Life history characteristics of the silky shark *Carcharhinus falciformis* from the central west Pacific

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Abstract. In the central west Pacific region, silky sharks (*Carcharhinus falciformis*) are commonly taken in fisheries, forming up to 95% of incidental elasmobranch bycatch. The present study examined the life history of silky sharks ($n = 553$) from Papua New Guinean waters. Age was analysed using sectioned vertebrae, and a multimodel approach was applied to the length-at-age data to fit growth models. Females ranged in length from 65.0- to 253.0-cm total length (TL), with the oldest estimated at 28 years. Males ranged in length from 68.4 to 271.3 cm TL and were aged to a maximum of 23 years. The logistic model provided the best fitting growth parameter estimates of length at birth $L_0 = 82.7$ cm TL, growth coefficient $g = 0.14 \, \text{year}^{-1}$ and asymptotic length $L_\infty = 261.3$ cm TL for the sexes combined. Females reached sexual maturity at 204 cm TL and 14.0 years, whereas males reached maturity at 183 cm TL and 11.6 years. The average litter size from 28 pregnant females was 8 (range of 3–13). The growth parameters and late ages of sexual maturation for silky sharks in the central west Pacific suggest a significant risk from fisheries exploitation without careful population management.

Additional keywords: intraspecific variation, logistic growth function, pelagic shark fisheries, vertebral ageing.

Introduction

Detailed biological information on life history (age, growth, reproductive traits and demography) of species exposed to fishing is critical to their sustainable management (Cailliet 2015). Aspects of the life history of chondrichthyans (sharks, rays and chimaeras) remain one of the most poorly understood among marine vertebrate groups. Although many elasmobranch species are widely distributed, considerable intraspecific variation in life history traits has been shown to exist between some populations in different geographic locations (e.g. Yamaguchi *et al.* 1998; Lombardi-Carlson *et al.* 2003; Smart *et al.* 2015). Therefore, region-specific life history data of a species is required to properly inform sustainable management plans (Simpfendorfer *et al.* 2011). Using life history parameters derived from one population to conspecifics in another region increases the risk of inaccuracies in population modelling (Chin *et al.* 2013; Smart *et al.* 2015). This can lead to inappropriate management approaches that risk negative consequences for those species and may lead to economic loss for those using the resource.

Sharks life histories are typically characterised by slow growth, low fecundity, late age of sexual maturation and often considerable longevity (Cortés 2000; Au *et al.* 2008). These traits collectively manifest low intrinsic population growth rates, reducing their resilience to fishing mortality (Campana 2001: Au *et al.* 2008). In recent decades, sharks have increasingly become a valuable commodity as catch of traditional teleost species has become more restrained (Dulvy *et al.* 2008) and demand for shark products has increased (Dent and Clarke 2015). Fuelled largely by the high market value of fins and demand for cheap sources of animal protein (Simpfendorfer and Dulvy 2017), targeted fishing effort for sharks, as well as the retention of incidentally caught sharks, has increased considerably both in coastal areas and on the high seas (Clarke *et al.* 2006; Dulvy *et al.* 2008). As exploitation increases, and the status of populations declines (Davidson *et al.* 2016), life history

data on key species taken in fisheries are needed to help improve their fisheries management and assessment.

The silky shark *Carcharhinus falciformis* is a pantropically distributed oceanic–epipelagic species (Last and Stevens 1994; Rigby *et al.* 2016) commonly caught by fisheries throughout their range. This species is placental viviparous and likely has a biennial reproductive cycle (Galván-Tirado *et al.* 2015). Maximum size is reported to be 371 cm and length-at-maturity ranges from 180 to 246 cm, with males and females estimated to reach maturity at 5–13 and 6–15 years respectively (Rigby *et al.* 2016). Silky sharks have a strong tendency to aggregate under floating oceanic debris and artificial fish aggregation devices (FADs), where they are commonly observed to follow schooling tuna (Strasburg 1958; Yoshimura and Kawasaki 1985). The tendency of silky sharks to migrate within schools of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*), both of which are heavily fished, has resulted in them being one of the most incidentally caught elasmobranch species (Hutchinson *et al.* 2015). Commercial purse seine and longline fishing operations report large amounts of silky shark catch (Poisson *et al.* 2014; Hutchinson *et al.* 2015). In addition, entanglement in FADs significantly contributes to the mortality of juvenile age classes in the Indo-Pacific and Indian Ocean regions (Filmalter *et al.* 2013). In recent years, the incidental catch rate of silky shark has fallen by 60% in the east Pacific (Minami *et al.* 2007), by up to 90% on longlines in the Atlantic (Baum and Myers 2004) and in the central Pacific, catch rate trends have fallen with decreases in the median size of individuals caught also observed (Clarke *et al.* 2011). Currently, the Western and Central Pacific Fisheries Commission (WCPFC) and International Commission for Conservation of Atlantic Tunas prohibit the retention of silky shark (Rice *et al.* 2015). In the Indian and east Pacific oceans, the deteriorating status of silky sharks has been noted (Minami *et al.* 2007; Hall *et al.* 2012), although adoption of conservation measures has yet to be reviewed and implemented. The Convention on International Trade in Endangered Species (CITES) lists the silky shark in appendix II (international trade only allowed if shown to have no detrimental to a population) and the silky shark is listed under the Conservation of Migratory Sharks (CMS) Memorandum of Understanding for Migratory Sharks (Rigby *et al.* 2016). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species assesses the silky shark as 'near threatened' throughout its range (Rigby *et al.* 2016).

Despite silky sharks being a common constituent of bycatch throughout their geographic range, life history parameters are lacking for some regions. Furthermore, previous studies on aspects of their growth and reproductive biology have produced variable results, underlining the need for region-specific data (Branstetter 1987; Oshitani *et al.* 2003; Hall *et al.* 2012). The central west Pacific is one such area where no detailed life history information exists for silky sharks. A dedicated shark longline fishery that operated in Papua New Guinea (PNG) until 2014 reported catch per unit effort (CPUE) of silky sharks to be as high as 17 per 1000 hooks set, with the species comprising ~50% of total landings (Kumoru 2003). Furthermore, silky shark reportedly constituted up to 95% of incidentally caught elasmobranchs in some areas of the WCPFC's range (Lawson 2011). High catch rates of this species since the inception of

management in 1995 indicate that the central west Pacific is an important region to this species and likely supports a large population (Clarke *et al.* 2013). However, gradual decreases in the median size of individuals caught since 1995 suggest this population may be declining as a result of prolonged fisheries exploitation (Rice and Harley 2013).

The aim of the present study was to estimate growth parameters from length-at-age analysis and to describe aspects of the reproductive biology for the silky shark in PNG waters. Information gathered was intended to produce sufficient life history data to inform improved fisheries management in PNG and the greater central west Pacific region.

Materials and methods

Samples were collected from seven commercial longline operators in the Bismarck and Solomon seas in May and June 2014 by fisheries observers from the PNG National Fisheries Authority. The vessels targeted various shark species by setting gear close to the surface (up to 1200 hooks per set) for 8–10 h (Kumoru 2003). In all, 553 silky sharks were collected for examination. Total length (TL) was measured to the nearest 1 mm for all individuals and photographs were taken for identification purposes. On-board observers recorded their reproductive status (see below) and a section of six to eight vertebrae was removed from 527 individuals anterior to the first dorsal fin. Vertebral samples were stripped of excess flesh and tissue before being stored frozen. Species validation of each individual was performed through the examination of the photographs taken.

