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Age and growth of the bull shark (*Carcharhinus leucas*) around Reunion Island, South West Indian Ocean

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Abstract:

Sharks exhibit varied demographic strategies depending on both the species and the population location, which make them more or less vulnerable to fishing. Accurate evaluation of local age and growth parameters is therefore fundamental for the sustainable management of their stocks. Although demographic parameters have been assessed for bull shark (*Carcharhinus leucas*) populations in several locations of the world, this information was missing so far around the Reunion Island, in the South West Indian Ocean. To fill this gap of knowledge, age and growth data was gathered from the vertebrae of 140 individuals of *C. leucas* (77 females and 63 males, mostly adults) fished around the island between 2012 and 2019. After verification of the annual deposition of growth band pairs on these structures using relative marginal increment analysis on 40 individuals, band pairs were counted along the vertebral centrum for each individual. Thanks to this approach, growth was shown to significantly differ between male and female *C. leucas* around the reunion island, with respective von Bertalanffy growth model equations of $L_t = 314\left(1 - e^{-0.0814(t+5.45)}\right)$ and $L_t = 321.5\left(1 - e^{-0.0999(t+3.420)}\right)$. Indeed, the females of the species fished in this area were significantly ($p < 0.001$) larger than local males, with an estimated difference in size of ~ 16.1 cm at 20 years old. They also apparently reach older ages, with an estimated maximum age of 33.50 years, against 29.75 years only for the males. The estimated size at birth around the island is larger than elsewhere in the world, varying from 92.30 to 100.00 cm depending on the method used. These results confirm that the population of *C. leucas* around the Reunion Island exhibits a K-selected strategy, which makes it highly vulnerable to fishing pressure.

Keywords:

Age determination, growth bands, Vertebrae, RMI analysis, Life history, Longevity

Introduction:

Sharks are often considered as key species in marine ecosystems, both because of their high trophic impact as predators and because they contribute to the connection of distant habitats through their migrations (Heithaus *et al*. 2008; Roff *et al*., 2016). Most shark species are targeted or taken as bycatch in a wide variety of fisheries worldwide (Campana *et al*., 2016), and a few are specifically targeted in shark control programs (McPhee 2014).

Depending on their reproductive strategies, some species are threatened with rapid extinction whereas others might withstand long-term fishing if their catches are restricted by adequate quotas throughout their distribution range (Dulvy *et al*. 2017). Accurate evaluation of age and growth is fundamental in shark fisheries management (Campana *et al*. 2016; Goldman 2005; Musick *et al*. 1999) because inaccurate age estimates can lead to serious error in stock assessments and possibly overexploitation (Campana, 2001). Precise size-at-age information is also required for producing robust estimates of essential parameters such as natural mortality and longevity (Goldman 2005).

The bull shark *Carcharhinus leucas* (Valenciennes, 1839) is a common tropical and subtropical coastal shark (Garrick, 1982) that can temporarily enter freshwater systems (Campagno, 1989). So far, its age and growth had been studied only in the Gulf of Mexico (Branstetter and stiles, 1987; Cruz-Martinez *et al*., 2005; Neer *et al*., 2005), in South Africa (Wintner *et al*., 2002), in Australia (Tillet *et al*., 2011) and in the Western North Atlantic (Natanson *et al*., 2014). These studies had shown that, like many other carcharhinids, *C. leucas* are long-lived, attaining maximum ages of 30 to >50 years. Females typically grow to larger sizes and mature later than males, and growth rates for both sexes are faster during the juvenile stage (Branstetter and Stiles, 1987; Castro, 1983; Compagno, 1984; Natanson *et al*., 2014; Snelson *et al*., 1984; Neer *et al*., 2005; Tillet *et al*., 2011; Werry, 2010; Wintner *et al*., 2002). However, *C. leucas* exhibit a wide variability in maximum age and length, growth rate and size and age at maturity among sampling locations. These spatial differences, supported by recent studies on the species' genetic structure (e.g. Pirog *et al*., 2019a, Tillet *et al*., 2011), suggest the existence of separate populations within exploited stocks that are currently structured by oceanic basins. This calls for more local studies on all the above-mentioned parameters, to implement efficient conservation and management strategies for the different populations of the species (Cailliet and Goldman, 2004), which face varied levels of fishing pressure. For example, in the Western North Atlantic Ocean and the Gulf of Mexico, commercial fishing of *C. leucas* stocks is not recent, and increased markedly in 1980s (Cortés *et al*., 2002; Natanson *et al*., 2014). Meanwhile, along the eastern coast of South Africa, the main source of fishing mortality is the local shark control program that started in 1966 to reduce the shark risk for sea users (Cliff and Dudley, 1991).

Around the reunion island in the Western Indian Ocean, commercial shark fishing is banned since 1999 due to a risk of food poisoning related to the presence of ciguatoxins (Quod *et al*., 2000). However, a spate of shark bites on humans since 2011 (Lagabrielle *et al*., 2018; Taglioni *et al*., 2018) resulted in the implementation of a local shark control program in 2012, to intercept sharks in coastal waters on the west coast of the island, close to the main local sites of water-based activities (Guyomard *et al.*, 2019). This prompted research interest on the local biology and ecology of *C. leucas*, one of the two species responsible for these incidences (Ballas *et al*., 2017) to avoid its local extinction as a result of the current shark control program. Despite this, knowledge on the demographic parameters of the species is still very limited in this area of the Indian Ocean. A recent study showed that male and female bull sharks around Reunion Island reach sexual maturity at ca. 234 and 257 cm total length respectively, and the local parturition period extends between October and December (Pirog *et al*., 2019b). However, to our knowledge, the present study is the first to report the age-length relationship and investigate the growth of *C. leucas* around the Reunion Island. For this size-at-age data was gathered for over 100 specimens of the species, by counting vertebral growth band pairs. Although it has recently been pointed out as probably leading to a systemic underestimation of shark age (Harry 2018), this method remains the most commonly used for estimating age in sharks (Cailliet *et al*. 2006; Panfili *et al*., 2002). It was expected that its application to assess the demographic parameters for *C. leucas* around the Reunion Island would bring in valuable knowledge for efficiently protecting human lives through the local shark control program without threatening the long-term maintenance of the local population and the ecosystem functions it sustains.

