarr Fishery used nets between 50–500 m in length with a square mesh size of 150–175 mm with a 16-mesh drop. In addition, several fishery-independent surveys were conducted in freshwater, estuarine and marine environments around Darwin including Darwin Harbour, and the Daly, Wildman,

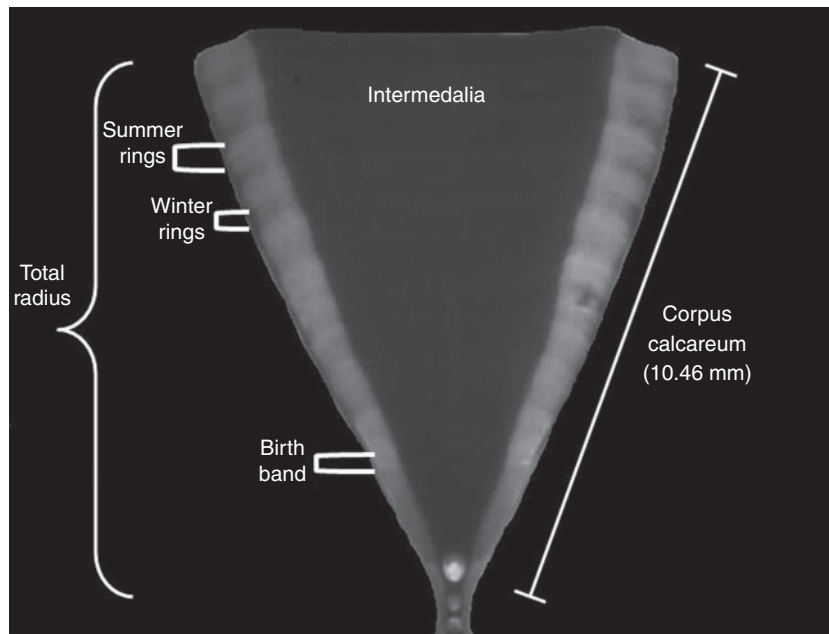


Fig. 2. Sagittal section of thoracic vertebrae showing growth increments and terminology. Bull shark (*Carcharhinus leucas*, 10 years old).

West Alligator, South Alligator and East Alligator Rivers (Fig. 1). In these surveys, animals were caught either using long-lines or nets. Long-lines were ~50 m long with 50 snoods (size 11/0) positioned 1 m apart, and nets were ~50 m long with a square-mesh size of 150–250 mm with a 16-mesh drop. Both were weighted and deployed along the bottom in depths ranging from 5 to 15 m. Sample sizes from each of these locations are given in the Accessory Publications. In total, 199 pig-eye and 94 bull sharks were sampled. All individuals were sexed based on the presence or absence of claspers and where possible, their total weight (TW), total length (TL) and fork length (FL) was measured. Age structure and growth dynamics are based on total length (TL). Small animals (<1-m TL) were examined for the presence of umbilical scars as an indication of time since birth. For each captured individual, a section of ~15 vertebrae were removed from beneath the first dorsal fin origin and stored frozen. Owing to the morphological similarities between members of the genus *Carcharhinus*, a small tissue fragment (~1 g) from each individual was also collected and tested genetically to confirm species identity.

Vertebral analysis

Vertebral samples were defrosted and excess tissue, neural and haemal arches were excised, exposing the centra. Individual centra were then separated and any connective tissue removed with a scalpel blade and Milli-Q water. Polished centra were then left to air dry causing any remaining tissue to become brittle and peel away. Cleaned vertebrae were weighed and embedded in a two-part epoxy resin. Sagittal sections were cut through the core using a low-speed diamond saw (IsoMet, Buehler) at ~240 rpm with 250 g-load weight. Sections were ground on wet and dry paper until ~0.4 mm thick and rinsed again in Milli-Q water to remove contaminants. They were then mounted on

glass slides using a neutral mounting medium (Crystal-bondTM509, Queensland, Australia).

Sections were viewed under a Leica DM 400B compound light microscope connected to a video camera (C3, jAi, Japan). The image was analysed using the computer imaging package OPTIMAS 6.5 (1999) (Media Cybernetics, Silver Spring, MD, USA). Age was estimated by counting growth bands (defined as one calcified, opaque ring and one less-calcified, translucent ring) visible along the *corpus calcareum* reading from the focus to the outer centrum edge (Fig. 2). The angle of change caused by differences in growth rate from intrauterine to post-natal life history stages was regarded as the point of birth, or birth mark, and recorded as year zero. Two readers made three non-consecutive counts. Readers were unaware of the total length or sex of specimens and each count was given a confidence rating from 1 (low confidence) to 3 (high confidence). Count reproducibility, as indicated by within and between reader variability, was determined by calculating an index of average per cent error (IAPE) (Beamish and Fournier 1981; Campana *et al.* 1997) and the coefficient of variation (CV) (Chang 1982; Campana *et al.* 1997). Consensus readings were determined for all individuals for which age estimates differed between readers, and if no consensus estimate could be reached, then samples were discarded.