Vertebrae preparation and sectioning

Vertebral sections were prepared for ageing following standard protocols (Goldman 2005). Vertebral samples were defrosted before being separated into individual centra. The neural arch, haemal arch and any residual tissue were cut from each centrum. Individual centra were then soaked in a 5% sodium hypochlorite solution for 30 min to remove any remaining soft tissue. Centra were rinsed thoroughly under running tap water and placed in a drying oven for 24 h at 60°C. One centrum from each individual was randomly selected to be sectioned for analysis. Centra were sectioned on a sagittal axis through the centrum focus using a low-speed circular saw with two diamond-tipped blades (Beuhler, Lake Bluff, IL, USA). Sections were cut to a thickness of ~400 μm, measured with digital callipers. Vertebral sections were mounted on microscope slides using Crystal Bond adhesive (SPI Supplies, West Chester, PA, USA). A binocular dissecting microscope with a transmitted light source was used to examine each section

Age determination

Ages were determined by counting translucent and opaque band pairs in the corpus calcareum of each centrum as per Cailliet and Goldman (2004). The birthmark was identified as a change in angle on the inner margins of the corpus calcareum representing the shift from embryonic development to postnatal growth (Cailliet and Goldman 2004). Following Cailliet *et al.* (2006), each pair of translucent and opaque bands thereafter was deemed to represent 1 year of growth (Fig. 1). No attempt to
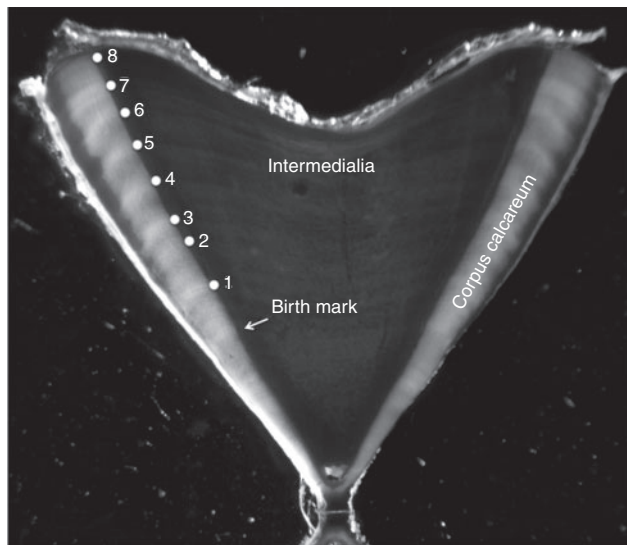
Fig. 1. Vertebral section of an immature male *Carcharhinus falciformis*, 148.8-cm total length, estimated to be 8 years old. The locations of the translucent annulus bands (white dots 1–8), the birthmark, intermedialia and corpus calcareum are shown.

determine the periodicity of band pair deposition could be made in the present study because samples were only collected over a 2-month period and hence methods of marginal increment analysis were not possible. However, annual band pair deposition has been verified by this method for silky sharks in regions adjacent to the present study site (Joung *et al.* 2008; Hall *et al.* 2012), and so annual band pair deposition was assumed for the present study.

Two readers independently counted band pairs on all sectioned vertebrae without prior knowledge of the length of the specimens. Each vertebral section was read twice by the primary reader (M. I. Grant) and once by an experienced second reader (J. J. Smart). A consensus age was recorded when primary reader counts agreed with the second reader count. All vertebrae with a band pair count discrepancy between readers were re-examined by both readers together to reach a consensus age. Vertebrae were disregarded from further analysis where a consensus age could not be agreed. Intra- and interreader precision was measured by indices of average percentage error (APE) and CV (Chang 1982), as recommended by Cailliet and Goldman (2004). Age bias plots were also constructed between each set of reads to identify the presence of systematic bias, which was formally tested by Bowker's test of symmetry (Bowker 1948; Evans and Hoenig 1998). All accuracy and precision calculations were conducted using the FSA package (D. H. Ogle, see https://fishr.wordpress.com/fsa/, accessed September 2016) in the R program environment (R Foundation for Statistical Computing, Vienna, Austria).

Modelling growth

A multimodel approach incorporating Akaike's information criterion (AIC; Akaike 1973) was used to select the most appropriate growth model (Smart *et al.* 2016). Three candidate models were selected *a priori* and each applied to the

Table 1. Three *a priori* model candidate equations used in the multi-model Akaike information criterion analysis

L_t, length at age t; L_0, length at age 0; L_∞, asymptotic length; k and g, respective growth coefficients of each model

Model	Growth function equation
Von Bertalanffy growth function	$L_t = L_0 + (L_\infty - L_0)\,(1 - \exp(-kt))$
Logistic function	$L_t = (L_\infty\,L_0\,(\exp(gt))) \div (L_\infty + L_0\,(\exp(gt) - 1))$
Gompertz function	$L_t = L_0\exp(\log(L_\infty \div L_0)\,(1 - \exp(-gt)))$

length-at-age data. The candidate models chosen were the von Bertalanffy growth function (VBGF; von Bertalanffy 1938), the logistic function (Ricker 1979) and the Gompertz function (Ricker 1975; Table 1). A form of each model incorporating the length-at-birth parameter L_0 was used because it has biological meaning and can be directly compared between models. The asymptotic length (L_∞) can also be directly compared between each of the candidate models, but the respective growth coefficient of each model (i.e. k for the VBGF, g for the logistic model and g for the Gompertz model) cannot because these coefficients represent different mathematical principles.

The best-fit parameter estimates for each model were identified using the non-linear least squares (nls) function in the R program environment (R Foundation for Statistical Computing). Each model was applied to the sexes combined data and to each sex separately. The AIC was then used to determine the 'best-fit' model for each of these datasets as follows:

$$AIC = n \log(\sigma^2) + 2k$$

where k is the total number of parameters being considered $+1$ for variance (σ^2) and n is the sample size. The model with the lowest AIC value (AIC_{min}) was selected as the most appropriate representation of the length-at-age data. Differences in AIC values (ΔAIC) were calculated for subsequently poorer fitting models as follows:

$$\Delta AIC = AIC_i - AIC_{min}$$

whereby a ΔAIC of 0–2 had the highest support, ΔAIC of 2–10 had considerably less support and $\Delta AIC > 10$ had no support (Burnham and Anderson 2002). AIC weights (w_i) were also calculated from AIC values, which described the probability of selecting the most suited model to the length-at-age dataset, as follows:

$$w_i = \frac{e^{\left(-\frac{\Delta_i}{2}\right)}}{\sum_{j=1}^{3} e^{\left(-\frac{\Delta_j}{2}\right)}}$$

where Δ_i is ΔAIC of each specified model and Δ_j is the ΔAIC of each individual model. Likelihood ratio tests (LRTs; Kimura 1980) were used to determine whether models for separate sexes should be used over a single model for combined sexes. The LRT was used to test whether the growth curves of each sex were coincident for all growth parameters combined, as well as each parameter individually, using Microsoft Excel (Bellevue, WA,

Table 2.   Characteristics used to classify maturity stages of female and male *Carcharhinus falciformis*
Adapted from White *et al.* (2001)

Maturity stage classification	Indicating characteristics
Females	
Stage 1: immature	Very small ovaries; uteri similar in size, thin and flaccid
Stage 2: maturing virgin	Functional (right) ovary contains small yolked ova; the two functional uteri beginning to enlarge but mostly thin and flaccid
Stage 3: mature, non-pregnant	Right ovary contains yolked ova >2.0 mm in diameter; uteri enlarged along entire length
Stage 4: mature, pregnant	Fertilised eggs or embryos in both uteri
Stage 5: mature, postpartum	Uteri very enlarged and flaccid from having recently released young
Males	
Immature	Claspers small, flexible and non-calcified
Maturing	Claspers enlarging and beginning to calcify and thus become rigid
Mature	Claspers fully developed and rigid from complete calcification

USA) according to the method outlined by Haddon (2001). Growth curves were tested only for equivalent age ranges (0–23 years) as per the assumptions of the LRT used (Haddon 2001).

Maturity analysis

The reproductive maturity status of 518 silky sharks was determined by examination of external and internal features. Male maturity was assessed by observers at the time of capture by inspection of clasper calcification. Female maturity was also examined at the time of capture by internal inspection of ovaries, uteri and ova (Table 2). Female silky sharks classified as Stage 1 and 2 were identified as those possessing an undeveloped right (functional) uterus and thus are not capable of conceiving, despite some small ova with indication of vitellogenic development. Females in Stage 3 contained larger (at least >2.0 mm) ova in conjunction with a developed uterus and were deemed capable of conceiving and were thus considered mature (White *et al.* 2001; Hall *et al.* 2012). Female maturity stages were later verified for each individual by reviewing photographs taken at the time of inspection. For pregnant females, the litter size and sex of embryos were recorded and the TL of each embryo measured. A Chi-Square test was used to test for any significant difference in the sex ratio of litters examined.