Material and methods:

Study site and local population sampling

The Reunion Island (21°08’S, 55°32’E) is a young volcanic island of 2,500 km^2 located in the Western Indian Ocean (Figure 1), characterised by a very narrow island shelf and a particularly small and discontinuous fringing coral reef on the leeward west coast. Between December 2012 and July 2019, 163 individuals of *C. leucas* were caught along the west coast of the island (Figure 1), within the frame of the local shark control program using bottom longlines and drumlines with catch-alive system (SMART drumline, Guyomard *et al.*, 2019). For 140 of these individuals (77 females and 63 males), biological information including sex, mass, maturity stage, total length (L_t) and fork length (L_f) was recorded and a section of the vertebral column was excised, approximately from below the anterior margin of the first dorsal fin. Two near full-term embryos of 79 cm L_t, 1 male and 1 female, recovered from a pregnant female caught in November (29/11/2016) were included in the growth analysis. As this size is very close to the size of the smallest free-swimming specimen caught around the island (78 cm) and to the maximum size-at-birth reported for the species locally (80 cm, Pirog et al. 2019b), these two embryos were considered to be due to born in December 2016. Therefore, their size was considered as that at birth and their age was estimated at -0.083 years (i.e. 1.00 month before birth).

Ethical statement

All sharks were caught as part of the local shark control program organized since 2012 by the French government around the island. This program aims at reducing the shark risk close to nautical activities and all catches are done by professional fishermen. The Reunion Island University takes opportunity of these catches to organize the dissection of the sharks captured in order to improve knowledge on the local biology and ecology of the species. As the death of the sharks is not primarily related to the gathering of scientific knowledge and samples or data are only taken from already dead animals, no ethical agreement is needed to conduct this research.

Vertebrae processing and sectioning

For each fish, individual vertebrae were separated, stored frozen until processed, and one was randomly selected for age estimation. Following common protocols (Cailliet and Goldman, 2004), the centrum of each vertebra was cleaned by removing the neural arch and any adherent soft tissues mechanically. When necessary, chemical cleaning by soaking the vertebra in 5% sodium hypochlorite for 5 minutes was used to remove residual tissues, as it does not affect the vertebra composition (Mohan *et al.*, 2017). The vertebrae were then rinsed in a bath of distilled water during 10 minutes and cut in the middle (sections of ca. 600 µm width) along the sagittal plane (Cailliet and Goldman, 2004) using a low-speed diamond saw (Isomet; Beuhler). Each vertebral section was then photographed twice, first dry and then immerged in 70% ethanol, under both reflected and transmitted lights using a binocular (Olympus® SZX12). The resulting pictures were used for age estimation and growth rate measurements, using the imageJ software. The radius of each vertebra centrum (R_{vc}) was measured from the centrum focus to the distal margin of the *corpus calcareum* (Goldman, 2004).

Centrum analysis and age verification

Although the count of vertebrae increments for bull shark's age estimation has already been verified in several previous studies (Branstetter and Stiles., 1987; Neer *et al*., 2005; Tillet *et al*., 2011; Wintner *et al*., 2002), verification of the approach is a crucial prerequisite in each new location investigated (Panfili *et al*., 2002). The Relative Marginal Increment analysis (RMI) is the most common method for this, when tagging (or chemically marking) the fish and recapturing them is impossible (Panfili *et al*, 2002). In this study, we used it to verify age estimates in our samples. For this, a sub-sample of individuals of both sexes and varied sizes were selected for the unequivocal status of their vertebrae margins. For each of these individuals, the width of the margin increment (i.e. the distance from the last growth band to the centrum edge) was divided by the width of the last (previously) fully formed band pair (Cailliet and Goldman, 2004). Resulting RMI values were then plotted as a function of the month of capture to confirm the annual periodicity of band pair formation. Following Okamura *et al*. (2013), a circular linear regression model with random effects was used to adjust three models of growth periodicity (acyclic, annual and biannual cycle) to the RMI data. The model, which best fits the data, was chosen using the Akaike information criterion (Burnham and Anderson, 2002).

Age determination and vertebral growth

In sharks, birth leaves a noticeable mark on the vertebrae: the birth mark (BM) identifiable as a marked change in the angle of the *corpus calcareum*. This mark, resulting from the difference between fast intra-uterine and slower post-natal growth (Walter and Ebert 1991), is commonly chosen to represent age 0 in sharks (Goldman, 2005). In this work, both the birth mark radius, i.e. the distance from the centrum focus to BM, and the width of the following growth band were measured on the *corpus calcareum* of each section.

To estimate age in this study, vertebral sections were randomly selected and analysed without any a priori knowledge regarding fish sex or size. For each individual fish, age was estimated by counting the number of band pairs (each formed by a pair of one opaque plus one translucent growth bands) after the birth mark on the corresponding vertebral section. Two separate readers independently made two non-consecutive counts of growth band pairs for each fish. Count reproducibility between readers was estimated using the index of average percentage error (APE; Beamish and Fournier, 1981) and the coefficient of variation (CV; Chang, 1982). When the difference in age estimates between the two readers was less than 10%, the mean of the two values was used, which can finally bring partial years (e.g. 0.5). Otherwise, both readers re-analysed the section until a consensus was found. Age estimates were evaluated for consistency within and between readers using age-bias plot (Campana *et al.*, 1995). Chi-square tests of symmetry were used to determine whether difference between counts were due to systematic bias or random error (Evans and Hoenig, 1998).

The relationship between R_{vc} and the shark's total length (L_t) was established using Pearson correlation test. Sex-related differences for this relationship and for birth mark radius were tested using an analysis of covariance (ANCOVA) and a Student test, respectively. Average size at birth for *C. leucas* was estimated as the L_t value corresponding to the mean birth mark width observed on the vertebrae when using the fitted R_{vc} - total length (L_t) regression.

Growth modelling and statistical analyses

Sex-related differences in age and length were tested using non-parametric Wilcoxon tests, since neither the normality nor the homoscedasticity of the data were confirmed. The von Bertalanffy growth model (von Bertalanffy, 1938) was fitted on the whole dataset (both sexes combined) and on the datasets produced for males and females, separately. For this, non-linear least-squares regressions were implemented on R (Version 3.5.1, (C) 2018 The R Foundation for Statistical Computing.) using the equation defined by von Bertalanffy (1938):

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

where L_t = predicted length at time t, L_∞ = theoretical asymptotic length, k = growth coefficient or growth completion rates and t_0 = theoretical age at zero length.

Sex-related differences in the parameters of this equation were assessed using analysis of covariance (ANCOVA) on the log-transformed linear form of the growth regression. Ages at maturity were determined following the L_{t50} criteria defined in Pirog *et al.* (2019b) for the bull shark in Reunion Island. Longevity was defined as the age at which 95 % of $L\infty$ is reached (Taylor, 1975).

Results:

RMI analysis on the vertebrae of 40 individuals (L_t = 121–271 cm) with unequivocal margin status supported the hypothesis that growth band pairs on vertebral sections, consisting each of one opaque and one translucent zone, are formed with an annual periodicity in the local bull shark population, starting between December and January each year (Figure 2). The annual cycle of growth-band pair deposition was further supported by the AIC values obtained for the three models of growth periodicity tested (-76.27 for the annual cycle model, against -8.93 for the acyclic and 12.18 for the biannual cycle ones).