Validation and verification

Deposition of annual bands in bull shark vertebrae has been verified by earlier studies from several different regions (Branstetter and Stiles 1987; Wintner *et al.* 2002; Cruz-Martinez *et al.* 2004; Neer *et al.* 2005). Consequently, we assumed that growth bands were deposited annually in the bull sharks we examined. As ours is the first study to estimate age and growth parameters for the pig-eye shark, there have been no validation

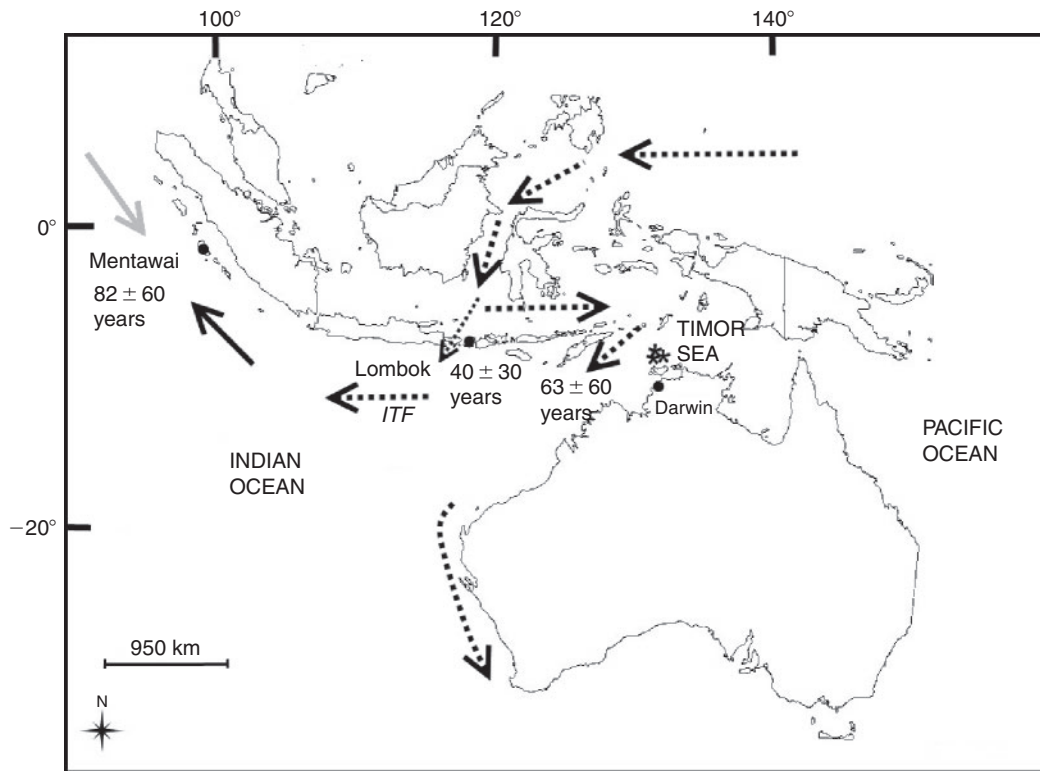


Fig. 3. Oceanic circulation patterns in northern Australia and adjacent seas indicating directional flow of major currents (adapted from Guilderson *et al.* 2009; and Hua *et al.* 2005). Dark arrows indicate direction of flow during the south-west monsoon, light arrows indicate flow during the north-east monsoon and the dashed arrows indicate year-round currents. ITF, Indonesian Through Flow. Numbers represent local or regional ΔR values for northern Australia, Lombok and Mentawai. * indicate capture locations of samples.

studies of band deposition patterns in the vertebrae of this species.

Radiocarbon analysis

Thermo-nuclear bomb testing began in the late 1950s to early 1960s, and elevated ^{14}C concentrations peaked in the atmosphere in the mid-1960s (Hua and Barbetti 2004). Via air-sea gas exchange, the excess ^{14}C was transferred to the ocean's surface, leading to an increase in oceanic ^{14}C , which reached its maximum ~ 10 years later than atmospheric ^{14}C (Druffel and Suess 1983; Nydal and Gislefoss 1996). Since then, the ^{14}C level in the ocean's surface has been decreasing as bomb radiocarbon has penetrated deeper into the ocean. By comparing ^{14}C concentrations present in the known-age shark vertebrae with a ^{14}C bomb curve from surrounding ocean waters, the date of vertebral matrix deposition can be determined and can then be used to validate age estimates from increment counts (Campana *et al.* 2002; Ardizzone *et al.* 2006; Kerr *et al.* 2006; Francis *et al.* 2007).