The TL at which 50% (L_{50}) and 95% (L_{95}) of females and males had attained maturity was calculated using the generalised linear model (GLM) with a logit-link function in the R environment (R Foundation for Statistical Computing). Following Hall *et al.* (2012), 1000 bootstrap estimates of the logistic parameters were produced to identify the probability of each individual of a given TL being mature. The 95% confidence limits were taken as the 2.5 and 97.5 percentiles of the 1000 estimates for the logistic parameters and probabilities of each individual being mature. The same process was used to estimate the age-at-maturity for the population at 50% mature (A_{50}) and 95% mature (A_{95}).

Results

Age estimates

Band pair counts by the primary reader (M. I. Grant) had a CV of 10.8% and an APE of 7.6%, both within reasonable limits for chondrichthyan age studies (Campana 2001). However,

systematic bias was present between Read 1 and Read 2 (both M. I. Grant) (Fig. 2), as detected by Bowker's test of symmetry (d.f. = 72, χ^2 = 149.2, $P < 0.001$). There were also levels of systematic bias detected between readers for both Read 1 (M. I. Grant) and Read 3 (J. J. Smart) (d.f. = 86, χ^2 = 229.6, $P < 0.001$) and Read 2 and Read 3 (d.f. = 92, χ^2 = 338.6, $P < 0.001$). Differences in age estimates were more pronounced in larger length classes (Fig. 2). To rectify age discrepancies, consensus counts were conducted for all age estimates that differed within all length classes. A third reader was used before commencing consensus counts to ensure consistency in first band pair identification, which is often the main systematic error source in chondrichthyan ageing techniques (Campana 2001). Age estimates were agreed upon for 526 samples (females = 254, males = 272) with only one vertebra deemed uninterpretable and omitted from the length-at-age data. Samples in the present study produced the oldest age estimates by vertebral analysis for both female and male silky sharks, with estimated ages ranging from 0 to 28 years for females and from 0 to 23 years for males. The sample size encompassed individuals ranging from 65 to 271 cm TL (Fig. 3).

Growth estimation

Results of the multimodel AIC analysis indicated that the logistic model was the best fit for the observed length-at-age data for sexes combined (Table 3; Fig. 4). Kimura's LRT showed that logistic growth curves for each sex separately were coincident, with no significant difference detected between curves (χ^2 = 2.49, d.f. = 3, $P < 0.05$). Furthermore, no significant difference was detected for each growth parameter produced by the logistic growth model between sexes ($P < 0.05$). Hence, the sexes combined logistic model growth parameter estimates (L_0 = 82.7 cm TL, g = 0.14 year^{-1}, L_∞ = 268.3 cm TL) were considered to appropriately represent the growth of both sexes (Fig. 4). Parameter estimates for length at birth (L_0) were within a reasonable biological range for this species across all models for both sexes combined and sexes separated.

Maturity analysis

Maturity status data were collected for 518 individuals (248 females, 269 males). The smallest observed mature female was 192 cm TL, whereas the largest observed immature female was
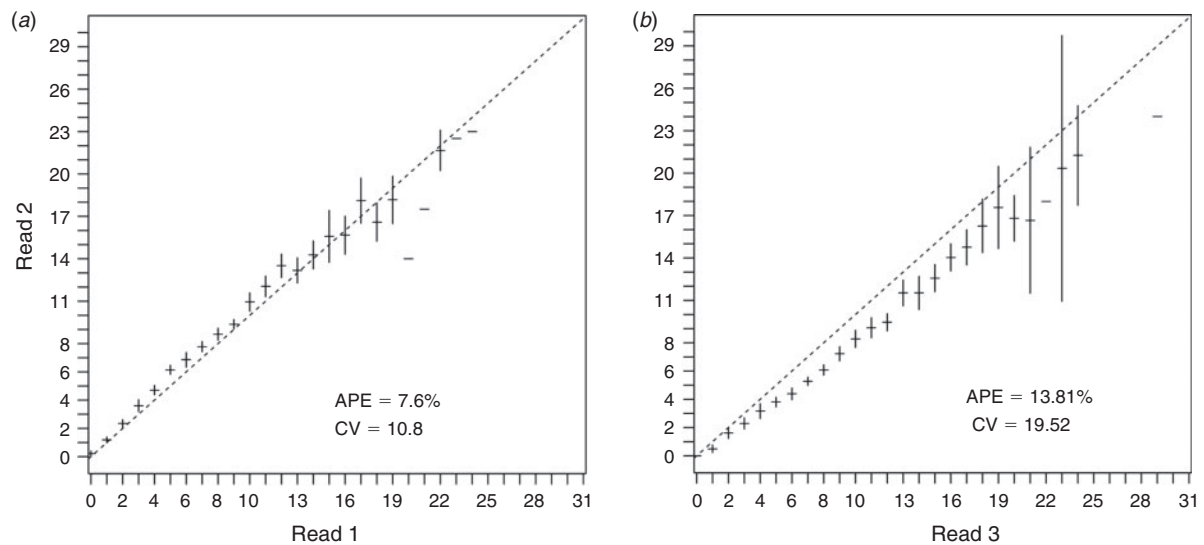
Fig. 2. Age-bias plots for *Carcharhinus falciformis*. Mean age-specific agreements between (*a*) Read 1 and Read 2 (both M. I. Grant) and (*b*) Read 2 (M. I. Grant) and Read 3 (J. J. Smart). The 95% confidence limits are plotted along a 1 : 1 equivalence line for comparison. APE, average percentage error. (The age-bias plot between Read 1 and Read 3 is shown in Fig. S1, available as Supplementary material to this paper.)
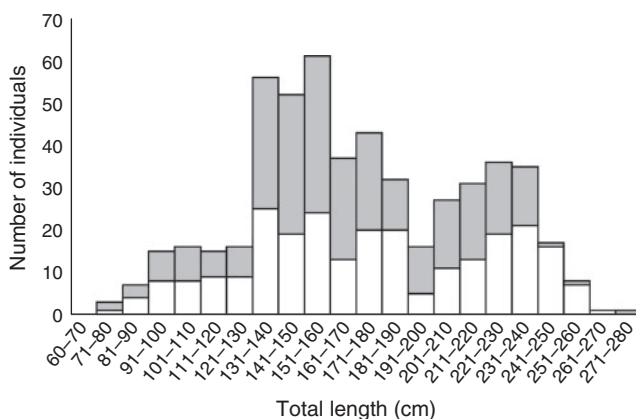

Fig. 3. Length–frequency distribution showing the range of *Carcharhinus falciformis* males (shaded) and females (white) used in the present study

213 cm TL. For males, the size range of mature individuals was greater, with the smallest mature male being 167 cm TL and the largest immature male being 200 cm TL. The length and age at which 50% and 95% of both females and males were mature showed a considerable difference, with males maturing earlier and at smaller sizes (Table 4). For males, L_{50} and L_{95} were 183 and 198 cm TL respectively, corresponding to an A_{50} and A_{95} of 11.6 and 13.7 years respectively. For females, L_{50} and L_{95} were 204 and 219 cm TL respectively, corresponding to an A_{50} and A_{95} of 14.0 and 16.5 years respectively (Figs 5, 6).

Of the mature females collected for ageing, 28 were pregnant with a mean (±s.d.) litter size of 8.6 ± 2.65. In total, there were 242 embryos (120 male, 122 female). The embryonic sex ratio did not differ significantly from 1 : 1 ($\chi^2 = 0.017$, d.f. = 1, $P = 0.90$). The largest observed litter size was 13 and the smallest was 3. No consistency in the length of embryos was

observed during the sampling period, with individuals between litters ranging from 9–12 to 66–71 cm TL.

Discussion

The results of the present study provide evidence that the growth characteristics of the silky shark vary throughout its pantropical distribution. Compared with previous length-at-age studies, silky sharks in the central west Pacific grow slower, mature later and possibly attain a smaller maximum size than conspecifics in the Atlantic (Branstetter 1987; Bonfil *et al.* 1993), Taiwan (Joung *et al.* 2008) and the central Pacific (Oshitani *et al.* 2003; Fig. 7; Table 5), whereas the results for growth parameters and ages at maturity were similar to those reported from Indonesia (Hall *et al.* 2012). Fecundity data and sex ratios for the western central Pacific showed similar trends to all other study regions (Oshitani *et al.* 2003; Hall *et al.* 2012).