Based on these findings, ages estimate from vertebrae reading in our sample (N = 140) ranged between 0.2 and 33.5 years, for *C. leucas* specimens between 78 and 327 cm L_t and from both sexes. This diversity allowed precising the local growth parameters of the species, with important implications for the sustainable regulation of its stock around the reunion island.

Precision in age estimates

The average percentage error (APE) between readers A and B for two independent counts was of 2.15% and the corresponding coefficient of variation (CV) was of 3.04%, suggesting that age estimation was precise for both readers (Table 1). Nevertheless, the second read was more precise than the first one for both readers and age estimates from reader B were more consistent than those from reader A (Table 1). Therefore, reader B was used as the reference (explanatory variable) for the comparison plot of ages assigned according to each reader (age-bias plot, Figure 3). The age-bias plot indicates high agreement around the 1:1 line and no systematic bias between readers (Figure 3). Chi-square tests of symmetry showed that the little differences in age estimates between readers were only due to random errors (n = 140; Bowker: $X^2 = 53.67$, df = 54, p = 0.49; Evans-Hoenig: $X^2 = 9.55$, df = 8, p = 0.30; McNemar: $X^2 = 2.85$, df = 1, p = 0.09).

Size-at-age distribution around the reunion island

The mean total length (L_t) of the bull sharks used in this work was 246.40 ± 57.20 (mean ± SD) cm. Females (L_t = 78-327 cm) were significantly ($p < 0.001$) larger than males (L_t = 101-310 cm), with mean lengths of 257.60 ± 60.97 and 232.80 ± 49.34 cm respectively. The average difference in size between them was of ~ 16.10 cm at 20 years old. Size frequency distributions were non-normal for both sexes, due to a lack of small sizes in the captures. Indeed, only 7 of the females and 4 males in our dataset were smaller than 150 cm and, in the 150-200 cm size-class, there were no female and only 9 males (Figure 4). The average age in the captures was of 15.11 ± 8.49 years (Figure 5), with females (0.20-33.50 years old) significantly ($p = 0.023$) older than males (0.25-29.75 years old) as mean ages for the two sexes were of 16.60 ± 8.98 and 13.29 ± 7.54 years, respectively.

A significant and robust linear relationship was found between the radius of the vertebrae (R_{vc}) and the total length (L_t) of individuals (Pearson test; $n = 135$; $R^2 = 0.974$; $p <0.001$; Figure 7) with no sex-related significant difference in its parameters (ANCOVA, $p = 0.09$). Based on the width of the birth mark (BM), ranging from 34.52 to 43.87 mm (mean ± SD: 39.11 ± 2.20 mm) with no significant difference between sexes (Wilcoxon test; $n= 137$; $W = 2729$; $p = 0.08$), the estimated range of body sizes at birth in our sample was estimated to be of 89.00 - 95.60 cm, around an average size of 92.30 ± 37.92 cm.

Local growth equations and minimum and maximum sizes

Von Bertalanffy growth equations for *C. leucas* in Reunion Island were estimated to be $L_t = 314\left(1 - e^{-0.0814(t+5.45)}\right)$ for males and $L_t = 321.5\left(1 - e^{-0.0999(t+3.420)}\right)$ for females (Table 2). Indeed, significantly different growth models were obtained for the two sexes (ANCOVA, $p < 0.001$). As a result, predicted local maximum sizes in the area (L_∞) differed between sexes, with estimates of 321 cm for the females and 314 cm for males (Table 2). Interestingly, while male *C. leucas* in our sample were all below 314 cm in size, three of the females captured in the area (of 322, 325 and 327 cm L_t) were larger than the maximum 321 cm predicted by the Von Bertalanffy growth equation obtained for predicting their growth. Using the corresponding models, the longevity of the species (95% of L_∞, Taylor, 1975) in the area was estimated to be 29.50 years (31.40 years for males and 26.30 years for females). Average ages at maturity were estimated to be of 11.30 and 12.70 years (from L_{t50} of 234 and 257 cm, Pirog et al., 2019) for males and females, respectively. Growth models including embryos did not differ significantly from those with only free-swimming individuals (ANCOVA, $p > 0.05$). Including the two embryos in the models however produced smaller estimates for both the global birth size, of 97.00 cm L_t instead of 100.00 cm L_t, and the asymptotic maximum size, of 307.3 cm L_t instead of 314 cm L_t for males and of 320.9 cm L_t instead of 321.5 cm L_t for females (Table 2, Figure 6). Therefore, both types of models are displayed in Table 2.

Discussion:

This study is the first to provide age and growth information for *C. leucas* around the Reunion Island, and the second in the Western Indian Ocean, after Wintner *et al*. (2002) in South Africa. Our results are consistent with previous findings on this species in other parts of the world (Branstetter and Stiles, 1987; Cruz-Martinez *et al*., 2004; Natanson *et al*., 2014; Neer *et al*., 2005; Tillet et al., 2011), and with the data gathered so far in other elasmobranchs (Caillet and Goldman, 2007; Cortés 2000). In particular, the low growth rate and the late age at maturity found here for *C. leucas* are typical of large carcharhinid species (Cortés 2000). The von Bertalanffy models obtained however suggest that life-history traits for the species in Reunion Island differ from those observed in other locations (Branstetter and Stiles, 1987; Cruz-Martinez *et al*., 2004; Natanson *et al*., 2014; Neer *et al*., 2005; Tillet *et al.,* 2011), with the exception of South Africa (McCord and Lamberth, 2010, Wintner *et al*. 2002) where similarly high maximum sizes and sizes at birth were described (Table 3). These results corroborate a recent study on *C. leucas* genetics, which suggested genetic isolation between *C. leucas* populations from the Western Indian Ocean and those from the Western Atlantic and Western Pacific Oceans (Pirog *et al*. 2019a). If true, this has important implications in terms of population management for *C. leucas* around the island, where fishing mainly targets large individuals.