Six pig-eye shark vertebrae were cleaned with deionised water to remove surface contamination. The birth band was then removed and ground to a fine powder, $\sim 6\text{--}19$ mg of which was used for bomb radiocarbon analysis. Following the method described in Ardizzone *et al.* (2006) and Kerr *et al.* (2006), each birth band sample was pre-treated to remove inorganic carbon

using 0.25M HCl at refrigerator temperatures. After 2 h, dilute acid solution was decanted and fresh dilute HCl was added into the sample vial, which was then placed in a fridge overnight to complete the demineralisation reaction. The organic residue was washed thoroughly with deionised water, and then transferred into a Vycor combustion tube. All water attached to the residue was removed using a vacuum pump. The pre-treated sample was combusted to CO_2 and converted to graphite following the methods described by Hua *et al.* (2001). Radiocarbon analysis was carried out using small tandem applied research (STAR) accelerator mass spectrometry (AMS) with a typical precision of 0.4% (Fink *et al.* 2004).

Reference bomb curves from the published literature appropriate to sea water around northern Australia were determined using local/regional radiocarbon marine reservoir corrections (ΔR). The ΔR value of a given location accounts for deviations from the model ^{14}C age of the 'global' surface ocean (e.g. Marine09 curve: Reimer *et al.* 2009) owing to variations in local ocean currents, ocean upwelling and in-flow of fresh water (Reimer and Reimer 2001; Ulm 2006). Values of ΔR have effectively been used to study ocean circulation and investigate sources of regional sea water (Southon *et al.* 2002; Hua *et al.* 2004). Surface waters around northern Australia are a mixture of the Indonesian Through-Flow (ITF) current and a seasonal south-east flow along the coast of Sumatra and local waters (Fig. 3). In addition, there is a similarity between the average

ΔR value for northern Australia of 63 ± 60 years (see SOM), the average ΔR value for Lombok, Indonesia of 40 ± 30 years calculated for the period 1938–1950 (Guilderson *et al.* 2009) and that for Mentawai, Indonesia of 82 ± 60 years calculated for 1944–1950 (Grumet *et al.* 2004). These suggest that sea waters around Lombok and Mentawai Islands, Indonesia are similar to that of northern Australia in terms of ^{14}C . Consequently, ^{14}C concentrations of the birth bands from adult sharks sourced within northern Australia were compared with the bomb curves from these regions to verify our age estimates for birth bands of pig-eye shark vertebrae.

Edge analysis

Owing to the lack of shark vertebrae of known age, annual deposition of growth increments was also confirmed by edge analysis. Under this protocol, the characteristics of the final growth increment before capture and subsequent death, i.e. translucent or opaque, was noted for all individuals and plotted against catch date. Only 46 mature individuals were included because they were all caught within the one month; juveniles less than one year old were excluded owing to the lack of clarity in band characteristics.

Growth models

After individual ages of sharks were estimated, five growth models were fitted to the length-at-age data with R cran v2.11.1 (R Development Core Team 2010). These included the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938), the two-parameter von Bertalanffy growth function (2VBGF; with both fixed and variable birth size: Fabens 1965; Hua *et al.* 2004), the two-phase von Bertalanffy growth function (TPVBGF: Soriano *et al.* 1992), the Gompertz growth function (GOMPertz: Ricker 1975) and the two-parameter Gompertz growth function (2GOMPertz; with both fixed and variable birth size: Mollet *et al.* 2002). Model parameters were estimated by least-squares nonlinear regression.

Size at birth was determined by the presence of open umbilical scars observed in juvenile sharks in the current study and from published values; and was set at 650 mm for pig-eye and 640 mm for bull sharks. The effect of variation in birth sizes on parameter estimates was determined by using Markov Chain Monte Carlo (MCMC) methods to simulate growth models over a range of described birth sizes (650–750 mm for pig-eye and 600–750 mm for bull sharks). Size at maturity (2100–2150 mm for male and female pig-eye sharks, respectively, and 2200–2300 mm for bull sharks) was taken from life history characteristics described in Last and Stevens (2009) and correlated with the slowing growth rate typical of carcharhinid sharks post-maturity. Age at maturity was calculated from estimated age at size at maturity.

Akaike's information criterion corrected for small sample size (AIC_c) was used to assess model performance (Burnham and Anderson 2002). The bias-corrected relative weight of evidence for each model, given the data and the suite of candidate models considered, was determined by calculating its Akaike weights (ω_i); the smaller the weight, the lower its contribution to parameter estimates (Burnham and Anderson 2002). Parameter estimates were then averaged by multiplying the growth coefficients by model ω_i and summing estimates

over all suggested candidate models. A student's *t* test compared whether growth rates between sexes were statistically different.

Results

Age and growth estimates

Totals of 199 pig-eye (89 females and 110 males) and 94 bull (47 females and 47 males) sharks were aged (see Accessory Publication). The total length for pig-eye sharks ranged from 678 mm (both sexes) to a maximum total length of 2550 mm for males and to 2560 mm for females. Few individuals of sizes from 1200 to 2000 mm total length were collected (see Accessory Publication). Bull sharks ranged between 645 mm to maximum total lengths of 2760 mm for males, and 3180 mm for females. The majority (57%) of bull sharks sampled were between 645 and 1000 mm in total length. There were no medium-sized individuals within the total length range of 1300–2200 mm (see Accessory Publication).