Multimodel growth analysis

The present study is the first to use a multimodel approach to the fitting of growth functions for the silky shark. All previous studies have *a priori* selected only the VBGF to fit length-at-age data, because the VBGF has traditionally been assumed to sufficiently estimate viviparous shark growth (Smart *et al.* 2016). However, it has been demonstrated that the VBGF does not always provide the best fit to shark length-at-age data and, in some instances, provides growth parameter estimates that are likely to be inaccurate (Katsanevakis 2006; Smart *et al.* 2016). The absence of a defined asymptote is not uncommon in many shark growth curves (Simpfendorfer *et al.* 2002; Smart *et al.* 2017), which can lead to biologically unrealistic L_∞ estimates, such as those observed for the VBGF in the present study. Comparatively, the logistic model L_∞ estimate was more comparable to the maximum size observed in the present study. Similarly, Carlson and Baremore (2005) found the logistic

Table 3. Summary of Akaike information criterion (AIC) results and model parameters for the length-at-age data

Where appropriate, data are given as the mean ± s.d. Bold values indicate the AIC selected logistic model growth parameters, n, number of individuals; Δ, difference in AIC values between models; w, AIC weight; L_∞, asymptotic length parameter; L_0, length-at-birth parameter; k, growth rate parameter for the von Bertalanffy growth function (VBGF). Both the Gompertz and logistic models use 'g' to represent their respective growth coefficient, so subscripts have been used to indicate which growth function 'g' refers to (i.e. g_{Gomp} and g_{Log} respectively). Confidence limits (95%) for parameter estimates are given in parenthesis. Only parameter values of L_∞ and L_0 are comparable between models

| Sex	Model	n	AIC	Δ	w	L_∞ (cm)	L_0 (cm)	k (year^{-1})	g_{Gomp} (year^{-1})	g_{Log} (year^{-1})
Combined	VBGF	526	4292.3	26.9	0.0	386.8 ± 57.4	77.6 ± 4.1	0.04 ± 0.01	–	–
	Logistic	**526**	**4264.1**	**0.0**	**100**	**268.3 ± 11.4**	**82.7 ± 3.1**	–	–	**0.14 ± 0.01**
	Gompertz	526	4275.6	11.1	0.0	296.4 ± 19.0	80.3 ± 3.5	–	0.09 ± 0.01	–
Male	VBGF	272	2234.0	2.8	24.2	659.1 ± 509.6	82.3 ± 6.0	0.02 ± 0.02	–	–
	Logistic	**272**	**2231.2**	**0.0**	**67.6**	**287.3 ± 31.8**	**85.8 ± 4.9**	–	–	**0.12 ± 0.02**
	Gompertz	272	2236.2	5.0	8.2	342.0 ± 61.4	84.0 ± 5.5	–	0.07 ± 0.02	–
Female	VBGF	254	2057.4	22.7	0.0	342.6 ± 45.1	74.8 ± 5.7	0.05 ± 0.01	–	–
	Logistic	**254**	**2034.7**	**0.0**	**99.9**	**261.6 ± 11.4**	**80.6 ± 4.3**	–	–	**0.15 ± 0.02**
	Gompertz	254	2044.0	9.3	0.01	282.7 ± 18.2	77.8 ± 4.9	–	0.09 ± 0.01	–
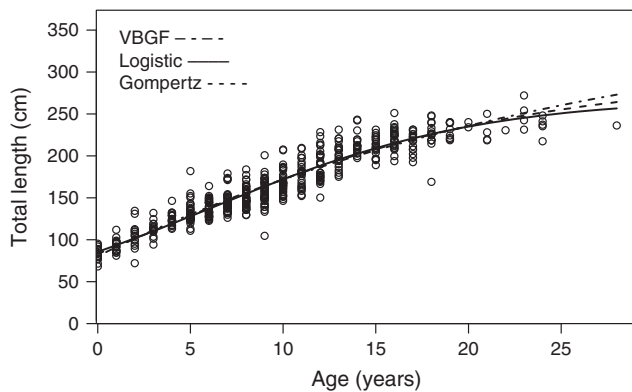
Fig. 4. Length-at-age data of *Carcharhinus falciformis* fitted with the three candidate models, namely the von Bertalanffy growth function (VBGF), logistic and Gompertz. Circles indicate the length at age of each individual. The logistic model provided the best fit for the observed length-at-age data.

Table 4. Total length (L_{50} and L_{95}) and age (A_{50} and A_{95}) estimates at which 50 and 95% of females and males are mature, together with 95% confidence limits (CL)

Maturity index	Females	Males
L_{50} (cm)	204.19	183.44
Lower CL	199.90	179.40
Upper CL	208.36	187.68
L_{95} (cm)	218.91	198.90
Lower CL	212.32	190.60
Upper CL	234.53	205.95
A_{50} (years)	14.0	11.6
Lower CL	13.4	11.2
Upper CL	14.5	12.0
A_{95} (years)	16.5	13.7
Lower CL	15.1	12.9
Upper CL	17.6	14.3

model also provided the best fit to length-at-age data for the spinner shark (*Carcharhinus brevipinna*), despite traditional *a priori* use of the VBGF for this species.

No significant difference was detected between growth parameters of each sex for the logistic models. Uniform growth between sexes has also been observed in all previous length-at-age studies of silky sharks and appears to be characteristic of this species. The growth coefficient attained from the logistic model ($g = 0.14$ year^{-1}) suggests that silky sharks in the central west Pacific reach their asymptotic length slowly compared with other regions (Fig. 7). For example, the blacktip reef shark *Carcharhinus melanopterus* from north-eastern Australia had an estimated g of 0.25 year^{-1} and was also considered to be a slow-growing species (Chin *et al.* 2013). A low growth coefficient for the silky shark was also observed in an adjacent study site, in Indonesia (Hall *et al.* 2012), whereas in the Gulf of Mexico (Branstetter 1987) and east (Sánchez-de Ita *et al.* 2011) and central Pacific (Oshitani *et al.* 2003) regions, silky sharks appear to reach their asymptotic length faster (Fig. 7; Table 5). Variation in the growth coefficient has been observed for other *Carcharhinus* species between regions, and may be a reflection of natural variation or differences in methodology and sampling design between studies (Casey and Natanson 1992; Smart *et al.* 2015).

Despite more individuals in larger size classes being sampled in the present study compared with the adjacent Pacific study sites, namely the central Pacific (Oshitani *et al.* 2003) and Taiwan (Joung *et al.* 2008), the L_∞ parameter estimated (268.3 cm TL) is still considerably lower than the observed maximum length of 371 cm TL for silky sharks (Serafy *et al.* 2012) in the Atlantic. Large (>300 cm TL) silky sharks are reported in the Atlantic (Bonfil *et al.* 1993) and occasionally in the east Pacific (Sánchez-de Ita *et al.* 2011), whereas around the Indo-Pacific reports of individuals >300 cm TL are rare. Sampling was only conducted over a 2-month period in the present study and it is possible that extremely large individuals were not present in the area at this time. However, the largest individuals observed in the present study are similar to those
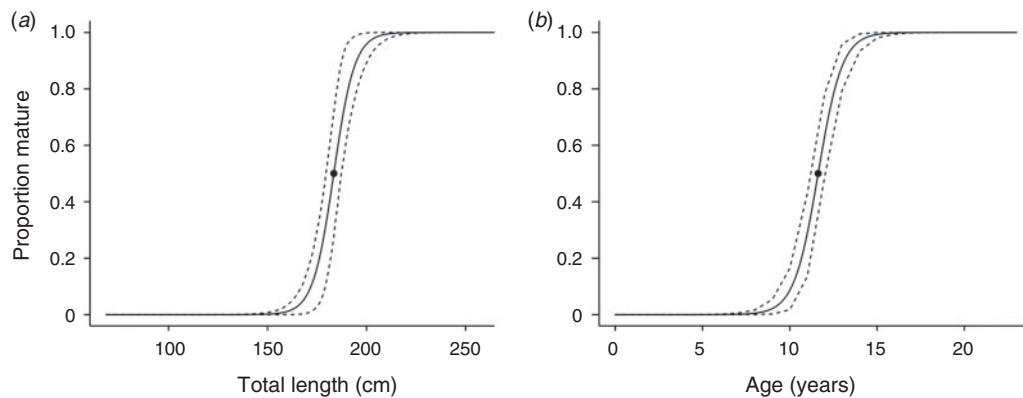
Fig. 5. Maturity ogives for male *Carcharhinus falciformis* from logistic generalised linear models of (*a*) observed length and (*b*) estimated age. Curves show the proportion of males that appear to be mature at a given length and age. Dotted lines indicate 95% confidence limits. The black circle indicates the point where the proportion mature is 50% (L_{50}, A_{50}).
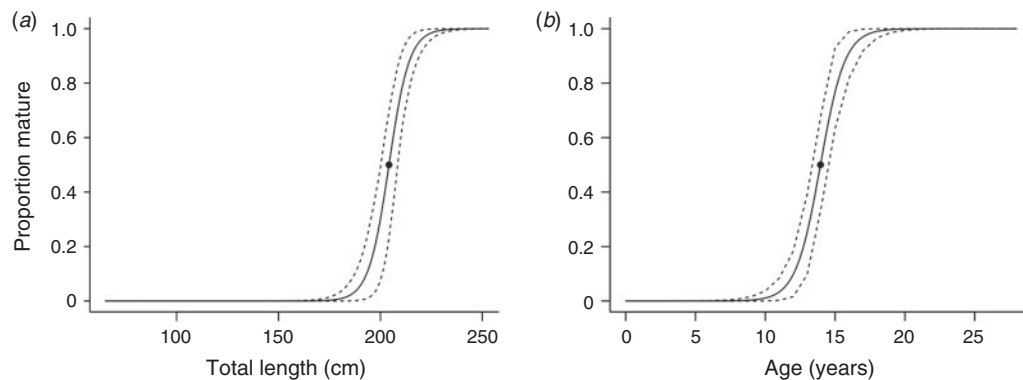