Verification and precision

Age underestimation is common for sharks and rays when counting annual growth band pairs on calcified structures (Harry, 2018). This is mainly due to the difficulty in distinguishing growth band pairs for older ages, because seasonal growth bands tend to be narrower as a result of the decrease in fish growth with age (Cruz-Martinez *et al*., 2004; Natanson *et al.*, 2014). For some species of sharks however, band pair deposition is annual for only a portion of the lifespan (Natanson *et al.*, 2018; Passerotti *et al.*, 2014), a process being referred to as of the "missing time" (Passerotti *et al*., 2014). Factors that influence the differential rate of calcium deposition in sharks' vertebrae centra are not well understood yet. Changes in temperature, diet (Stevens, 1975) and stress-related activities such as migration (Pratt and Casey, 1983) have been suggested. This highlights the importance of validating the method, including for old specimens, before applying it for age estimation. In the present study, RMI analysis suggested that growth band pairs, consisting each of an opaque plus a translucent zone, were formed annually on the vertebrae of *C. leucas* specimens captured in Reunion Island, as already observed for this species in other locations (Branstetter and Stiles, 1987; Neer *et al*., 2005; Tillet *et al*., 2011; Wintner *et al*., 2002). However, this analysis was performed on the vertebrae of 40 individuals only (28.58 % of our total sample) for which the last growth bands were easily measurable. These fish were mainly small individuals, with sizes of 121-271 cm L_t, which calls for caution when interpreting our age estimates, especially for large and old individuals. To our knowledge, missing time has never been observed for *C. leucas* so far. However, other validation methods such as tetracycline injection (Cailliet and Goldman, 2004; Panfili *et al.*, 2002) or capture-recapture might improve the accuracy of size-at-age estimates and lead to the production of more robust models for local growth in the species. This being said, the coefficient of variation (CV, Chang 1982) in this study did not exceed the 5% level recommended by Campana (2001) and the APE, age-bias plot and symmetry tests produced are among the most precise obtained for the species so far (Cruz-Martinez *et al.*, 2004; Neer *et al.*,2005; Wintner *et al.*, 2002). This substantiate our ability to correctly interpret vertebral band pairs for *C. Leucas* in our study area and confirms previous conclusions that *C. leucas* is relatively easy to age for a shark species.

Size, growth and age of *Carcharhinus leucas* in Reunion Island

Due to a combination of problems in sampling and growth band pairs reading on the vertebrae, maximum predicted lengths in sharks are usually lower than those observed in the field (Harry, 2018). This was the case here, and in most studies involving *C. leucas* worldwide, exception made of one study in Northern Australia, where the maximum total length observed for *C. leucas* (318 cm L_t) was smaller than the average maximum length ($L\infty$ = 350.7 cm) predicted by the von Bertalanffy growth model (Tillet *et al*, 2011). This might reflect an artificial inflation of the L_∞ estimate though, due to the lack of large individuals in the local dataset since parameter estimates with the von Bertalanffy equation are greatly influenced by extreme values (Haddon 2001; Natanson *et al*., 2014).

With total lengths up to 327 cm and an average predicted maximum size of 321.57 cm, the *C. leucas* specimens caught around the Reunion Island are globally larger than those from other locations (Table 3, Figure 8), as already pointed out by Blaison *et al*. (2015). Indeed, studies in the Gulf of Mexico reported local maximum total lengths of 231.21 cm and 258.00 cm for female and male bull shark, respectively (Branstetter and Stiles, 1987; Cruz-Martinez *et al*., 2004; Neer *et al*., 2005) and, to our knowledge, the largest individual of the species ever observed was a female of 400.00 cm tagged in the Breede River, along the South Eastern coast of South Africa (McCord and Lamberth, 2010). These results support the hypothesis that *C. leucas* from Indian Ocean populations are larger than those from Atlantic ones (Pirog *et al*. 2019a, b). In sharks, life history traits can differ between conspecific populations, reflecting spatial differences in population dynamics and resilience to exploitation (Dulvy *et al*. 2008). This could explain the larger sizes observed in this work. However, all other life-history parameters derived from the von Bertalanffy model fall within the range of the values from other studies (Table 3). Alternatively, because until 2012 and the beginning of the shark control program in Reunion Island, the local *C. leucas* population was barely fished, the presence of large individuals in this population could reflects its pristine state. A last explanation could lie in the use of different fishing gears (with different size-related selectivity) among locations. Around the Reunion Island, the shark control program uses large hooks to target large individuals and to limit bycatches (Guyomard *et al*., 2019). Even if the size-related selectivity cannot explain all differences, as in all studies both large and small individuals were caught, it remains an important factor to consider.

The von Bertalanffy growth model is the most commonly applied in elasmobranch studies (Cailliet and Goldman, 2004). It has been largely used to describe growth in *C. leucas* (e.g. Branstetter and Stiles, 1987; Neer *et a*l., 2005), which explain its use for the present work.

Yet, it does not always provide the best fit with size-at-age data in fish (Cailliet and Goldman, 2004). Several models and multi-model combinations exist and can be used to describe shark growth (Smart *et al.*, 2016). The use and comparison of these different models could improve growth description for the local population of *C. leucas* in the future. For example, in the Western North Atlantic, Natanson et al. (2014) found the Gompertz and the logistic models to provide better descriptions of growth for *C. leucas* males and females, respectively. Still, such model comparisons should be made with caution, as growth modelling in a given shark population can provide different results depending on the age or length distribution in the sample (Natanson *et al*., 2014; Neer *et al*., 2005). In particular, the lack of small and old individuals in the sample can significantly influence growth model estimates (Goodman *et al*., 2012; Haddon 2001; Natanson *et al.*, 2014; Neer *et al*., 2005; Wintner *et al*., 2002). This highlights the need for a better scientific monitoring of the bull shark population around the Reunion Island to improve the quality of the local size-at-age dataset.

In this study, *C. leucas* growth rate was found to differ between sexes, with a 3 to 5% smaller maximum size predicted in the males than in the females. This confirms sex-related differences in growth parameters already reported for the species at other locations (Figure 8, Table 3), and is in agreement with the 10% size difference between sexes in favour of the females observed by Cortès (2000) on 164 species of sharks and the 7% found by Garrick (1982) on 24 species of the genus *Carcharhinus*. A characteristic of the dataset in the present study though is the absence of females for the 150-200 cm L_t range. To our knowledge, this sex-related difference in the size distribution (nine males and zero females) has never been reported in other *C. leucas* populations. Scientific sampling efforts around the island in the future should aim at determining whether this current size gap in the catches reflects a local particularity in the behaviour or the ecology of 150-200 cm L_t females. Further investigations could also help understanding the biology of *C. leucas* juveniles and sub-adults around the island, which is still largely unknown. Indeed, small size classes (< 200 cm L_t) were poorly represented in our samples for both sexes (Figure 4), probably because the large size hooks gear used in the shark control program targets the largest individuals in the population. However, because access to estuarine ecosystems is of key importance for both parturition and early development in *C. leucas* (Werry *et al*. 2011), it is likely that the newborns and juveniles of the species remain near the mouths of local perennial rivers, which are mostly located on the rainy eastern coast of the island. As the focus for the shark control program is on the western coast of the island, near coral reefs with limited freshwater inputs (Figure 1), this habitat preference may also partly explain the low representation of small size classes in our sample.

Around the Reunion Island, both sexes of *C. leucas* were found to mature at ages between 11 and 13 years, which falls within the values reported for the species at other locations (Table 3), and between the ages at maturity found in Australia (Tillet *et al*. 2011) and in South Africa (Wintner *et al*. 2002). The longevity estimates found (29.50 years) are also similar to those previously reported at other locations (Table 3), with one noticeable exception: South Africa, where longevity was estimated to be >50 years (Wintner *et al*. 2002).