Within-reader precision for both species was high and between-reader variation was low (see Accessory Publication). Between-reader consensus age estimates were attained for all samples for both species; consequently, all individuals were deemed readable. IAPE for individual vertebrae were consistently less than 20% (Wintner *et al.* 2002) (see Accessory Publication for age-specific within- and between-reader variability). Confidence levels were moderate (two) to high (three) consistently across all total lengths for both species.

Individuals of \leq one year old were prevalent in both species (26.13 and 54.26% of pig-eye and bull sharks respectively). Most other age classes of pig-eye sharks were also well represented, except ages 4–11 years and >21 years, which only accounted for 10.5 and 1.5%, respectively, of the total sample (combined sexes). The oldest male pig-eye shark was 2370 mm in length and 21 years old, and the oldest female was 2490 mm in length and 24 years old. There were four female pig-eye sharks collected at size at maturity and these were between 13 and 14 years of age. Similarly, there were four males at size at maturity, aged between 12 and 14 years. Only 26% of bull sharks were greater than 2000 mm in size; consequently, most individuals (74.3%) were juveniles four years and younger. The oldest male bull shark was 2840 mm in length and 22 years of age and the oldest female was 26 years of age. There was only one nine-year-old female and no male bull sharks at size at maturity.

Verification

Edge analysis

No opaque banding was found in the final growth increment that was deposited immediately before capture during the months of March to August. The occurrence of opaque bands increased after September, although we lacked samples from December to February (Fig. 4). These results suggest annual band deposition.

Radiocarbon analysis

Radiocarbon contents of five birth date bands agreed well with those from Mentawai and Lombok bomb curves within 2σ uncertainties (Fig. 5). There is only one sample (OZL652 – PE170) whose $\Delta^{14}\text{C}$ level for the estimated birth year was higher

than that recorded in Mentawai but agreed with the value for Lombok within 2σ uncertainty.

Growth parameter estimates

Growth parameters were averaged across all candidate models based on their Akaike weights (ω_i). The TPVBGF could not be fitted to either species because it over-parameterised the VBGF. For female pig-eye sharks, the GOMPERTZ function was the top-ranked growth model according to AIC_c (Table 1;

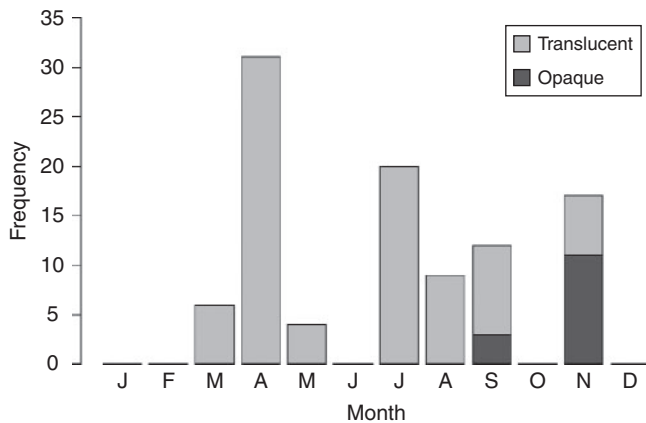


Fig. 4. Frequency of final growth increment characteristics (translucent or opaque) per month for the pig-eye shark (*Carcharhinus amboinensis*); $n = 99$.

Fig. 6a). Incorporating variability in birth size only increased model weight in the 2GOMPERTZ. The weighted-average predicted values (and s.e.) of theoretical asymptotic lengths (L_∞) (\pm s.e.) and growth coefficient (k) were 2672 (\pm 11.94) mm and 0.145 year⁻¹, respectively. Corresponding age at maturity was \sim 13 years and was estimated an approximate maximum age (defined at 1% of its asymptotic length) at $>$ 30 years (Fabens 1965) (Table 2). Juvenile growth rate was 151 mm year⁻¹ for the first 5 years, slowing to $<$ 25 mm year⁻¹ post-maturity.

For male pig-eye sharks, the 2GOMPERTZ function was top-ranked (Table 1; Fig. 6a) although both the 2GOMPERTZ and GOMPERTZ had similar AIC_c values. As for females, incorporating variability in birth size only reduced model ranking in 2GOMPERTZ (Table 1). Model-averaged growth parameters were 2540 (\pm 13.056) mm and 0.161 year⁻¹ for the theoretical asymptotic length (L_∞) (\pm s.e.), and growth coefficient (k), respectively. Age at maturity of males was similar to females, with males maturing slightly earlier at \sim 12 years. Maximum age was $>$ 26 years. Juvenile growth rate resembled that of females and was estimated as 147 mm year⁻¹ for the first 5 years, slowing to $<$ 20 mm year⁻¹ post-maturity. Growth rates were not significantly different from female conspecifics ($t_{179,8} = -1.614$, $P = 0.1083$).