Fig. 6. Maturity ogives for female *Carcharhinus falciformis* from logistic generalised linear models of (*a*) observed length and (*b*) estimated age. Curves show the proportion of males which appear to be mature at a given length and age. Dotted lines indicate 95% confidence limits. The black circle indicates the point where the proportion mature is 50% (L_{50}, A_{50}).
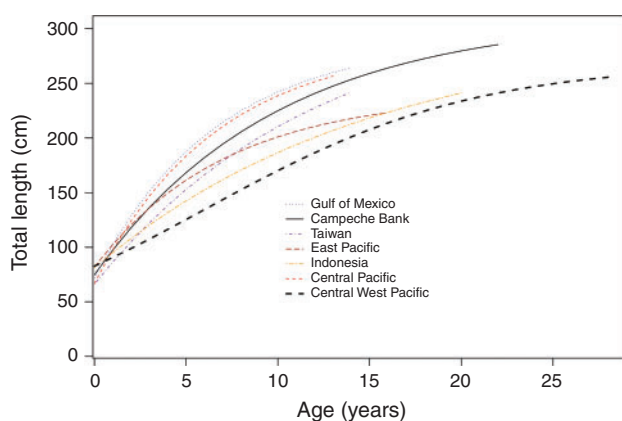

Fig. 7. Comparison of growth curves for *Carcharhinus falciformis* from the Gulf of Mexico (Branstetter 1987), Campeche Bank (Bonfil *et al.* 1993), Taiwan (Joung *et al.* 2008), east Pacific (Sánchez-de Ita *et al.* 2011), Indonesia (Hall *et al.* 2012), central Pacific (Oshitani *et al.*, 2003) and central west Pacific (present study). The von Bertalanffy growth function was used in all regions to fit length-at-age data, except for the central west Pacific, where the logistic growth function provided the best fit from Akaike information criterion analysis.

reported by Hall *et al.* (2012), who sampled year-round in comparable latitudes in Indonesia. It is possible that silky shark populations around the Indo-Pacific do not reach the maximum sizes that conspecifics do in the Atlantic. This is supported by older age estimates derived in the present study, which indicate that several individuals of 20–28 years have only attained lengths of ∼250 cm TL. Silky sharks at similar lengths were also aged at ∼20 years by Hall *et al.* (2012) in Indonesia, whereas in the Atlantic Branstetter (1987) estimated his largest specimen, measuring 267 cm TL, to be 13 years old. However, the absence of large (>300 cm TL) silky sharks in the Indo-Pacific may be a consequence of intensive historical targeting of large sharks for the Asian fin trade (Clarke *et al.* 2006, 2013). Within the WCPFC's range particularly, silky sharks have incurred very heavy fisheries pressure since the mid-1990s, with an average of ∼175 000 individuals caught annually in longline and purse seine fisheries since 1995 (Lawson 2011).

Sources of variation between silky shark studies

There are a few possible sources of variation within silky shark length-at-age studies that may have been responsible for the observed regional differences in growth parameters (Table 5)

Table 5. Comparison of life history characteristics presented for *Carcharhinus falciformis* in each region studied

TL, total length; L_0, length-at-birth parameter; L_∞, asymptotic length parameter; k, von Bertalanffy growth coefficient; g, logistic growth function growth coefficient; A_{50}, age at which 50% of individuals sampled have obtained maturity, calculated using a generalised linear model (GLM); L_{50}, length at which 50% of individuals sampled have obtained maturity, calculated using a GLM; F, female; M, male

Region	Maximum observed age (years)	Maximum observed TL (cm)	Growth parameter estimates				Sexual maturation			Study
			L_0 (cm TL)	L_∞ (cm TL)	k (year^{-1})	g (year^{-1})		Age (years)	TL (cm)	
Atlantic										
Gulf of Mexico	14	267	72	291	0.15	–	F	7–9	>225	Branstetter (1987)
							M	6–7	210–220	
Campeche Bank	22	314	74.7	311	0.1	–	F	>12	232–245	Bonfil *et al.* (1993)
							M	10	>225	
Pacific										
East Pacific	16	260	81.9	240	0.14	–	F	8	180–182	Hoyos-Padilla *et al.* (2012),
							M	8	180–182	Sánchez-de Ita *et al.* (2011)
Central Pacific	13	292	66.8	288	0.15	–	F	6–7	204	Oshitani *et al.* (2003)
							M	5–6	>186	
Taiwan	14	256	68.3	332	0.083	–	F	9–10	210–220	Joung *et al.* (2008)
							M	9 (A_{50})	213 (L_{50})	
Central west Pacific	28	271	82.7	268	–	0.14	F	14 (A_{50})	204 (L_{50})	Present study
							M	12 (A_{50})	183 (L_{50})	
Indian										
Indonesia	20	260	81.2	299	0.066	–	F	15 (A_{50})	216 (L_{50})	Hall *et al.* (2012)
							M	13 (A_{50})	208 (L_{50})	

and subsequent growth curves (Fig. 7). There is a paucity of information available with regard to distributional patterns of silky shark stocks and a better understanding is needed of population structure and size segregations within populations. Clarke *et al.* (2015) investigated the global population connectivity of silky sharks using mitochondrial DNA markers and suggested one population in the west Atlantic and two distinct populations (east and west) in both the Pacific and Indian oceans. Hence, variations in growth parameters between regions studied may be attributed to natural variation between these suggested populations. However, differences between growth parameters in west Pacific study sites, namely Taiwan (Joung *et al.* 2008), the central Pacific (Oshitani *et al.* 2003) and the present study, are inconsistent with the population structure proposed by Clarke *et al.* (2015), although latitudinally segregated populations were not considered in their study.

Differences in sampling design and methodology may have contributed to regional growth parameter variances. Growth models are sensitive to missing data points on either end of the length spectrum and a lack of juvenile or large adult size classes can lead to false inferences of growth rate (Smart *et al.* 2016). Bonfil *et al.* (1993) noted size class distributions within the sample size of the two respective Atlantic silky shark studies likely contributed to the observed growth parameter differences between these geographically adjacent regions. A lack of large samples in the Gulf of Mexico (Branstetter 1987) produced a low asymptotic length and higher growth coefficient estimate compared with Campeche Bank to the south (Bonfil *et al.* 1993). The variation in growth models produced between these studies is significant because Clarke *et al.* (2015) suggest one population in the west Atlantic. This indicates that these variations in

growth parameters are likely to have resulted from methodological differences or sampling design. In the east (Sánchez-de Ita *et al.* 2011) and central (Oshitani *et al.* 2003) Pacific studies, most individuals collected were <240 cm TL and, similarly, these regions had comparatively high growth coefficient estimates compared with the present study and that in Taiwan (Joung *et al.* 2008), where more individuals in larger size classes were sampled (Table 5).