Size at birth of *Carcharhinus leucas* in Reunion Island

Size at birth is particularly difficult to evaluate in *C. leucas*, due to the worldwide variability in its life-history traits. The mean birth size reported for the species is of 78.33 ± 2.56 cm, but it is apparently larger (97.73 cm) in South Africa (Wintner *et al*., 2002) than in the Atlantic (70-80 cm, Branstetter and Stiles, 1987; Castro, 1983; Compagno, 1984; Natanson *et al*., 2014; Neer *et al*., 2015; Rodriguez de la Cruz *et al*., 1996; Snelson *et al*., 1984). Around the Reunion Island, Pirog *et al*. (2019b) estimated the birth size of the species to be between 70 and 80 cm, based on the analysis of 16 litters, and local anglers reported free-swimming juveniles of 68-79 cm (T. Poirout, pers. obs.). In this study, the growth model predicted a birth size of 100 cm, however this estimate decreased to 97 cm when including near full-term embryos in the dataset. The lack of newborns and juveniles in our sample likely led to birth size overestimation using von Bertalanffy growth modelling. Indeed, when using the local relationship between R_{vc} and body total length (L_t) in the species, birth mark widths suggested a mean birth size of 92.30 cm, which better fits with local field observations. Cortés (2000) highlighted a universal positive correlation between female and offspring body sizes in sharks. It seems plausible that in bull sharks as well, larger and older females produce larger offspring. Larger female sizes in Reunion Island could therefore explain the local larger birth size, when compared to most of the other study sites. This idea is also supported by the variability in birth mark widths observed among vertebrae (34.52 – 43.87 mm), which might reflect individual differences in mother sizes. Finally, the larger birth size estimates found in this study, but also in South Africa (Wintner *et al*., 2002), is an additional argument supporting the hypothesis of a distinct population of bull sharks, with higher demographic parameters, in the Western Indian Ocean.

Shark risk and shark control program

The results of this work confirm that bull sharks around the Reunion Island exhibit typical characteristics of a K-selected fish population, with large maximum sizes, high longevity, late maturity, low fecundity and slow growth for both sexes (Stearns, 1992). These K-selected characteristics make populations particularly vulnerable to the removal of large and mature individuals. Depending on the population size and its degree of connectivity with other populations in the Indian Ocean, the on-going shark control program could significantly affect the local population dynamics. As a matter of fact, the high abundance in the captures of old individuals, larger than at most other locations where studies were conducted, suggests that, until the beginning of the shark control program in 2012, the *C. leucas* population around the island was relatively pristine. Knowledge on the local natural populations' dynamics is needed however to appreciate whether the current fishing pressure acts as an additive or a compensatory source of mortality (Allen *et al.*, 2006). Indeed, the local shark control only aims to eliminate potentially dangerous specimens that would swim close to coastal areas where human activities develop, so the idea is to only reduce the local population size to a threshold for which the probability of shark bites will be close to nil. A long-term follow-up of the catches could help identify trends in *C. leucas* body length and possible indirect effects of this targeted fishing (Stevens *et al*., 2000). Fishing pressure, especially on large individuals, can lead to changes in the structure and life-history traits in some populations (Stevens *et al.*, 2000). In response to demographic changes, changes in growth rate (Sminkey and Musick, 1995) or in reproductive parameters (Holden, 1973, Walker *et al.*, 1998) can be observed in elasmobranch populations (Roff *et al.*, 2018; Stevens *et al.*, 2000). Fecundity tends to increase with body size so that populations with a higher proportion of larger fish have greater reproductive potential. A better understanding of the general ecology of this species and a follow-up of its catches around Reunion Island are essential to predict the consequences of the shark control program on the risk of human attack by *C. leucas* and the local population dynamics of the species. It is also vital to infer the possible impact of the program on the functioning of local ecosystems. Indeed, large shark individuals are rare in most ecosystems, yet they have a unique functional role as true apex predators (Roff *et al*. 2016). The removal of these individuals from the coastal habitats around the Reunion Island could have unexpected consequences on the goods and services provided by these ecosystems.

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Contributions

S.J. and A.D. designed the research; F.H., T.P. and L.J. contributed to data acquisition and generation; F.H. and M.L. prepared samples; F.H. analyzed the data and wrote the original draft, all authors contributed to the writing of the manuscript.

Table 1 Average percentage of error (APE) and coefficient of variation (CV) in the age estimates obtained by two successive vertebra readings (first and second reads) by each of the two independent readers (A and B). In each case, n indicates the number of fish aged.

Reader	**First read**		**Second read**		**n**
	APE	CV	APE	CV	
A	-	-	1.94	2.74	140
B	-	-	0.80	1.13	140
A vs B	3.84	5.44	2.15	3.04	140

Table 2 Summary of the biometric and growth parameters data for the 140 bull sharks from Reunion Island, with the inclusion or not of embryos in the von Bertalanffy model. All lengths (except BM) are in cm. L_T: Total Length; Age and longevity in years; BM: birth mark width in mm; L_∞, t_0 et k: parameters of von Bertalanffy growth model; L_{T50}: size at maturity for each sex (from Pirog *et al*., 2019b).

Bull shark (C. leucas)	***Free swimming individuals***			***Embryos included***		
	Combined sexes	Males	Females	Combined sexes	Males	Females
Sample size	140	63	77	142	64	78
L_t min	78	101	78	78	79	78
L_t max	327	310	327	327	310	327
L_t mean	246.4	232.8	257.6	244.1	230.4	255.3
Age min	0.20	0.25	0.20	-0.083	-0.083	-0.083
Age max	33.5	29.7	33.5	33.5	29.7	33.5
Age mean	15.1	13.3	16.6	14.9	13.1	16.4
BM mean	39.11	38.70	39.44	39.11	38.70	39.44
L_∞	321.6	314	321.5	319.6	307.3	320.9
t_0	-4.231	-5.450	-3.420	-3.921	-4.551	-3.300
k	0.0889	0.0814	0.0999	0.0923	0.0911	0.1013
Estimated size at birth	100	112.4	93.1	97	104	91.2

Longevity	29.5	31.4	26.3	28.5	28.1	26.3
$L_{t\,50}$	-	234	257	-	234	257
Age at maturity	-	11.34	12.7	-	11.18	12.63

Table 3 Summary of main relative information on length, age and life history traits from different studies.