We did not estimate sex-specific growth parameters for bull sharks owing to the lack of large individuals; rather, growth was determined for both sexes combined (Table 2; Fig. 6b). The GOMPERTZ function was top-ranked model for this dataset (Table 1). Comparison between model-specific growth parameters and model-averaged estimates displayed similar

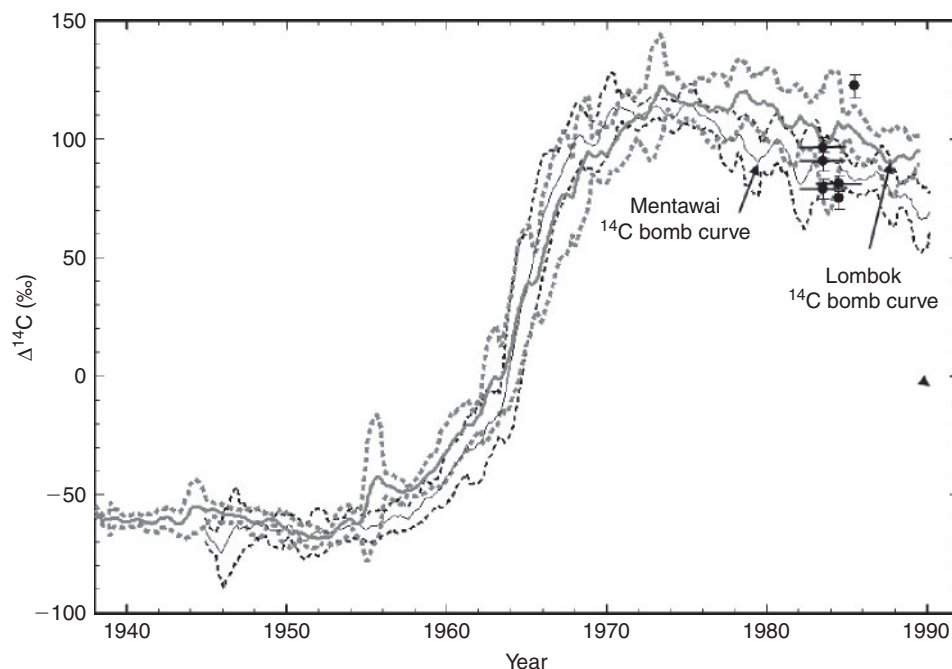


Fig. 5. Comparison of $\Delta^{14}C$ values in birth bands of seven pig-eye sharks, *Carcharhinus amboinensis*, collected from the Timor Sea with those of the reference oceanic ^{14}C bomb curves from Mentawai (solid black line) and Lombok (solid grey line), shown in 1-year running mean values. Dashed lines represent 2σ uncertainties. The birth band samples are plotted against their estimated ages based on band counting. Vertical and horizontal error bars, shown in 1σ , represent ^{14}C analytical and band counting uncertainties, respectively.

Table 1. Information-theoretic growth model ranking for pig-eye, *Carcharhinus amboinensis* (males $n = 110$ and females $n = 89$) and bull, *Carcharhinus leucas* (sexes combined $n = 94$) sharks

AIC, Akaike's information criterion; ΔAIC_c , differences between model AIC values; ω_i , AIC_c weights. Model ranking criteria: TPVBGF, two-phase von Bertalanffy growth function; VBGF, von Bertalanffy growth function; 2VBGF-*fixed*, two-parameter von Bertalanffy growth function fixed birth size; 2VBGF-*variable*, two-parameter von Bertalanffy growth function with variable birth size; GOMPERTZ, Gompertz growth function; 2GOMPERTZ-*fixed*, two-parameter Gompertz growth function fixed birth size; 2GOMPERTZ-*variable*, two-parameter Gompertz growth function with variable birth size

Model	AIC _c		ΔAIC_c		AIC _c weights (ω_i)	
	Female	Male	Female	Male	Female	Male
Pig-eye shark						
TPVBGF	–	–	–	–	–	–
GOMPERTZ	1071.469	1324.503	0.000	1.371	0.871	0.334
2GOMPERTZ- <i>variable</i>	1075.527	1338.890	4.058	15.758	0.115	0.000
2GOMPERTZ- <i>fixed</i>	1079.751	1323.132	8.282	0.000	0.014	0.664
2VBGF- <i>fixed</i>	1088.065	1336.139	16.596	13.007	0.000	0.001
VBGF	1088.716	1337.244	17.247	14.112	0.000	0.001
2VBGF- <i>variable</i>	1098.372	1359.392	26.903	36.260	0.000	0.001
Bull shark	Both sexes		Both sexes		Both sexes	
TPVBGF	–		–		–	
GOMPERTZ	1145.556		0.000		0.985	
2GOMPERTZ- <i>fixed</i>	1154.599		9.043		0.010	
2GOMPERTZ- <i>variable</i>	1157.606		12.050		0.002	
2VBGF- <i>fixed</i>	1159.104		13.548		0.001	
VBGF	1161.036		15.480		0.000	
2VBGF- <i>variable</i>	1185.775		40.219		0.000	

patterns, as for pig-eye sharks (Table 2). Model-averaged growth parameters for these length-at-age data are theoretical asymptotic length (L_∞) (\pm s.e.) = 3119 (\pm 9.803) mm and a growth coefficient (k) = 0.158 year⁻¹ respectively. Age at maturity was 9.5 years and like pig-eye sharks, bull sharks are long-lived with a predicted longevity of >27 years (Table 2). Juvenile growth rate was 186 mm year⁻¹ for the first five years and then slowed to 45 mm year⁻¹ post-maturity.