From data presented within silky shark length-at-age studies, it is not possible to deduce whether the apparent limitations on the availability of size classes sampled is due to temporal gear selectivity or undocumented segregation of size classes in each study region. All previous length-at-age studies on silky sharks have obtained samples from longline fishing methods, although little comparable information is given for soak time, depth and hook size. However, location of habitat fished may be a factor. For example, between the Atlantic studies, larger individuals (>240 cm TL) were caught on the continental shelf (Bonfil *et al.* 1993), whereas Branstetter (1987) collected samples from a pelagic swordfish fishery resulting in smaller size classes ranging from 100 to 210 cm TL. Conversely, in Indonesia, Hall *et al.* (2012) noted a higher presence of smaller individuals (<140 cm TL) in gill net fisheries operating on the outer continental shelf and larger individuals (>140 cm TL) were collected from longline fisheries off the continental shelf in pelagic environments. Thus, size class segregations may occur between shelf and pelagic habitats for silky sharks, although it is unclear whether this is a function of gear selectivity. In the Pacific, seasonal size class segregations are observed in the east (Sánchez-de Ita *et al.* 2011; Galván-Tirado *et al.* 2015) although similar data are lacking for other regions within the Pacific.

Further to methodological differences in sample collection, it is also possible that differences in the interpretation of vertebral growth band pairs have affected growth curves between studies. Silky shark age and growth studies have been conducted over the past 30 years and, throughout this period, the methodological approaches to length-at-age estimation for elasmobranchs have become more refined (Cailliet 2015). All studies used the traditional technique of counting opaque and translucent band pairs to estimate ages (Cailliet and Goldman 2004), except for Oshitani *et al.* (2003) in the central Pacific, who counted convex and concave structures on vertebral sections. Maximum observed age estimates of females and males in the central Pacific were only 13 and 8 years respectively. Low maximum observed age estimates were also reported in the east Pacific (females 16 years, males 14 years; Sánchez-de Ita *et al.* 2011), Taiwan (females 11 years, males 14 years; Joung *et al.* 2008) and in the Gulf of Mexico (females 14 years, males 13 years; Branstetter 1987). These observations are substantially lower than studies in the Campeche Bank (females 22 years, males 20 years; Bonfil *et al.* 1993), Indonesia (females 19 years, males 20 years; Hall *et al.* 2012) and the present study (females 28 years, males 23 years). It is suggested that growth band counts incorporate at least two readers with some form of precision, accuracy and bias measurement (Cailliet and Goldman 2004). Previous length-at-age studies on silky sharks (Branstetter 1987; Bonfil *et al.* 1993; Oshitani *et al.* 2003; Joung *et al.* 2008; Sánchez-de Ita *et al.* 2011; Hall *et al.* 2012) did not always use multiple readers and, where they did, there has been no indication of precision and bias in growth band counts, limiting the confidence that can be taken from length-at-age estimates and subsequent growth parameter estimates. It is likely that the intraspecific variation observed for the silky shark between regions can be attributed, in part, to a combination of sampling differences and limitations or varied band pair interpretation across studies. Between-laboratory comparisons would be useful to test the assumptions about the interpretation of band pairs for the purpose of ageing by different institutions and remains an area in need of further investigation (Cailliet *et al.* 1990; Tanaka *et al.* 1990).

The present study produced the oldest age estimations for female and male silky sharks. In the management of exploited populations, longevity of the species is an important consideration and underestimation can seriously impede management (Cailliet and Andrews 2008; Cailliet 2015; Harry 2017). However, maximum ages derived from vertebral ageing techniques have proven to underestimate longevity in several *Carcharhinus* species. Determinate methods of validation confirm that the maximum age of adult sandbar sharks *Carcharhinus plumbeus* and blacktip reef sharks may be underestimated by more than 11 years by vertebral analysis techniques (Andrews *et al.* 2011; Chin *et al.* 2013). Based on these and similar studies, it is apparent that adult sharks may cease annual band pair deposition in vertebral centra, despite validation in juveniles and subadults, (Casey and Natanson 1992; Harry *et al.* 2013; Passerotti *et al.* 2014; Harry 2017). For silky sharks, there is reasonably good evidence that band pair depositions occur on an annual basis until at least the age of 20 years in the Indo-Pacific, as evidenced by methods of marginal increment analysis (Joung *et al.* 2008; Hall *et al.* 2012). Moreover, in the east Pacific during an annual

period of high sea surface temperature, vertebrae with opaque borders were observed in subadult and adult silky sharks (Sánchez-de Ita *et al.* 2011). This supports evidence from marginal increment analysis that the translucent band forms in winter months during early development in silky sharks throughout their geographic range (Branstetter 1987; Bonfil *et al.* 1993; Joung *et al.* 2008; Hall *et al.* 2012). However, the absence of deterministic age validation on silky sharks in different regions and throughout different age classes limits the confidence that can be taken in directly comparing growth parameter estimates between studies. There is a need for validation of the periodicity of silky shark band pair formation throughout their geographic distribution and within different age classes.

Reproductive biology

Lengths of embryos were highly variable across a short time span (weeks), supporting the conclusion of asynchronous parturition for silky sharks in the Indo-Pacific (Oshitani *et al.* 2003; Hall *et al.* 2012; Galván-Tirado *et al.* 2015). The litter sizes observed in the present study were also consistent with previous observations of fecundity suggesting silky sharks most commonly birth 8–12 young (Oshitani *et al.* 2003). The smallest neonate observed in the present study was 65 cm TL, whereas the largest embryo was 71 cm TL. The estimated size-at-birth parameter L_0 was marginally larger than reported in previous studies (Table 5). Collectively, these observations and L_0 estimates are within the range of birth sizes (65–85 cm TL) commonly observed for this species, supporting evidence that silky sharks can have a relatively wide length range at birth (Oshitani *et al.* 2003).

Maturity ogives indicate that males reach sexual maturity at a younger age and smaller size than females. Lengths estimated in the present study were smaller than at other study sites, although it has been suggested here that silky sharks in the central west Pacific may not reach the maximum lengths observed in other regions. Interestingly, the lengths at maturity are very similar to the lengths proposed for the central Pacific (Oshitani *et al.* 2003), although the ages at which those lengths are reached vary considerably (Table 5). However, this may be due to the different technique used in estimating age in the central Pacific study (Oshitani *et al.* 2003). The ages at maturity estimated in the present study are most comparable to those reported for studies in Indonesia (Hall *et al.* 2012) and Campeche Bank (Bonfil *et al.* 1993), suggesting that silky sharks are slow to reach sexual maturity. This late onset of sexual maturity indicates slow population growth potential and a higher risk of exploitation from fisheries (Smith *et al.* 1998; Musick 1999).

Conclusions

The growth parameters estimated herein provide the requisite biological information for further demographic analysis and are intended to inform fisheries and conservation sectors in the central west Pacific region. Data from the present study indicate that silky sharks have a slow growth rate and late age of sexual maturity. Coupled with previous studies on fecundity and evidence of a biennial reproductive cycle, it is suggested here that this species is vulnerable to the intensive fishing pressure it

currently faces in the central west Pacific region. Information on population structure and validation of annual band pair deposition for silky sharks is recommended in future studies to further refine the life history data for this cosmopolitan species.

Conflicts of interest

The authors declare that they have no conflicts of interest for any material contained within this manuscript.

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References

Akaike, H. (1973). Information theory as an extension of the maximum likelihood. In 'Proceedings of the Second International Symposium on Information Theory, 1973' (Eds B. N. Petrov and F. Csaki.) pp. 267–228. (Akademiai Kiado: Budapest, Hungary.)

Andrews, A. H., Natanson, L. J., Kerr, L. A., Burgess, G. H., and Cailliet, G. M. (2011). Bomb radiocarbon and tag–recapture dating of sandbar shark (*Carcharhinus plumbeus*). *Fishery Bulletin* **109**, 454–465.

Au, D. W., Smith, S. E., and Show, C. (2008). Shark productivity and reproductive protection, and comparison with teleosts. In 'Sharks of the Open Ocean: Biology, Fisheries & Conservation'. (Eds M. D. Camhi, E. K. Pikitch, and E. A. Babcock.) pp. 298–308. (Blackwell Publishing: Oxford, UK.) . doi:10.1002/9781444302516.CH26

Baum, J. K., and Myers, R. A. (2004). Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters* **7**, 135–145. doi:10.1111/J.1461-0248.2003.00564.X

Bonfil, R., Mena, R., and de-Anda, D. (1993). Biological parameters of commercially exploited silky sharks, *Carcharhinus falciformis*, from the Campeche Bank, Mexico. *NOAA Technical Report NMFS* **115**, 73–86.