Bull shark (C. leucas)	***Compagno (1984)***	***Branstetter and Stiles (1987)***	***Rodriquez de la Cruz et al. (1996)***	***Wintner et al. (2002)***	***Cruz-Martinez et al. (2004)***	***Neer et al. (2005)***	***Tillet et al. (2011)***	***Natanson et al. (2014)***	**This present study**
L_t (cm) mean	NA	F=242-268 M=213-245	206.2	NA	NA	NA	NA	NA	F=257.6 M=232.8
L_t (cm) max	340	F=268 M=245	F=334	F=284 M=278	F=271 M=254	F=271,21 M=245.80	F=318 M=276	F=269 M=254	F=327 M=310
Age max (years)	14	F=24 M=21	NA	F=32 M=29	F=28 M=23	F=29 M=25	F=26 M=22	F=27 M=25	F=33.5 M=29.7
L_∞ ***T_0*** ***K***	NA	285 -3.00 0.076	NA	295,3 -5.120 0.071	256,4 -1.935 0.1397	377.7 -6.844 0.042	350,7 -2.485 0.082	259 NA NA	321.6 -4.231 0.0889
Length (cm) to maturity	250	F>225 M=210-220	F=204 M=190-200	F=249 M=246	F=204 M=190-200	NA	NA	F=228 M=208	F=257 M=234
Age (years) to maturity	6	F>18 M=14-18	NA	F=21	F=10 M=9-10	NA	9.5	F=15 M=16	F=12.7 M=11.34
Gestation time (months)	10-11	10-11	10-11	NA	NA	NA	NA	NA	NA
Birth size (cm)	56-81	75	78	89-97	NA	56-97	NA	76	92-100
Number of pups	1-13	NA	1-22	NA	NA	NA	NA	NA	NA
Study locations	Symposis of world data	Northern Gulf of Mexico	Gulf of Mexico	South-Africa	Southern Gulf of Mexico	Northern Gulf of Mexico	North Australia	Western North Atlantic	Reunion Island

(Indian Ocean)

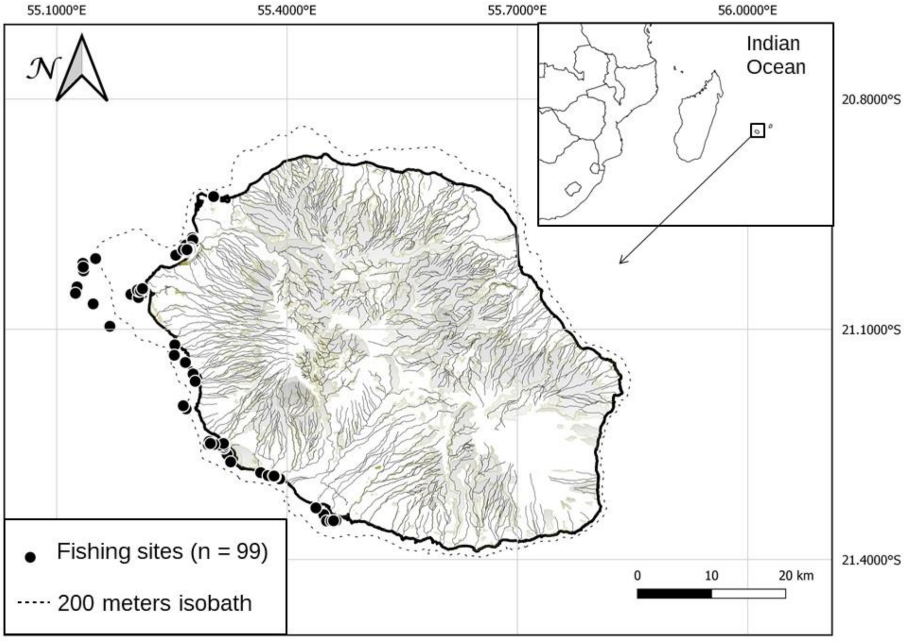

Figure 1 Fishing sites for the bull sharks (Carcharhinus leucas) captured around the Reunion Island between December 2012 and July 2019.

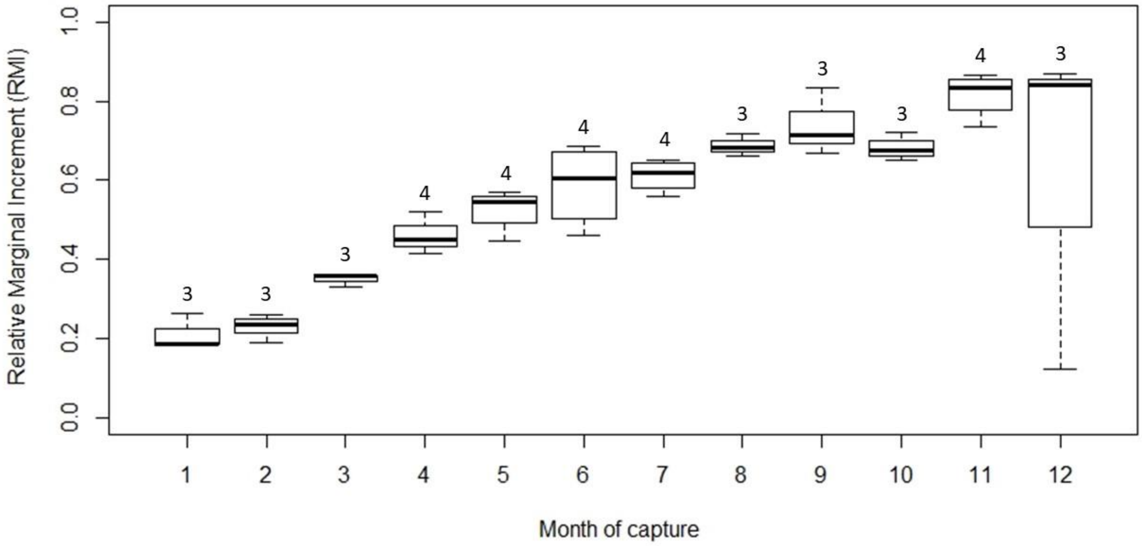

Figure 2 Relative marginal Increment (RMI) by month of capture for 40 individuals bull shark (Carcharhinus leucas). The thick line in the boxplots represents the median value for each month, and box lower and upper margins represent the first and third quartiles, respectively.