Discussion

Age and growth parameters of bull and pig-eye sharks

We have provided the first estimates of age and growth for the pig-eye shark, despite its global distribution in tropical and subtropical waters and its targeted and passive take as bycatch by Australian commercial fisheries. The age and growth estimates show the K -selected life history traits (slow growth, late maturity and long-lived) typical of other large carcharhinids and indicative of high susceptibility to over-exploitation (Campana *et al.* 2002; Simpfendorfer *et al.* 2002; Field *et al.* 2009). Management strategies regulating acceptable mortality due to fishing must reflect these pressures.

The notoriety of the bull shark as one of the most aggressive sharks in the world, and the high frequency of human interactions with this species, has increased public awareness of it and the pressure to quantify species resilience. For this reason, multiple age and growth studies are available from different locations within its distribution (Branstetter and Stiles 1987; Wintner *et al.* 2002; Cruz-Martinez *et al.* 2004; Neer *et al.* 2005). Our estimates of age and growth parameters confirm that bull sharks in northern Australia obtain greater total lengths than conspecifics from other locations, and like pig-eye sharks, they have also evolved slow vital rates.

Regional differences in age and growth parameters have been used to distinguish population structure in other carcharhins, suggesting Australian bull sharks have diverged from other populations (Carlson and Baremore 2005; Carlson *et al.* 2006; Romine *et al.* 2006). Current estimates of juvenile growth rates within northern Australia reinforce predictions by Thorburn and Rowland (2008) and suggest that juvenile bull sharks have similar growth rates to those estimated from other populations (Branstetter and Stiles 1987). However, as they mature, Australian bull sharks appear to grow at a high rate, similar to those in South African waters, but mature earlier than individuals from the Gulf of Mexico (Branstetter and Stiles 1987; Wintner *et al.* 2002; Cruz-Martinez *et al.* 2004). Despite Australian bull sharks obtaining larger sizes than in other locations, individuals from all populations are equally long-lived (Branstetter and Stiles 1987; Wintner *et al.* 2002; Neer *et al.* 2005).

Our growth-parameter estimates for both species are biologically realistic, but slightly underestimate maximum total length (Last and Stevens 2009). This might arise because few very large and old individuals were collected by our study. The lack of sex-specific variation in parameter estimates in the pig-eye shark also seems reasonable, as these do not differ between sexes in other large carcharhinids (Branstetter and Musick 1994; Joung *et al.* 2008). Restricted sample sizes prevented statistical testing of the effects of gender on growth of Australian bull sharks, although the differences we noted in maximum sizes between sexes hint at this possibility. It is possible that the similar growth rates between species in our study, despite bull sharks maturing larger and obtaining greater total lengths than pig-eye sharks, reflects the counteraction of sex-specific age and growth trends. Not all bull shark populations exhibit these sex differences (Wintner *et al.* 2002; Neer *et al.* 2005), and the

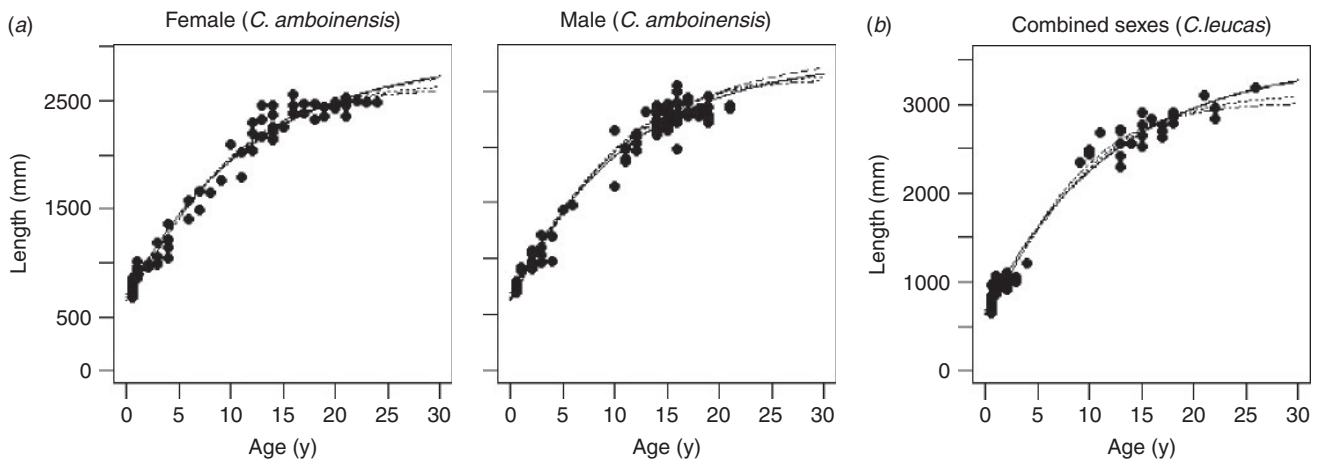


Fig. 6. Growth models fitted to total length (mm)-at-age (years) data. Solid line, von Bertalanffy Growth Function (VBGF); dashes, two parameter von Bertalanffy growth function (2VBGF); dotted, Gompertz growth function (GOMPERTZ); dot-dash, two-parameter Gompertz growth function (2GOMPERTZ). Growth functions do not incorporate variation in birth size. (a) Pig-eye shark (*Carcharhinus amboinensis*); (b) Bull shark (*Carcharhinus leucas*).