Bowker, A. H. (1948). A test for symmetry in contingency tables. *Journal of the American Statistical Association* **43**, 572–574. doi:10.1080/01621459.1948.10483284

Branstetter, S. (1987). Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. *Environmental Biology of Fishes* **19**, 161–173. doi:10.1007/BF00005346

Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodel Inference: a Practical Information-theoretic Approach', 2nd edn. (Springer: New York, NY, USA.)

Cailliet, G. M. (2015). Perspectives on elasmobranch life history studies: a focus on age validation and relevance to fishery management. *Fish Biology* **87**, 1271–1292. doi:10.1111/JFB.12829

Cailliet, G. M., and Andrews, A. H. (2008). Age-validated longevity of fishes: its importance for sustainable fisheries. In 'Fisheries for Global Welfare and Environment, 5th World Fisheries Congress 2008'. (Eds K. Tsukamoto, T. Kawamura, T. Takeuchi, T. D. Beard Jr, and M. J. Kaiser.) pp. 103–120. (TERRAPUB: Tokyo, Japan.)

Cailliet, G. M., and Goldman, K. J. (2004). Age determination and validation in chondrichthyan fishes. In 'Biology of Sharks and Their Relatives'. (Eds J. C. Carrier, J. A. Musick, and M. R. Heithanus.) pp. 399–447. (CRC Press: Boca Raton, FL, USA.) . doi:10.1201/9780203491317.PT3

Cailliet, G. M., Yudin, K. G., Tanaka, S., and Taniuchi, T. (1990). Growth characteristics of two populations of *Mustelus manazo* from Japan based upon cross-readings of vertebral bands. *NOAA Technical Report NMFS* **90**, 167–176.

Cailliet, G. M., Smith, W. D., Mollet, H. F., and Goldman, 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

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**, 197–242. doi:10.1111/J.1095-8649.2001.TB00127.X

Carlson, J. K., 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.

Casey, J. G., and Natanson, L. J. (1992). Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumeus*) from the western north Atlantic. *Canadian Journal of Fisheries and Aquatic Research* **49**(7), 1474–1477. doi:10.1139/F92-162

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**(8), 1208–1210. doi:10.1139/F82-158

Chin, A., Simpfendorfer, C., Tobin, A., and Heupel, M. (2013). Validated age, growth and reproductive biology of *Carcharhinus melanopterus*, a widely distributed and exploited reef shark. *Marine and Freshwater Research* **64**(10), 965–975. doi:10.1071/MF13017

Clarke, S. C., McAllister, M. K., Milner-Gulland, E. J., Kirkwood, G. P., Michielsens, C. G. J., Agnew, D. J., Pikitch, E. K., Nakano, H., and Shivji, M. S. (2006). Global estimates of shark catches using trade records from commercial markets. *Ecology Letters* **9**(10), 1115–1126. doi:10.1111/J.1461-0248.2006.00968.X

Clarke, S. C., Harley, S., Hoyle, S., and Rice, J. (2011). An indicator-based analysis of key shark species based on data held by SPC-OFP. In 'Scientific Committee Seventh Regular Session', 9–17 August 2011, Pohnpei, Federated States of Micronesia. WCPFC-SC7-2011/EB-WP-01. (Western and Central Pacific Fisheries Commission: Kolonia, Federated States of Micronesia.) Available at https://www.wcpfc.int/system/files/EB-WP-01%20%5BIndicator-based%20Analysis%20of%20SPC%20Shark%20Data%5D.pdf [Verified 12 January 2018].

Clarke, S. C., Harley, S. J., Hoyle, S. D., and Rice, J. S. (2013). Population trends in Pacific oceanic sharks and the utility of regulations on shark finning. *Conservation Biology* **27**(1), 197–209. doi:10.1111/J.1523-1739.2012.01943.X

Clarke, C. R., Karl, S. A., Horn, R. L., Bernard, A. M., Lea, J. S., Hazin, F. H., Prodohl, P. A., and Shivji, M. S. (2015). Global mitochondrial DNA phylogeography and population structure of the silky shark, *Carcharhinus falciformis*. *Marine Biology* **162**(5), 945–955. doi:10.1007/S00227-015-2636-6

Cortés, E. (2000). Life history patterns and correlations in sharks. *Reviews in Fisheries Science* **8**(4), 299–344. doi:10.1080/10408340308951115

Davidson, L. N. K., Krawchuk, M. A., and Dulvy, N. K. (2016). Why have global shark and ray landings declined: improved management or overfishing? *Fish and Fisheries* **17**(2), 438–458. doi:10.1111/FAF.12119

Dent, F., and Clarke, S. (2015). State of the global market for shark products. *FAO Fisheries and Aquaculture Technical Paper* **590**, 1–187.

Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J. V., Cortés, E., Domingo, A. S., Fordham, S., Fowler, S., Francis, M. P., Gibson, C., Martinez, J., Musick, J. A., Soldo, A., Stevens, J. D., and Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation* **18**(5), 459–482. doi:10.1002/AQC.975

Evans, G. T., and Hoenig, J. M. (1998). Testing and viewing symmetry in contingency tables, with application to readers of fish ages. *Biometrics* **54**, 620–629. doi:10.2307/3109768

Filmalter, J. D., Capello, M., Deneubourg, J. L., Cowley, P. D., and Laurent, D. (2013). Looking behind the curtain: quantifying massive shark mortality in fish aggregating devices. *Frontiers in Ecology and the Environment* **11**(6), 291–296. doi:10.1890/130045

Galván-Tirado, C., Galván-Magaña, F., and Ochoa-Báez, R. I. (2015). Reproductive biology of the silky shark *Carcharhinus falciformis* in the southern Mexican Pacific. *Journal of the Marine Biological Association of the United Kingdom* **95**(3), 561–567. doi:10.1017/S0025315414001970

Goldman, K. J. (2005). Age and growth of elasmobranch fishes. In 'Management Techniques for Elasmobranch Fishes'. (Eds J. A. Musick and R. Bonfil.) pp. 76–102 (FAO: Rome, Italy.)

Haddon, M. (2001). 'Modeling and Quantitative Methods in Fisheries.' (CRC Press: Boca Raton, FL, USA.)

Hall, N. G., Barton, C., White, W. T., Dharmadis, T., and Potter, I. C. (2012). Biology of the silky shark *Carcharhinus falciformis* (Carcharhinidae) in the eastern Indian Ocean, including an approach to estimating age when timing of parturition is not well defined. *Fish Biology* **80**, 1320–1341. doi:10.1111/J.1095-8649.2012.03240.X

Harry, A. V. (2017). Evidence for systemic age underestimation in shark and ray ageing studies. *Fish and Fisheries*. [Published online early 23 August 2017]. doi:10.1111/FAF.12243

Harry, A. V., Tobin, A. J., and Simpfendorfer, C. A. (2013). Age, growth and reproductive biology of the spot-tail shark, *Carcharhinus sorrah*, and the Australian blacktip shark, *C. tilstoni*, from the Great Barrier Reef World Heritage Area, north-eastern Australia. *Marine and Freshwater Research* **64**, 277–293. doi:10.1071/MF12142

Hoyos-Padilla, E. M., Ceballos-Vázquez, B. P., and Galván-Magaña, F. (2012). Reproductive biology of the silky shark *Carcharhinus falciformis* (Chondrichthyes: Carcharhinidae) off the west coast of Baja California Sur, Mexico. *Journal of Applied Ichthyology* **18**, 15–24.

Hutchinson, M. R., Itano, D. G., Muir, J. A., and Holland, K. N. (2015). Post-release survival of juvenile silky sharks captured in a tropical tuna purse seine fishery. *Marine Ecology Progress Series* **521**, 143–154. doi:10.3354/MEPS11073

Joung, S., Chen, C., Lee, H., and Liu, K. (2008). Age, growth and reproduction of silky sharks, *Carcharhinus falciformis*, in northeastern Taiwan waters. *Fisheries Research* **90**, 78–85. doi:10.1016/J.FISHRES.2007.09.025

Katsanevakis, S. (2006). Modelling fish growth: model selection, multi-model inference and model selection uncertainty. *Fisheries Research* **81**, 229–235. doi:10.1016/J.FISHRES.2006.07.002

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* **77**(4), 765–776.