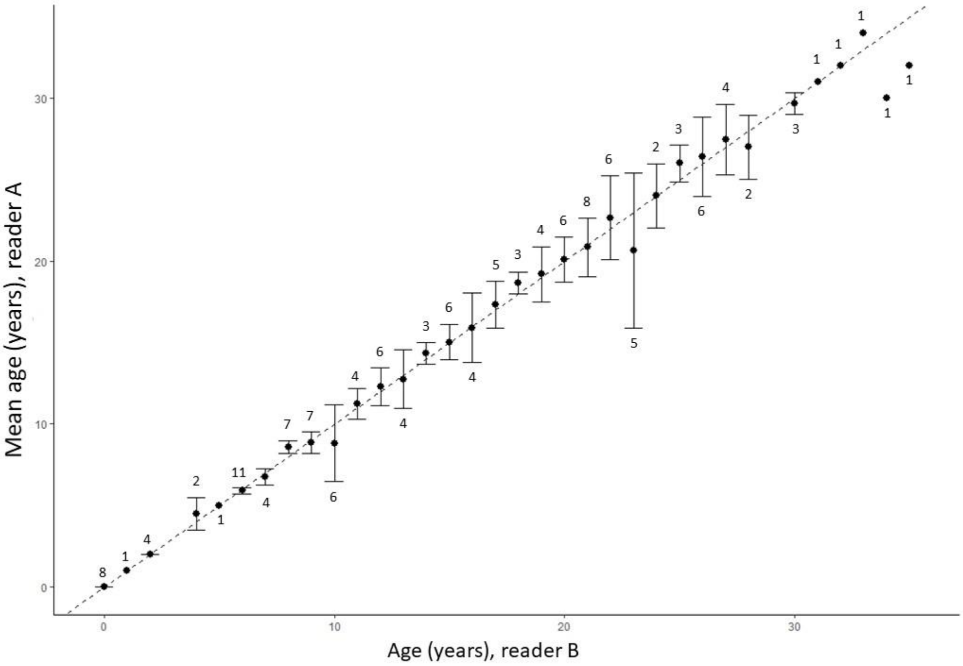

Figure 3 Reader-linked biases in age estimation from vertebral growth bands' counts in the 140 bull sharks (Carcharhinus leucas) investigated in this work. Numbers along the 1:1 equivalence line (dotted line) indicate sample size for each age. Error bars in each case represent the 95 % confidence intervals for the mean age assigned by reader B to all the fish assigned a given age by reader A

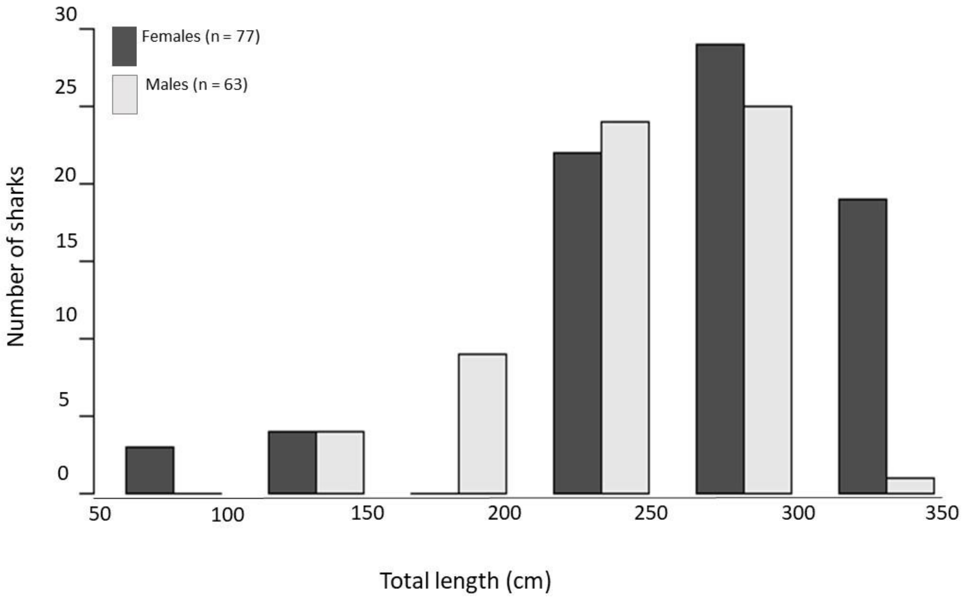

Figure 4 Number of bull shark (Carcharhinus leucas) individuals studied by size class (L_t, cm) and sex.

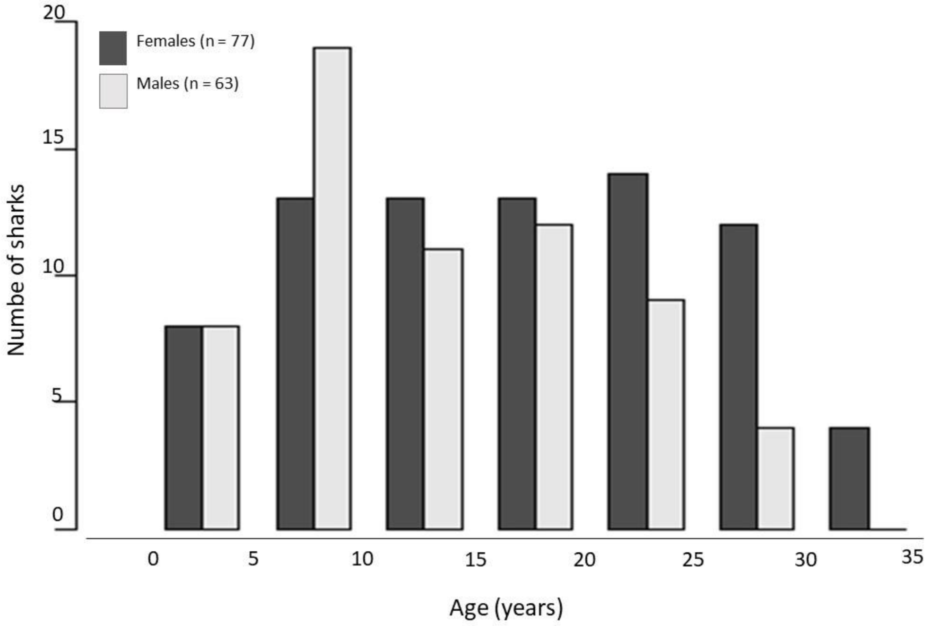

Figure 5 Age distribution for the females (n=77) and males (n=63) bull shark (Carcharhinus leucas) caught around Reunion island.