Table 2. Age and growth parameter estimates for pig-eye sharks, *Carcharhinus amboinensis* (males $n = 110$; females $n = 89$), and bull sharks, *Carcharhinus leucas* (sexes combined $n = 94$)

L_{∞} , theoretical asymptotic length; k , growth rate; t_0 , age when the individual would be zero length. AIC, Akaike's information criterion; ΔAIC_c , differences between model AIC values; ω_i , AIC_c weights. Model ranking criteria: TPVBGF, two-phase von Bertalanffy growth function; VBGF, von Bertalanffy growth function; 2VBGF-fixed, two-parameter von Bertalanffy growth function fixed birth size; 2VBGF-variable, two-parameter von Bertalanffy growth function with variable birth size; GOMPERTZ, Gompertz growth function; 2GOMPERTZ-fixed, two-parameter Gompertz growth function fixed birth size; 2GOMPERTZ-variable, two-parameter Gompertz growth function with variable birth size

Model	L_{∞} (\pm s.e.) (mm)		Max. age (years)		k (year ⁻¹)		t_0		Age at maturity (years)	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Pig-eye shark										
TPVBGF	–	–	–	–	–	–	–	–	–	–
GOMPERTZ	2668 (45.66)	2550 (53.20)	>30	>26	0.146	0.158	1.944	1.863	13	12
2GOMPERTZ-variable	2710 (48.63)	2665 (68.41)	>31	>29	0.136	0.133	–	–	13	13
2GOMPERTZ-fixed	2620 (38.20)	2529 (42.33)	>30	>27	0.160	0.163	–	–	12.5	12
2VBGF-fixed	2855 (75.45)	2847 (99.12)	>38	>36	0.090	0.085	–	–	13	12.5
VBGF	2895 (92.28)	2794 (106.92)	>38	>33	0.085	0.091	-3.125	-2.794	13	12
2VBGF-variable	3035 (116.4)	3135 (188)	>41	>39	0.072	0.065	–	–	12	13
Model averaged	2672 (11.94)	2540 (13.06)	>30	>26	0.145	0.161	–	–	13	12
Bull shark										
	Both sexes		Both sexes		Both sexes		Both sexes		Both sexes	
TPVBGF	–	–	–	–	–	–	–	–	–	–
GOMPERTZ	3120 (65.65)	–	>27	–	0.158	–	2.601	–	9.5	–
2GOMPERTZ-fixed	3025 (50.25)	–	>25	–	0.179	–	–	–	9	–
2GOMPERTZ-variable	3241 (78.44)	–	>30	–	0.137	–	–	–	9.5	–
2VBGF-fixed	3481 (115)	–	>38	–	0.084	–	–	–	9.5	–
VBGF	3507 (143.3)	–	>37	–	0.082	–	-2.485	–	9.5	–
2VBGF-variable	3979 (249.3)	–	>43	–	0.059	–	–	–	10	–
Model averaged	3119 (9.80)	–	>27	–	0.158	–	–	–	9.5	–

presence of this trend might again support the divergence of Australian populations from those of other regions. The lack of medium-sized individuals in this study most likely reflects age-based habitat partitioning.

Verification of annual band deposition in the pig-eye shark

Annual-band deposition was supported by both independent methods (edge analysis and bomb-radiocarbon dating). Unfortunately, intense tropical weather prevented acquisition of

samples from December to February for edge analysis. The lack of opaque banding between March and August, and its subsequent increase in prevalence after September, strongly suggests annual deposition of growth increments in pig-eye sharks.

The present study is the first to apply bomb radiocarbon dating to corroborate age estimates of large sharks from the Indo-Pacific region. Campana *et al.* (2002) confirmed that ¹⁴C concentrations are temporally stable with no leaching of ¹⁴C into consecutive growth bands post-deposition or metabolic reworking of vertebral material. Consequently, the quantified

vertebral ^{14}C concentrations we measured were real and representative of the environments inhabited while increments were being deposited. The good agreement between $\Delta^{14}\text{C}$ values calculated based on estimated shark birth dates and those of the reference oceanic ^{14}C bomb curves from Mentawai and Lombok (Indonesia) confirms that our age estimates are likely to be realistic in most cases, and is further evidence that band deposition is likely to be annual, as occurs in other carcharhinids. The lack of correlation between ^{14}C concentration within one individual and the Mentawai reference bomb curve might represent a different birth location and subsequent migration to the capture location, which is typical of large marine predators.