Kumoru, L. (2003). The shark longline fishery in Papua New Guinea. In 'Proceedings of the Billfish and By-catch Research Group, 176th Meeting of the Standing Committee on Tuna and Billfish', 9–16 July 2003, Mooloolaba, Qld, Australia. pp. 1–5. (National Fisheries Authority: Port Moresby, Papua New Guinea.)

Last, P. R., and Stevens, J. D. (1994). 'Sharks and Rays of Australia.' (CSIRO Publishing: Melbourne, Vic, Australia.)

Lawson, T. (2011). Estimation of catch rates and catches of key shark species in tuna fisheries of the western and central Pacific Ocean using observer data. In 'Scientific Committee Seventh Regular Session', 9–17 August 2011, Pohnpei, Federated States of Micronesia. WCPFC-SC7 EBIP-02. (Western and Central Pacific Fisheries Commission: Kolonia, Federated States of Micronesia.) Available at https://www.wcpfc.int/system/files/EB-IP-02%20%5BEstimation%20of%20Catch%20Rates%20and%20Catches%20of%20Key%20Shark%20Species%5D.pdf [Verified 12 January 2018].

Lombardi-Carlson, L. A., Cortés, E., Parsons, G. R., and Manire, C. A. (2003). Latitudinal variation in the life-history traits of bonnethead sharks, *Sphyrna tiburo*, (Carcharhiniforms: Sphyrnidae) from the eastern Gulf of Mexico. *Marine and Freshwater Research* **54**, 875–883. doi:10.1071/MF03023

Minami, M., Lennert-Cody, C. E., Gao, W., and Roman-Verdesoto, M. (2007). Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. *Fisheries Research* **84**, 210–221. doi:10.1016/J.FISHRES.2006.10.019

Musick, J. A. (1999) Ecology and conservation of long-lived marine animals. In 'Life in the Slow Lane: Ecology and Conservation of Long Lived Marine Animals, American Fisheries Society Symposium 23'. (Ed. J. A. Musick.) pp. 1–10. (American Fisheries Society: Bethesda, MD, USA.)

Oshitani, S., Nakano, H., and Tanaka, S. (2003). Age and growth of the silky shark *Carcharhinus falciformis* from the Pacific Ocean. *Fisheries Science* **69**, 456–464. doi:10.1046/J.1444-2906.2003.00645.X

Passerotti, M. S., Andrews, A. H., Carlson, J. K., Wintner, S. P., Goldman, K. J., and Natanson, L. J. (2014). Maximum age and missing time in the vertebrae of sand tiger shark (*Carcharias taurus*): validated lifespan from bomb radiocarbon dating in the western North Atlantic and southwestern Indian Oceans. *Marine and Freshwater Research* **65**, 674–687. doi:10.1071/MF13214

Poisson, F., Filmalter, J. D., Vernet, A. L., and Dagorn, L. (2014). Mortality rate of silky sharks (*Carcharhinus falciformis*) caught in the tropical tuna purse seine fishery in the Indian Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **71**(6), 795–798. doi:10.1139/CJFAS-2013-0561

Rice, J., and Harley, S. (2013). Updated stock assessment of silky sharks in the western and central Pacific Ocean. In 'Scientific Committee Ninth Regular Session', 6–14 August 2013, Pohnpei, Federated States of Micronesia. WCPFC-SC9 SA-WP-03. (Western and Central Pacific Fisheries Commission: Kolonia, Federated States of Micronesia.) Available at https://www.wcpfc.int/system/files/SA-WP-03-Silky-Shark-SA.pdf [Verified 12 January 2018].

Rice, J., Tremblay-Boyer, L., Scott, R., Hare, S., and Tidd, A. 2015. Analysis of stock status and related indicators for key shark species of the Western Central Pacific Fisheries Commission. In 'Scientific Committee Eleventh Regular Session', 5–13 August 2015, Pohnpei, Federated States of Micronesia. (Western Central Pacific Fisheries Commission.)

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. In 'Bulletin 191 of the Fisheries Research Board of Canada'. pp. 313–314. (The Blackburn Press.) Available at http://www.dfo-mpo.gc.ca/Library/1485.pdf [Verified 15 November 2017].

Ricker, W. E. (1979). Growth rates and models. In 'Fish Physiology'. (Eds W. S. Hoar, D. J. Randall, and J. R. Brett.) pp. 677–743. (Academic Press: New York, NY, USA.)

Rigby, C. L., Sherman, C. S., Chin, A., and Simpfendorfer, C. A. (2016). *Carcharhinus falciformis* (silky shark). In 'The IUCN Red List of Threatened Species 2016', e.T39370A2909465. (International Union for Conservation of Nature and Natural Resources.) Available at http://www.iucnredlist.org/details/39370/0 [Verified 1 November 2017].

Sánchez-de Ita, J. A., Quinonez-Velazquez, C., Galvin-Magana, F., Bocanegra-Castillo, N., and Felix-Uraga, R. (2011). Age and growth of the silky shark *Carcharhinus falciformis* from the west coast of Baja California Sur, Mexico. *Applied Ichthyology* **27**, 20–24. doi:10.1111/J.1439-0426.2010.01569.X

Serafy, J. E., Orbesen, E. S., Snodgrass, D. J. G., Beerkircher, L. R., and Walter, J. F. (2012). Hooking survival of fishes captured by the United States Atlantic pelagic longline fishery: impact of the 2004 circle hook rule. *Bulletin of Marine Science* **88**(3), 605–621. doi:10.5343/BMS.2011.1080

Simpfendorfer, C. A., and Dulvy, N. K. (2017). Bright spots of sustainable shark fishing. *Current Biology* **27**(3), R97–R98. doi:10.1016/J.CUB.2016.12.017

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

Simpfendorfer, C. A., Heupel, M. R., White, W. T., and Dulvy, N. K. (2011). The importance of research and public opinion to conservation management of sharks and rays: a synthesis. *Marine and Freshwater Research* **62**, 518–527. doi:10.1071/MF11086

Smart, J. J., Chin, A., Tobin, A. J., Simpfendorfer, C. A., and White, W. T. (2015). Age and growth of the common blacktip shark *Carcharhinus limbatus* from Indonesia, incorporating an improved approach to comparing regional population growth rates. *African Journal of Marine Science* **37**(2), 177–188. doi:10.2989/1814232X.2015.1025428

Smart, J. J., Chin, A., Tobin, A. J., and Simpfendorfer, C. A. (2016). Multimodel approaches in shark and ray growth studies: strengths, weaknesses and the future. *Fish and Fisheries* **17**(4), 955–971. doi:10.1111/FAF.12154

Smart, J. J., Chin, A., Baje, L., Tobin, A. J., Simpfendorfer, C. A., and White, W. T. (2017). Life history of the silvertip shark *Carcharhinus albimarginatus* from Papua New Guinea. *Coral Reefs* **36**(2), 577–588. doi:10.1007/S00338-016-1533-X

Smith, S. E., Au, D. W., and Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **49**(7), 663–678. doi:10.1071/MF97135

Strasburg, D. W. (1958). Distribution, abundance and habits of pelagic sharks in the central Pacific Ocean. *Fishery Bulletin* **58**, 335–361.

Tanaka, S., Cailliet, G. M., and Yudin, K. G. (1990). Differences in growth of the blue shark, *Prionace glauca*: technique or population. *NOAA Technical Report NMFS* **90**, 177–187.

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

White, W. T., Platell, M. E., and Potter, I. C. (2001). Relationship between reproductive biology and age composition and growth in *Urolophus lobatus* (Batoidea: Urolophidae). *Marine Biology* **138**, 135–147. doi:10.1007/S002270000436

Yamaguchi, A., Taniuchi, T., and Shimizu, M. (1998). Geographic variation in growth of the starspotted dogfish *Mustelus manazo* from five localities in Japan and Taiwan. *Fisheries Science* **64**(5), 732–739. doi:10.2331/FISHSCI.64.732

Yoshimura, H., and Kawasaki, S. (1985). Silky shark (*Carcharhinus falciformis*) in the tropical water of Western Pacific. *Report of the Japanese Group for Elasmobranch Studies* **20**, 6–10.