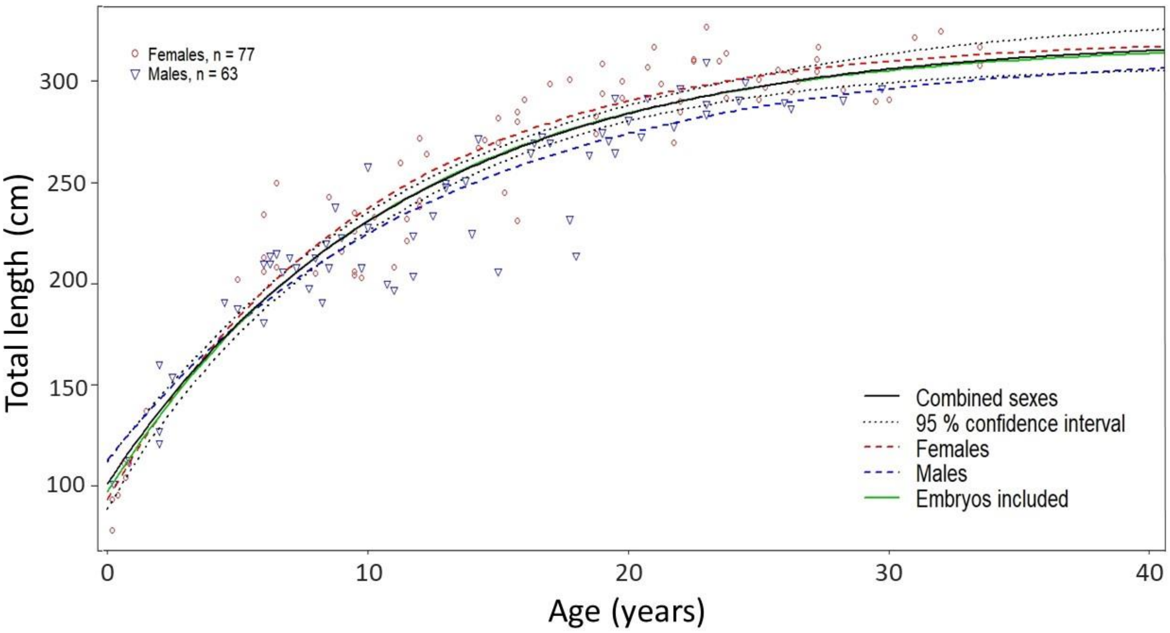

Figure 6 Fitted von Bertalanffy growth model for the bull shark (*Carcharhinus leucas*) in Reunion Island, for only free-swimming individuals (combined sexes, females and males) and for free-swimming with embryos included (only combined sexes).

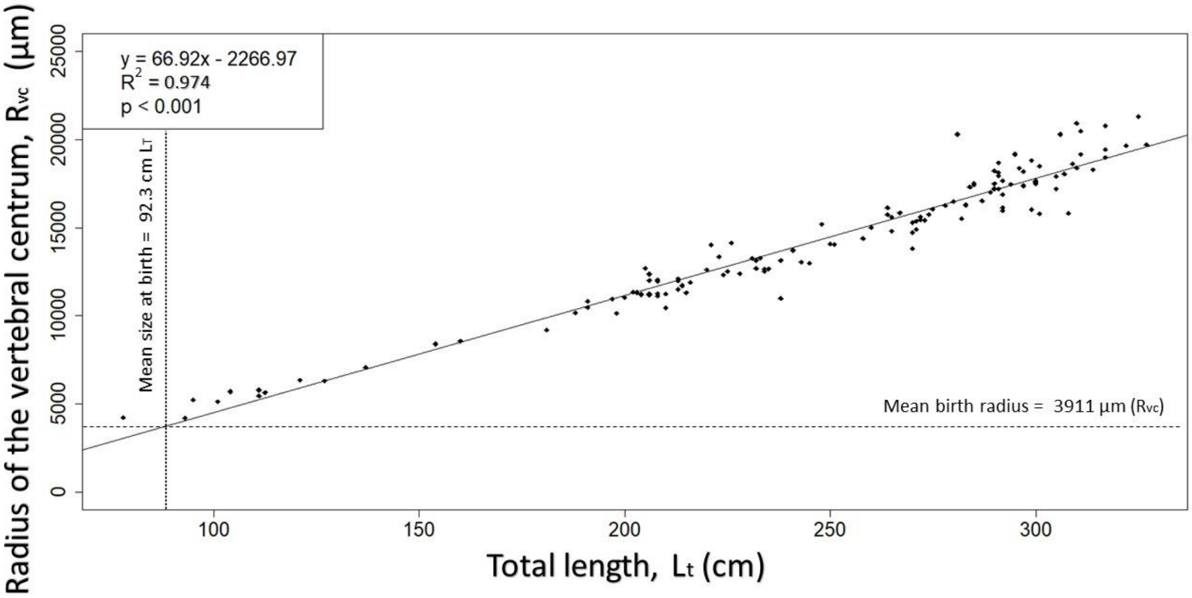

Figure 7 Relationship between the radius of the vertebral centrum (Rvc) and the body total length (L_t) for 136 individuals of bull shark (Carcharhinus leucas). The horizontal dashed line represents the mean radius of the vertebral centrum (R_{vc}) of the birth mark and the vertical dashed line represents the mean size at birth (L_t).

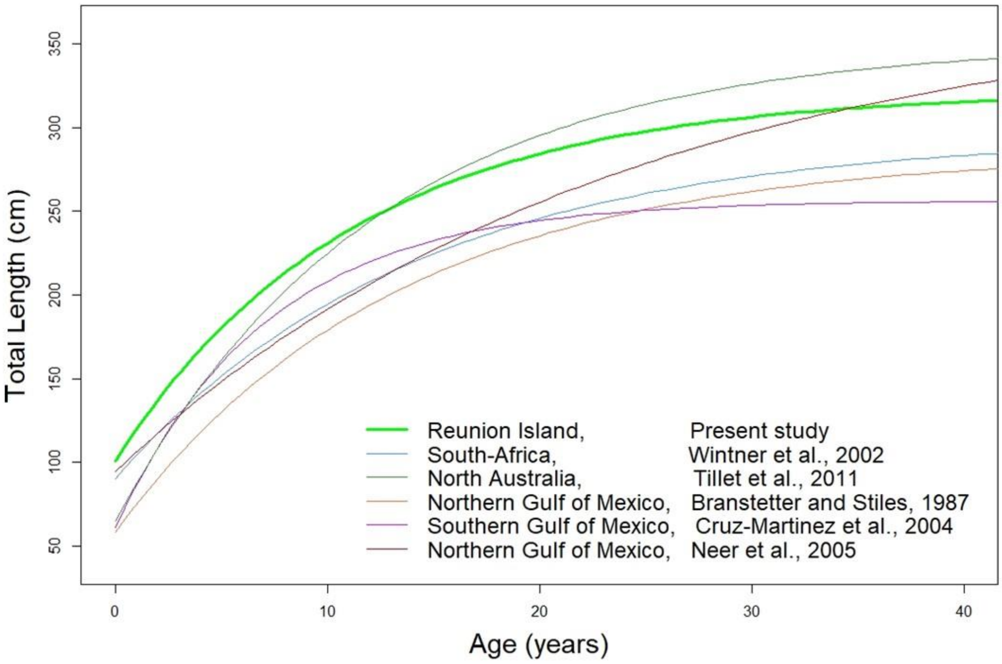

Figure 8 Comparison of the von Bertalanffy growth curve fitted for the bull shark (Carcharhinus leucas) in Reunion Island (present study) with those obtained in other published studies