Unfortunately, we were unable to obtain vertebrae from known-age sharks born during the 1960s to 1970s correlating with the region of the bomb curve with the greatest change in atmospheric ^{14}C providing the highest resolution on the bomb curve. Furthermore, the recent development of this application as a tool for ageing marine fauna in this region compared with other studies limited comparative bomb curves to carbonates, such as coral, rather than other sharks or teleost fishes that have similar mineralisation processes to those of our study species (Campana *et al.* 2002; Cruz-Martinez *et al.* 2004; Ardizzone *et al.* 2006; Francis *et al.* 2007). The use of shallow inshore nurseries by juveniles supports the assumption that these sharks are not embarking on seasonal migrations and remained in shallow coastal waters when the birth band was deposited. This method also assumes that juveniles are not moving far from nursery grounds as adults, which is supported by both isotopic and genetic analyses (B. Tillett *et al.* unpubl. data). Despite the limitations of this method, analysis of bomb radiocarbon enabled a definitive classification of broad-scale trends, such as *K*-selected life history traits, which have important implications for fisheries management and our understanding of species' ecological roles.

Influence of birth-size variability on parameter estimates

Incorporating variability in birth size weakened the performance of two-parameter growth functions in all length-at-age datasets, except data for female pig-eye sharks. Inclusion of variability in this trait within candidate models increases the flexibility within the shape of that function and, as a consequence, models become more susceptible to overestimating longevity should the dataset lack larger, older individuals, as was typically the case in the present study. Only the datasets for length-at-age of female pig-eye sharks attained a natural asymptote, and thus did not require a model to predict this plateau. For these sharks, the addition of variability in birth size produced more biologically realistic parameter estimates that were nearer to recorded maximum TL for both species within Australia. Neer *et al.* (2005) also concluded that including variability in birth size produced more biologically realistic estimates of growth parameters for bull sharks in the Gulf of Mexico, although this study only fitted the von Bertalanffy growth function and its derivatives to datasets.

Accuracy and precision of parameter estimates

Our metrics of precision (index of average percent error and coefficient of variation) were within the lower range of estimated error rates for carcharhinids (Santana and Lessa 2004; Carlson and

Baremore 2005). The predominance of juvenile bull sharks aged ≤ 1 year in our samples might have downwardly biased our estimated error, although no error for individual vertebra exceed 20%. Consistent with age studies on other sharks, within-reader variation for both bull and pig-eye sharks increased with increasing total length, reflecting the compression of annuli as growth rate slows in older individuals (Officer *et al.* 1996). The challenge of ageing larger, older individuals may be further complicated by the stability of the tropical environment from which the sharks were sampled (Lessa *et al.* 2006).

Low numbers of individuals at maturity, particularly for bull sharks, might have influenced the inflexion point of the growth models. This could have caused an underestimation of age at maturity and an overestimation of the growth coefficient. Additionally, the lack of large, older individuals could be responsible for the relatively poor performance of the von Bertalanffy growth models and its derivatives. No asymptote was attained by these models, potentially causing an overestimation of the theoretical asymptotic length, and underestimating the growth coefficient. The *S*-shaped logistic curve of the Gompertz growth models forces the relationship to an asymptote, thus providing more biologically realistic growth estimates. The predominance of juveniles ≤ 1 year provided a non-variable base to the functions, commonly lacking in other studies, and the difference in longevity estimates arises depending on how candidate models project growth in the older individuals that were lacking in our study and would have removed variability in that portion of the function.

Summary

Our results reinforce the notion that these two species of apex predator are highly susceptible to over-exploitation. The lack of larger individuals of both species needs to be further investigated, with changes in policy effected to reduce the fishery mortality of these larger size classes and those near maturity, to ensure the species' reproductive potential is not reduced. Additionally, the ecological diversity within the genus *Carcharhinus* requires region- and species-specific understanding of these predators' functional roles in the ecosystem. Similar size does not necessarily imply analogous function, although in the present study it does imply similar resilience and susceptibility to over-exploitation. Despite the larger total length obtained by bull sharks, its demographic similarity with the pig-shark suggests that it is just as vulnerable to over-exploitation and as such, its IUCN Red List classification should be upgraded to Near Threatened, as it is for the bull sharks. Furthermore, this study reiterates the need for better management of marine resources across northern Australia, as this region remains one of the last strong-holds for the marine megafauna of tropical South East Asia (Field *et al.* 2009).

Accessory publications

Accessory publications for this article are available on the Journal's website.

Acknowledgements

This study was funded by the Tropical Rivers and Coastal Knowledge Research Hub, Charles Darwin University, Darwin, the Australian Institute

of Marine Science and the Australian Institute of Nuclear Science and Engineering (AINSE). Sampling was undertaken with the kind support of fishermen, Wildlife Resources Inc., Kakadu National Park and the Department of Resources – Fisheries, Northern Territory. K. Strobel, Charles Darwin University assisted with shark ageing. Samples were collected under the S17 fisheries permit number 27134 and Kakadu permit number RK 689. Research was in agreement with animal ethics clearance number A07001. We thank the reviewers for their comments.

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Manuscript received 1 November 2010, accepted 1 March 2011